

RESEARCH ARTICLE

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Key Points:

- Deoxygenation processes occur in the northern limit of OMZ off Mexico
- Thinning of the hypoxic layer affects its inhabitants in different ways
- Fish larvae of some species show resilience to changes of dissolved oxygen

Supporting Information:

- Supporting Information S1

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Larval Fish Habitats and Deoxygenation in the Northern Limit of the Oxygen Minimum Zone off Mexico

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Abstract The present state of deoxygenation in the northern limits of the shallow oxygen minimum zone off Mexico is examined in order to detect its effects on larval fish habitats and consider the sensitivity of fish larvae to decreased dissolved oxygen. A series of cruises between 2000 and 2017 indicated a significant vertical expansion of low oxygen waters. The upper limit of suboxic conditions ($<4.4 \mu\text{mol/kg}$) has risen ~ 100 m at 19.5°N off Cabo Corrientes and ~ 50 m at 25°N in the mouth of the Gulf of California. The larval habitat distribution was related to the geographic variability of dissolved oxygen and water masses between these two latitudes. One recurrent larval habitat, with *Bregmaceros bathymaster* larvae as the indicator species, extended throughout the water column off Cabo Corrientes from Subtropical Subsurface Water (suboxic conditions) to the surface ($220 \mu\text{mol/kg}$). The second recurrent habitat was located between the oxycline ($>44 \mu\text{mol/kg}$) and the surface in association with the Gulf of California Water, with *Benthosema panamense* as the indicator species. During the warm El Niño event of 2015–2016, a tropical larval fish habitat (*Auxis* spp.) associated with Tropical Surface Water appeared to change the larval habitat distributions. These results indicate that some species are resilient to changes of dissolved oxygen and temperature generated by El Niño events and by continuing deoxygenation, although other species with more limited environmental windows could be affected by deoxygenation, probably leading to a change of the pelagic ecosystem over time.

Plain Language Summary Dissolved oxygen in the ocean is crucial for the biological cycles of all organisms. There are vast zones in the ocean where the oxygen has dropped to levels that only a few, very well adapted, organisms can live. Dissolved oxygen measurements in the past two decades in the Mexican Pacific have shown that the concentrations have decreased, and water layers with nearly no oxygen are now closer to the surface, potentially impacting larval fish species that are not adapted to extremely low oxygen concentrations. Nevertheless, there is a set of fish larvae that is well adapted to low dissolved oxygen concentrations, principally small forage fish, which have a permanent presence in the poorly oxygenated waters, while some larvae of species with fisheries interest, like small tunids, only live in the well-oxygenated surface layer and are more abundant in warm years. The loss of oxygen in the Mexican Pacific has not had an effect on the small forage fish larvae but can affect those larvae of fish of commercial interest, with less adaptation to low oxygen concentrations.

1. Introduction

Deoxygenation in the oceans, which has been documented mainly on global scales (Bograd et al., 2008; Breitburg et al., 2018; Schmidtko et al., 2017; Stramma et al., 2008; Stramma et al., 2010), is of major concern for its potential effects on the nutrient cycles, the structure of marine trophic chains, and therefore availability of fishery resources (Prince & Goodyear, 2006; Chavez & Messié, 2009; Schmidtko et al., 2017; Cheng et al., 2015). However, more research needs to be done to precisely evaluate the consequences of deoxygenation in marine systems.

In oceanic regions where dissolved oxygen is already low, such as the shallow oxygen minimum zones (OMZs) of the eastern North Pacific Ocean (Cepeda-Morales et al., 2013; Schmidtko et al., 2017; Stramma et al., 2010), the deoxygenation process can affect the habitat of pelagic organisms from zooplankton to

top predators (Diaz & Rosenberg, 2008; Ekau et al., 2010; Hofmann et al., 2011; Longhurst, 1967; Prince & Goodyear, 2006). Previous studies in this shallow OMZ (Fernandez-Alamo & Farber-Lorda, 2006, Sánchez-Velasco et al., 2016, 2017, Ruvalcaba-Aroche et al., 2018) reported that the zooplankton biomass and total larval fish and cephalopod paralarvae had the highest abundances in the oxygenated surface layer ($>44 \mu\text{mol/kg}$) and decreased toward the hypoxic ($<44 \mu\text{mol/kg}$) and suboxic ($<4.4 \mu\text{mol/kg}$) conditions of the deeper layers. This is similar to findings on the vertical distribution of zooplankton in other shallow OMZs in the southeastern Pacific, Benguela and Angola Currents, and the Arabian Oceans (Madhu et al., 2003, Ekau & Verheye, 2005, Escribano et al., 2009, Hirche et al., 2014).

The loss of dissolved oxygen in OMZs may have severe implications at the species level because critical survival thresholds may be surpassed (Schmidtko et al., 2017; Vaquer-Sunyer & Duarte, 2008; Wishner et al., 2018), particularly for zooplanktonic organisms like fish larvae and cephalopod paralarvae, which are highly sensitive to dissolved oxygen changes (Koslow et al., 2011; Kreiner et al., 2009; Ruvalcaba-Aroche et al., 2018). Understanding the consequences of sustained deoxygenation for taxa in the planktonic life stage in OMZs is a challenge due to the lack of knowledge of how different species respond to suboxic conditions. The possible scenarios tend to be bleak because most of the physiological processes of the organisms depend on dissolved oxygen levels (Breitburg et al., 2018; Brewer & Peltzer, 2016; Hofmann et al., 2011; Tremblay et al., 2010). However, the resilience of species to extreme changes in the environment has received little attention, probably because of the logistical difficulty of studying the issue (Tett et al., 2013).

Previous studies focusing on interannual events found that warm phases of El Niño–Southern Oscillation (ENSO) increase the diversity of the planktonic assemblages, with replacement of dominant temperate assemblages by tropical ones, while during cold phases the corresponding diversity decreases. In the absence of ENSO events, it has been assumed that most species return to their original state (Lavaniegos et al., 1998, Sánchez-Velasco et al., 2000, Cavole et al., 2016, Mcclatchie et al., 2016, Sánchez-Velasco et al., 2017); that is, most species are resilient to ENSO events. Nevertheless, it has been reported that species like northern anchovy *Engraulis mordax* and jumbo squid *Dosidicus gigas* extended their distributions to colonize adjacent ecosystems (Bazzino et al., 2010; Green-Ruiz & Hinojosa-Corona, 1997; Hammann & Cisneros-Mata, 1989; Zeidberg & Robison, 2007) and did not return their distributions to pre-El Niño conditions. The northeastern Pacific Ocean contains the planet's most extended shallow OMZ (Stramma et al., 2008; Stramma et al., 2010). One of the first challenges is to know the degree of deoxygenation at local scales in that region. Even though Stramma et al. (2010) reported that the shallow OMZs have expanded and intensified globally during the past 50 years, in areas like the shallow OMZ off Mexico the lack of in situ data (Márquez-Artavia et al., 2019; Sánchez-Velasco et al., 2017) limits analysis and predictions of local conditions. The strong stratification of the water column throughout the year (Godínez et al., 2010), the intense mesoscale eddy activity of the region (Kurczyn et al., 2012), and the interannual variability dominated by the ENSO events (Godínez et al., 2010) can render difficult the detection of deoxygenation trends. The extent of the shallow OMZ off Mexico is largely governed by the convergence of surface (California Current, Gulf of California, and Tropical Surface) and intermediate (Subtropical Subsurface) water masses (Portela et al., 2016). The intermediate water mass is characterized by hypoxic and suboxic oxygen concentrations (Cepeda-Morales et al., 2013; Davies et al., 2015; Sánchez-Velasco et al., 2016).

The OMZ off Mexico can be split into two regions: the transitional area, north of 20°N , and the tropical domain, south of 20°N (Cepeda-Morales et al., 2013). In the tropical domain the hydrographic conditions are similar through the year, with high surface temperature ($>27^{\circ}\text{C}$), low surface salinity ($>34.6 \text{ g/kg}$; Portela et al., 2016), and shallow ($\sim 60 \text{ m}$) hypoxic waters (Cepeda-Morales et al., 2013; Sánchez-Velasco et al., 2017). In the transition zone the surface temperatures oscillate between 18 and 30°C , and surface salinity varies from 35.1 to 34 g/kg during spring and autumn, respectively (Fiedler & Talley, 2006). In spring and winter, the intrusion of the tropical branch of the California Current (Kurczyn et al., 2012) ventilates the hypoxic subsurface waters, while during summer and autumn the influence of the Mexican Coastal Current (Lavín et al., 2006; Portela et al., 2018) transport hypoxic and suboxic waters from the tropical domain to the transition zone, rising the hypoxic waters in the area (Márquez-Artavia et al., 2019).

Baseline information on the present state of the pelagic ecosystem is needed at local scales to evaluate future changes caused by the loss of oxygen in this OMZ. Fish larvae of tropical and subtropical species that inhabit the northeast Pacific Ocean (Moser, 1996) are good biological indicators of dissolved oxygen changes

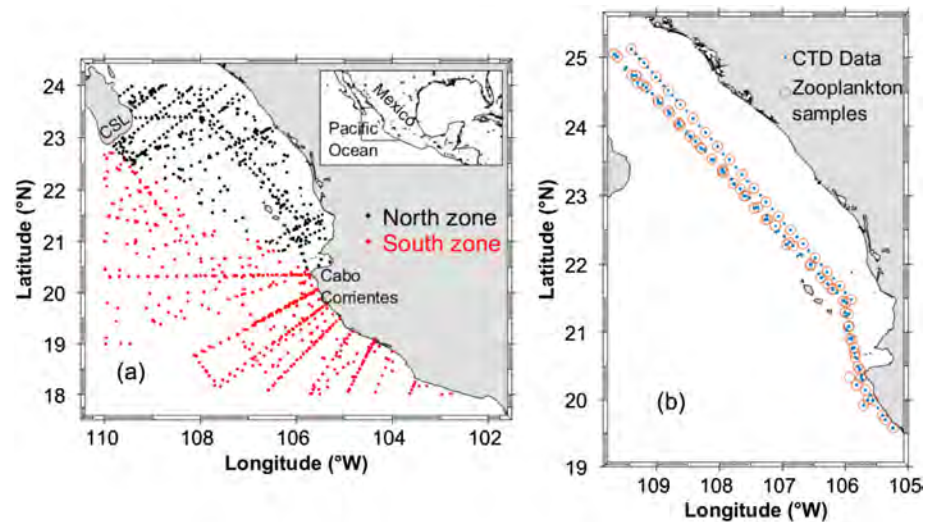


Figure 1. (a) Geographic distribution of the profiles of dissolved oxygen made from 2000 to 2017 in the northern limit of the shallow oxygen minimum zone of the tropical-subtropical convergence of the northeastern Pacific Ocean. Black points = north zone; red points = south zone. CL = Cabo San Lucas. (b) Location of CTD and zooplankton stations obtained from five oceanographic cruises made during February 2010, April 2012, June 2015, March 2016, and October 2017. Blue points = CTD data; red circles = zooplankton samples.

because of their sensitivity to the hydrographic gradients in the water column (Apango-Figueroa et al., 2015; Contreras-Catala et al., 2016; Davies et al., 2015; Moser & Smith, 1993; Sánchez-Velasco et al., 2017).

As a contribution to these emergent topics, in this study, the northern limit of the shallow OMZ is examined off Mexico. Evidence of progressive deoxygenation by the elevation of the oxypleths is investigated in a data set covering 2000 to 2017. It is expected that the loss of oxygen could be seen in the reduction of the hypoxic layer more than in the oxygenated layer considering the strong stratification of the water column in the study region over the year. It is also expected that any deoxygenation tendency might modify the distribution of the larvae of the fish species that inhabit that region and therefore the extension of the larval fish habitats. Due to differences in behavior and life histories, different fish species may exhibit differing responses to deoxygenation.

In this context, the aims of this study were to determine the present state of deoxygenation in the northern limit of the shallow OMZ off Mexico and to detect the effects of the dissolved oxygen gradients on the distribution of the larval fish habitats.

2. Methodology

2.1. Temporal Series of Profiles of Dissolved Oxygen

From a series of 19 oceanographic data cruises (along 10 years) made from 2000 to 2017 (see details in supporting information S1) in the northern limit of the shallow OMZ of the tropical-subtropical convergence of the northeastern Pacific Ocean, between 25°N and 18°30'N and 110°W and the coastline (~106°W and 104°30'W) (Figure 1a), 1,161 vertical profiles of dissolved oxygen were analyzed to detect evidence of latitudinal and vertical expansion of that shallow OMZ. Even though the spatial and temporal coverage of the cruises is irregular, the data provide a good indicator of the evolution of the dissolved oxygen conditions in the region.

On the basis of previous studies that described latitudinal dissolved oxygen gradients from SE to NW (Cepeda-Morales et al., 2013; Davies et al., 2015; Ruvalcaba-Aroche et al., 2018) and the marine ecoregions defined according to species distribution (Santamaría-del-Ángel et al., 2011), the dissolved oxygen profiles were divided into two regions: the north zone located at the mouth of the Gulf of California and the south zone off Cabo Corrientes (Figure 1a). Particularly, the northwest conductivity, temperature and depth (CTD) stations (between 20.5°N and 23°N) are considered part of the north zone according to the Gulf of California marine ecoregion mentioned above.

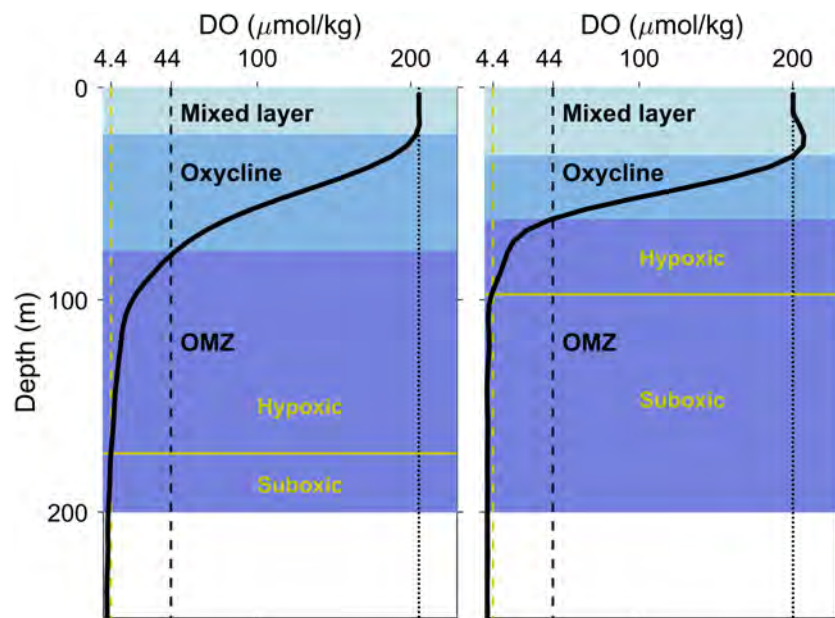


Figure 2. Example of the depth levels of the zooplankton hauls as a function of the dissolved oxygen profile in two different water columns. The continuous black line is the dissolved oxygen profile, the dashed black line is the 44 $\mu\text{mol/kg}$ oxygen concentration, the dotted line is the surface dissolved oxygen concentration, the continuous yellow line is the limit between hypoxic and suboxic waters, and the dashed yellow line is the 4.4 $\mu\text{mol/kg}$ oxygen concentration. The zooplankton hauls strata are represented in background colors, mixed layer (gray blue), oxycline (light blue), and oxygen minimum zone (dark blue).

The annual average depth of the 44 and 4.4 $\mu\text{mol/kg}$ oxypleths and the vertical distance between these oxypleths were calculated, as well as the temperature and salinity of the 4.4 $\mu\text{mol/kg}$ oxypleth in each region through the time series (see details of the data in supporting information S1). The selection of oxypleths was made on the basis of previous studies in this region (e.g., Davies et al., 2015, Sánchez-Velasco et al., 2016, Sánchez-Velasco et al., 2017, Ruvalcaba-Aroche et al., 2018). A conceptual model shows an example of the CTD profile with the oxypleths used to define the hypoxic and suboxic layers (Figure 2). For this study, we considered the 44 $\mu\text{mol/kg}$ oxypleth, which marks the lower limit of the oxycline, as the level below which conditions are hypoxic, while the 4.4 $\mu\text{mol/kg}$ oxypleth is the limit of suboxic conditions. The temporal trend of each variable (oxypleth depth, oxypleth difference, temperature, and salinity) was tested with a simple linear correlation test (Agresti, 2015).

2.2. Synoptic Vision of the Zooplankton Samples and Hydrography

CTD data and zooplankton samples were obtained from five oceanographic cruises with similar station distributions made during February 2010, April 2012, June 2015, March 2016, and October 2017 (see details in Table 1 and Figure 1b). The cruises were located in temporal context on the series of monthly average values of the multivariate ENSO index and the Pacific Decadal Oscillation (PDO) index (<https://www.esrl.noaa.gov/psd/data/climateindices/list/>) from 2000 to 2018.

Before zooplankton hauls, vertical profiles were obtained at each station using a SeaBird 911plus CTD probe equipped with dissolved oxygen and fluorescence sensors. Conservative temperature Θ ($^{\circ}\text{C}$) and absolute salinity (S_A , g/kg) were calculated from in situ temperature and practical salinity, respectively, with the TEOS-10 (Thermodynamic Equation of Seawater-2010) software, which was downloaded from <http://www.TEOS-10.org> (IOC, SCOR, IAPSO, 2010, Pawlowicz et al., 2010).

The ocean surface mixed layer depth was calculated following the methodology of Kara et al. (2000), which consists of a gradient-based criterion having a fixed temperature difference of 0.8 $^{\circ}\text{C}$ and variable salinity. The thermocline was defined as the temperature band ± 1 $^{\circ}\text{C}$ centered on the depth of the maximum temperature gradient ($\delta T/\delta z$), which varied between cruises.

Table 1
Details of the All Oceanographic Cruises Made in the Northern Limit of the Oxygen Minimum Zone off México

| General data | Cruise name | | | | |
|----------------------------|--------------------------------|--------------------------------|---------------------------|---------------------------|---------------------------------------|
| | MARIAS1002 | MARIAS1204 | MARIAS1506 | MARIAS1603 | MARIAS1710 |
| Cruise date | From 14 to 27 February 2010 | From 26 April to 4 May 2012 | From 3 to 16 June 2015 | From 2 to 8 March 2016 | From 28 October to 8 November 2017 |
| No. of physical stations | 27 | 41 | 32 | 24 | 24 |
| No. of zooplankton hauls | 14 | 19 | 14 | 16 | 16 |
| No. of zooplankton samples | 33 | 57 | 32 | 38 | 39 |

The zooplankton hauls were carried out over three depth intervals selected according to the water column structure. The first stratum was essentially the oxygenated surface mixed layer from the sea surface to the upper limit of the oxycline. The second covered the oxycline layer, from the base of the mixed layer down to the 44 $\mu\text{mol/kg}$ oxypleth, and the third was from the base of the oxycline, at the 44 $\mu\text{mol/kg}$ oxypleth, to 200 m depth. The depth of each net haul for zooplankton was selected after a visual inspection of the CTD oxygen profile. Figure 2 shows the depth levels of the zooplankton hauls in relation to two CTD oxygen profiles. The profiles of dissolved oxygen for all stations can be found in Godínez, Beier, Sánchez Velasco, & Lavín, 2010, Godínez et al., 2012, Godínez et al., 2015, Godínez et al., 2016, Godínez et al., 2017).

The hauls were performed day and night using opening-closing conical zooplankton nets with a 60 cm mouth diameter, 250 cm net length, and 505 μm mesh size (<http://www.generaloceanics.com>). Standard speeds of deployment (50 m/min) and recovery (5 m/min with 30 min bottom for stabilization) were made according to Smith and Richardson (1979). To estimate the true depth of each plankton tow, the depth of the net was calculated by the cosine of the wire angle method, following the standard specifications of Smith and Richardson (1979). The volume of filtered water was calculated using calibrated flow meters placed in the mouth of each net. Samples were fixed with 5% formalin buffered with sodium borate.

Zooplankton displacement volume (Beers, 1976; Kramer et al., 1972; Smith, 1971) was standardized to ml/1,000 m³. Fish larvae were removed from all samples. These were identified according to the descriptions in Moser (1996), and abundance was standardized to number of larvae per 10 m² (Moser & Smith, 1993; Smith & Richardson, 1979).

2.3. Fish Larvae and Hydrographic Statistical Analysis

In this study a larval fish habitat was considered as the place where a group of species coexisted during their planktonic phase (Costello, 2009). To determine the areas or habitats of fish larvae along the transects of each cruise, a cluster analysis was applied based on a species abundance matrix versus sample location (Clarke & Ainsworth, 1993). In order to consider only the most representative species of the study area, species contributing less than 5% of the total abundance and with a frequency of occurrence <2 were excluded from the matrices. To reduce the weight of the most abundant species, the standardized data were fourth-root transformed. Dendrograms were constructed with the flexible agglomerative clustering method (Bray-Curtis dissimilarity index; Field et al., 1982). The cut line in the dendrograms were chosen visually, according to common practice in zooplankton and fish larvae studies (i.e., Atwood et al., 2010; Doyle et al., 1993; Moser & Smith, 1993). To detect significant differences among the dissimilarity of the distinct larval fish habits, we applied a one-way analysis of similarities as a test of the significance of the habitats that had been defined a priori. The null hypothesis is that there are no differences between the members of the habitats (Clarke & Ainsworth, 1993; Clarke & Green, 1988).

The Phi coefficient (Tichý & Chytrý, 2007) was applied in order to obtain the indicator (or diagnostic) p value of a species with respect to the components of each larval fish habitat. This coefficient considers only the presence/absence of data. The Phi coefficients range from -1 (perfect negative indication) to 1 (perfect positive indication). The perfect indication means that the presence of a species points exclusively to a habitat without error, at least with the available data. The null hypothesis is that the indicator value is not larger than it would be expected at random, meaning that the species has no indicator p value. If the value is less than 0.05, the null hypothesis is rejected, meaning that the species has p value as an indicator.

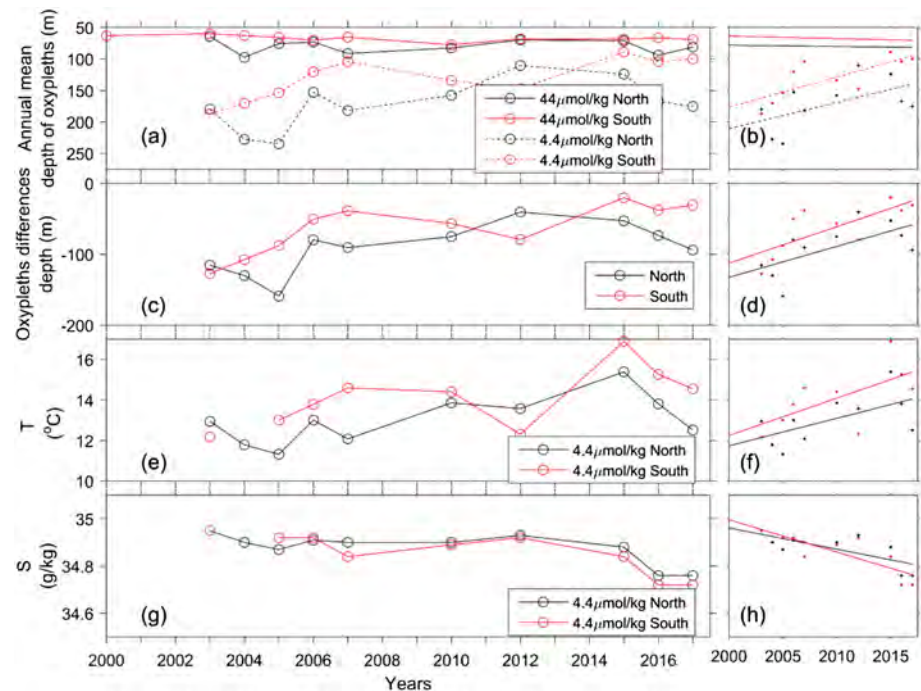


Figure 3. (a) Temporal trend of the depth of the 44 and 4.4 $\mu\text{mol/kg}$ oxypleths from 2000 to 2017 and (b) linear regression of their trends. (c) Temporal trend of the oxypleth difference depth (m), and (d) linear regression of their trends. (e) Temporal trend of temperature values in the 4.4 $\mu\text{mol/kg}$ oxypleths and (f) linear regression of their trends. (g) Temporal trend of salinity values in the 4.4 $\mu\text{mol/kg}$ oxypleths and (h) linear regression of their trends.

A redundancy canonical analysis (Legendre & Legendre, 1998) was run to define the relationship between environmental variables and larval fish distribution for the five cruises, after fourth-root transformation of the standardized biological data. This matrix contained the stratum-average values of conservative temperature (Θ , $^{\circ}\text{C}$), absolute salinity (S_A , g/kg), chlorophyll *a* (mg/m^3), and dissolved oxygen ($\mu\text{mol/kg}$).

3. Results

3.1. Temporal Series of Profiles of Dissolved Oxygen

The 44 $\mu\text{mol/kg}$ oxypleth did not show significant tendency in depth through time in either zone (Figures 3a and 3b and Table 2). This oxypleth was located between ~ 75 and 100 m depth in the north zone (black continuous line) and between ~ 65 and 75 m depth in the south zone (red continuous line). However, the 4.4 $\mu\text{mol/kg}$ oxypleths showed a rising tendency over time in both zones (Figures 3a and 3b), with significant correlation in the south zone (red dashed line) (Table 2). This oxypleth shoaled from ~ 200 to ~ 90 m depth, sinking slightly in 2017. The 4.4 $\mu\text{mol/kg}$ oxypleth in the north (black dashed line) was elevated from ~ 225 m depth in the beginning of the 2000s to ~ 120 m depth in 2016 but sinking to ~ 160 m depth in 2017.

In the north zone the difference in depth between the 44 and 4.4 $\mu\text{mol/kg}$ oxypleths (black continuous line) was reduced significantly from ~ 150 m at the beginning of the 2000s to ~ 50 m depth in 2016, while in the south zone (red continuous line) it decreased also significantly from ~ 150 m in the 2000s to ~ 20 m depth at the end of the series (Figures 3c and 3d and Table 2). In both cases the difference in depth between the oxypleths in 2017 increased.

The average temperature and salinity values at the depth of the 44 $\mu\text{mol/kg}$ oxypleths did not show any significant tendency through time in either zone (not shown). However, the average temperature values at the depth

Table 2

Linear Regression of the Trends of the Depth of the 44 and 4.4 $\mu\text{mol/kg}$ Oxypleths, and Temperature (T) and Salinity (S) Values in the Depth of These Oxypleths in the North (NZ) and South (SZ) Zones in the Northern Limit of the Shallow Oxygen Minimum Zone off México

| Variable | Estimate | D.f. | R^2 | t value | p value |
|---------------------------------|----------|------|-------|---------|---------|
| NZ, 44 $\mu\text{mol/kg}$ | 0.2039 | 8 | 0.01 | 1.084 | 0.794 |
| SZ, 44 $\mu\text{mol/kg}$ | 0.4062 | 9 | 0.25 | 0.985 | 0.119 |
| NZ, 4.4 $\mu\text{mol/kg}$ | -4.1580 | 8 | 0.31 | -1.368 | 0.096 |
| SZ, 4.4 $\mu\text{mol/kg}$ | -4.7797 | 8 | 0.57 | -2.700 | 0.011 |
| NZ, oxypleths difference | 4.3618 | 8 | 0.41 | 1.885 | 0.046 |
| SZ, oxypleths difference | 5.1677 | 8 | 0.58 | 2.744 | 0.010 |
| NZ, T at 4.4 $\mu\text{mol/kg}$ | 0.1359 | 8 | 0.36 | 1.668 | 0.069 |
| SZ, T at 4.4 $\mu\text{mol/kg}$ | 0.1842 | 7 | 0.40 | 2.172 | 0.066 |
| NZ, S at 4.4 $\mu\text{mol/kg}$ | -0.0090 | 8 | 0.52 | -2.850 | 0.018 |
| SZ, S at 4.4 $\mu\text{mol/kg}$ | -0.0137 | 7 | 0.66 | -3.725 | 0.007 |

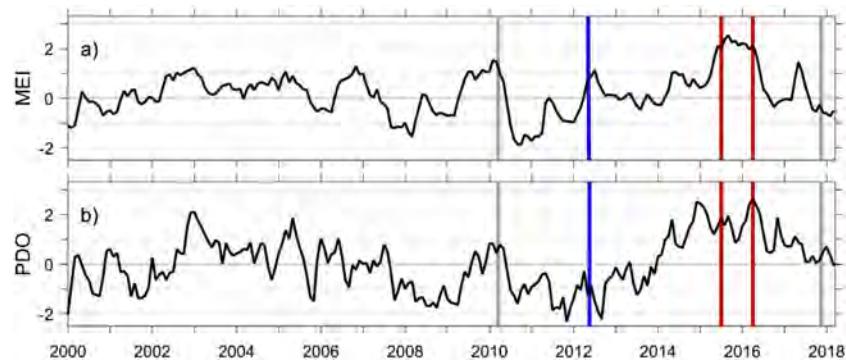


Figure 4. Fluctuations of the (a) multivariate ENSO index (MEI) and (b) Pacific Oscillation Decadal (PDO) index from 2000 to 2017. Vertical bars = period when the oceanographic cruises were made; blue line = under negative anomalies; red line = under positive anomalies; gray line = close to zero according to the PDO index.

of the $4.4 \mu\text{mol/kg}$ oxypleths showed a tendency to rise over time as a function of the elevation of the $4.4 \mu\text{mol/kg}$ oxypleths close to the values of significance in both zones (Figures 3e and 3f and Table 2). In the north zone (black continuous line) the temperature tended to increase from $\sim 12^\circ\text{C}$ at the beginning of the 2000s to $\sim 14^\circ\text{C}$ in 2015, decreasing to $\sim 12^\circ\text{C}$ in 2017. In the southern zone (red continuous line), it tended to increase from ~ 12 to $\sim 17^\circ\text{C}$ in 2015, decreasing to 2°C in 2017, but fluctuated strongly. The salinity at the depth of the $4.4 \mu\text{mol/kg}$ oxypleths showed a significant decreasing tendency in both zones, like in the case of the temperature, as a function of the elevation of the $4.4 \mu\text{mol/kg}$ oxypleths (Figures 3g and 3h and Table 2).

3.2. Geographic Variability of Dissolved Oxygen, Temperature, and Salinity

The temporal context of the cruises that sustain the biological samplings in relation to the series of monthly average values of the multivariate ENSO index and the PDO index from 2000 to 2018 is shown in Figure 4. The cruise dates were represented with vertical lines (red lines, the two cruises that encountered the warmest conditions). The indexes displayed strong variability throughout the period, consistent between both series. Positive anomalies ≥ 2 were observed in both indexes from mid-June 2015 to the beginning of 2016, during the warmest period of the series (red lines, June 2015 and March 2016). In contrast, negative anomalies ≥ 2 were observed in the PDO Index series at the time of the oceanographic cruise of April 2012 (gray line).

The geographic variability of the dissolved oxygen during the five selected oceanographic cruises (Figure 5) was typified by fluctuations in the depth of the $44 \mu\text{mol/kg}$ oxypleth of ~ 100 m in the mouth of the Gulf and ~ 80 m off Cabo Corrientes. The exception was in April 2012, when this oxypleth rose from 80 m near the Gulf to ~ 40 m depth off Cabo Corrientes. The $4.4 \mu\text{mol/kg}$ oxypleth ranged from ~ 90 to ~ 300 m depth in all cruises, except in April 2012, when this was elevated to 50 m depth off Cabo Corrientes.

Stronger geographic variability in the salinity values were observed in the first 100 m depth of the water column (Figure 6), where Gulf of California Water (GCW, >35.1 g/kg), Transitional Water (TW), and Tropical Surface Water (TSW, <34.6 g/kg) converge. In February 2010, GCW was recorded in the mouth of the Gulf, TSW was found from the Islas Marias to north of Cabo Corrientes, and TW (>34.6 and <31 g/kg) between these. In April 2012, most of the transect was occupied by GCW, decreasing in depth from the mouth of the Gulf to Cabo Corrientes. TSW was absent in this period. In the other three cruises, June 2015, March 2016, and October 2017, TSW was extended to the north, mainly in June 2015, when it was detected near the mouth of the Gulf. Below the surface water masses, TW and Subtropical Subsurface Water (StSsW) occurred.

Geographically, the temperature values also showed vertical gradients in the first 100 m of the water column (Figure 7). The mixed layer depth fluctuated between 30 and 50 m in most of the cruises, but it was shallowest ~ 20 m and deepest ~ 80 m off Cabo Corrientes in April 2012 (~ 20 and 24°C) and June 2015 (~ 26 and 30°C), respectively. The thermocline depth followed a similar tendency to the mixed layer in all periods, being shallowest in April 2012 (~ 30 m) and deepest in June 2015 (>100 m) off Cabo Corrientes.

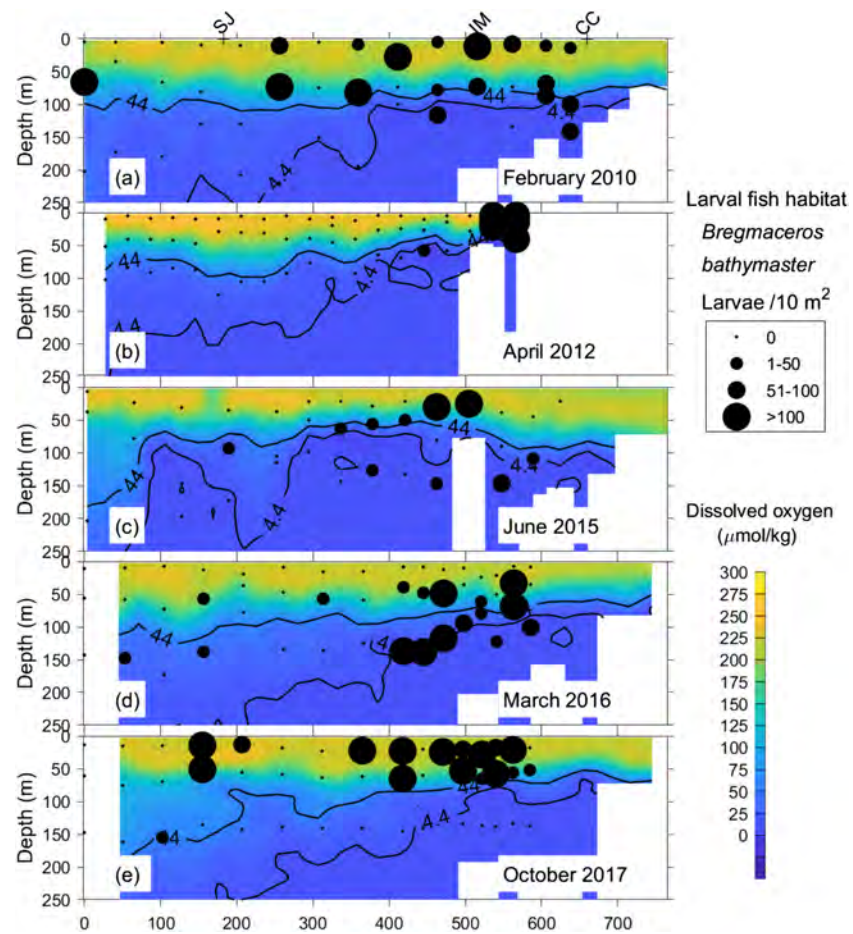


Figure 5. Dissolved oxygen concentration (color) and larval fish habitat *Bregmaceros bathymaster* (black circles) in the northern limit of the shallow oxygen minimum zone of the tropical-subtropical convergence of the northeastern Pacific Ocean. The 44 and 4.4 $\mu\text{mol/kg}$ oxypleths are marked (black lines). The x axis represents distance (km) from the first station in the Gulf of California entrance along the transect shown in Figure 1b.

3.3. Geographic Distribution of Larval Fish Habitats

The total mean larval abundance and the specific richness showed strong variability among the cruises (Table 3). Nevertheless, the Bray-Curtis dissimilarity index defined three groups of samples or larval fish habitats in each cruise analyzed to a cut of $\sim 20\%$ of information remaining of the data set (not shown), which were significantly different (analysis of similarities: $R = 0.5$, $p < 0.001$) in the five cruises. Based on the exploration of the indicator species of each habitat (Table 3) and their geographical location (Figures 5–7), two of the three larval fish habitats were recurrent but with changes in their distribution in response to environmental events.

A recurrent larval fish habitat (LFH 1) was observed mainly around the Islas Marias to north off Cabo Corrientes, extending to the north but in lower abundance and frequency. In April 2012 this habitat was concentrated only around the Islas Marias (Figure 5). Vertically, this habitat, although it was found throughout the observed water column (0–250 m), showed high abundance and frequency below the oxycline in oxygen concentrations $< 44 \mu\text{mol/kg}$, mainly in June 2015 and March 2016. This habitat had high mean larval abundance and specific richness in February 2010 but had the highest specific richness in October 2017 and the lowest mean larval abundance of the habitats in most of the cruises (June 2015, March 2016, and October 2017) (Table 3). *Bregmaceros bathymaster* was the indicator species of the habitat according to the Phi coefficient during the five cruises (Table 3). *Etropus crossotus* and *Caranx caballus* larvae were also indicator species, but in only three of the five cruises.

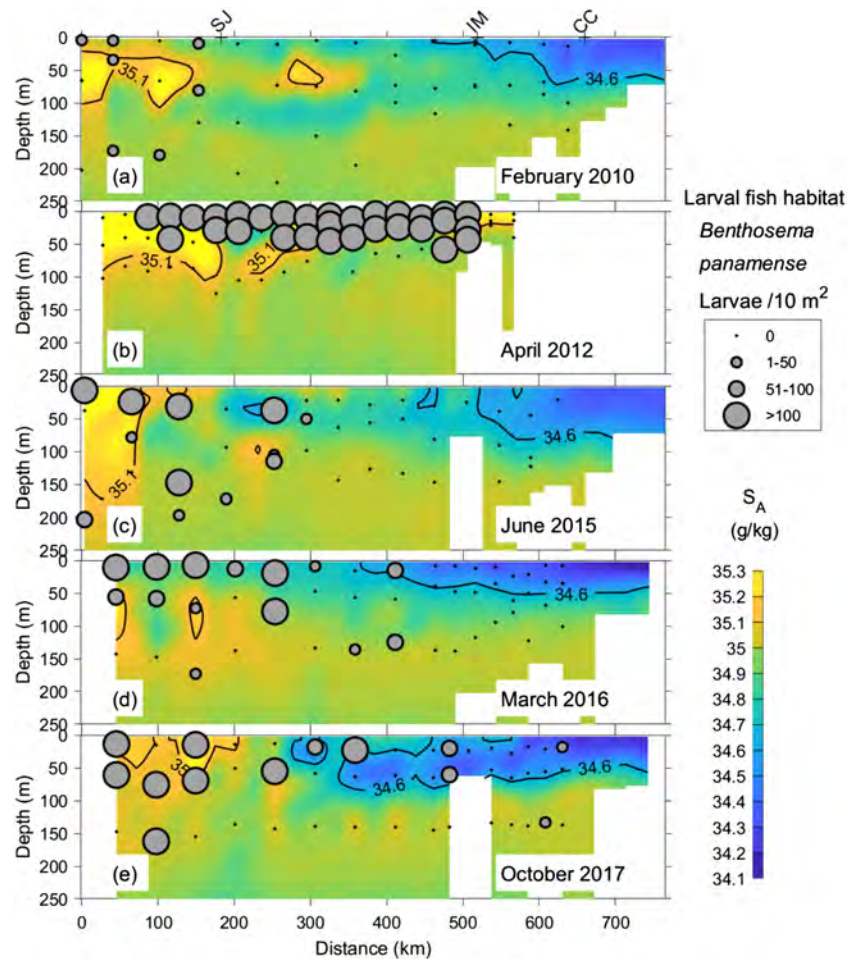


Figure 6. Salinity (color) and larval fish habitat *Benthosema panamense* (gray circles) in the northern limit of the shallow oxygen minimum zone of the tropical-subtropical convergence of the northeastern Pacific Ocean. The 34.6 and 35.1 g/kg isohalines are marked (black lines) as they are the indicators of Tropical Surface Water and Gulf of California Water. The x axis represents distance (km) from the first station in the Gulf of California entrance along the transect shown in Figure 1b.

The second recurrent larval fish habitat (LFH-2) was located mainly in the mouth of the Gulf of California, extending to the south in April 2012 and October 2017 (Figure 6). It was observed vertically throughout the sampled water column but with greater abundance from the oxycline to the surface ($\geq 44 \mu\text{mol/kg}$), although in April 2012 this habitat was concentrated only in the oxygenated layer. Its mean larval abundance and its species richness were the highest in April 2012 and October 2017, and both biological descriptors were relatively high in June 2015 and March 2016 (Table 3). *Benthosema panamense* was the indicator species of the habitat, except in October 2017, where other indicator species of the habitat, *Vinciguerria lucetia* and *Lampanyctus parvicauda*, were recorded (Table 4).

A larval fish habitat (LFH-3) located mainly under the oxycline along the transect was detected in February 2010, April 2012, and October 2017 (Figure 7). This habitat had relatively low larval abundance and the lowest specific richness (Table 3). *Diogenichthys laternatus* was the indicator species of this habitat during the three cruises (Table 3). In June 2015 and March 2016, another larval fish habitat (LFH-4) occurred mainly from the oxycline to the surface near Islas Marias (Figure 7), with *Auxis* spp. as the indicator species, together with *Paranthias colonus* and *Syacium ovale* (Table 3).

3.4. Environmental Variables and Larval Fish Habitats

In the redundancy canonical analysis, environmental variables account for 12.8% of the total variance, and the first two canonical axes explain 12% of the variance (Figure 8 and Table 4). The first canonical axis was

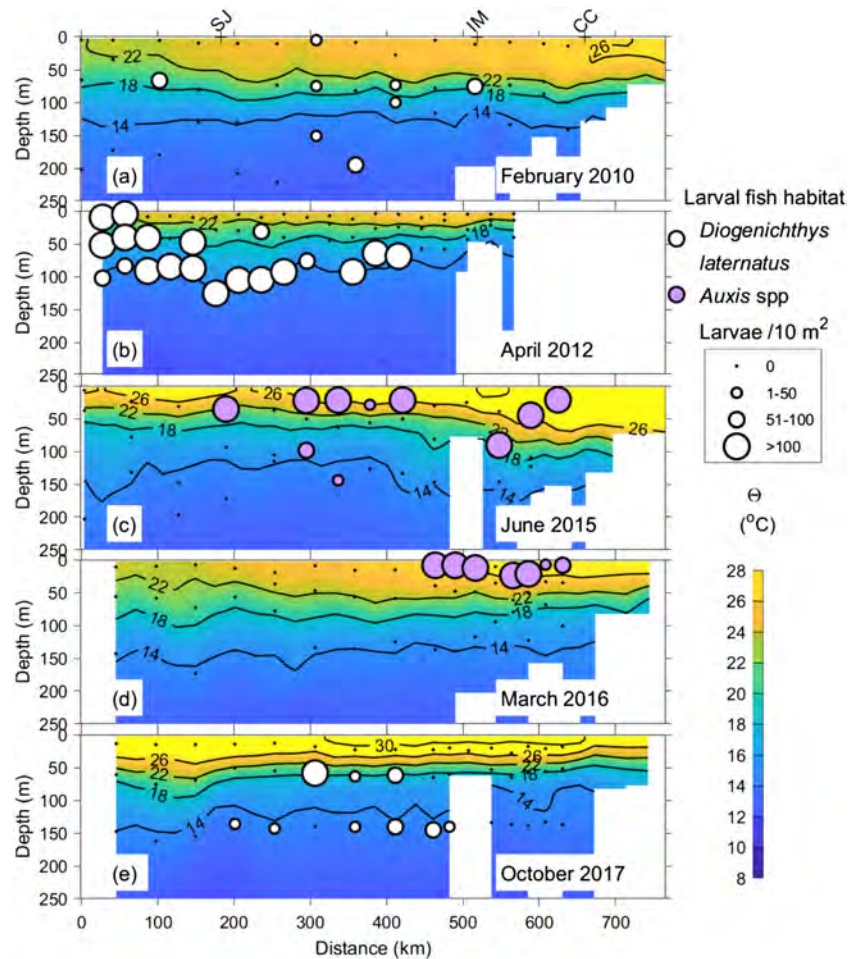


Figure 7. Conservative temperature (color) and larval fish habitats *Diogenichthys laternatus* (white circles) and *Auxis* spp. (purple circles) in the northern limit of the shallow oxygen minimum zone of the tropical-subtropical convergence of the northeastern Pacific Ocean. The x axis represents distance (km) from the first station in the Gulf of California entrance along the transect shown in Figure 1b.

related to horizontal gradients, in which salinity was the more correlated variable ($r = 0.4$). The second canonical axis was related to vertical gradients, where temperature ($r = 0.5$) and the dissolved oxygen ($r = 0.4$) were the variables with stronger correlations.

The ordination of the recurrent larval fish habitats showed a preference to specific environmental conditions. The LFH-1 observed around the Islas Marias indicated by *B. bathymaster* (black circles) was inversely correlated with the salinity and the dissolved oxygen, while the LFH-2 indicated by *B. panamense* detected near the Gulf of California (gray circles) was correlated with high values of temperature, salinity, and dissolved oxygen (Figure 8).

The less recurrent larval fish habitats also showed a relationship with the environmental conditions. The LFH-3, dominated by *D. laternatus* under the oxycline in February 2010, April 2012, and October 2017 (white circles), was inversely correlated with temperature and dissolved oxygen. Also, the LFH-4, dominated by *Auxis* spp. associated with the warm surface layer in June 2015 and March 2016 (purple circles), was correlated with high temperature and low salinity (Figure 8).

In addition, the indicator species of each habitat overlaid on Θ - S_A diagrams (Figure 9) showed different affinities to the water masses. Although *B. bathymaster* (LFH-1) and *B. panamense* (LFH-2) indicator species of recurrent habitats were widely distributed among the water masses, *B. bathymaster* was more frequent in TSW in relation to *B. panamense*, and this last species was more frequent in GCW. In contrast, *D.*

Table 3
Species Indicators for Each of the Larval Fish Habitat (LFH) Determined by the Indicator Species Analysis in the Northern Limit of the Shallow Oxygen Minimum Zone off México.

| Species | February 2010 | | | April 2012 | | | June 2015 | | | March 2016 | | | October 2017 | | |
|---------------------------------|---------------|-------|-------|------------|-------|-------|-----------|-------|-------|------------|-------|-------|--------------|-------|-------|
| | LFH-1 | LFH-2 | LFH-3 | LFH-1 | LFH-2 | LFH-3 | LFH-1 | LFH-2 | LFH-4 | LFH-1 | LFH-2 | LFH-4 | LFH-1 | LFH-2 | LFH-3 |
| <i>Bregmaceros bathymaster</i> | 0.62 | | | 0.42 | | | 0.47 | | | 0.51 | | | 0.71 | | |
| <i>Etropus crossotus</i> | 0.33 | | | 0.63 | | | | | | | | | 0.41 | | |
| <i>Caranx caballus</i> | 0.33 | | | | | | 0.17 | | | 0.21 | | | | | |
| <i>Bentosema panamense</i> | | 0.51 | | | 0.64 | | | 0.70 | | | 0.52 | | | 0.57 | |
| <i>Vinciguerria lucetia</i> | | | 0.14 | | 0.27 | | | 0.44 | | | 0.36 | | | | 0.26 |
| <i>Lamparyctus parvicauda</i> | | | | | 0.61 | | | 0.23 | | | | | | | 0.48 |
| <i>Diogenichthys laternatus</i> | | | 0.52 | | | 0.63 | | 0.68 | | 0.20 | | | | | 0.38 |
| <i>Auxis</i> spp | | | | | 0.40 | | | | 0.32 | | | 0.92 | | 0.35 | |
| <i>Paranthias colonus</i> | | | | | | | | | 0.18 | | | 0.58 | | | |
| <i>Syacium ovale</i> | | | 0.23 | | | | | | 0.85 | | | 0.57 | | 0.31 | |
| Specific richness | 17 | 10 | 10 | 10 | 21 | 15 | 10 | 17 | 21 | 12 | 15 | 19 | 37 | 36 | 12 |
| Samples | 18 | 7 | 8 | 6 | 30 | 21 | 10 | 12 | 10 | 17 | 14 | 7 | 17 | 13 | 9 |
| Average abundance | 75 | 29 | 40 | 725 | 1919 | 458 | 61 | 302 | 385 | 83 | 177 | 249 | 143 | 288 | 52 |

laternatus (LFH-3) and *Auxis* spp. (LFH-4) showed a clear affinity to a different water mass. *D. laternatus* was concentrated in StSsW and *Auxis* spp. in TW.

4. Discussion

4.1. Temporal Changes in Dissolved Oxygen Concentrations

In the context of the deoxygenation of the oceans, the dissolved oxygen series from cruises (2000 to 2017) that covered the northern limit of the shallow OMZ off Mexico suggested a vertical expansion of suboxic water ($\leq 4.4 \mu\text{mol/kg}$) in the present century (Figure 3). As in previous studies on the shallow OMZs (e.g., Schmidtko et al., 2017; Stramma et al., 2008; Stramma et al., 2010), the databases used were temporally and spatially irregular. The deoxygenation trend is evident despite the high mesoscale activity modulated by seasonality and interannuality in this region of the Pacific Ocean off Mexico (Godínez et al., 2010a; Kurczyn et al., 2012).

The vertical expansion of the suboxic water ($\leq 4.4 \mu\text{mol/kg}$ oxypleth) over time shown in this study (Figure 3) is an indicator of the progress of the deoxygenation in the shallow OMZ off Mexico, but many details of its development remain unknown. In the northern limit of the shallow OMZ off Mexico, the strong stratification characteristic of the water column (Godínez et al., 2010a; Davies et al., 2015; Portela et al., 2016) may be limiting the expansion of the hypoxic water ($\leq 44 \mu\text{mol/kg}$ oxypleth) to the sea surface, that is, the oxycline. However, the suboxic water is raised to depths near to the lower limit of oxycline ($\sim 44 \mu\text{mol/kg}$ oxypleth), particularly in the zone south of Cabo Corrientes (Figure 5). This trend demonstrates that the hypoxic layer (from ~ 4.4 to $44 \mu\text{mol/kg}$ oxypleths) has been thinning through time (Figure 3). The implications could be drastic for zooplankton species that live under hypoxic conditions and species that migrate between the oxycline and the hypoxic layer for feeding and to avoid depredation (Davies et al., 2015; Koslow et al., 2011; Kreiner et al., 2009; Sánchez-Velasco et al., 2017). Most of these species live near their physiological limits, similar to the deep (~ 400 m) copepod species reported by Wishner et al. (2018).

In addition, in this study the temperature values at the depth of the oxycline did not show significant changes over time, but the temperature at the depth of the $4.4 \mu\text{mol/kg}$ oxypleth showed some significant increase due to the ascent of that oxypleth (Figure 3), which may be a major

Table 4
Eigenvalues and Explained Variation of the Explanatory Variables and Correlations Among Environmental Variables and Ordination Axes by the Canonical Correspondence Analysis

| Variable | Axis 1 | .Axis 2 | Axis 3 |
|---|--------|---------|---------|
| Statistics | | | |
| Eigenvalue | 0.0846 | 0.035 | 0.0082 |
| Explained variation (cumulative) | 8.46 | 11.95 | 12.78 |
| Pseudo-canonical correlation | 0.6341 | 0.5635 | 0.3979 |
| Explained fitted variation (cumulative) | 66.18 | 93.55 | 100 |
| Correlation variable | | | |
| Conservative temperature (Θ) | 0.0284 | 0.5176 | 0.1564 |
| Absolute salinity (S_A , g/kg) | 0.3944 | 0.0051 | -0.3116 |
| Dissolved oxygen ($\mu\text{mol/kg}$) | 0.303 | 0.4085 | 0.1974 |

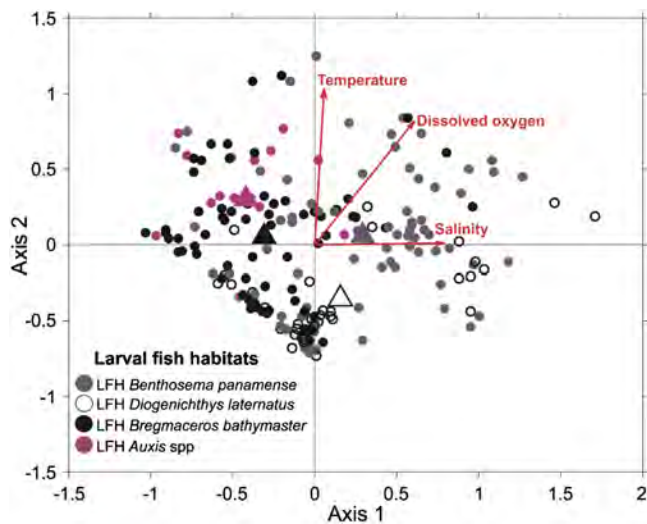


Figure 8. Biplot of the canonical correspondence analysis conducted for fish larvae and environmental variables in the northern limit of the oxygen minimum zone of the tropical-subtropical convergence of the northeastern Pacific Ocean. Triangles indicate the centroid of each larval fish habitat. Larval fish habitats are color coded as in Figures 4–6.

stress for the organisms. The shallowing of the 4.4 $\mu\text{mol/kg}$ oxypleth, besides reducing the hypoxic layer, also exposes the organisms to warmer temperatures and less saline conditions, which may impact the physiology and behavior of the organisms (Deutch et al. 2015). These environmental changes may also increase the stress and mortality rate of some diel vertical migrators that are physiologically limited by suboxic conditions.

Relationships between ocean warming and deoxygenation are complex and indirect. Authors like Cheng et al. (2015) analyzed a global-averaged ocean temperature trend, observed that even though the ocean has continued to gain heat in this century (XXI), the pattern of change is different in the interior ocean. The sea surface layer (1–100 m depth) temperature has decreased in the recent years, accompanied by heating in the 101–300 m layer as a result of changes in the frequency of the warm and cold ENSO phases. In addition, the subsurface ocean from 301 to 700 m experienced a cooling, which Cheng et al. (2015) indicates is “another instance of variability in the natural ocean.” In the shallow OMZ off Mexico, the hypoxic layer and upper limit of the suboxic layer fall between 101 and 300 m depth, corresponding with the layer that is warming according to Cheng et al. (2015). The heating of this critical layer could be a trigger of the deoxygenation and loss of the hypoxic habitats for many marine organisms.

Our results are consistent with the global tendencies of deoxygenation and expansion of the shallow OMZs (Bograd et al., 2008; Schmidtko et al., 2017; Stramma et al., 2008; Stramma et al., 2010), but the processes that generate this deoxygenation remain uncertain. It is therefore difficult to predict how deoxygenation effects will proceed in this region. Authors like Meier et al. (2018) reported that the changes in dissolved oxygen in the deep waters of the Baltic Sea are primarily caused by the increase of organic matter. In studies based on physical data, thermal stratification has been identified as the main cause of the deoxygenation in the ocean (Schmidtko et al., 2017). Other research groups (Duteil et al., 2018) pointed out that the phase changes of the PDO relate to the dissolved oxygen concentration. Positive PDO conditions explain a significant part of the current deoxygenation occurring in the eastern Pacific Ocean (Breitburg et al., 2018). However, Brewer (2018) mentioned that there are clearly multiple processes at work on the deoxygenation in the oceans that could only be explained by multidisciplinary studies focused on global ocean-atmosphere interconnections. Multidisciplinary studies and the maintenance of long time series must be priorities for the understanding of the varied response of marine life to the deoxygenation and warming of the oceans.

4.2. Geographic Variability of Larval Fish Habitats and Water Masses

The distribution of the larval fish habitats defined in this study was related to the dissolved oxygen gradients and the water masses that converge in the Pacific Ocean off Mexico. Despite the inherent seasonal and inter-annual variations in the zooplankton samples that support this study, recurrent larval fish habitats were defined, but with changes in their distribution clearly linked to the ENSO phases (Figures 5–7).

The recurrence of the LFH-1 indicated by *B. bathymater* and LFH-2 indicated by *B. panamense* showed that their components were tolerant to environmental changes; that is, these species had a wide environmental window defined by strong gradients of dissolved oxygen, temperature, and salinity. However, the LFH-1 was mostly located off Cabo Corrientes associated with highly oxygenated TSW, and with StSsW, characterized by low oxygen concentrations, while the LFH-2 was detected to be mostly associated with GCW, water with high dissolved oxygen (Figure 9). Conversely, the LFH-3 indicated by *D. laternatus* and LFH-4 indicated by *Auxis* spp. showed that their components inhabited a reduced environmental window, where the LFH-3 had high affinity with StSsW and the LFH-4 with TSW (Figure 9).

The influence of ENSO phases in the region was evident in the larval fish habitats with a reduced environmental window. During the warm phase of the ENSO (June 2015 and March 2016), the LFH-3 of a more southern origin and immersed in TSW (Figure 9) replaced the LFH-4 during two different warm seasons, showing that its presence in the study area was not random (Figure 7). The presence of the LFH-4 in the

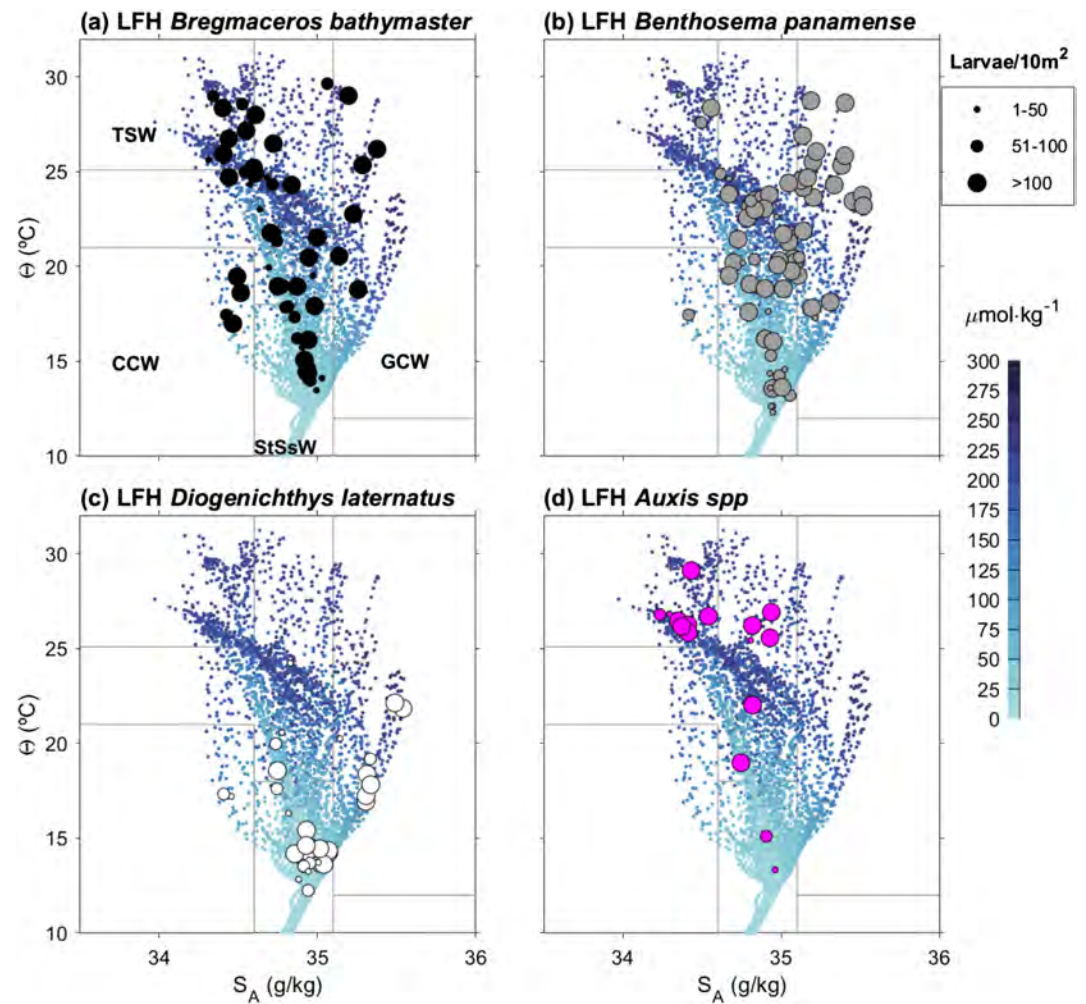


Figure 9. Θ - S_A diagrams with larval fish habitats *Bregmaceros bathymaster* (black circles), *Benthosema panamense* (gray circles), *Diogenichthys laternatus* (white circles), and *Auxis* spp. (purple circles) of the northern limit of the shallow oxygen minimum zone of the tropical-subtropical convergence of the northeastern Pacific Ocean. Water masses are Tropical Surface Water (TSW), Gulf of California Water (GCW), California Current Water (CCW), and Subtropical Subsurface Water (StSsW), according to Portela et al. (2016). Dissolved oxygen is shown in color.

region also modified the distribution of the recurrent habitats. The LFH-4 displaced the LFH-1 to a greater depth, and the LFH-2 to further north in both warm periods. In contrast, during the cold phase of the ENSO (April 2012), the LFH-2 was extended along the oxycline further south into GCW, and the LFH-1 was concentrated in the Islas Marias region. Besides, the LFH-3 was elevated close to the oxycline in water with low oxygen concentrations (Figures 5–7).

The recurrence of larval fish habitats with high abundance in different seasons and ENSO phases shows their resilience to the environment in the context of deoxygenation. Previous studies (Gallo & Levin, 2016; Koslow et al., 2011) have reported that dissolved oxygen concentrations in the OMZs are lower than lethal concentrations determined for many fish species in the laboratory. However, OMZs are not devoid of fish. Therefore, the results of this study support the idea that some fish species (i.e., *B. bathymaster*, *D. laternatus*, and *B. panamense*), from early phases to adult stages, have developed evolutionary physiological adaptations to strong dissolved oxygen gradients and to seasonal and interannual changes in the characteristics of the shallow OMZ off Mexico. These results are similar to descriptions for demersal fish species in the Gulf of California that are also adapted to live under the extremely low oxygen conditions characteristic of the Gulf of California OMZ (Gallo et al., 2019).

Previous studies have reported that the fish can respond to changes in oxygen over a range of time scales from rapid (hours to days) changes in gene expression (Gracey & Somero, 2001, Tiedke et al., 2014) to longer time scales through changes in the presence and density of specific species leading to altered community structures (Chu & Tunnicliffe, 2015; Keller et al., 2015). It can be expected that if deoxygenation continues, the frequency and abundance of species adapted to low thresholds of dissolved oxygen, including specific mesopelagic species examined in this study, will increase. Continuous monitoring is strongly recommended in the context of climatic change and deoxygenation.

5. Conclusion

Based on a series of 19 oceanographic cruises (1,515 profiles) between 2000 and 2017 made in the northern limit of the shallow OMZ off Mexico, a significant vertical expansion of the upper limit of suboxic conditions ($<4.4 \mu\text{mol/kg}$) was detected. In this context, one recurrent larval fish habitat (indicated by *B. bathymaster* larvae) extended throughout the water column off Cabo Corrientes from StSsW (suboxic conditions) to the surface ($220 \mu\text{mol/kg}$). The second recurrent larval fish habitat (*B. panamense*) was located between the oxycline ($>44 \mu\text{mol/kg}$) and the surface in association with GCW. During the warm El Niño event of 2015–2016, a tropical larval fish habitat (*Auxis* spp.) associated with TW appeared to change the larval habitat distributions. These results indicate that some species are resilient to changes of dissolved oxygen and temperature generated by both intermittent events (ENSO phases) and continuing processes (deoxygenation). However, other groups of species, with reduced environmental windows, could be affected by deoxygenation and warming associated, as well others variables not considered here.

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