Larval fish assemblages, environment and circulation in a semienclosed sea (Gulf of California, Mexico)

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ABSTRACT

Fish larvae and hydrographic data collected in the Gulf of California (GC) in December 2002 are used to describe larval fish assemblages (LFAs) and to explore their relationships with environmental variables (temperature, salinity, dissolved oxygen, fluorescence maximum, ψ and superficial chlorophyll a). The Bray–Curtis dissimilarity index defined three LFAs, distributed in areas with distinctly different environmental conditions. The affinity of most of the species with the environmental characteristics of their areas of distribution could be interpreted as an indication that spawning occurred inside those areas. Particle tracking in current fields from a 3D numerical model and connectivity matrices are used to assess larval retention in the LFA areas. The technique is well suited for seats like the GC that have well-defined particle trajectories. On time scales around 30 days, retention (from 56% to 73% of the particles) occurred (1) for the North LFA in the Upper GC, (2) for the Channel-Center LFA in the anticyclone over the Northern GC and in Ballenas Channel, and (3) for the South LFA in the eddy over San Pedro Mártir basin and in the shallow zone off the peninsula. Therefore, the Lagrangian analysis revealed that the observed LFAs have a permanency long enough to allow fish larvae to remain in a favorable environment until they develop motility. The main particle export path (less than 26% of the particles) was from the North to the South LFA, following the anticyclonic main flow and coinciding with the gradient in species number and larval abundance.

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1. Introduction

Numerous studies have indicated that the early life stages of fish are sensitive to variability in the marine environment because of their meroplanktonic condition (e.g. Fiedler 1986; Somarakis et al., 2002). Advantageous environmental conditions for larval survival can be both biological (e.g. high abundance of food and low abundance of predators) and physical (e.g. temperature and salinity, and circulation patterns promoting retention or transport to nursery areas) (Ahlstrom and Moser, 1976). Larval fish assemblages (LFA) can be retained or transported until larvae have the motile capabilities to search for a favorable habitat (epipelagic, mesopelagic, coastal demersal, etc.) for subsequent development (Heath, 1992; Somarakis et al., 2002).

For example, Iles and Sinclair (1982) and Sinclair (1988) explained that the variations in larval fish survival and recruitment are associated with geographic retention mechanisms by oceanographic processes. Modeling the dispersion of Sardinops melanosticlus larvae in the Kuroshio Current showed that current variability determined the larval dispersion routes (Heath et al. 1998). Studies on larval fish dispersion in the Scotian Shelf using particle dispersion indicated that larval retention in low-energy areas resulted from the interaction of spawning locations, geostrophic currents, and bathymetric steering and required neither convergence nor larval behavioral response (Reiss et al., 2000).

A large number of fish species spawn in the Gulf of California (GC) (Fig. 1). Some are of commercial importance, such as the northern anchovy Engraulis mordax, the Monterey sardine Sardinops sagax, and the mackerel Scomber japonicus (e.g., Cisneros-Mata et al., 1997), while others are an important link in the trophic web, such as the mesopelagic lamp fish Vinciguerria lucita (e.g., De la Cruz-Aguüero, 1997). The interaction between spawning of species in different habitats with particular environmental dynamics (described below) produces complex LFAs (e.g., Moser et al., 1974; Avalos-García et al., 2003), which may vary in their boundaries and permanency.
There are in the GC several dynamic processes that can promote enrichment of the upper ocean layers and transport (or trapping) of fish eggs and larvae (e.g., see review by Lavín and Marinone, 2003). These include: (a) strong tidal currents and intense tidal stirring in the Midriff Archipelago Region (henceforth, MAR) and in the shallow Upper GC (Delfín and Wagner basins), (b) a well defined seasonally-reversing circulation in the shelf-deep Northern region (Delfín and Wagner basins), (c) wind-induced upwelling in the deep Southern GC (which occurs on the main land side during winter and spring, and on the peninsula side during summer) as a response to the monsoonal wind regime (Badan-Dangon et al., 1991), and (d) gulf-wide eddies that dominate the circulation both in the Northern and Southern regions. The most important tidal mixing areas within the MAR (Paden et al., 1991; Argote et al., 1995) are the sills that delimit the two ends of Ballenas Channel and the sill between San Esteban and San Lorenzo Islands. In Ballenas Channel, which is part of the MAR, tidal mixing and convergence-induced upwelling generate the lowest sea-surface temperature (SST) in the GC (Paden et al., 1991; López et al., 2006). This minimum is limited to the south and north by sharp SST fronts, which frequently show convolutions, eddies, and filaments (Navarro-Olache et al., 2004).

The seasonal surface circulation of the GC is forced mainly by the geostrophic coastal circulation of the eastern tropical Pacific (Ripa, 1997; Marinone, 2003; Zamudio et al., in press) and to a lesser degree by the surface winds, with a small contribution from buoyancy flux (Beier, 1997; Ripa, 1997). The direct observations of currents (Lagrangian and Eulerian) made by Lavín et al. (1997) and Palacios-Hernández et al. (2002), and the analytical and numerical models of Ripa (1997), Beier (1997), Marinone (2003) and Zamudio et al. (in press) have established that the surface circulation in the entire GC is anticyclonic from late autumn to early spring and cyclonic in summer. One of the best-described features of the GC circulation is the eddy that dominates the circulation in the Northern GC, which is cyclonic from June to September and anticyclonic from November to April (Lavín et al., 1997; Lavín and Marinone, 2003; Gutiérrez et al., 2004). The seasonal circulation patterns are very energetic because the seasonal forcings by the eastern tropical Pacific coastal currents and by the surface winds happen to be in phase (Beier, 1997; Ripa, 1997). The seasonal currents are dominant in the Southern GC, while in the Northern GC they are similar to the tidal currents (except in shallow bays, including the Upper GC). Although Badan-Dangon et al. (1991) reported variability in the subtidal frequencies of the surface winds, the surface drifters of Lavín et al. (1997) showed a dominance of the seasonal signal in the Northern GC, as did the current meter data of Palacios-Hernández et al. (2002). This circulation pattern is so well established that it has become a benchmark for numerical models, and the basis for connectivity studies (Marinone et al., 2008).

Within this environmental context, Moser et al. (1974) made the first study on distribution and abundance of fish larvae in the GC (to date the most extensive ichthyoplankton work in the GC). More recent studies on larvae and eggs of small pelagic fish species such as Sardinops sagax (Hammann et al., 1988; Sánchez-Velasco et al., 2002), Scomber japonicus (Esqueda-Escárciga, 1995) and Engraulis mordax (Green-Ruiz and Hinojosa-Corona, 1997), and studies on LFAs (Avalos-García et al., 2003; Aceves-Medina et al., 2004; Sánchez-Velasco et al., 2004) have related distributional patterns only to SST (measured in situ or from satellite data) as the environmental indicator.

Studies relating larval fish distributions to oceanographic variables (other than SST), and especially to the circulation (i.e., connectivity) within the GC are quite scarce. Recently, Sánchez-Velasco et al. (2006) found a strong relationship between LFAs and geostrophic surface flow in and around La Paz Bay, in the Southern GC. Calderón-Aguílera et al. (2003) and Marinone et al. (2008) found relationships between the circulation in the Upper GC and the distribution of blue shrimp (Litopenaeus stylirostris) and coastal rocky reef fish larvae respectively, by using a three-dimensional (3D) numerical model for tracking particles. This suggests that the circulation in the GC may be affecting the distribution of fish eggs and larvae. Therefore, the objectives of this study are to describe the LFAs in the northern and central regions of the GC, to investigate their relationship with several observed environmental variables,
to assess the permanency of the assemblages in their areas of influence, and to explore the connectivity paths (larval export routes) among LFA areas. For the last two objectives, particle-tracking techniques based on the circulation from a 3D numerical model are used.

2. Materials and methods

Plankton and physical data were collected from December 7 to 13, 2002, on board the R/V Francisco de Ulloa in a sampling grid consisting of 32 stations (Fig. 1) covering the area from ~27° N in the Central GC to ~31° N in the Upper GC. The cruise was timed to take place under the typical anticyclonic circulation conditions of the GC, which occur from November to April (Lavin et al., 1997; Palacios-Hernández et al., 2002). In addition to the field data, daily chlorophyll a and SST images from the AQUA-MODIS satellites (4 km × 4 km resolution) were obtained from http://oceancolor.gsfc.nasa.gov/cgi/level3.pl.

2.1. Fish larvae data

Zooplankton hauls were made using a Bongo net 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 where bottom depths permitted. These hauls were in a circular trajectory at a speed of 2.5 knots, following the methodology recommended by Smith and Richardson (1979). The volume of water filtered was calculated using calibrated flow meters placed in the mouth of the nets. Each sample was fixed with 5% formaldehyde buffered with sodium borate. Fish larvae were removed from the 505 μm mesh samples and identified according to the descriptions in Moser et al. (1996). Larval abundance was standardized to number of larvae per 10 m² of sea surface, following Smith and Richardson (1979).

Before calculating the Bray–Curtis dissimilarity index, the standardized data were root-root transformed in order to reduce the weight of the most abundant species. This index was used because it was not affected by joint absences and was therefore sufficiently robust for marine data, yet it does give more weight to abundant species than to rare ones (Bray and Curtis, 1957). The Bray–Curtis index has the form

$$\delta_{jk} = \frac{\sum (Y_{ij} - Y_{ik})}{\sum (Y_{ij} + Y_{ik})}$$

where $Y_{ij}$ = score for the ith species in the jth sample; $Y_{ik}$ = score for ith species in the kth sample; $\delta_{jk}$ = dissimilarity between the jth and kth samples summed over all species. $\delta_{jk}$ ranges from 0 (identical scores for all species) to 1 (no species in common) (Field et al., 1982).

Unweighted pair-group average (UPGA), which joins two groups of samples together at the average level of dissimilarity between all members of one group and all members of the other (Sneath and Sokal, 1973), was the hierarchical sorting strategy to produce a dendrogram from the dissimilarity matrix. Groups of stations were defined based on the dendrograms and on previous knowledge on the spawning areas and the environmental affinity of the fish species that inhabit the GC (Hammann et al., 1988; Esqueda-Escárcega, 1995; Green-Ruiz and Hinojosoa-Corona, 1997; Sánchez-Velasco et al., 2002). The collection of larval species characteristic of each group of stations was called a LFA and the geographic area occupied by that group was called the LFA area.

The characteristic species, or dominant species, of each LFA (e.g., Sanvicente-Añorve et al., 1998), were defined as those whose values of abundance and relative frequency surpassed the average of both. The Olmstead–Tukey test analyzed the average relative abundance, against the percentage of the appearance frequency of each species (Sokal and Rohlf, 1985).

These analyses (Bray–Curtis dissimilarity index, dendrogram, and Olmstead–Tukey tests) were made with two types of matrices, one of them with all the species, and the other excluding the species with >80% of occurrence-frequency (i.e. species of wide distribution) and high abundance. This was done in order to observe the contribution of the rest of the species to the community of fish larvae.

2.2. Environment data

A factory-calibrated SBE-19 Sea-Bird conductivity, temperature, and depth (CTD) recorder was used to obtain vertical profiles of potential temperature ($\theta$), salinity (S), dissolved oxygen (O2) and fluorescence (F). The potential temperature and salinity profiles were used to calculate the potential density anomaly $\gamma(z) = \rho(z) - 1000$ where $\rho$ is density and z the vertical coordinate (positive upwards, zero at the surface). Two parameters that measure the strength of stratification, or stability, were calculated:

(a) The local stability parameter $E(z) = -\rho^{-1}d\rho/dz$, which measures stratification at depth z, and is maximum at the depth where the pycnocline is strongest.

(b) The integral stratification parameter $\phi$ (Simpson, 1981)

$$\phi = \frac{1}{h} \int_{-h}^{0} (\rho - \bar{\rho}) g dz$$

where $h$ is the maximum depth of integration (200 m in our case), and $g$ is the gravitational acceleration. The stratification parameter $\phi$ represents the quantity of work per cubic meter (J m⁻³) necessary to mix the water column completely to depth $h$, and is an integral measure of stability. Argote et al. (1995) previously discussed the relationship of this parameter with stratification and tidal mixing in the GC.

Water samples were taken with Niskin bottles to determine the average concentration of chlorophyll a from surface waters. From these samples 1.5 l of water were vacuum-filtered (~1/3 atm) through GF/F filters and conserved in liquid nitrogen for later analysis. For the spectrum-photometric determination of chlorophyll a, extractions were done from the filters by placing them in 10 ml of 90% acetone for 24 h (as recommended by Venrick and Hayward, 1984), and the equations of Jeffrey and Humphrey (1975) were used to calculate chlorophyll a concentrations in mg m⁻³.

To assess the permanency of the LFAs in their respective LFA areas, the 3D baroclinic numerical model of Marinone (2003) was used to provide an approximate description of the circulation in the GC at the time of the cruise. The model had a mesh size of 2.5° × 2.5° (~3.9 × 4.6 km) in the horizontal and 12 layers in the vertical [see Supplementary Data 1, and Marinone (2003) for more details]. The most important forcing, that by the eastern tropical Pacific geostrophic coastal currents, was applied by specifying the observed annual variability of hydrography in the GC entrance. Forcing by the monsoonal wind pattern was applied with a sinusoidal seasonally-reversing, along-gulf wind stress. Tidal forcing was applied as tidal elevations with the seven most important tidal constituents, namely M2, S2, N2, K2, K1, O1, and P1, which account for more than 95% of the total tidal variance. The harmonic constants were estimated from several years of observations in Mazatlán, at the mainland side, and in Cabo San Lucas, at the tip of the Baja California peninsula. From these points, the sea surface elevation was obtained at each time step and then interpolated along the open boundary. Buoyancy forcing was applied by specifying the fluxes of heat and moisture. This model has been proven to give an acceptable description of the mean and seasonal overall circulation; the
seasonally-reversing circulation observed by Lavin et al. (1997) and Palacios-Hernández et al. (2002) in the Northern GC was very well reproduced.

Outputs from the Marinone (2003) model have previously been used to describe the movement of particles released in the northern GC, as an approximation to larval transport (Calderón et al., 2003; Marinone, 2006; Marinone et al., 2008). Although the wind forcing of the model does not include wind-event variability, the use of its outputs for this study were acceptable because most fish larvae have planktonic periods longer than a week; at time scales exceeding that, the effect of the seasonal currents on LFAs was more important than that due to the wind variability. Hourly wind data from a meteorological buoy installed in the northern GC from December 1994 to January 1995 (Leal and Lavin, 2002) showed that wind speeds rarely exceeded 15 m s\(^{-1}\) and deviations from the dominant NW direction lasted only a couple of days. An analysis of daily mean winds in the same region for the autumn–winters of 1982–1987 (Reyes and Laviń, 1997) showed that the mean wind for those seasons was from the NW and had a speed \(\approx 5 \pm 1.3 \text{ m s}^{-1}\), with episodic variability rarely exceeding 10 m/s. Assuming a wind episode of 10 m s\(^{-1}\) and a surface drift of 2% of the wind (i.e. 0.2 m s\(^{-1}\)), the particles would have been transported \(\approx 17\) km per day. This was much smaller than the spatial scales examined in this study (hundreds of kilometers).

Two thousand particles were released at the position of each sampling station on December 1st, and then tracked for 30 days, which was considered a maximum extent for the larval period. The 3D Lagrangian trajectories were due to the Eulerian velocity field plus a random-walk contribution related to turbulent eddy diffusion processes and they were calculated following the advection/diffusion scheme described by Proehl et al. (2005). For more details on the technique see supplementary data 1 and for applications in the GC see Cutiérrez et al. (2004) and Marinone et al. (2008).

3. Results

3.1. Fish larvae

A total of 3750 fish larvae were collected, and 88 taxa included within 38 families were identified. The most abundant species were *Engraulis mordax* (*Engraulidae*) and *Benthosema panamense* (*Myctophidae*), which represented 62% of the total larval abundance. Both species were considered of wide distribution due to their frequency of occurrence (>80%) in the study area (see Supplementary Data 2).

The application of the Bray–Curtis dissimilarity index to the matrix of fish larvae identified three groups of stations, representing three distinct LFAs. Fig. 2 shows these groups and their distributions for the case including the wide-distribution species. The geographic distributions of the LFAs for the case excluding the wide-distribution species were very similar (not shown), which means that their structures were firmly established. Due to their geographic location, the LFAs were named North, Channel-Center and South. The areas of the LFAs are shown superimposed on SST and chlorophyll a satellite images (for December 10, 2002) in Fig. 3. The North LFA, which according to the satellite images was associated with SSTs between 21 and 22 °C and chlorophyll a concentrations >1 mg m\(^{-3}\) (Fig. 3), presented the lowest larval abundance and taxa number (20). The dominant species in this LFA were *Engraulis mordax*, *Sardinops sagax* (*Clupeidae*) (both coastal-pelagic species), and *Benthosema panamense* (a mesopelagic species) (Table 1). The dominant species excluding *B. panamense* and *E. mordax* were *S. sagax*, *Synodus luciocephs* (*Synodontidae*, shallow-demersal species) and *Scomber japonicus* (*Scombridae*, coastal-pelagic).

The Channel-Center LFA was associated with the lowest SSTs (<20 °C) and the highest chlorophyll a concentrations (>1.5 mg m\(^{-3}\)) (Fig. 3). This LFA presented the highest larval abundance and an intermediate number of taxa (35). *Benthosema panamense*, *Engraulis mordax* and *Citharichthys fragilis* (Paralichthyidae, shallow-demersal) were the dominant species (Table 1). Excluding *B. panamense* and *E. mordax*, the dominant species were *C. fragilis* and *Etrupus crotosus* (Paralichthyidae, demersal) and *Triphoturus mucianus* and *Diogenichthys laternatus* (*Myctophidae*, mesopelagic).

The South LFA, located south of the MAR, was associated with the warmest SSTs, between 22 and 23 °C, and the lowest chlorophyll a concentrations, <1 mg m\(^{-3}\) (Fig. 3). It presented an intermediate larval abundance and the highest taxa number (65). The dominant species were *Engraulis mordax*, *Benthosema panamense*, *Triphoturus mucianus*, *Vinciguerria lucetia* (*Physicithyidae*, mesopelagic), *Etrumeus teres* (*Clupeidae*, coastal-epipelagic), *Diogenichthys laternatus* and *Scorpaenodes xyris* (*Scorpaenidae*, demersal) (Table 1). The dominant species excluding *B. panamense* and *E. mordax* were *T. mucianus* and *V. lucetia*, *Sardinops sagax*, *Pontinus sp.* (*Scorpaenidae*, demersal), *Albula sp.* (*Albulidae*, demersal) and *Eleotris picta* (*Eleotridae*, demersal).

3.2. Environment

3.2.1. Vertical profiles

Vertical profiles of temperature (°C), salinity, dissolved oxygen (ml l\(^{-1}\)), fluorescence (mg l\(^{-1}\)) and stability (m\(^{-1}\)), selected as representative of the regions occupied by the LFAs, are shown in Fig. 4. The North LFA was found in a relatively shallow area (<120 m) that included the Upper GC and the northern shelf of Delfín Basin. Station 22 (Fig. 4a) showed a tendency of vertical homogeneity in temperature with increased salinities toward the bottom indicating vertical convection and probably gravity currents; the stability profile indicated well-mixed conditions in the top 20 m and some stratification near the bottom. At this station, \(\bar{\rho} = 10\) J m\(^{-3}\), a low value due to both the shallowness and the weak stratification due to the intense mixing, by tidal currents and by vertical convection.

The Channel-Center LFA was in a deeper area (200–500 m), and included the deeper part of Delfín Basin, the basin to the east of Ángel de la Guarda Island (*AGI*), and most importantly, Ballenas Channel (maximum depth \(\sim 1600 m\)). The hydrographic structure of the latter was very different from that of the rest of the GC, consistently showing the lowest SSTs of the GC, and intermediate stratification. At Station 26 (Fig. 4b) in Ballenas Channel, temperature and salinity decreased with depth with no sharp thermocline or halocline. The stability profile indicated well-mixed conditions in the top 20 m and some stratification near the bottom. At this station, \(\bar{\rho} = 143\) J m\(^{-3}\), an intermediate value due to the moderate stratification.

The South LFA was also in a deep area (450–800 m), but somewhat away from the tidally energetic MAR. Therefore, Station 32 (Fig. 4c) was strongly stratified in all the variables (below a 40 m-deep surface mixed layer); the stability values in the first 200 m were the highest in the study area with the strongest thermocline, halocline and oxycline. At this station, \(\bar{\rho} = 310\) J m\(^{-3}\), reflecting strongly stratified conditions.

3.2.2. Horizontal distributions

The spatial distributions of environmental variables in the top 10 m of the water column are shown in Fig. 5, and the data are given in Supplementary Data 3. The temperature and salinity showed a gradual change along the gulf (Fig. 5a and b): the former increased southward (from 18 °C in the Upper GC to 22 °C in the south of the study area) while the latter increased northward (from 35.3 in the

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These trends are due to the seasonal diminishing heat gain through the surface and the increase of evaporation and wind mixing, whose effects are most noticeable in the shallow Upper GC. Ballenas Channel also has low SST, which is due to mixing and convergence-induced upwelling (López et al., 2006). The \( \phi \) parameter (Fig. 5c) increased from north to south with the lowest values in the shallow Upper Gulf (0.3–3 J m\(^{-3}\)) and the highest in the deep south (\( \geq 350 \) J m\(^{-3}\)). The oxygen concentration (Fig. 5d) was high in the Upper GC and in Ballenas Channel (3.7 ml l\(^{-1}\)), and low north of Tiburón Island and in the south (2.9 ml l\(^{-1}\)). The fluorescence maximum (Fig. 5e) presented three zones of high concentration: in the center of the MAR (5 \( \mu \)g l\(^{-1}\)), and on both ends of the study area (\( \geq 2 \) \( \mu \)g l\(^{-1}\)). The highest surface chlorophyll \( a \) concentrations (\( \geq 1.2 \) mg m\(^{-3}\)) (Fig. 5f) were located in the Northern Gulf and over the sills in the southern end of Ballenas Channel.

In this context, the environmental characteristics of the LFA areas were as follows: the North LFA was located in an area with the highest salinities (35.7–36.7) and the lowest temperatures (18–20.5 °C) and \( \phi \) (\( \leq 20 \) J m\(^{-3}\)); the Channel-Center LFA (Fig. 2) had intermediate value intervals of all the variables, and the South LFA had the highest temperatures (>21.5 °C) and \( \phi \) (>280 J m\(^{-3}\)), and the lowest salinity (<35.4). The mean values of these variables were statistically different between the North LFA and the South LFA areas (ANOVA \( p < 0.05 \)) (see Supplementary Data 3).

### 3.3. Circulation from the numerical model

The numerical model low-passed (or residual) surface current in the northern region of the GC on December 9, 2002 (Fig. 6), was representative of the surface circulation during the cruise (i.e., anticyclonic overall, with a main anticyclonic eddy in the center of

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**Fig. 2.** (a) Dendrogram of sampling station groups defined by the Bray–Curtis dissimilarity index and UPGA agglomerative method, and (b) their location in the Gulf of California during December 2002.
the Northern GC). This circulation pattern included northward flow in the peninsular side of the edge of Delfín and Wagner basins, and very strong southeastward currents parallel to the mainland coastline. This coastal current veered west in the area to the east of AGI, and then split into two branches: one returned to the northwest into the main anticyclonic eddy, and the other flowed to the southeast to form an overall flow out of the Northern GC. Both the main anticyclonic eddy and the outward flow were part of the seasonal circulation pattern of the GC as described (e.g.) by Lavin and Marinone (2003). The anticyclonic eddy just south of the MAR, over San Pedro Mártir Basin, was a persistent feature that had also been detected in the mean geostrophic flow (Mateos et al., 2006). The surface flow in Ballenas Channel was weak to the SE, and somewhat stronger close to the southern end, where it was influenced by the southward branch described above.

The tracks of the particles released at each station are shown in Fig. 7, separated by the LFAs. The connectivity between the areas at a stated time (e.g., $t = 15$ days) after releasing the particles was quantified by the connectivity matrix $C_{ij}$, where $i$ was given in the vertical and represents the release area, and $j$ was given in the horizontal and represents the position of particles after $t$ days. The connectivity matrices corresponding to Fig. 7 are shown in Table 2; for example, $C_{30}(2,3) = 18.9$ means that after 30 days 18.9% of the particles released in the Channel area were found in the Southern GC. The main diagonal represents the percentage of the particles that remained in their area of origin after the stated time.

The tracks from the three northernmost areas of the North LFA (Fig. 7a and b) showed retention in the Upper GC resulting from weak flow. However, after 30 days the overall anticyclonic flow toward the mainland led some particles to enter the fast southeastward coastal flow by the end of the tracking period. The particles released in the eastern side showed fast southeastward displacement, which slowed down north and west of Tiburón Island, where there appeared to be a retention zone. By the end of the period, some of the particles from this retention zone had escaped into the main flow, with some moving north toward the main eddy and some continuing slowly south, following the circulation patterns described above. After 15 days 64% of the particles remained in the area, while after 30 days 56% still remained in the area (Table 2). After 30 days more particles from the North LFA area were found in the South LFA area (26%) than in the Channel-Center LFA area (14%), indicating more connectivity between the North LFA and South LFA areas than between the North LFA and Channel-Center LFA areas.

The particles released in the stations of the Channel-Center LFA (Fig. 7c,d) showed retention in the first 15 days for most sites, except close to the mainland because of the coastal current. The most retentive area was Ballenas Channel because of the weak residual currents. The particles released in the stations north of Ballenas Channel were affected by the main anticyclonic eddy and showed some dispersion. After 30 days, the effect of the circulation pattern became more apparent (Fig. 7d), with retention in the main anticyclonic eddy, in Ballenas Channel and in the San Pedro Mártir eddy. The connectivity matrices (Table 2) showed that this area was very retentive, with ~70% of the particles remaining in the area.

### Table 1

Dominant taxa of the larval fish assemblages defined in the Gulf of California during December 2002 by the Olmstead–Tukey test. $X$, mean abundance; $\%F$, frequency of occurrence. Abundance is expressed as number of larvae per 10 m$^2$.

<table>
<thead>
<tr>
<th>Dominant taxon</th>
<th>North$^a$</th>
<th>Channel-Center$^b$</th>
<th>South$^c$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Engraulis mordax</td>
<td>44</td>
<td>328</td>
<td>277</td>
</tr>
<tr>
<td>Sardinops sagax</td>
<td>15</td>
<td>34</td>
<td>30</td>
</tr>
<tr>
<td>Benthosema panamense</td>
<td>7</td>
<td>344</td>
<td>245</td>
</tr>
<tr>
<td>Citharichthys fragilis</td>
<td>27</td>
<td>83</td>
<td></td>
</tr>
<tr>
<td>Triphoturus mexicanus</td>
<td>245</td>
<td>100</td>
<td></td>
</tr>
<tr>
<td>Vinciguerra lucia</td>
<td>93</td>
<td>100</td>
<td></td>
</tr>
<tr>
<td>Etrumeus teres</td>
<td>33</td>
<td>40</td>
<td></td>
</tr>
<tr>
<td>Diogenichthys laternatus</td>
<td>25</td>
<td>50</td>
<td></td>
</tr>
<tr>
<td>Scorpaenodes xyris</td>
<td>22</td>
<td>50</td>
<td></td>
</tr>
</tbody>
</table>

$^a$ Number of taxa 20; number of stations 8.

$^b$ Number of taxa 35; number of stations 12.

$^c$ Number of taxa 64; number of stations 10.
Fig. 4. Selected vertical profiles for stations typical of the area occupied by the different LFAs, in the Gulf of California during December 2002. (a) North LFA area, Station 22; (b) Channel-Center LFA area, Station 26; (c) South LFA area, Station 32. Stability (Einst/1000 m$^2$), Oxygen (ml l$^{-1}$), Fluorescence ($\mu$g l$^{-1}$), Temperature (°C), Salinity.
after 30 days, 20% going to the South area and only 9% moving to the North area.

The tracks of the particles released in the stations corresponding to the South LFA showed trapping during the first 15 days for most stations (Fig. 7e), except for those off the mainland coast south of Tiburón Island, which were carried away by the southeastward costal current. The particles released over San Pedro Mártir basin and on the peninsular side remained in the neighborhood of the release areas even after 30 days. After 30 days (Fig. 7f), most of the particles released north and west of Tiburón Island remained in the area, although some moved north into the anticyclonic eddy, and a few were taken out of the Northern GC by the circulation. After 15 days, 80% of the particles remained in the area with only 5% moving to the Channel-Center LFA, while after 30 days 73% still remained in the area with 9% moving to the Channel-Center LFA (Table 2).

Fig. 5. Spatial distribution of the environmental variables in the study area in December 2002. (a) Temperature (°C), (b) Salinity, (c) φ (J m⁻³) to 200 m, (d) Dissolved oxygen concentration (ml l⁻¹), (e) fluorescence maximum (µg l⁻¹), and (f) surface chlorophyll a (mg m⁻³) in the study area for December 2002. The LFA areas are marked.
3.4. Synthesis of results

The North LFA area (an area, which excluding the wide-distribution species Engraulis mordax and Benthosema panamense, was dominated by coastal-demersal species such as Synodus lucioceps), had the highest salinity and the lowest temperature, fluorescence and oxygen concentration, and had a relatively homogenous water column. These environmental conditions have been reported as typical for the Northern GC (\(<100\, \text{m}\)) from late fall to early spring (Lavín and Marinone, 2003). The fact that the lowest larval abundance and number of species were observed in this LFA suggested that the environmental conditions were unfavorable for the larval development of most of the species recorded in this study. The southern boundary of the North LFA coincided with the edge of the anticyclonic eddy that occupied most of the Northern GC (Fig. 6). The tracks from the particles released in the northern-most stations of the North LFA remained inside the boundaries of this LFA (Fig. 2) for the 30 days of tracking (Fig. 7a and b; Table 2); in other words, particle retention was shown in the Upper GC associated with the relatively weak flow in that area. However, the tracks of the North LFA stations that were near to the mainland were transported to the northern boundary of the Channel-Center.
LFA (Fig. 7b), showing connection between these two LFAs, although after 30 days there was more connectivity with the South LFA area.

The Channel-Center LFA (with the highest larval abundance dominated by mesopelagic species Triphoturus mexicanus and Diogenichthys laternatus, coastal-depositional species Etrumeus teres and Lythrypnus dalli, and coastal-epipelagic species Etrumeus teres), covered the anticyclonic gyre zone (Northern GC), Ballenas Channel and two stations east of AGI. As noted above, the area covered by this LFA had intermediate values of salinity, oxygen, temperature, and stratification in the water column. The mixture of species from different habitats and the intermediate environmental variable values of the Channel-Center LFA, were probably a consequence of the various environments encompassed by the LFA area. Lavín and Marinone (2003) and López et al. (2006) indicated that Ballenas Channel was characterized by strong vertical mixing and convergence-induced upwelling that resulted in low values of temperature and high oxygen concentration throughout the year. As mentioned above, the anticyclonic eddy was an established feature of the circulation for this season; according to our results, it was characterized by low chlorophyll a and oxygen concentrations and warm water (Fig. 5), typical characteristics of anticyclonic eddies. The trajectories (Fig. 7b,c) and the connectivity matrices (Table 2) indicated retention of this LFA in the central part of the main eddy, and in Ballenas Channel, both at 15 and 30 days. The tracks from the eastern stations suggested that part of this LFA may have been affected by the southeastward flow parallel to the mainland coast, e.g., between AGI and the mainland, particles were either recirculated into the main eddy or carried southward (20% cross the sills, Table 2). Therefore, it appears that the Channel-Center LFA was mostly retained within its area of influence for at least 30 days.

The South LFA (with the highest diversity and dominated by mesopelagic species like Benthosema panamense, Vinciguerra lucetia and Diogenichthys laternatus) had the most stratified water column and the highest values of SST, oxygen and fluorescence, and the lowest salinity. These conditions are typical of the Southern GC, according to Lavín and Marinone (2003). The tracks from the South LFA defined two contrasting areas (Fig. 7e,f): one with the strongest southward current off the mainland coast, and the other off the peninsula over the San Pedro Mártir anticyclonic eddy. The particles released in the first area were rapidly transported to the southeast, while those released in the second showed particle (and probably larval) trapping during the 30 days of tracking. The connectivity matrices (Table 2) showed that this area was very retentive.

4. Discussion

We investigated the relationship between the areas occupied by the LFAs in December 2002 with the environmental characteristics of those areas, and the likely effect of the circulation on the permanency of those LFAs in their respective areas. We found three LFAs (defined by the Bray–Curtis dissimilarity index): the North LFA, the Channel-Center LFA and the South LFA (see Fig. 2). While in the literature it is common to relate LFAs to SST (e.g. Avalos-García et al. 2003, Aceves-Medina et al. 2004, Sánchez-Velasco et al. 2004), we used several physical parameters to characterize the environment. It was found that the geographic areas occupied by the LFAs had distinctly different environmental conditions. The connectivity exercise based on the circulation predicted by a 3D numerical model, summarized in Table 2, showed that within time scales less than 30 days, 60–70% of the particles remained within the LFA areas while up to 26% were exported to the other areas. That export was almost exclusively from the North LFA to the South LFA, and from the South LFA out of the domination.

The LFA areas appeared to define planktonic habitats, a concept supported by the affinity (within LFAs) of most of the fish larvae with the environmental characteristics. We defined planktonic habitat as a set of physical, chemical, and biological conditions (e.g., temperature, food availability and physical retention processes) favorable for larval survival and subsequent recruitment.

LFAs in well-defined planktonic habitats have been recognized in other seas (Moser and Smith, 1993; Richards et al., 1993; Olivar and Shelton, 1993) and in regions of the GC (Sánchez-Velasco et al., 2006). However, the question of the permanence of the LFAs beyond the time of the cruise had not been addressed before. The importance of the connectivity study was that it showed that the LFAs can remain inside areas with propitious conditions during the larval stage (assuming that it lasts less than 30 days) despite being advected and dispersed by currents within the LFA boundaries.

Even though the connectivity matrix showed high particle retention inside the boundaries of each LFA area, the percentage of particles that were transported (up to 26% exported from the original LFA area to another) indicated a north-to-south flow due to the predominant current direction, which resulted in changes in larval abundance and species diversity. The North LFA had the lowest larval abundance (90 larvae per 10 m2) and number of taxa (20) and the highest connectivity values with the Channel-Center LFA and the South LFA. On the other hand, the South LFA had the highest number of taxa (65), high larval abundance (1105 larvae per 10 m2) and no south-to-north connectivity. These connectivity features may explain previous findings (Moser et al., 1974; Aceves et al., 2004; and herein) that larvae of species that spawn exclusively in the South LFA (like the mesopelagic Vinciguerra lucetia and Diogenichthys laternatus, or the deep-demersal Bathycongrus macrurus) are not found in the north region of the GC, at least during periods with hydrographic and circulation conditions like those from the current study. This suggests spawning strategies that ensure the permanency of the larvae in areas appropriate for their later recruitment.

Previous applications of the Marinone (2003) GC model to study the effect of circulation on planktonic larvae have focused on pathways of connectivity. Calderón et al. (2003) investigated the relationship between circulation patterns and the recruitment of blue-shrimp larvae in the Upper GC during summer, finding that larvae were exported from the continental coast (from different reproduction units) to the peninsular coast by surface currents. Marinone et al. (2008) studied larval dispersion of rocky-habitat species, and the connectivity between the two coasts of the Northern GC in summer by simulating the dispersion of particles released from spawning areas described in the literature, observing a cyclonic downstream connectivity along the coast dominated by residual flows. Like previous studies, this work also studied larval transport by currents, but it focused on the permanency of particles within (and the export out of) the boundaries defined by the LFAs. This different approach is made possible by the presence of the LFA areas, and the importance of the results stems from the fact that the
areas were not defined arbitrarily (like in Marinone et al., 2008), since they came out of a statistical analysis (Bray–Curtis dissimilarity index). In addition, since there is affinity of most of the species of the LFAs with the environmental characteristics of those areas, we have been able to quantify the permanency of the LFAs in favorable environments.

Most previous larval studies based on particle tracking focused on mid-latitude species, usually of commercial value, where a cumulus of knowledge could be input into the particle-release experiments (e.g., areas and time of spawning, aggregation, and recruitment). Some examples: (a) Heath et al. (1998) used dispersion of particles based on observed currents to simulate the dispersion of eggs and larvae of Japanese sardine (Sardinops melanostictus) in the Kuroshio Current. They observed that the current pattern variations affected larval dispersion and subsequent recruitment. (b) Reiss et al. (2000) assessed the spatial distribution of sardine larvae (Clupea harengus) and hake (Merluccius bilinearis), by simulating the transport of particles by geostrophic currents in the Scotian Shelf. They found small larvae in areas where the geostrophic flow was weak (retention), and an increase in size related with geostrophic flow (transport). (c) Hinrichsen et al. (2001) used a 3D numerical physical oceanographic model in the Baltic Sea, in which cod larvae (Gadus morhua) were represented as Lagrangian drifters released in the main spawning ground. They found that variations in larval transport and subsequent horizontal distributions were caused by seasonal and interannual variations in meteorological forcing.

Ours results and those of previous studies agree that oceanographic processes affect the distribution of fish larvae, although in different spatial-temporal scales. All of these studies concur with the postulate of Illes and Sinclair (1982) and Sinclair (1988), that geographic retention in early age larvae (as a result of physical forces and spawning area and intensity) is the most important factor for larval fish survival. However, it is notable that the previous studies did not use the concept of connectivity (retention against transport).

In our case, although we know little about each particular species, with the use of LFAs and connectivity we were able to deduce or infer valuable knowledge about the ecosystem (e.g., that LFAs were found in well-defined planktonic habitats). In an ecological sense, studying LFAs is more valuable than studying a single species (e.g. Heath et al., 1998; Reiss et al., 2000) and considering that the tropical and subtropical seas are very rich in species, this kind of work is particularly relevant. In addition, considering the valuable information obtained with the methodology used here from a widely-spaced array of stations (made with prospective purposes), this suggests that its application to historical data bases could be used to estimate larval permanency and the export paths of larval associations.

It is important to mention that the numerical model used here has limitations, e.g., the lack of short-term wind variability, which could be important for fish species whose larval periods are shorter than 1 week. This was not the case for the fish species found in this study as the larval periods of the dominant species Benthostoma panamense and Engraulis mordax and the other abundant species were longer than 1 week (Moser, 1996). However, it remains to be investigated if short-term wind variability can affect variability and connectivity at lower frequencies by nonlinear effects. Further investigation is also needed to determine if the between-year wind variability is as relevant to larval transport in the GC as it is in other seas (e.g.: Heath et al., 1998). Also, there are many biological unknowns that limit the usefulness of the numerical model, such as the sites and dates of spawning of the different species, the duration of their larval periods, etc.; these unknowns are inherent in the use of LFAs. However, the model did succeed in providing a rough estimate of the likely permanence of LFAs on their respective areas of influence. Future studies could include vertical distribution, for which the numerical model could use in situ meteorological forcing, and the particle-tracking scheme could include species behavior.

The technique of particle tracking from numerical models, and the associated connectivity matrices, can be used as tools to assess retention or transport of LFAs and plankton in general in the GC. The technique can also be used in other regions of the world in which the circulation has well-defined patterns in time and space.

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Appendix A. Supplemental material
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References
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