Larval fish assemblages and circulation in the Eastern Tropical Pacific in Autumn and Winter

CRISTINA A. LEÓN-CHÁVEZ1,2, LAURA SÁNCHEZ-VELASCO2,*, EMILIO BEIER3, MIGUEL E. LAVÍN4, VICTOR M. GODÍNEZ5,6 AND JAIME FÄRBER-LORDA4


*CORRESPONDING AUTHOR: lsvelasc@gmail.com

Received September 29, 2009; accepted in principle November 20, 2009; accepted for publication December 10, 2009

Corresponding editor: Roger Harris

In this work, we linked larval fish assemblages with water masses and circulation in the Eastern Tropical Pacific off Mexico, during autumn 2005 and winter 2007. Four assemblages were defined. (i) The “Transitional” assemblage, with the lowest mean larval abundance and dominated by tropical mesopelagic *Vinciguerria lucetia* and *Diogenicthys laternatus*. It was associated with modified California Current Water in winter and with modified Tropical Surface Water in autumn. (ii) The “Coastal-oceanic” assemblage was found off Cabo Corrientes, with high larval abundance, and dominated by *Bregmaceros bathymaster*; part of this assemblage was trapped by coastal cyclonic eddies. (iii) The “Tropical A” assemblage was associated with Tropical Surface Water. It had the highest abundance and richness, and the largest number of dominant species (*e.g.* *D. laternatus*, *Auxis* spp.); it covered a wider area in winter than in autumn. (iv) The “Tropical B” assemblage, distinguished by the highest abundance of *V. lucetia*, was present only in autumn; it was associated with overall anticyclonic circulation of warm Tropical Surface Water. The agreement between larval fish assemblage distributions, water masses and mesoscale dynamics indicates that the formation and permanence of assemblages depends on the interaction of spawning strategies of different species with large-scale and mesoscale processes.

INTRODUCTION

The Eastern Tropical Pacific (ETP) off Mexico (Fig. 1) is a transitional ocean region associated with the confluence of tropical water brought to the area by the poleward Mexican Coastal Current (Beier et al., 2003; Lavín et al., 2006) and subarctic water transported by a branch of the California Current system which, instead of flowing westward to join the North Equatorial Current, flows equatorward parallel to the coast of Mexico (Kessler, 2006). This confluence or transitional zone has a seasonal signal (Wyrtki, 1965a, b; Fiedler and Talley, 2006; Kessler, 2006) with the local branch of the California Current having its maximum southward extent in March–May and its minimum in September–December. Superimposed on the seasonal circulation is an intense mesoscale activity consisting of eddies, fronts and filaments (sometimes associated with coastal
upwelling). These structures are almost always present in satellite images of sea surface temperature and chlorophyll of the area (Torres-Orozco et al., 2005; Zamudio et al., 2007). The mesoscale accounts for around 30% of the local total variance of the surface dynamics, a contribution similar to that explained by the seasonal signal (Godínez et al., 2010).

Numerical models of the ETP off Mexico can reproduce eddies (Fig. 1), some of which appear to be generated by instabilities of the Mexican Coastal Current (Zamudio et al., 2007), unlike the eddies in the Gulf of Tehuantepec that are mainly produced by the offshore-directed wind jet typical of that gulf (Willett et al., 2006). The Tehuantepec eddies show the westward drift characteristic of Rossby waves (Willett et al., 2006), but this behavior has not been described for the eddies of the ETP off Mexico.

Regardless of their origin, mesoscale oceanographic structures may act as mechanisms that concentrate or disperse nutrients and planktonic organisms (Fiedler, 1986; Bakun, 2006); therefore, they may impact the productivity of the ocean (Pennington et al., 2006; López-Sandoval et al., 2009) and the heterogeneity of the composition and distribution of zooplankton, including fish eggs and larvae (Färber-Lorda et al., 2004; Fernández-Alamo and Färber-Lorda, 2006). The possible biological consequences of the eddies of the ETP off Mexico, such as the effect on fish larval survival, has not yet been studied.

Fish larvae composition and distribution in the ETP off Mexico have previously been examined, both offshore (Ahlstrom, 1971; Ahlstrom, 1972; Loeb and Nichols, 1984), and in limited near-shore areas of the continental shelf (e.g. Franco-Gordo et al., 2002; Franco-Gordo et al., 2004). The community is represented by more than 150 species belonging to 50 families, which vary in abundance and distribution in different periods of the year. However, there are no studies on the relation between oceanographic processes that can influence the spawning of the different species and the formation and permanence of larval fish assemblages.

Previous work on fish larvae in the coastal region (e.g. Franco-Gordo et al., 2002) indicated that the California Current affected the area from January to May, but no detailed physical (temperature and salinity values) or biological (fish larvae-specific composition) evidence was provided. Studies in the ETP open sea have suggested that the highest larval abundance is found in the thermocline (Loeb and Nichols, 1984). Recently, Vilchis et al. (Vilchis et al., 2009) found that the neustonic ichthyoplankton in the open-sea western subtropical region is more resilient to ENSO-driven environmental variability than ichthyoplankton in the eastern coastal upwelling areas. These earlier contributions did not identify the physical and biological processes that affect the formation and permanence of the larval fish assemblages nor their hydrographic boundaries, both of which are necessary to understand larval survival and subsequent recruitment in the region.

The aim of this study is to examine the distribution of larval fish assemblages in the ETP off Mexico and their hydrographic and dynamics boundaries in autumn (November 2005) and winter (March 2007) using direct observations and satellite data. In particular, we discuss the relationships between assemblage distributions and large-scale and mesoscale physical processes.

**METHOD**

The zooplankton and physical data were obtained on board the R/V “Francisco de Ulloa” (CICESE) during two oceanographic campaigns, in 8–21 November 2005, and 7–22 March 2007. The sampling area, shown in Fig. 1, extended from the tip of the Baja California Peninsula (23°N) to south of Cabo Corrientes (17°N). Around 150 hydrographic stations were made on each cruise, 50 of which included biological sampling (zooplankton samples). The vertical profiles of temperature and salinity were measured to 1000 m depth (or to ~5 m above the bottom if shallower) with a factory-calibrated SeaBird SBE-911 plus...
CTD, with primary and secondary sensors and a sampling rate of 24 Hz. The data were processed and averaged to 1 dbar (Godínez et al., 2010). Salinity (S) was calculated with the Practical Salinity Scale 1978. The potential temperature, θ (°C), and the density anomaly, γθ (kg m$^{-3}$), were calculated according to UNESCO (UNESCO, 1991). The surface geopotential anomaly was obtained (after smoothing the temperature and salinity cross-sections by objective mapping) relative to 500 m, following Lavín et al. (Lavín et al., 2006).

In addition to the field data, mean weekly images of chlorophyll and temperature were obtained from the AQUA-MODIS satellites (4 km x 4 km resolution) (ftp://oceans.gsfc.nasa.gov/MODISA), as support for the interpretation of the hydrographic data, in particular to identify features such as eddies and fronts. The altimeter sea surface height anomaly (SSHA) data of 1/3 degree resolution produced by SSALTO/DUACS (Developing Use of Altimetry for Climate Studies) and distributed by Aviso (Archiving Validation and Interpretation of Satellite Oceanographic Data), with support from CNES (http://www.aviso.oceanobs.com), were also obtained.

Zooplankton hauls were made using bongo nets with a mouth diameter of 60 cm and mesh sizes of 505 and 333 μm. Hauls were oblique, from near the bottom to the surface, or from 200-m depth to the surface when the bottom depth was greater. 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 displacement volume (Beers, 1976; Smith, 1971), was standardized to mL/1000 m$^3$. Fish larvae were removed from the samples and identified, mainly following Moser (Moser, 1996). Larval abundance was standardized to number per 10 m$^2$ of sea surface.

Similarities among stations were based on taxa with a frequency of occurrence ≥5% in each period. To reduce the weight of the most abundant species, the standardized data were fourth-root transformed. Groups of stations were defined using the Bray–Curtis dissimilarity index, a technique which is sufficiently robust for marine data because it 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). Dendrograms were constructed with the flexible agglomerative clustering method (Field et al., 1982). The Olmstead–Tukey test, which takes into account the frequency and abundance of each species, was used to determine the characteristic species of each station group (Sokal and Rohlf, 1969).

**RESULTS**

**Zooplankton biomass**

In November 2005, the zooplankton biomass ranged between 21 mL/1000 m$^3$ and 893 mL/1000 m$^3$, with a mean of 186 mL/1000 m$^3$. The highest values were found (Fig. 2A) in the coastal zone off and south of Cabo Corrientes, while the lowest values were in the oceanic area off Cabo Corrientes and to the north of the study area. In March 2007, the zooplankton biomass values had a wider range than in November 2005, between 12 mL/1000 m$^3$ and 1847 mL/1000 m$^3$.

**Fig. 2.** Spatial distribution of zooplankton biomass (mL/1000 m$^3$) in the Eastern Tropical Pacific off Mexico during (A) November 2005 and (B) March 2007.
Fish larvae composition

A total of 7095 fish larvae were identified in November 2005, which were included in 57 families and 131 taxa. *Vinciguerria lucetia* (46%), *Bregmaceros bathymaster* (12%), *Diogenychthys laternatus* (9%), *Diaphus pacificus* (4%), *Benthosema panamense* (3%), *Auxis* Type I (3%), *Auxis* Type II (2%) and *Cubiceps pasciradiatus* (2%) comprised more than 80% of the total larval abundance. Most of the species were of tropical affinity (Supplementary data, Annex S1).

In March 2007, the larval abundance was higher than in November 2005, but the species richness was lower. A total of 9737 fish larvae were collected and identified in 44 families and 97 taxa. *Vinciguerria lucetia* (31%), *B. bathymaster* (22%), *D. laternatus* (22%), *Myctophum aerolatermatum* (3%) and *D. pacificus* (3%) made up more than 80% of the total larval abundance (Supplementary data, Annex S1).

Larval fish assemblages

Larval fish assemblages were defined by the Bray–Curtis dissimilarity index at a level near one; four in November and three in March (Fig 3). The assemblages were named according to their distribution area and their association with the water masses (to be presented later) as follows: Transitional assemblage, Coastal-oceanic assemblage, Tropical A assemblage and Tropical B assemblage.

The transitional assemblage was present, in both cruises, in the northwestern sector of the sampled area (Fig 4A and B), a region with low values of zooplankton biomass (Fig 2A and B). The mean larval abundance was ≤498 larvae/10 m² with a specific richness of 15 and 23 taxa in November and March, respectively. The dominant species (all mesopelagic, Table I) were *V. lucetia* and *D. laternatus* on both cruises, as well as *D. pacificus* in November and *Hygophum atratum* in March.

On both cruises, the Coastal-oceanic assemblage was defined in the neighborhood of Cabo Corrientes (Fig 4A and B), where the zooplankton biomass was high (Fig 2A and B). This assemblage had high larval abundance and high specific richness on both cruises, with a mean larval abundance ≥969 larvae/10 m² and specific richness ≥46 taxa. This assemblage was characterized by the dominance of a mixture of coastal and oceanic species. The neritic—mesopelagic species *B. bathymaster* strongly dominated this assemblage on both cruises. In addition, *Dormitator latifrons* (coastal shallow demersal), *Bathylagoides nigrogryns* (mesopelagic species), *Pennesio* (oceanic epipelagic species), *V. lucetia*, *D. laternatus*, *Citharichthys platophrys* (coastal shallow demersal), *B. panamense* (mesopelagic species) and *D. pacificus* also dominated in November; *V. lucetia* and *D. laternatus* larvae did so in March (Table I).

The Tropical A assemblage covered broadly the central and southern parts of the sampled area in March, but in November it was restricted to the southern part (Fig 4A and B). This assemblage had high mean larval abundance (≥960 larvae/10 m²), high specific richness (≥60 taxa) and the largest number of dominant species (Table I). In November 2005, the dominant species were *V. lucetia*, *D. laternatus*, *Auxis* Type I and *Auxis* Type II (coastal epipelagic species), *B. panamense*, *B. bathymaster*, *D. pacificus*, *Xyrichtys mundiceps* (shallow demersal species), *C. pasciradiatus* (oceanic epipelagic) and *P. sio*. In March 2007, the dominant species were *V. lucetia*, *D. laternatus*, *M. aerolatermatum*, *D. pacificus*, *Lestidiops neles* (mesopelagic species), *B. bathymaster*, *Symphurus chabanaudi* (shallow demersal species) and *H. atratum*.

The Tropical B assemblage was defined only in November and was located in a wide oceanic area (Fig 4A), in which the zooplankton biomass showed intermediate values. This assemblage had an intermediate larval fish abundance (886 larvae/10 m²) and intermediate specific richness (20 taxa), with a lower number of dominant species than the Tropical A assemblage (Table I). The dominant species were *V. lucetia* (with its highest abundance in the study at 564 larvae/10 m²), *D. laternatus*, *D. pacificus* and *C. pasciradiatus*.

Sea surface temperature (SST), chlorophyll concentration (CHL) and larval fish assemblages

Satellite images of SST showed a NW–SE large-scale gradient around the dates of both cruises (Fig 5A and B), but with higher SST values in November than in March. In November, the SST ranged from 25.8 to 28.9°C with a mean of 27.7°C, while in March, the range was from 20.4 to 27.2°C and the mean was 24.9°C. In both sampling periods, the lowest SST values were in the northwest, and the highest in the southeast of the sampled area. In November, a local SST minimum occurred in the coastal zone off Cabo Corrientes, which suggested upwelling; this was confirmed by the vertical hydrographic sections (data not shown). Superimposed
on the large-scale NW–SE gradient, intense mesoscale activity was suggested in both periods.

The corresponding CHL satellite images (Fig. 6A and B) show that the highest concentrations were located near the coast (>0.7 mg/m³), in particular in the coastal zone off and to the southeast of Cabo Corrientes (consistent with upwelling as suggested by the SST in November). There were offshore extensions of the coastal highs of CHL, apparently associated with mesoscale features such as eddies (e.g. the cold-core cyclonic eddy C2 in Fig. 6A).

The distributions of the assemblages were related to the spatial distribution of SST (Fig. 5) and CHL (Fig. 6). The Transitional assemblage (blue squares) was associated with the lowest SST and chlorophyll concentrations, while the Coastal-oceanic assemblage (green marks) was associated with the highest concentrations of CHL and the highest SST.
triangles) was located in coastal zones, specifically south and off Cabo Corrientes with low SST and high chlorophyll concentration. Both the Tropical A and Tropical B assemblages (red stars and cyan circles, respectively) were located in oceanic areas with the highest SST and low chlorophyll concentration.

**Surface circulation, water masses and larval fish assemblages**

The surface geostrophic circulation during the two cruises is presented in Figs 7 and 8, calculated from the gradient of the geopotential anomalies relative to 500 m depth (upper panels, with the surface salinity as background) and of the SSH anomalies (lower panels). The two fields can be compared only qualitatively because the SSH data are anomalies of the mean surface level. However, the overall agreement between the two fields in this zone has been demonstrated by Godinez et al. (Godinez et al., 2010), and is also apparent in Figs 7 and 8. By combining the two fields, a more complete description of the circulation is obtained. The poor SSH coverage near the coast is largely compensated by the ship sampling.

The water masses present in the surface layer in the sampled area during the two cruises are shown in the \( \theta - S \) diagrams of Fig. 9, which were built by averaging the temperature and salinity profiles (5-m means) that corresponded to each assemblage (Fig. 4). The assemblage-averaged profiles to 125 m depth (Fig. 9) include the pycnocline (found from \( \sim 30 \) to \( \sim 100 \) m depth), where most of the fish larvae tend to concentrate (Loeb and Nichols, 1984; Sánchez-Velasco et al., 2007). The water-mass classification in Fig. 9 is based on Wyrtki (Wyrtki, 1965b), Fiedler and Talley (Fiedler and Talley, 2006) and Durazo and Baumgartner (Durazo and Baumgartner, 2002). The surface water masses in this region and their characteristics are: California Current Water with salinity \( >34.5 \) and temperature \( <21^\circ C \), Tropical Surface Water with salinity \( \leq 34.5 \) and temperature \( \geq 25^\circ C \), and Gulf of California Water with salinity \( >34.9 \). These boundaries are marked as vertical and horizontal lines in Fig. 9; also notice the "transitional zone", marked in light gray. According to Wyrtki (Wyrtki, 1965b), the properties of water masses are well defined at the center of the formation areas, but the boundaries between them are not because properties change gradually, particularly in a transition region like the ETP off Mexico. Consequently, large bodies of transitional waters are located between the water masses. In Fig. 9, whenever the properties of the surface water go below or above the temperature or salinity ranges given above, they are denoted as "warmed", "cooled" or "evaporated" to indicate their transitional condition. Below the surface water masses, the salinity maximum \( (\sim 34.8) \) of the Subtropical Subsurface Water is found between 100 and 150 m depth.

The circulation in November 2005 (Fig. 7) showed an overall southward flow in the sampled area, and northward flow just west of it (more evident in Fig. 7B). Both flows meandered around a series of mesoscale eddies that dominated the circulation pattern. The three principal cyclonic eddies, C1 just south of the tip of the peninsula, C2 west of Cabo Corrientes and C3 in the
Table I: Dominant species of the sampling stations groups and their larval fish assemblages in the Eastern Tropical Pacific off Mexico determined by the Olmstead–Tukey test

<table>
<thead>
<tr>
<th>Dominant taxon</th>
<th>November 2005</th>
<th>March 2007</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Transitional</td>
<td>Coastal-oceanic</td>
</tr>
<tr>
<td>Auxis Type II</td>
<td>9.9</td>
<td>95.2</td>
</tr>
<tr>
<td>Auxis Type I</td>
<td>7.6</td>
<td>72.6</td>
</tr>
<tr>
<td>Bathylagoides nigrenys</td>
<td>2.2</td>
<td>21.7</td>
</tr>
<tr>
<td>Benthosema panamense</td>
<td>7.8</td>
<td>75.4</td>
</tr>
<tr>
<td>Bregmaceros bathymaster</td>
<td>44.6</td>
<td>431.9</td>
</tr>
<tr>
<td>Citharinchthys platophys</td>
<td>1.9</td>
<td>18.7</td>
</tr>
<tr>
<td>Cubiceps paucradiatius</td>
<td>2.9</td>
<td>28.2</td>
</tr>
<tr>
<td>Diaphus pacificus</td>
<td>8.0</td>
<td>39.6</td>
</tr>
<tr>
<td>Diogenichthys laternatus</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dormitator latifrons</td>
<td>2.3</td>
<td>21.9</td>
</tr>
<tr>
<td>Hygophum atratum</td>
<td>9.6</td>
<td>35.1</td>
</tr>
<tr>
<td>Lestidiops neles</td>
<td>3.1</td>
<td>42.6</td>
</tr>
<tr>
<td>Myctophum aurolaternatum</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pseses sio</td>
<td>1.8</td>
<td>17.5</td>
</tr>
<tr>
<td>Symphurus chabanaudi</td>
<td>84.1</td>
<td>418.5</td>
</tr>
<tr>
<td>Vinciguerria lucetia</td>
<td>108.1</td>
<td>343.6</td>
</tr>
<tr>
<td>Xyrichtys mundiceps</td>
<td>343.6</td>
<td>564.2</td>
</tr>
<tr>
<td>Number of taxa</td>
<td>15</td>
<td>60</td>
</tr>
<tr>
<td>Number of stations</td>
<td>5</td>
<td>10</td>
</tr>
<tr>
<td>Mean larval abundance (larvae/10 m²)</td>
<td>498</td>
<td>966</td>
</tr>
<tr>
<td>Adult habitat (%)</td>
<td>60 (mp)</td>
<td>44 (dp)</td>
</tr>
<tr>
<td>Mean larval abundance (larvae/10 m²)</td>
<td>24 (mp)</td>
<td>27 (mp)</td>
</tr>
<tr>
<td>Faunistic affinity (%)</td>
<td>80 (tr)</td>
<td>63 (tr)</td>
</tr>
</tbody>
</table>

%F, frequency; X, mean larval abundance. Adult Habitat: (mp) mesopelagic; (d) demersal. Faunistic affinity: (tr) tropical.
coastal area south of Cabo Corrientes, are identified in Fig. 7B. The anticyclonic eddies that affected the sampled areas were A1, west of cyclone C2, and A2, southwest of cyclone C1.

During November 2005, the Transitional assemblage was associated with high-salinity water flowing around cyclonic eddy C1 (Fig. 7A and B). The $\theta$–$S$ diagram (Fig. 9A) suggests that this warm and salty surface water was Tropical Surface Water whose salinity had increased beyond its nominal maximum of 34.5. The Coastal-oceanic and the Tropical A assemblages were found in high-salinity waters close to the coast, probably evaporated Tropical Surface Water (Fig. 9A). These two assemblages were clearly interspersed by the circulation associated with cyclonic eddies C2 and C3 (Fig. 7A and B). The Tropical B assemblage was found in the offshore low-salinity and warm water, which Fig. 9A suggests to have been Tropical Surface Water, associated with northward flow and with anticyclonic flow around eddy A1.

In March 2007, the surface circulation (Fig. 8) showed an overall southward flow, except close to the coast, where a poleward coastal current was apparent south of Cabo Corrientes (Fig. 8A). The southward flow presented wide meanders, associated with eddies visible in the SSH

![Fig. 5. Larval fish assemblages and mean weekly images of sea surface temperature obtained from the AQUA-MODIS satellites (4 km × 4 km resolution). (A) 17–24 November 2005. (B) 6–13 March 2007. Assemblage color code: insert square.](image)

![Fig. 6. Larval fish assemblages and mean weekly images of chlorophyll obtained from the AQUA-MODIS satellites (4 km × 4 km resolution). (A) 17–24 November 2005. (B) 6–13 March 2007. Assemblage color code: insert square. C2 marks a chlorophyll maximum associated to a cyclonic eddy (Fig. 7B).](image)
A strong anticyclonic eddy was evident south of the tip of the peninsula (A3), a cyclonic eddy south Cabo Corrientes (C4) appeared to affect the coastal current and a cyclonic eddy (C5) was situated close to the mainland in the northeast of the sampled area.

During the March 2007 cruise, the Transitional assemblage was found in the cool medium-salinity water (Figs 6B and 8A) that flowed southward in the northwest of the sampled area. This water was probably evaporated transitional California Current Water (Fig. 9B). The anticyclonic eddy A3 seemed to have trapped most of the elements of this assemblage (Fig. 8B).

The Coastal-oceanic assemblage was found close to the mainland coast, both south of Cabo Corrientes associated with poleward-flowing, low-salinity and warm Tropical Surface Water, and in the northernmost transect associated with evaporated Tropical Surface Water (Fig. 8A). Eddy C4 seemed to have trapped part of this assemblage, and spread it offshore. The Tropical A assemblage covered a large proportion of the sampled area, which caused the large variability in temperature and salinity (Fig. 9B). It was immersed in transitional water and mostly southward flow. The decrease of salinity toward the surface in both the Coastal-oceanic and the Tropical A assemblages (Fig. 9B) is a trend typical of the Tropical Surface Water.
DISCUSSION

The northern boundary of the Tropical Surface Water lies near 15°N, and presents a seasonal movement of about 5° of latitude during the year (Wyrtki, 1965b). The autumn cruise (November 2005) took place at the time of the year when the Tropical Surface Water was beginning its southward retreat from its maximum summer northward intrusion (Wyrtki, 1965b; Fiedler and Talley, 2006; Kessler, 2006). The macroscale circulation was to the south and the SST was high (Fig. 5A). During the winter cruise (March 2007), the retreat of the Tropical Surface Water was evident (Fig. 5B); the local branch of the California Current was close to its maximum southward extension and the SST was low in most of the area.

The surface dynamics of the studied region can be decomposed into the large-scale annual circulation and the local eddies, both scales with the same proportion of explained variance (Godínez et al., 2010). The annual variability of the dynamics can be explained in terms of a long Rossby wave radiated from the coast and forced locally by the annual harmonic of the wind stress curl (Kessler, 2006; Godínez et al., 2010). This annual-scale dynamical model explains the seasonal variability of the confluence of the local branch of the California Current with the Mexican Coastal Current. This in turn determines the seasonal variability of the distribution of the California Current Water and the Tropical Surface Water in the area.

We propose that in the ETP off Mexico, the large-scale distribution of the assemblages is correlated with the different water masses (which in turn vary with the seasonal dynamics), while the mesoscale eddies would define boundaries within which part of a particular assemblage may get trapped.

For instance, some mesopelagic species such as V. lucetia, D. laternatus and D. pacificus were present in most of the assemblages defined in the region, but with a marked gradient of abundance and frequency (Table I). In view of the great extent of the area, the dominance of these mesopelagic species throughout the region may be explained as due to the spawning of distinct fish populations of the same species in different water masses, whose environmental differences would result from the large-scale annual circulation in the region. However, the eggs and larvae may be either retained or dispersed by the different mesoscale hydrodynamic features that occurred in the distribution area of each assemblage. We are proposing that although the composition and distribution of the assemblages may change seasonally and from year to year, their distribution would be controlled by that of the water masses and by large-scale and mesoscale hydrodynamic processes, as described for our data sets.

The Transitional larval fish assemblage

Biologically, the Transitional assemblage was characterized by the lowest zooplankton biomass values (Fig. 2),
low larval abundance and low specific richness, and by the overwhelming dominance of the tropical mesopelagic *V. lucetia* and *D. laternatus*. This occurred in both sampling periods, despite the assemblages being found in Tropical Surface Water in autumn and in California Current Water in winter (Fig. 9A and B). This suggests that this assemblage represented the northern limit of the tropical assemblages in this zone in both seasons.

Support for the idea of a northern limit of the tropical assemblages comes from the absence in the Transitional assemblage of species of subarctic affinity such as *Engraulis mordax*, *Sardinops sagax* and *Merluccius productus*, which are dominant in the California Current System and in the cool areas of the Gulf of California during autumn and winter. The cause of their absence was probably that the temperature was above their optimal spawning range; i.e., this Transitional assemblage was located beyond the southern limit of these species. In contrast, the tropical mesopelagic species *V. lucetia* and *D. laternatus* are also frequent and abundant in the California Current System off California and Baja California Peninsula (e.g. Loeb et al., 1983; Moser and Smith, 1993), and in the Gulf of California (e.g. Moser et al., 1974; Acese-Medina et al., 2004).

Most of the Transitional assemblage stations in March appeared to be trapped in the anticyclonic eddy A3, which could have been holding together this assemblage. The interaction of this assemblage with eddies C1 and A2 in November is not very clear because of the scant sampling.

**Coastal-oceanic assemblage**

The definition of the Coastal-oceanic assemblage in the coastal zone south of Cabo Corrientes was associated with Tropical Surface Water (Figs 7A, 8A and 9), and with relatively low SST, high CHL and high zooplankton biomass, which indicates that there was a specific larval environment in both periods. The very high larval abundance and specific richness of this assemblage may be associated with the influence of coastal processes such as coastal upwelling, as observed in our November 2005 cruise. López-Sandoval et al. (López-Sandoval et al., 2009) studied the upwelling area of Cabo Corrientes, where they recorded high primary productivity, and pointed out that this zone is one of the richest of the ETP off Mexico, which is congruent with the biological characteristics of this assemblage.

There was a striking coincidence of the distribution of this assemblage with the cyclonic eddies C2, C3 (Fig. 7) and C4 (Fig. 8), which suggests that its biological richness may have been influenced by these eddies. The eddies may be trapping eggs and larvae of this assemblage during their formation (together with the high chlorophyll, as seen in eddy C2, in Fig. 6A), while at the edges they would intermingle coastal and oceanic species, as suggested by the distribution of assemblages around eddy C2 in Fig. 7. This is a complex but interesting scenario, only suggested by our data, but the coexistence of abundant coastal and oceanic species may be an indicator of this dynamics. For instance, the coastal species of this assemblage have also been recorded in the near-shore coastal area off Jalisco and Colima (e.g. Franco-Gordo et al., 2002; Franco-Gordo et al., 2004), and on the other hand the neritic-mesopelagic *B. bathymaster* was dominant both in the near-shore mainland coastal area and in the more extended area covered by our Coastal-oceanic assemblage.

The eddies may also carry the Coastal-oceanic assemblage environment toward the interior ocean (e.g. eddy C2 in Figs 6A and 7) when they detach from the coast and drift west (Zamudio et al., 2007). Considering the biological characteristics of the Coastal-oceanic assemblage, the repeated detachment of such features would be an important enrichment process for the oceanic region of the ETP off Mexico. Despite studies of eddies and their transport of eggs and larvae into the ocean (e.g. Fiedler, 1986; Muhling et al., 2007), their biological impact has not yet been fully understood.

Previous work on larval distribution in the coastal zone of the area covered by the Coastal-oceanic assemblage (Jalisco and Colima, see Fig. 1) has suggested the influence of the California Current in late autumn and winter (Franco-Gordo et al., 2002; Franco-Gordo et al., 2004). In contrast, we find that the water properties of the upper-layer (temperature and salinity) and the biological indicators (assemblage composition and distribution) do not show the presence of California Current Water in the surface layer much further south than the tip of Baja California Peninsula.

**Tropical A and Tropical B assemblages**

The Tropical A assemblage may be considered representative of the Pacific Ocean environment off Mexico, as it resided in Tropical Surface Water (Fig. 9), a water mass that is transported by the Mexican Coastal Current from the tropical region (Kessler, 2006; Lavin et al., 2006). The Tropical A assemblage was characterized by the highest mean larval abundance and specific richness, and by dominance of the largest number of species (e.g. *V. lucetia*, *D. laternatus*, *D. pacificus*, *Auxis* sp.). This assemblage broadly covered the central and southern parts of the sampled area in March, but in November it was restricted to the coastal area, probably...
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tropical neritic-mesopelagic

Bregmaceros bathymaster

Diogenicthys laternatus

larvae. This assemblage was

becoming an enrichment process for the open sea.

most of this assemblage was trapped by coastal cyclo-

cyclic eddies, which upon detaching from the coast

might carry this assemblage toward the west, thus

becoming an enrichment process for the open sea.

(1) The “Transitional” assemblage, which was located

in the northwestern sector of the study region in

both seasons, had the lowest mean larval abun-

dance and specific richness. It was dominated by

the tropical mesopelagic Vinciguerria lucetia and

Diogenicthys laternatus larvae. This assemblage

was associated with modified California Current Water

in winter and with modified Tropical Surface Water in autumn, and it was affected (retained) by eddies observed in this transitional region.

(2) The “Coastal-oceanic” assemblage was found adja-

cent to the coast off and south of Cabo Corrientes in

both seasons, with high larval abundance and

specific richness. It was strongly dominated by the

tropical neritic-mesopelagic Bregmaceros bathymaster.

Most of this assemblage was trapped by coastal cyclic eddies, which upon detaching from the coast

might carry this assemblage toward the west, thus

becoming an enrichment process for the open sea.

(3) The “Tropical A” assemblage was associated with

Tropical Surface Water. It had the highest abun-

dance and specific richness of the study, and the

largest number of dominant species (e.g. V. lucetia,

D. laternatus, D. pacificus, Auxis spp.). This assemblage

covered the central and southern parts of the

sampled area in winter, but in autumn it was

restricted to a narrow zone west of the

Coastal-oceanic assemblage; this was probably due to

seasonal changes in water masses and
circulation.

(4) The “Tropical B” assemblage, distinguished by the

highest abundance of V. lucetia, was present only in

autumn; it was associated with overall anticyclonic

due to the offshore intrusion from the south of Tropical

Surface Water (Fig. 9A). This water mass was associated

with the definition of the ‘Tropical B’ assemblage. The

latter assemblage had less abundance and specific rich-

ness than the ‘Tropical A’ assemblage, but V. lucetia larvae

presented its highest observed abundance. The separa-

tion of the Tropical assemblages implies that the

large-scale environmental variability may affect the

spawning area and spawning intensity of the species

that inhabit the region, as in the case of V. lucetia.

At the same time, and independently of the origin of

the Tropical B assemblage in November, the distri-

bution of this assemblage was strongly affected by the

eddies present in the region (Fig. 7B). It was found in

the outer edges of cyclonic eddies C2 and C3 linked to

the Coastal-oceanic assemblage, and around anticyclo-

nic eddy A1. There are no antecedents in the region on

the relationships between zooplankton distribution and

oceanographic processes that can support the proposed mechanism. An oceanic assemblage in the Eastern

Pacific Warm Pool (which includes a part of our

sampled area) with a larval composition similar to that

of the Tropical A assemblage was observed by Vilchis

et al. (Vilchis et al., 2009), but they did not examine the

role of the oceanographic processes on the larval fish
distribution.

In general, the results obtained in this study provide
evidence that the spawning of fish species that inhabit

the ETP off Mexico is linked to the large-scale circula-
tion; the water-mass characteristics would be species-
specific spawning triggers. However, while the adult fish

can cross planktonic boundaries, their eggs and larvae

will be restrained by mesoscale processes, such as the

eddies described in this work. If the environment is

favorable for their survival (e.g. food availability, preda-
tion level), the larvae will develop in different environ-

ments during their planktonic phase, and will

subsequently recruit in common adult populations. This

would explain the dominance of the mesopelagic

species in the assemblages defined in this work.

To explain the spatial distribution of the assem-
blages, we have used the annual surface circulation

reported by Godínez et al. (Godínez et al., 2010) which

was linked with the distribution of the water masses.

The high correlation between the distribution of these

environmental variables and the assemblages offers the

possibility of using the assemblages as tracers of the

surface circulation in the ETP, which will contribute to

the understanding of its ecosystem. We consider

that continued extensive multidisciplinary work in the

ETP is necessary to improve understanding of the for-

mation and maintenance of larval fish assemblages in

the open sea.

CONCLUSIONS

The analysis of the larval fish assemblage composition

and distribution in the Eastern Tropical Pacific off

Mexico from data collected during autumn of 2005 and

winter of 2007 showed that the interaction of fish

spawning and the large-scale and mesoscale processes

affect the formation and permanence of the assemblages.

The tropical mesopelagic species V. lucetia, D. laternatus

and D. pacificus were present in the four assemblages

defined in the region, but with a marked gradient of

abundance and frequency. Their dominance may be

explained as due to the spawning of distinct fish popu-

lations of the same species in the different water masses

detected in the region. However, the eggs and larvae

may be retained or dispersed by the eddies that

occurred in the distribution area of each assemblage.

(1) The “Transitional” assemblage, which was located

in the northwestern sector of the study region in

both seasons, had the lowest mean larval abun-

dance and specific richness. It was dominated by

the tropical mesopelagic Vinciguerria lucetia and

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Most of this assemblage was trapped by coastal cyclic eddies, which upon detaching from the coast

might carry this assemblage toward the west, thus

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sampled area in winter, but in autumn it was

restricted to a narrow zone west of the

Coastal-oceanic assemblage; this was probably due to

seasonal changes in water masses and
circulation.

(4) The “Tropical B” assemblage, distinguished by the

highest abundance of V. lucetia, was present only in

autumn; it was associated with overall anticyclonic
circulation of Tropical Surface Water in the study area, which contained most of the assemblage.

SUPPLEMENTARY DATA

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

ACKNOWLEDGEMENTS

Thanks to Carlos Cabrera (CICESE) for satellite image processing, to Arturo Ocampo (CICESE) for his support in sampling at sea and to Dr E.D. Barton for grammar and style improvements. We thank the skipper and crew of the B/O Francisco de Ulloa.

FUNDING

This is a product of project “Dinámica, termodinámica y producción primaria de la Corriente Costera Mexicana” supported by CONACyT (SEP-2003-C02-42941/A-1). Additional support from CGPI-Instituto Politécnico Nacional (projects SIP 20090578 and SIP 20080496). C.A.L.-C. and V.M.G. held CONACyT postgraduate scholarships; the former also held a SNI-CONACyT assistantship.

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