Three-dimensional distribution of larval fish assemblages in an anticyclonic eddy in a semi-enclosed sea (Gulf of California)

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Transects of CTD (to 1000 m) and zooplankton stations (to 200 m in 50 m strata) were made across an anticyclonic eddy in the southern Gulf of California during October 2007 to determine its influence upon the three-dimensional distribution of larval fish assemblages. The eddy was ≏90 km in diameter and ≏70 m deep. A larval fish assemblage, representing a mix of oceanic and coastal species, was defined mainly in the eddy from 200 m depth to the surface. Mesopelagic species, such as Vinciguerria lucetia, were dominant. Coastal reef (Diplodactylus sp.) and pelagic (Auxis spp.) species were found mainly in the surface layer. This suggests that, because of the Gulf’s relative narrowness, the eddy trapped coastal fish larvae during its formation and trajectory southward, retaining larvae of different adult habits. Another larval fish assemblage was defined off the eastern coast; its high larval abundance and specific richness was probably associated with coastal upwelling. Mesopelagic species (e.g. Triphoturus mexicanus) dominated this assemblage, and coastal demersal species that were absent from the eddy (e.g. Symphurus williamsi) were recorded in the surface layer, suggesting that the thermocline was a vertical boundary in this assemblage. The 3D differentiation of planktonic habitats was the result of the mesoscale hydrodynamics in the area sampled, in particular that associated to the eddy life history and characteristics (radius, depth and velocity), and to coastal upwelling, promoting larval retention of a mix of species of different adult habits.

KEYWORDS: fish larvae; vertical distribution; anticyclonic eddy; Gulf of California

INTRODUCTION

Mesoscale hydrographic structures, such as eddies and fronts, may act as mechanisms of enrichment, concentration and retention of zooplankton (Iles and Sinclair, 1982), with eddies and coastal upwelling two of the main promoters of productivity in the oceans (Bakun, 1996). Distributions of fish larvae relative to hydrographic conditions in and around oceanic eddies have been observed in diverse ecosystems, such as the California Current (Fiedler, 1986), the Kuroshio...
The Gulf of California (Fig. 1a) is a semi-enclosed narrow sea (~120 km wide) with abrupt bathymetry in the midriff section, which is characterized by high productivity (Álvarez-Borrego and Lara-Lara, 1991; Santamaría-del-Angel et al., 1994), and high species diversity (Moser et al., 1974; Aurioles-Gamboa, 1993). This biological richness is associated with enrichment processes that occur within the Gulf, such as inverse-Mediterranean thermohaline circulation, tidal mixing, wind-driven coastal upwelling and mesoscale structures (Álvarez-Borrego and Lara-Lara, 1991; Lavin and Marinone, 2003). Some of these processes and structures are observable in remotely sensed imagery as sharp gradients in sea surface temperature (SST) and chlorophyll-a (Chl a), such as those shown in Fig. 1; in general, cooler SST and high Chl a concentration represent upwelling of cool nutrient-rich subsurface water. Tidal mixing is very important year-round in the midriff archipelago, while coastal upwelling occurs off the eastern coast in autumn-spring (Fig. 1b and c) and off the western coast in summer as a response to the seasonal along-gulf winds, which blow from the NW in spring-autumn and from the SE in summer (Santamaría-del-Angel et al., 1994; Lluch-Cota, 2000; Bordoni et al., 2004).

Although previously speculated upon, the significance of eddies in affecting the distribution and ecology of planktonic biota in the Gulf of California remains poorly understood. Hammann et al. (Hammann et al., 1998) suggested that eddies and associated filaments might be important for the transport of eggs and larvae of sardine, Sardinops sagax, from the east to the west coast of the Gulf of California. This is not confirmed, but these ideas were fundamental in promoting the study of the mechanisms responsible for plankton transport in the Gulf. Using geostrophic currents and larval fish assemblages, Sánchez-Velasco et al. (Sánchez-Velasco et al., 2006) investigated a cyclonic eddy in Bahía de La Paz (southwestern Gulf of California) and this is the first study of its kind in the region.

Recent studies in the Gulf of California have shown the importance of the thermocline and the mixed layer for the vertical distribution of fish larvae (Danell-
Jiménez et al., 2009; Inda-Díaz et al., 2010). Studies focused on the effect of eddies upon the three-dimensional distribution of fish larvae have not been made in the Gulf of California and similar studies are scarce in the tropical–subtropical transitional region of the Pacific Ocean, despite the importance of eddies in promoting productivity (Bakun, 1996).

Because mesoscale eddies are structures with a defined lifetime (months) and continuously evolving, the coupling between the spawning strategies of fish relative to hydrographic structures (such as eddies) might be important for the survival of fish larvae in the pelagic system. In the Gulf of California, the proximity of eddies to the coast suggests that they might entrain eggs and larvae of coastal demersal and oceanic fishes, which implies that these eddies may be important as nursery areas, as well as affecting the recruitment of those species.

Here, we analyze the three-dimensional distribution of larval fish assemblages in and around an anticyclonic eddy in the southern Gulf of California during October 2007. We examine the relationship between the horizontal and vertical distributions of larval fish assemblages and the hydrodynamic structure of the eddy and adjacent waters, as well as the fish larvae distribution in relation to the habits of the adults.

**METHODS**

The mesoscale eddy visible in the Chl a image in Fig 1c, centered at 24°40'N, 109°50'W, was sampled aboard the R/V Francisco de Ulloa from 14 to 22 October 2007. A grid of 36 sampling stations was occupied where concurrent physical and biological (zooplankton) oceanographic measurements were made (Fig 2). Three cross-sections were surveyed through the eddy and extended into the surrounding waters, including the eastern Gulf of California coast, where the images of Figs 1b, 1c and 2b suggested coastal upwelling. Vertical profiles of temperature and conductivity were obtained at each station with a SeaBird 911+CTD that was also equipped with dissolved oxygen (SBE-13, resn. ± 0.02 mL/L) and fluorescence sensors. The data were processed using the manufacturer’s software and averaged to 1 dbar (Godínez-Sandoval et al., 2010). Salinity (S) was calculated with the Practical Salinity Scale 1978. Potential temperature (θ (°C)) and potential density anomaly, γ₀ (kg m⁻³), were calculated according to UNESCO (UNESCO, 1991). The fluorescence data were converted to Chl a values (µg m⁻³) by the sensor (Seapoint, resn. ± 0.02 µg m⁻³); in this article, we refer to these data as “Chl a”. The methods used for processing these data were documented by García-Córdova et al. (García Córdova et al., 2008). Although discrete water samples for Chl a were collected using Niskin bottles, only the fluorescence-derived Chl a concentrations (µg m⁻³) are used herein.

Geostrophic velocity relative to the minimum common sampling depth of pairs of stations (usually 1000 m) was calculated from objectively mapped potential temperature (θ) and salinity. A standard objective-mapping interpolation was used, with a classic Gaussian correlation function with relative errors of 0.1, a 50-km horizontal length scale, and a 70-m vertical scale.

Remotely sensed SST and ocean color images (4 × 4 km) from the Aqua/MODIS satellites were obtained from http://oceancolor.gsfc.nasa.gov/cgi/level3.pl.
Wind data (6-hourly CCMP winds, with horizontal resolution \(0.25^\circ \times 0.25^\circ\)) were obtained from http://podaa.jpl.nasa.gov/DATA_CATALOG/ccmpinfo.html. Lagrangian surface currents were measured with WOCE surface drifters with a 10-m holey sock drogue centered at 15 m, and tracked with the ARGOS satellite telemetry system. These data were quality-controlled and interpolated at 6-h intervals by NOAA’s Global Drifter Program, as described by Hansen and Poulain (Hansen and Poulain, 1996).

Oblique zooplankton hauls were made during day and night at four depth strata (from 200 to 150 m, from 150 to 100 m, from 100 to 50 m and from 50 m to the surface), using opening–closing conical zooplankton nets, with a 50 cm mouth diameter, 250-cm net length and 505-µm mesh size (http://www.generaloceanics.com). To ensure accurate sampling of each depth stratum, the depth of the net was calculated by the cosine of the wire angle method, following the standard specifications of Smith and Richardson (Smith and Richardson, 1979). This stratified sampling technique has been used successfully in previous studies (Danell-Jiménez et al., 2009). 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 biomass, estimated by the displacement volume (Kramer et al., 1972), was standardized to mL/1000 m³. Fish larvae were removed from all samples and identified according to the descriptions in Moser (Moser, 1996), and abundance was standardized to number of larvae per 10 m² (Smith and Richardson, 1979; Moser and Smith, 1993).

The non-parametric Kruskal–Wallis test (Sokal and Rohlf, 1985; Siegel and Castellón, 1988) was used to assess the statistical significance of differences in zooplankton biomass and total larval abundance between daytime and nighttime, and among the different depth strata. When the null hypothesis was rejected, a Tukey multiple-comparison test was used to establish whether significant differences occurred between pairs of strata (Daniel, 2008).

Similarities among the different depth strata were based on taxa with a frequency of occurrence ≥5%. The standardized data were fourth-root transformed to reduce the weight of the most abundant species (Field et al., 1982). Planktonic habitats or groups of strata were defined using the Bray–Curtis dissimilarity index, a technique that is not affected by multiple absences and gives more weight to abundant species than to rare ones (Bray and Curtis, 1957; Field et al., 1982). A dendrogram was made by the flexible agglomerative-clustering method (Sokal and Sneath, 1963). One-way ANOSIM was applied to test the null hypotheses of no difference in larval fish assemblages.

The dominant fish species of each habitat were obtained in accordance with the Olmstead–Tukey test (Sokal and Rohlf, 1985), which takes into account the abundance and relative frequency of each species. The dominant species were considered the representative species of each larval fish assemblage. Diversity was calculated with the Shannon Wiener Index (Ludwig and Reynolds, 1988).

Average similarity and the percentage of contribution of specific species to the identity of each assemblage were determined using the Similarity Percentage (SIMPER) routine (PRIMER; Clarke and Warwick, 2001).

A canonical correspondence analysis (Ter-Braak, 1986) was applied to define the relation between environmental variables and larval fish assemblages. Before calculating the canonical correspondence analysis, the standardized biological data and the matrix of environmental indicators were root–root transformed. The matrix of environmental indicators contained the stratum-average values of zooplankton biomass (mL/1000 m³), depth (m), temperature (°C), salinity, Chl a (µg m⁻³) and dissolved oxygen (mL/L). The result is shown as a biplot (the two first ordination axes) with environmental indicators as vectors and the sampling strata as symbols (Ter-Braak, 1986; De la Cruz-Agüero, 1994).

RESULTS

Environmental variables

Satellite imagery (Figs 1b, 1c and 2b) shows an eddy centered at ~24°40'N, 109°50'W, which was characterized by central maxima in Chl a concentration (≥0.2 µg m⁻³) and sea surface temperature (≥28.5°C), relative to the surrounding water. A time series of chlorophyll images (not shown) indicated that the eddy started forming around 10–11 September in the mainland bight at 26°30'N, 109°30'W, then propagated southwestward toward Isla San José and finally to the southeast at 4–10 km/day. It dissipated on 24–25 October due to tropical storm Kiko.

The hydrographic variables along transect A, which crossed the eddy near its center, are shown in Fig. 3 (temperature cross-sections for the other two transects are presented in Supplementary data, Fig. S1). The geostrophic velocity distribution (isolines, Fig. 3a) shows that the eddy was anticyclonic and this was confirmed by the drifter trajectories (Fig. 2b). The branch of the
eddy current entering the Gulf of California close to the peninsula had a maximum speed \( \approx 35 \text{ cm s}^{-1} \), while the outgoing current had a maximum speed of \( \approx 50 \text{ cm s}^{-1} \). Using the isolachs of Fig. 3a to visually define the eddy dimensions, it was \( \approx 90 \text{ km} \) in diameter (stations A1–A10), and the center was \( \approx 20 \text{ km} \) wide (stations A5–A7); the accuracy of these estimates is around \( \pm 5 \text{ km} \). The eddy was a relatively shallow feature and was \( \approx 70 \text{ m} \) deep at its center. The eddy was a relatively shallow feature and was \( \approx 70 \text{ m} \) deep at its center.

Temperatures (isolines, Fig. 3b) were warmest (\( \geq 28^\circ \text{C} \)) at the eddy center and homogeneous in the first 20 m. Stations toward the eastern coast displayed raised isotherms that are consistent with coastal upwelling, with values \( < 28^\circ \text{C} \). The Chl \( a \) maximum (color, Fig. 3b) was found in the thermocline over most of the cross-section, except in the eddy center (stations A5–A7) where the Chl \( a \) maximum occupied the entire surface mixed layer.

The water masses above 500 m in this region of the Gulf of California (e.g. Lavín et al., 2009) are marked in Fig. 3c. In the upper 150 m, Gulf of California Water (GCW, \( S > 34.9, \theta \geq 12^\circ \text{C} \)) is found in most of the Gulf, and Tropical Surface Water (TSW, \( S < 34.9, \theta \geq 18^\circ \text{C} \)) is found in the entrance and in the southern part of the Gulf of California. A shallow salinity minimum (modified California Current Water) is sometimes found in a narrow layer at \( \approx 50 \text{ m} \) depth. Subtropical Subsurface Water (StSsW, \( 34.5 < S < 35.0, 9 \leq \theta \leq 18^\circ \text{C} \)) is found between \( \approx 100 \) and \( \approx 400 \text{ m} \). Pacific Intermediate Water (PIW, \( 34.5 < S < 34.8, 4 \leq \theta < 9^\circ \text{C} \)) is found below \( \approx 400 \text{ m} \). Therefore, Fig. 3c shows Tropical Surface Water in the eddy body, surrounded by Gulf of California Water off both coasts. The eddy lay over StSsW. The likely sources of the salinity

![Fig. 3. Vertical distribution of hydrographic variables along Transect A (see Fig. 2). (a) Geostrophic speed (cm s\(^{-1}\), isolachs) and potential density anomaly (\( \gamma_0, \text{ kg m}^{-3} \), color): for geostrophic speed, negative values indicate flow to the SE, positive flow to the NW. (b) Potential temperature (\(^\circ\text{C}\)) and Chl \( a \) (\( \mu \text{g m}^{-3} \), color map). (c) Salinity and isotherms marking water masses. (d) Dissolved oxygen (mL L\(^{-1}\)). Water masses code in (c): GCW, Gulf of California Water; TSW, Tropical Surface Water; StSsW, Subtropical Subsurface Water; PIW, Pacific Intermediate Water.](https://academic.oup.com/plankt/article-abstract/34/6/548/1575418)
minima in the eddy center are TSW or the shallow salinity minimum for the peak at ~40 m, and StSw for that at ~100 m. The latter idea is supported by the concave shape of the 1 mL/L oxypleth (which marks the upper limit of the Minimum Oxygen Zone of the eastern tropical Pacific) at ~90 m depth just below the eddy.

In the study area, zooplankton biomass (Fig. 4) ranged from 3.2 to 362.8 mL/1000 m³. There were no statistically significant differences in biomass between day and night ($P > 0.05$, $P = 0.33$), but there were among the four strata ($P < 0.05$, $P = 0.0005$). The Tukey test indicated that these differences were between the shallowest (0–50 m depth) and deepest strata (150 to 200 m depth). Although a horizontal gradient of surface zooplankton biomass was present between the shallowest (0–50 m depth) and the deepest stratum (150–200 m depth). The biomass in the eastern coastal area (Fig. 4), the difference was not significant ($P > 0.05$, $P = 0.25$). The highest biomass, >100 mL/1000 m³, roughly corresponded with the thermoline.

Three-dimensional distribution of larval fish assemblages

There were no statistically significant differences in total larval abundance between day and night ($P > 0.05$, $P = 0.10$). However, there were significant differences in total larval abundance among the four strata ($P < 0.05$, $P = 0.009$), similar to the case of zooplankton biomass. The Tukey test defined that these differences were between the shallowest (0–50 m depth) and the deepest strata (100–150 and 150–200 m depth).

A total of 5850 fish larvae were collected, representing 61 families and 166 taxa (Supplementary data, Table S1). The dominant species were the bathypelagic Vinciguerria lucetia (20%), and the mesopelagics Benthosema panamense (27%), Triphoturus mexicanus (9%), Diaphus pacificus (6%), Diogenichthys lateratus (6%) and Cubiceps pauciradiatus (6%); they formed more than 70% of the total larval fish assemblage. Most of the larvae (>75%) were in preflexion–flexion stage.

The Bray–Curtis dissimilarity index defined three groups of strata (using data from the three transects), with larval fish assemblages that differed in composition and abundance at a level >1.4 (Supplementary data, Fig. S2). These assemblages were significantly different (ANOSIM: $R = 0.55$, $P < 0.001$). The larval fish assemblages were named according to their location in the eddy and are defined as “Eddy larval fish assemblage”, “Eastern larval fish assemblage” and “Edge larval fish assemblage”. An unnamed small group (five strata) was also formed. In addition, the three main larval fish assemblages were subdivided in two subgroups at a level 1.2; some of these subdivisions were related with the vertical structure of the larval fish assemblages (Supplementary data, Fig. S2). The larval fish assemblage distributions on transects B and C are shown in Supplementary data, Fig. S1.

The Eddy larval fish assemblage was located mostly in the eddy center and body and some of its surroundings, from 200 m depth to the surface (Fig. 5a); it was formed by 52 strata and 52 taxa (Supplementary data, Table S1). This larval fish assemblage had a mean abundance of 289 larvae/10 m² and a diversity of 3.4 (Table I). Its highest abundance and specific richness was in the 0 to 50 m stratum, decreasing with depth. It was dominated by larvae of species of different adult habits (Table I) such as the bathypelagic $V$. lucetia and the mesopelagics B. panamense, D. pacificus and C. pauciradiatus. $V$. lucetia (Fig. 6a) and C. pauciradiatus (Fig. 6b) larvae were distributed almost homogenously through the water column in the eddy center (stations A05–A07), but B. panamense was also present in the other larval fish assemblages. Larvae of reef demersal species such as the serranids Hemanthias sp. and Diploprion sp. (Fig. 6c), and the epipelagic Auxis spp. (Fig. 6d) were found in this assemblage from 150 m depth to the surface, but the latter species with maximum abundance in the surface stratum. The contribution of each species to this assemblage was >11%, with B. panamense (22%) and $V$. lucetia (17%) the species with the highest contribution.

Fig. 4. Vertical distribution of zooplankton biomass (mL/1000 m³) on potential temperature (isotherms) on Transect A (Fig. 2). Data symbols represent values integrated in 50-m strata from the surface to 200 m.
Subgroup Eddy A consisted mostly of strata located directly in the eddy center, from surface to 200 m depth (black circles, Fig. 5a); it was dominated by fish larvae of all adult habitats (see above). Its mean larval abundance was double that of subgroup Eddy B. This last subgroup was located mainly from 200 to 50 m depth (open circles, Fig. 5a) and was dominated by bathypelagic and mesopelagic species.

The Eastern larval fish assemblage, formed by 40 strata and 64 taxa (Supplementary data, Table S1 and Table II), was located between the eastern side of the eddy and the mainland from 200 m depth to the surface (squares, Fig. 5b), but with the highest abundance in the first 100 m. It had a mean abundance of 468 larvae/10 m² and a diversity of 3.7 (Table I); this was the larval fish assemblage with the highest abundance and diversity.

Larvae of *B. panamense* and the mesopelagic *T. mexicanus* dominated this assemblage, which were distributed outside the eddy in the first 100 m; however, these species were also present in deep layers of the Eddy larval fish assemblage (Fig. 7a and c). In addition to the dominant species, this larval fish assemblage was characterized by the occurrence of demersal species such as *Syacium ovale* (Fig. 7b), *Symphurus williamsi* (Fig. 7d), *Synodus lucioceps* and Gobiidae types; these species were restricted to this larval fish assemblage. *Benthosema panamense* (38%), *T. mexicanus* (13%) and *S. ovale* (11%) contributed >60% to the formation of the assemblage.

Subgroup Eastern A was formed mostly of shallow strata (black squares, Fig. 5b). This subgroup had the highest larval abundance of the study but its assemblage had a shared affinity to that which characterized the Eastern larval fish assemblage. Subgroup Eastern B was located in the deeper strata (open squares, Fig. 5b), and was dominated by two mesopelagic species and *S. ovale*.
The Edge larval fish assemblage was mostly around the eddy assemblage between 100 m depth and the surface (Fig. 5c). It was formed by 27 strata and 44 taxa (Supplementary data, Table S1 and Table III) with a mean larval abundance of 227 larvae/10 m² and a di-

Relation between larval fish assemblages and environmental variables

The larval fish assemblages were also detected by canonical correspondence analysis (Fig. 8a), which had high multiple correlations in the three ordination axes ($R > 0.65$). The Eastern larval fish assemblage was clearly correlated with all variables, although subgroup Eastern A was correlated with the highest values of temperature, salinity, dissolved oxygen and fluorescence, while subgroup Eastern B, was inversely correlated with these variables, and strongly correlated with depth. The Eddy larval fish assemblage and the Edge larval fish assemblage showed a wide interval of environmental variables; but most of the strata of subgroups Eddy A and Edge A were correlated with intermediate values of temperature, dissolved oxygen, fluorescence and zooplankton biomass.

The $\theta–S$ diagram corresponding to the first 200 m of the water column (Fig. 8b) shows the location of the larval fish assemblages in relation to the water masses. The Eastern larval fish assemblage was mostly in GCW, with high salinities and low temperature, but its deeper strata were in StSsW. The Eddy larval fish assemblage and the Edge larval fish assemblage were mostly in TSW, and their deeper strata also in StSsW. The Edge larval fish assemblage was also related with GCW.

DISCUSSION

This is the first study focused on understanding the effects of an anticyclonic eddy on the three-dimensional distribution of meroplankton, indicated by fish larvae, in the tropical–subtropical transitional region of the Pacific Ocean. The Gulf of California is a highly productive ecosystem (Cisneros-Mata et al., 1997; Sánchez-Velasco et al., 2009) and some of this productivity may be associated with the continuous presence of mesoscale eddies and fronts, which have been recorded by several authors (Lavin et al., 1997; Zamudio et al., 2008). These eddies may have important effects upon the life cycle of the species inhabiting the region.

Larval fish habitats and hydrographic boundaries

The physical characterization of the eddy using geostrophic currents showed that the eddy was anticyclonic, ~90 km in diameter and ~70 m deep. The satellite images showed that the eddy center was warm and had higher Chl a biomass compared to surrounding Gulf of California water (however, note that the surface layers of the Gulf of California are oligotrophic in summer and autumn; concentrations in the thermocline and the eddy center were <0.35 $\mu$g m$^{-3}$). This surface central enrichment may be due to wind/eddy interactions, which can generate upward nutrient fluxes by Ekman pumping and submesoscale processes at the periphery of the eddy (McGillicuddy et al., 2007; Mahadevan et al., 2008). This mechanism could explain the striking distribution of Chl a in the eddy center, and therefore be an enriching process in the Gulf.
Fig. 6. Vertical distribution of larvae of some species (larvae/10 m²) on the thermal structure, along transect A (Fig. 2): (a) *Vinciguerria lucetia* prefexion–flexion larvae, (b) *Cubiceps pauciradiatus* prefexion–flexion larvae, (c) *Diplectrum* sp. prefexion–flexion, (d) *Auxis* spp. prefexion–flexion larvae. The Eddy larval fish assemblage area is indicated by the dashed polygon, based on the Bray–Curtis Index and flexible agglomerative dendrogram method. Data symbols represent values integrated in 50-m strata from the surface to 200 m.

Table II: Dominant species in Eastern larval fish assemblage in the southern Gulf of California during October 2007

<table>
<thead>
<tr>
<th>Taxa</th>
<th>X</th>
<th>%F</th>
<th>% Contribution</th>
<th>Adult habitat</th>
<th>Faunistic habitat</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Benthosema panamense</em></td>
<td>142</td>
<td>100</td>
<td>38.21</td>
<td>MP</td>
<td>Tr</td>
</tr>
<tr>
<td><em>Triphoturus mexicanus</em></td>
<td>51</td>
<td>75</td>
<td>13.33</td>
<td>MP</td>
<td>Sbtr</td>
</tr>
<tr>
<td><em>Syacium ovale</em></td>
<td>23</td>
<td>67.5</td>
<td>10.62</td>
<td>D</td>
<td>Tr</td>
</tr>
<tr>
<td><em>Vinciguerria lucetia</em></td>
<td>100</td>
<td>65</td>
<td>9.98</td>
<td>BP-MP</td>
<td>Tr-Sbtr</td>
</tr>
<tr>
<td><em>Diogenichthys laternatus</em></td>
<td>53</td>
<td>40</td>
<td>3.37</td>
<td>BP</td>
<td>Tr</td>
</tr>
<tr>
<td><em>Cubiceps pauciradiatus</em></td>
<td>20</td>
<td>40</td>
<td>2.77</td>
<td>BP</td>
<td>Tr</td>
</tr>
<tr>
<td><em>Symphurus williamsi</em></td>
<td>19</td>
<td>42.5</td>
<td>3.93</td>
<td>D</td>
<td>Tr</td>
</tr>
</tbody>
</table>

Number of taxa 64
Number of stratum 40
Mean larval abundance larvae/10 m² 468
Mean zooplankton biomass mL/1000 m³ 143.01
Diversity bits/ind. 3.74

%F, frequency; X, mean larval abundance. Adult habitat: B, bathypelagic; MP, mesopelagic; BP, benthepelagic; D, demersal. ND, undetermined. Adult faunistic affinity: Tr, tropical; Sbtr, subtropical.
Fig. 7. Vertical distribution of larvae of some species (larvae/10 m²) on the thermal structure (isotherms), along transect A (Fig. 2); (a) *Benthosema panamense* prefexion–flexion larvae, (b) *Triphoturus mexicanus* prefexion–flexion larvae, (c) *Syacium ovale* prefexion–flexion larvae, (d) *Symphurus williamsi* prefexion–flexion larvae. The Eddy larval fish assemblage area is sketched by the dashed polygon broken line, based on the Bray–Curtis Index and the flexible agglomerative dendrogram method. Data symbols represent values integrated in 50-m strata from the surface to 200 m.

Table III: Dominant species in Edge larval fish assemblage in the southern Gulf of California during October 2007

<table>
<thead>
<tr>
<th>Taxa</th>
<th>X</th>
<th>%F</th>
<th>% Contribution</th>
<th>Adult habitat</th>
<th>Faunistic habitat</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Vinciguerria lucetia</em></td>
<td>59</td>
<td>100</td>
<td>44.49</td>
<td>BP-MP</td>
<td>Tr-Sbtr</td>
</tr>
<tr>
<td><em>Benthosema panamense</em></td>
<td>44</td>
<td>74.1</td>
<td>21.4</td>
<td>MP</td>
<td>Tr</td>
</tr>
<tr>
<td><em>Cubiceps pauciradiatus</em></td>
<td>34</td>
<td>59.3</td>
<td>10.7</td>
<td>BP</td>
<td>Tr</td>
</tr>
<tr>
<td><em>Triphoturus mexicanus</em></td>
<td>15</td>
<td>48.1</td>
<td>6.77</td>
<td>MP</td>
<td>Sbtr</td>
</tr>
<tr>
<td><em>Auxis</em> spp.</td>
<td>18</td>
<td>29.6</td>
<td>2.13</td>
<td>EP</td>
<td>Tr</td>
</tr>
<tr>
<td><em>Diaphus pacificus</em></td>
<td>44</td>
<td>25.9</td>
<td>1.84</td>
<td>MP</td>
<td>Tr</td>
</tr>
<tr>
<td>Number of taxa</td>
<td>44</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Number of stratum</td>
<td>27</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean larval abundance</td>
<td>larvae/10 m²</td>
<td>227</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean zooplankton biomass</td>
<td>ml/L/1000m³</td>
<td>115.6</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Diversity</td>
<td>bits/ind.</td>
<td>3.36</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

%F, frequency; X, mean larval abundance. Adult habitat: B, bathypelagic; MP, mesopelagic; BP, bathypelagic; D, demersal. ND, undetermined. Adult faunistic affinity: Tr, tropical; Sbtr, subtropical.
The elevation of the 1 mL/L oxypleth just below the eddy suggests that it may have been in the decline phase during sampling. However, the clear definition of larval fish assemblages as a function of the eddy structure indicates that this eddy still had a strong influence on the three-dimensional distribution of the fish larvae community.

The Eddy larval fish assemblage was defined from 200 m depth to the surface in the eddy body, but the eddy depth (∼70 m) strongly corresponded with the thermocline. The surface layer contained well-oxygenated Tropical Surface Water with high Chl a, indicating a well-differentiated planktonic habitat. The Eastern larval fish assemblage was associated with warmer, saltier Gulf of California Water where a tilted pycnocline indicated coastal upwelling. This represented a different planktonic habitat to that of the eddy.

Fig. 8. (a) Graphic of the canonical correspondence analysis in the southern Gulf of California during October 2007. (b) θ–S diagram (from CTD) and larval fish assemblages: Eddy larval fish assemblage, circles. Eastern larval fish assemblage, squares. Edge larval fish assemblage, triangles. Black symbols indicate subgroups A and open symbols subgroups B. Data symbols represent values integrated in 50-m strata from the surface to 200 m.
Vertically, the thermocline depth marked different planktonic habitats, below which there was cooler, less saline StSsW that was also low in dissolved oxygen and fluorescence. Zooplankton biomass and total larval abundance were significantly higher in the mixed layer than in the deeper strata as a response to this vertical boundary; however, the dominant species of the larval fish assemblages showed a differential response. In the Eddy larval fish assemblage, prefexion–flexion larvae of _V. lucetia_ and _C. pauciradiatus_ were distributed throughout the water column, suggesting permeability to the thermocline boundary; meanwhile prefexion–flexion larvae of _B. panamense_ and _T. mexicanus_ dominated in the mixed layer in the Eastern larval fish assemblage. This differential response of the mesopelagic larvae suggests that the thermocline may or may not be a vertical boundary for the same zooplankton and fish larvae, depending on their biology and interaction with the production sources (e.g., eddies, upwelling). Futures studies may further explain this differential behavior of the mesopelagic species.

**Larval fish abundance as a function of eddy structure**

The Eddy larval fish assemblage had a mean larval-fish abundance and specific richness lower than that in the Eastern larval fish assemblage. This seems to contradict the biological response recorded in anticyclonic eddies observed in other oceanic ecosystems, such as off Alaska (Mackas and Galbraith, 2002), the Canary Islands (Rodríguez et al. 2004) and the Leeuwin Current (Holliday et al., 2011), where anticyclonic eddies had the highest larval abundance and species richness in the center rather than at the edge and periphery. The Eastern larval fish assemblage was associated with an area of upwelling, suggesting that the greater larval abundance corresponded with enhanced productivity; zooplankton biomass was the highest in this area. Because the Gulf of California is a semi-enclosed sea with relatively little distance between its two coasts (150–200 km), coastal physical processes, such as upwelling, may interact strongly with mesoscale oceanic structures such as eddies and fronts, and generate complex patterns in the distributions of fish larvae as shown in this study.

The lowest larval abundance and species richness at the edge of the eddy reflected the higher production at the eddy center due to mechanisms of accumulation (Bakun, 1996) and upwelling to the cast, although the sampling resolution (one sampling station in the edge per transect) was somewhat limited.

**Ecological implications of eddy entrainment upon larval fish composition**

Larvae of different adult habitats coexisted in the eddy: bathypelagic and mesopelagic species (e.g. _V. lucetia_, _B. panamense_, _T. mexicanus_, from 200 m depth to the surface), pelagic species (e.g. _Auxis spp._) and coastal reef species (e.g. _Diplectrum sp._) mainly from 150 m depth to the surface. The occurrence of coastal species in the eddy center is considered to be indicative of coastal water entrainment by the eddy which, given its proximity to the coast, probably continues throughout the life of the eddy. The presence of reef species (e.g. _Diplectrum sp._) suggests that coastal water came from the peninsular side, where rocky-reef systems are frequent (~40% of the area) (De la Cruz-Aguero et al., 1997). While there are few studies on the coastal demersal larvae in the Gulf, _Diplectrum sp._ larvae have been reported near the west coast of the southern Gulf of California during fall (Sánchez-Velasco et al. 2006; Sánchez-Velasco et al. 2007), the same sampling season as this study.

Trapping of coastal water and neritic larval species in oceanic eddies has been reported in the Leeuwin Current (Holliday et al., 2011) and in the Gulf Stream (Myers and Drinkwater, 1989) during eddy formation and is suggested to negatively influence recruitment of these species. In contrast, in the narrow Gulf of California, we suggest that the continuous formation of eddies with trapping of coastal water may be a mechanism that favors the integrity of the fish-larvae populations and promotes the recruitment of neritic and oceanic species inside them.

**Implications of eddy effects on the species that inhabit the region**

The large number of different larvae, representing adult species with different habitats (mesopelagic, bathypelagic, epipelagic and coastal demersal) demonstrated that the eddy has an important, but as yet undefined influence upon the spawning and nursery areas of fish species inhabiting the Gulf of California. Certainly, the recurrent nature of these eddies (Lavín et al., 1997, 2009; Pegau et al., 2002; Lavín and Marinone, 2003; Zamudio et al., 2008) and of upwelling (Santamaria-del-Angel et al., 1994) has important ecosystem effects within the Gulf of California. In particular, we hypothesize the following main eddy effects on the fish spawning products: (i) trapping eggs and larvae of oceanic and coastal species in the eddy body as suggested by Bakun (Bakun, 1996) for coastal upwelling, (ii) limiting the coastal-oceanic distribution gradients for coastal species as in frontal zones (Danell-Jiménez et al., ...
2009), and (iii) transporting eggs and larvae from coast to coast as suggested by Hammann et al. (Hammann et al., 1998). Future studies in the Gulf of California focused on testing these hypotheses will allow a better understanding of the relation between eddy dynamics and recruitment of meroplanktonic species in this complex subtropical–tropical transitional region.

CONCLUSIONS

This study of the three-dimensional distribution of fish larvae in and around an anticyclonic eddy in the southern Gulf of California during October 2007 showed different spatial and vertical planktonic habitats as function of the mesoscale hydrographic structure and dynamics of the eddy (radius and depth), and the interaction of the eddy with surrounding coastal processes; this seems to favor larval retention of species of different adult habits in this complex transitional region.

The difference in species composition between the Eddy larval fish assemblage and the Eastern larval fish assemblage suggested that the rotation effects of the eddy could function as horizontal planktonic limit between the two assemblages; and the thermocline as a vertical boundary for the some zooplankton organisms and fish larvae in the Eastern larval fish assemblage, which was associated with coastal upwelling, a common process in the Gulf of California from autumn to spring.

The mixed coastal and oceanic species found in the Eddy larval fish assemblage indicated that because of the narrowness of the Gulf, the anticyclonic eddy might have trapped coastal species during its formation or during its trajectory south; this is an indicator of strong interaction of coastal and oceanic processes in the Gulf of California.

SUPPLEMENTARY DATA

Supplementary data can be found online at http://plankt.oxfordjournals.org.

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