



## Research papers

## Larval fish habitats and hydrography in the Biosphere Reserve of the Upper Gulf of California (June 2008)

L. Sánchez-Velasco<sup>a,\*</sup>, M.F. Lavín<sup>b</sup>, S.P.A. Jiménez-Rosenberg<sup>a</sup>, J.M. Montes<sup>b</sup>, P.J. Turk-Boyer<sup>c</sup><sup>a</sup> Centro Interdisciplinario de Ciencias Marinas, Ave. Inst. Politécnico Nacional s/n, La Paz, Baja California Sur 23096, Mexico<sup>b</sup> Departamento de Oceanografía Física, CICESE, Carretera Ensenada-Tijuana 3918, Zona Playitas, Ensenada, Baja California 22860, Mexico<sup>c</sup> Centro Intercultural para el Estudio de Desiertos y Océanos—CEDO, Edificio Agustín Cortés, Fraccionamiento Las Conchas, Apartado Postal 53, Puerto Peñasco, Sonora, Mexico

## ARTICLE INFO

## Article history:

Received 11 July 2011

Received in revised form

31 October 2011

Accepted 18 November 2011

Available online 25 November 2011

Dedicated to Biol. José Campoy (RIP),  
Director of the Upper Gulf of California  
Biosphere Reserve from 1999 to 2011.

## Keywords:

Fish larvae

Larval fish habitat

Biosphere Reserve

Upper Gulf of California

## ABSTRACT

The Upper Gulf of California (UGC) is a Biosphere Reserve that despite its extreme environmental conditions (macrotidal inverse estuary) houses a high fish species richness. An intensive sampling of fish larvae and hydrography was carried out during June 2008 in the UGC. From 56 zooplankton sampling stations with a maximum of three sampling strata (each 5 m deep, from 0 to 15 m), a total of 29,505 fish larvae were collected, included in 99 taxa and 32 families. The Bray–Curtis Index defined three main larval fish habitats that varied in composition. (i) The “Mixed” larval habitat was mostly defined in the vertically mixed western sector of the UGC; the coastal pelagic *Anchoa* spp. presented high abundance in this habitat, associated with demersal species such as *Gobulus crescentalis* and Scianidae type 1. The lowest diversity and abundance, and the highest salinity, temperature and chlorophyll distinguished this larval habitat. (ii) The “Front” habitat was located mostly on the physical–chemical frontal zone between the UGC and the Northern Gulf; it had the highest specific richness and larval abundance. The dominant species were the coastal pelagics *Anchoa* spp. and *Opisthonema* sp. 1; the latter was almost limited to the north by the frontal zone. (iii) The “Shelf” habitat, found over the shelf off the mainland, was the deepest and less salty, and was also dominated by *Opisthonema* sp. 1, but included epipelagic species such as Scombridae (e.g., *Scomber japonicus*, *Auxis* spp., *Scomberomerus sierra*), probably from the adjacent deeper zone. These larval fish habitats had well-defined limits that coincided with marked environmental gradients, with the lowest larval diversity in the saltiest environment; this suggests that the human-induced shift to hypersaline conditions may have reduced the preferred larval habitat for some species. The habitats most likely change with the seasons, with implications for the management of the reserve.

© 2011 Elsevier Ltd. All rights reserved.

## 1. Introduction

Management and conservation of ecosystems is a complex task, since it involves defining and coupling physical and biological interactions at multiple spatial and temporal scales, as well as anthropogenic factors (Cudney-Bueno et al., 2009; Pollnac et al., 2010). Although marine reserves are considered an important tool for sustaining ocean ecosystems (Nowlis and Friedlander, 2005), they are often established using a precautionary approach, and without in-depth knowledge of the species that inhabit them, their spawning strategies (e.g. areas, periods and intensity) and their relationships with physical environmental processes (Borguez et al., 2009; Cudney-Bueno et al., 2009). In this article we describe summer-time oceanographic conditions

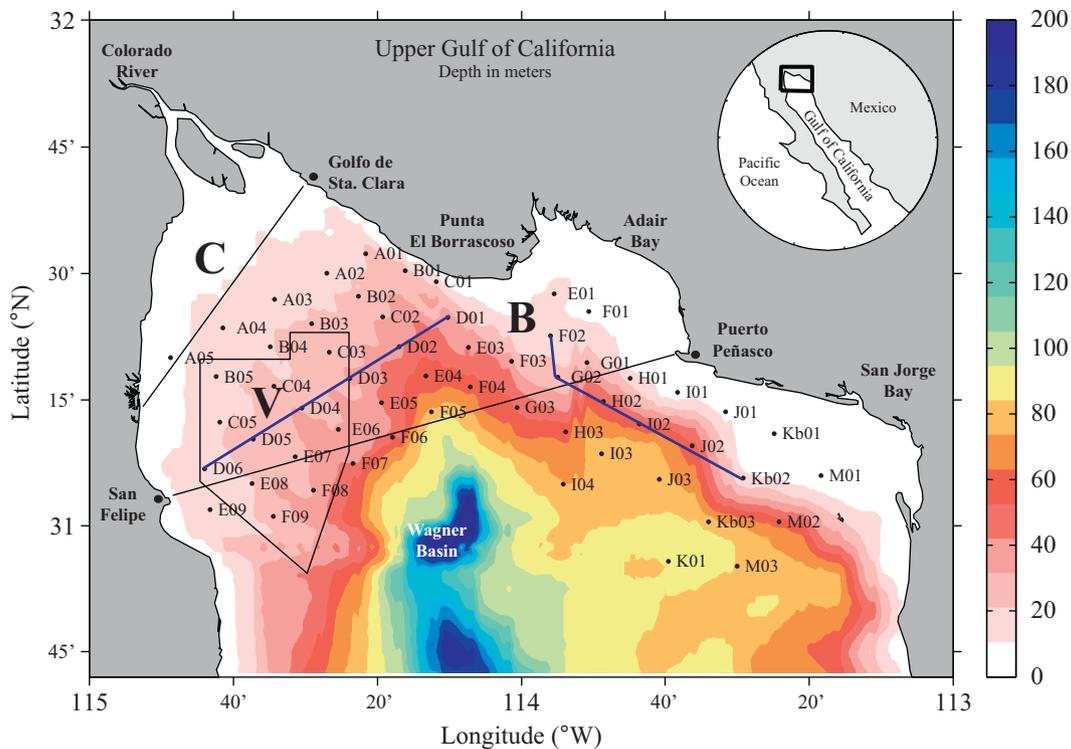
and distinct fish larval communities in the Upper Gulf of California (UGC), and compare these bioregions to established conservation zoning.

The UGC (Fig. 1) was declared a Biosphere Reserve in 1993, largely due to its importance for endemic fish species, such as Totoaba (*Totoaba macdonaldii*), the Bigeye Croaker (*Micropogonias megalops*), the curvina golfina (*Cynoscion othonopterus*) and the endemic and critically endangered marine mammal Vaquita (*Phocoena sinus*; Rojas-Bracho et al., 2006). To provide additional protection for the Vaquita, in 2005 the Mexican Government decreed a “Vaquita Refuge” in the central part of the species range (e.g., Jaramillo-Legorreta et al., 1999,2005; Fig. 1).

The reserve is divided into two management areas: the “Buffer Zone” and the “Core Area” (marked B and C, respectively, in Fig. 1); the latter, located in the northwestern extreme of the UGC, is vertically mixed and so shallow that it is accessible only by small boats. The “Vaquita Refuge” (marked V in Fig. 1) is located on the western side of the Buffer Zone, and it has a small section

\* Corresponding author.

E-mail address: lsvelasc@gmail.com (L. Sánchez-Velasco).



**Fig. 1.** The Upper Gulf of California, with bathymetry (in meters) and named coastal features. Capital letters indicate marine protected areas: C=core zone of the UGC Reserve, B=buffer zone of the UGC Reserve and V=Vaquita Refuge. (For interpretation of the references to color in the text, the reader is referred to the web version of this article.)

extending outside the UGC Reserve. The Reserve is supported by a management program that is charged with promoting sustainable activities and maintaining biodiversity. In the Core Zone all fishing activities are banned, while in the Buffer Zone controlled fishing activities, including shrimping (*Litopenaeus stylirostris*), are allowed. In the Vaquita Refuge fishing activities have been restricted and gillnets banned since 2005, but effective enforcement did not begin until fall 2008 (Gerrodette and Rojas-Bracho, 2011).

From the physical oceanography perspective, the UGC is a highly seasonal, shallow (< 30 m deep) macrotidal inverse estuary, with temperatures ranging from ~14 °C in winter to over 32 °C in summer (Alvarez-Borrego and Galindo-Bect, 1974; Alvarez-Borrego et al., 1975; Lavín et al., 1998). The inverse-estuarine conditions that exist today, characterized by salinities that increase from 35.4 in the open Northern Gulf to above 39 in the shallowest areas of the UGC, are the consequence of the damming and diversion of the entire Colorado River flow for agricultural and domestic use, the almost null rainfall and the high evaporation rate (~0.9 m year<sup>-1</sup>; Alvarez-Borrego et al., 1975; Lavín and Organista, 1988; Lavín et al., 1998). Tidal range is ~6 m during spring tides, and strong tidal currents up to 1 m s<sup>-1</sup> cause resuspension of sediments and elevated turbidity (Alvarez and Jones, 2002), in addition to a tidal-mixing front separating the well-mixed UGC from the deeper and stratified Northern Gulf (Argote et al., 1995).

Despite these extreme physical conditions, the UGC holds a high diversity of fish species (260 species) representing 29% of the Gulf's total ichthyofauna (Hastings and Findley, 2007). High diversity has also been recorded for other taxonomic groups in the UGC (Felger and Broyles, 2007), such as birds (> 350 species), marine mammals (12 species regularly sighted, but up to 22 other species occurring occasionally) and macroinvertebrates (~1045 species). In addition, Calderon-Aguilera et al. (2002) and Galindo-Bect et al. (2010) reported that the preferred spawning zone of

the shrimp *L. stylirostris* in the Northern Gulf is in the eastern part of the Reserve's Buffer Zone, south of Punta El Borrascoso (Fig. 1).

The management zones in the UGC Reserve coincide approximately with areas with particular physical characteristics previously defined in hydrography and sediment studies. For example, during summer the highest temperature and salinity are found in the well-mixed NW side of the UGC, and the lowest values in the deeper, stratified SE side; in winter the thermal gradient reverses while that of salinity remains, as does the tidal-mixing front between the stratified and the well-mixed zones (Alvarez-Borrego and Galindo-Bect, 1974; Alvarez-Borrego et al., 1975; Argote et al., 1995; Lavín et al., 1998). There is also a sediment particle-size regionalization, with the largest particles (sands) in the north and east areas of the UGC, and the smallest (silts and clays) in the shallow western side (Carrquiry and Sánchez, 1999).

In this context, the hypothesis in the present work was that there should be at least two distinct larval fish habitats that respond to the UGC extreme environmental gradients: mixed and stratified. Based on observations carried out in the UGC in June 2008, this study aims to: (i) identify larval fish habitats indicated by fish larvae composition and abundance and (ii) relate these habitats to hydrographic characteristics or processes. The relationship between the larval habitats and the zonation of the reserve will be discussed.

## 2. Methods

### 2.1. Study area

The UGC Reserve is located in the northern part of the Gulf of California, Mexico (Fig. 1). It is triangular in shape, covering an area of approximately 5000 km<sup>2</sup>. The southern limit is marked by an imaginary line between the town of San Felipe on the Baja

California Peninsula and Cerro Prieto, just north of Puerto Peñasco on the mainland. The Reserve's northern limit is the old mouth of the Colorado River (Lavín et al., 1998).

## 2.2. Field methods

Physical, chemical and zooplankton data were obtained during neap tides from the *R/V Francisco de Ulloa*, from 6 to 12 June 2008, in the 56 stations shown in Fig. 1. Temperature and conductivity profiles were obtained at each station with a SeaBird 911*plus* CTD (conductivity, temperature and depth profiler), including recently calibrated dissolved oxygen and fluorescence sensors. The fluorescence data were converted to chlorophyll values ( $\mu\text{g/L}$ ) by the sensor, and in this article we will refer to these data as “chlorophyll”. The methods used for processing these data were documented by García-Córdova et al. (2008).

Two sampling station transects (marked in blue in Fig. 1) were selected from the grid of stations in order to describe the vertical hydrographic structure of the water column and relate it to biological data: (i) Line D (sampling stations from D01 to D06) is transversal across the UGC, from San Felipe towards Punta El Borrascoso and (ii) Line L (stations from F02 to Kb02) is an along-gulf transect offshore the eastern coast from Adair Bay to San Jorge Bay.

Sea surface temperature and surface chlorophyll Aqua/MODIS images were obtained from <http://oceancolor.gsfc.nasa.gov/cgi/level3.pl>.

## 2.3. Zooplankton methods

Oblique zooplankton hauls were made during day and night hours at three depth strata (from 15 to 10 m, 10 to 5 m and 5 m to surface), using opening–closing conical zooplankton nets with a mouth diameter of 50 cm, 250 cm of net length and 505  $\mu\text{m}$  mesh size (<http://www.generaloceanics.com/genocean/1000DT.htm>). The volume of filtered water was calculated using calibrated flow meters placed at the mouth of each net. The closed net was lowered to the bottom of the stratum to be sampled, and was then opened with a manual brass messenger at the onset of the haul. When the upper level of the sampling stratum was reached, the net was closed with another messenger, and the haul was terminated. This system effectively avoids entrance of organisms from other strata. This closing system was very precise, since it responded almost instantaneously for surface hauls (5 m–surface), while the maximum delay was for the deepest hauls (15–10 m). The depth for each stratum was calculated by the cosine of the wire angle method, following the standard specifications of Smith and Richardson (1979). This stratified sampling technique has been successfully used in previous studies (e.g., Espinosa-Fuentes and Flores-Coto, 2004; Danell-Jiménez et al., 2009).

Samples were fixed with 5% formalin buffered with sodium borate. Zooplankton biomass was estimated by displacement volume (Beers, 1976), and standardized to  $\text{mL}/1000\text{m}^3$ . Fish larvae were sorted out, removed from the samples and identified to the lowest possible taxonomic level, mainly using Moser (1996), and specific guides for certain families (e.g., Jiménez-Rosenberg et al., 2006). Larval abundance was standardized to number of larvae per  $10\text{m}^2$  for comparison with adjacent regions (Smith and Richardson, 1979).

The non-parametric Kruskal–Wallis test (Sokal and Rohlf, 1985) was used to assess the statistical significance of differences of the total larval abundance between day and night hours and among the different depth strata.

To identify fish larval habitats (clusters of similar samples), a matrix of fish larvae composition per stratum was used (only taxa with frequency occurrence  $>5$ ). The standardized data were fourth-root transformed before applying 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). A nonparametric test that does not require assumptions of normality of variance, the multi-response permutation procedure (MRPP; McCune and Grace, 2002), was applied for testing the hypothesis of no difference between habitat groups, using PC-ORD version 6.0. The MRPP test statistic ( $T$ ) describes the separation between the groups (the stronger the separations the more negative the value of  $T$ ), and the chance-corrected within-group agreement ( $A$ ) describes the within-group homogeneity, compared to the random expectation, using Sørensen's distance. The highest possible value for  $A$  is 1, and occurs when all items are identical within groups. If heterogeneity within groups equals expectation by chance, then  $A=0$ . In community ecology, values of  $A$  are commonly below 0.1, an  $A > 0.3$  is fairly high (McCune and Grace, 2002).

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 as the representative species of each planktonic habitat.

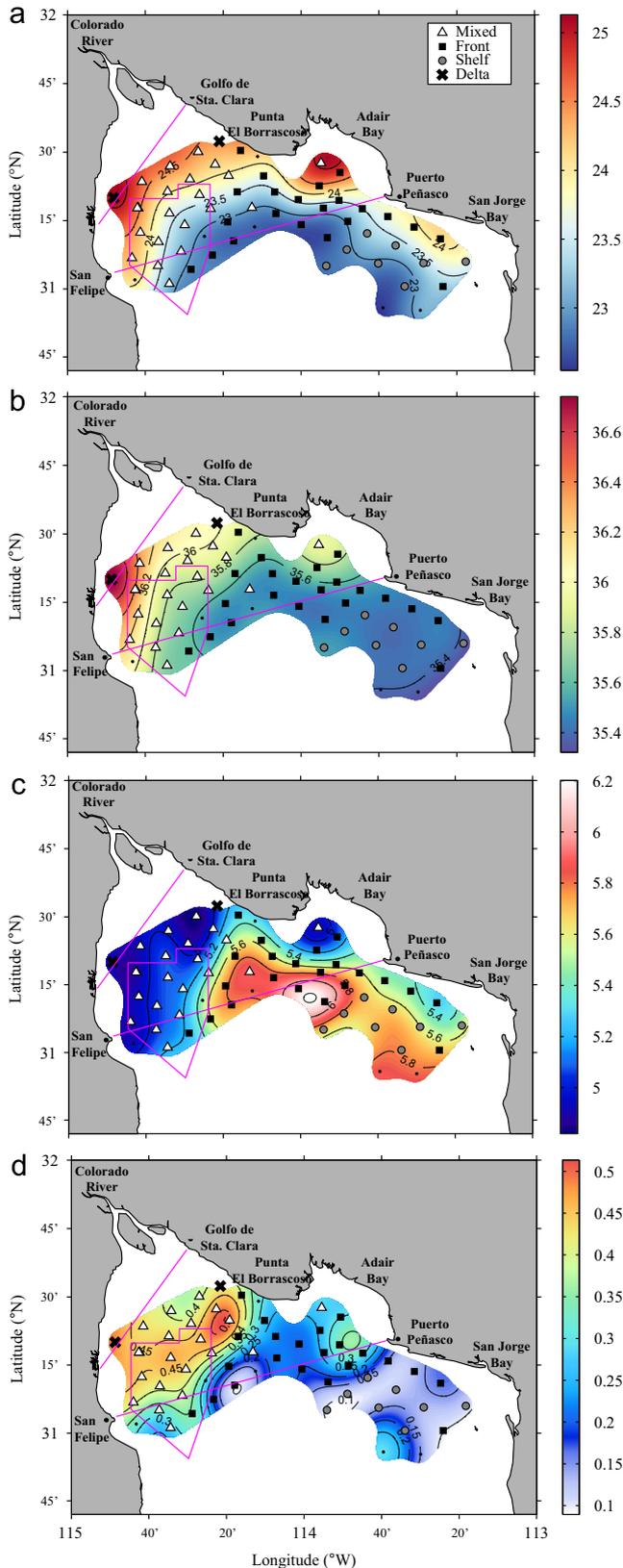
A canonical correspondence analysis (Ter Braak, 1986) was applied to define the relation between the environmental variables and the larval habitats (clusters of strata abundance). Before calculating the canonical correspondence analysis, the standardized biological data and the matrix of environmental indicators were root–root transformed, to reduce the weight of the most abundant species (Field et al., 1982). The matrix of environmental indicators contained the average values of station depth, temperature ( $^{\circ}\text{C}$ ), salinity, chlorophyll ( $\mu\text{g/L}$ ) and dissolved oxygen ( $\text{mL/L}$ ) in the water column. A Monte Carlo test of significance was applied (McCune and Grace, 2002). The result is shown as biplot (the two first ordination axes) with environmental indicators as a vector and the sampling stations as symbols in the ordination space (Ter Braak, 1986; De la Cruz-Agüero, 1994).

## 3. Results

### 3.1. Horizontal distribution of physical and chemical variables

For the description of the horizontal distribution of the physical and chemical variables, averages over the upper 10 m were used. Sea surface temperature (SST, Fig. 2a) ranged from  $<23^{\circ}\text{C}$  in the southern, deeper ( $>40\text{m}$ ) area of the study zone, to  $>25.5^{\circ}\text{C}$  at the head of the gulf and in the coastal zones. As the SST satellite image for June 8 shows (Fig. 3a) it is a locally enhanced thermal gradient; this is a tidal-mixing frontal area, separating well-mixed water in the shallow zone from stratified water in the deep zone (Argote et al., 1995), as shown in Section 3.2. The surface salinity values (Fig. 2b) were high in all the UGC, ranging from 35.4 in the south to 36.6 in the NW, with a haline front with a difference of 1.0. The shape of the 35.6 isohaline south of Punta Borrascoso suggests an intrusion of offshore water toward the coastal zone (Fig. 2b), which is also apparent in the surface isotherms in that area (Fig. 2a) and in the satellite images (Fig. 3).

Surface dissolved oxygen values were relatively high in all the study area (Fig. 2c), ranging from 4.8  $\text{mL/L}$  in the shallow NW side of the UGC and in Adair Bay to 6.2  $\text{mL/L}$  in the deep sector; a strong surface oxygen front separated these two extreme values.



**Fig. 2.** Surface hydrography (top 10 m averages): (a) temperature ( $^{\circ}\text{C}$ ), (b) salinity, (c) dissolved oxygen (mL/L) and (d) chlorophyll *a* from fluorescence ( $\mu\text{g/L}$ ). Symbols indicate fish larval habitats (see text). White triangles: "Mixed" habitat. Black squares: "Front" habitat. Gray circles: "Shelf" habitat. Black crosses: "Delta" habitat.

The oxygen front also suggests intrusions of surface water from the deep area: northward towards Punta Borrascoso and eastward towards San Jorge Bay.

Surface chlorophyll ranged from  $0.45 \mu\text{g/L}$  in a large portion of the UGC to  $0.1 \mu\text{g/L}$  in the SE part of the study area (Fig. 2d). A strong chlorophyll front separated the high values in the UGC from the low values in the deep area, a pattern also shown in the satellite image (Fig. 3b), which shows a low-chlorophyll area in most of the Northern Gulf. This front coincided with the dissolved oxygen front (Fig. 2c), but while the latter continued eastward toward Puerto Peñasco, the former was interrupted at Punta Borrascoso. This interruption of the chlorophyll front appears to be due to the northward intrusion mentioned above. An eastward intrusion of low-chlorophyll water ( $< 0.1 \mu\text{g/L}$ ) was found in the southeastern sector of the study area, which was also suggested by the dissolved oxygen distribution (Fig. 2c), and the chlorophyll satellite image (Fig. 3b) indicates that it is part of the large offshore chlorophyll minimum zone.

### 3.2. Vertical distribution of physical and chemical variables

The vertical distributions of the physical and chemical variables on transects across and along the Gulf axis (Lines D and L, marked blue in Fig. 1) help complete the hydrographic description of the UGC.

In Line D, from San Felipe to Punta El Borrascoso, temperature, salinity and dissolved oxygen (Fig. 4a–c) showed well-mixed conditions in the shallow western side of the UGC (as a result of strong tidal mixing) and slightly stratified conditions in the deeper eastern side.

In the case of temperature (Fig. 4a), the  $23.5^{\circ}\text{C}$  isotherm broke the surface in the center of the section, forming a surface front on both sides (contrast  $\sim 0.5^{\circ}\text{C}$ ). Temperature was vertically mixed in the shallow western side and increased toward the mainland. The bottom temperature front (where the thermocline touches the bottom) is stronger than the surface front, with a contrast of  $\sim 1^{\circ}\text{C}$ . Salinity was almost vertically mixed, with values of 35.6 in the east increasing to 36.2 in the west; there was a haline front on the peninsula side. The oxypleths (Fig. 4c) showed that the less shallow zone (between stations D03 and D01) was the most oxygenated and was stratified with the highest values ( $> 5.5 \text{ mL/L}$ ) in the surface layer, while the shallow zone to the west was the least oxygenated ( $\sim 4.9 \text{ mL/L}$ ) and vertically mixed. There was a dissolved oxygen front at station D03, very similar in shape and location to the temperature front (Fig. 4a). The chlorophyll distribution (Fig. 4d) shows high values ( $> 0.5 \mu\text{g/L}$ ) in a core between D04 and D02, with maximum in D03 at  $\sim 15 \text{ m}$  depth; it seems to be centered in the thermocline–oxycline in the warm side of the temperature front.

In Line L, which is along-gulf close to the mainland coast (from Adair Bay to San Jorge Bay), the isotherms (Fig. 5a) are almost horizontal in the deeper south sector, with a thermocline at  $\sim 20 \text{ m}$  depth. The isotherms dive towards the bottom from station H02 to F02 (depth  $< 25 \text{ m}$ ) forming a strong bottom front. Salinity shows an inversion, with a near-bottom maximum in F02 (35.8) and at mid-depth in G02 (35.7), which suggests (together with the coincident oxygen inversion) a gravity current coming out of Adair Bay, similar to those reported by Lavín et al. (1998) for the UGC. In the deep southern sector there is a subsurface salinity minimum (35.4) at stations J02 and Kb02 at  $10\text{--}20 \text{ m}$  depth, and a halocline below. The vertical oxygen distribution (Fig. 5c) shows that the top 20 m were well oxygenated, with a strong oxycline below, and intermediate values associated with the gravity current. The chlorophyll distribution registers the gravity current as a bottom maximum ( $0.5 \mu\text{g/L}$ ), which suggests that it may be due to sediment load rather than to phytoplankton chlorophyll. The lowest chlorophyll ( $\sim 0.1 \mu\text{g/L}$ ) is found in a 15 m thick surface layer at stations J02 and Kb02; there is a chlorophyll front starting north of station I02 and ending at station H02, in agreement with Figs. 2d and 3b.

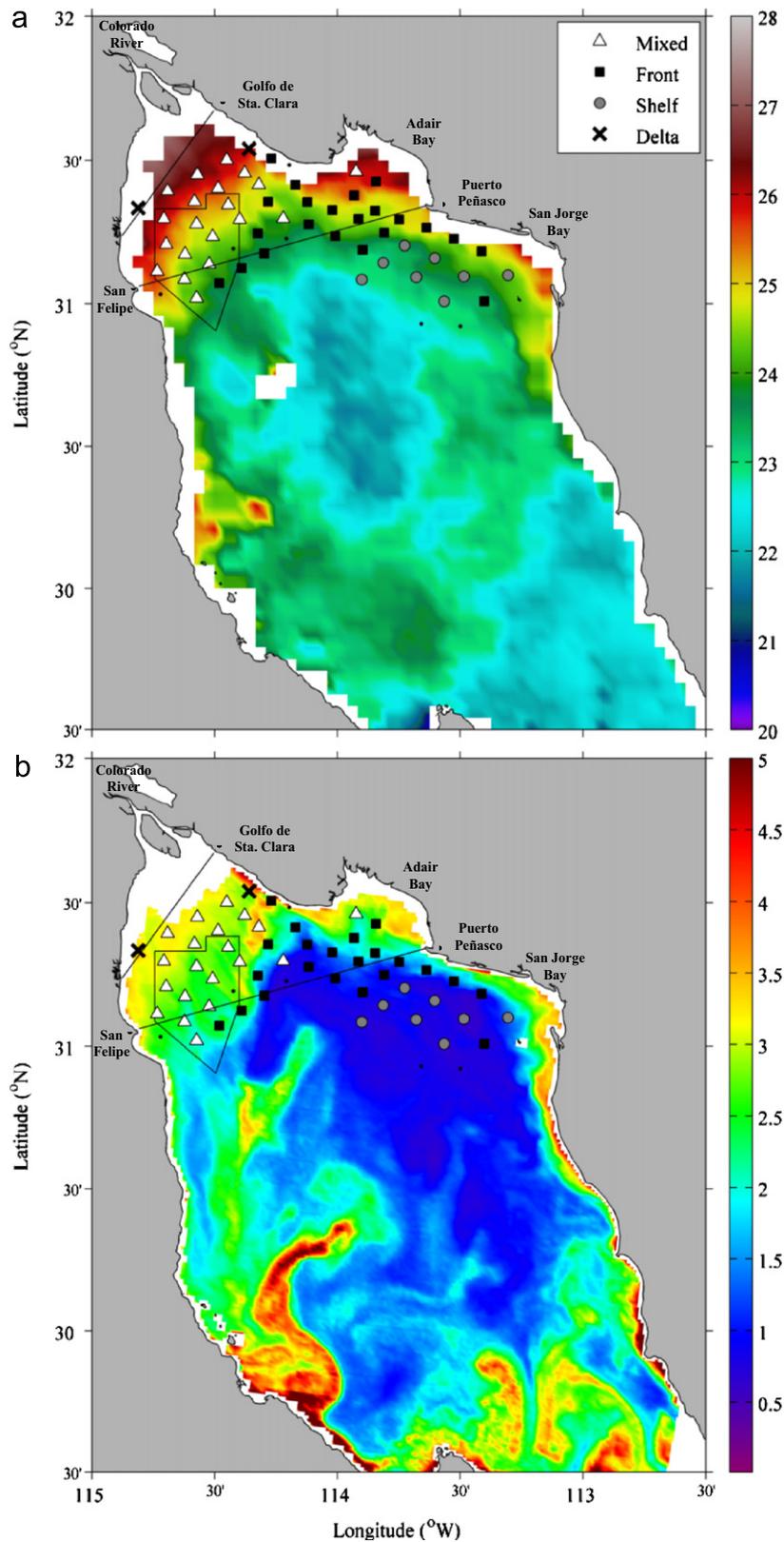
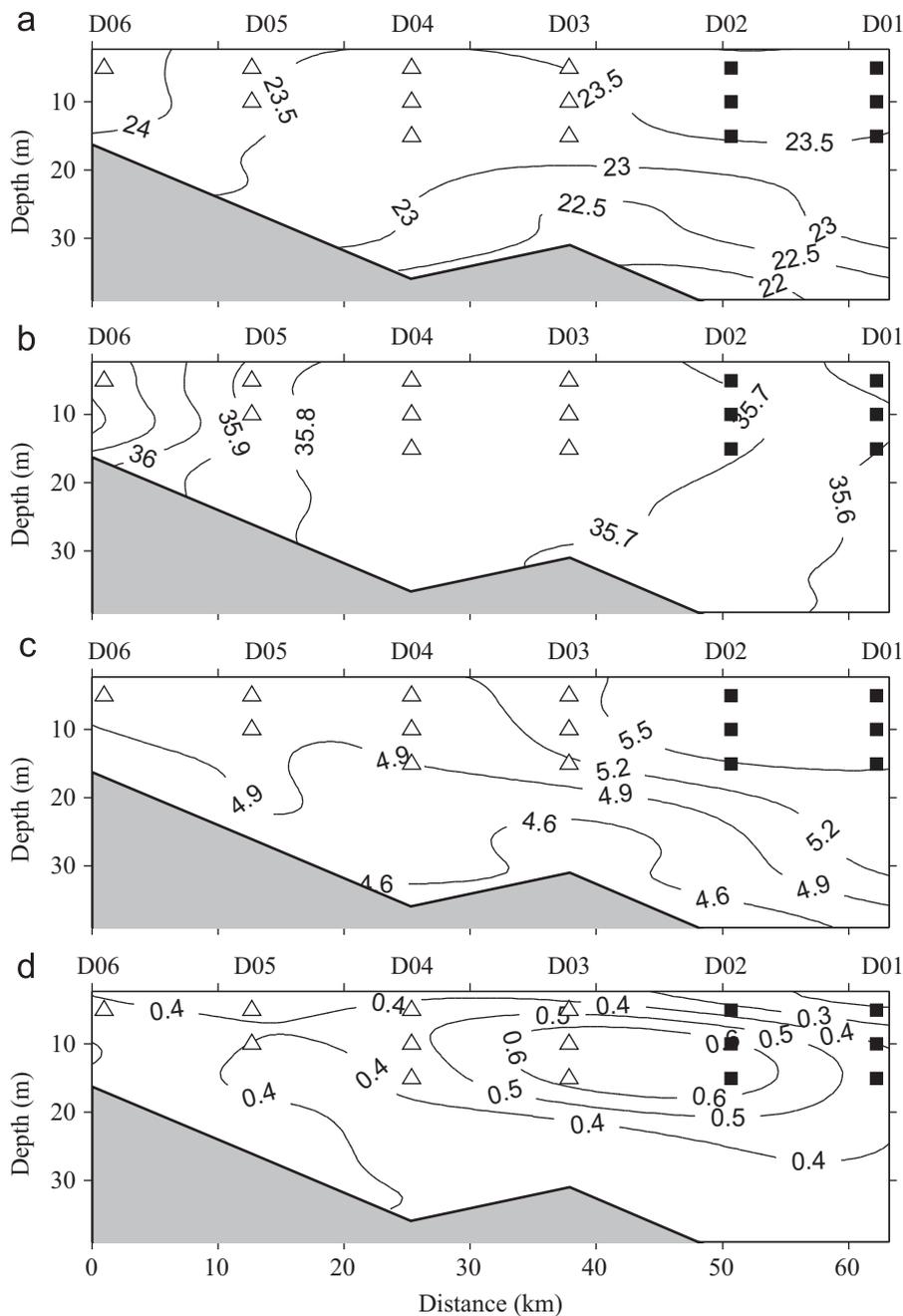


Fig. 3. Aqua/MODIS satellite images for June 8, 2008: (a) sea surface temperature ( $^{\circ}\text{C}$ ;  $4\text{ km} \times 4\text{ km}$ ) and (b) surface chlorophyll  $a$  ( $\text{mg m}^{-3}$ ;  $1\text{ km} \times 1\text{ km}$ ).

### 3.3. Zooplankton biomass

Zooplankton biomass values ranged from 10 to  $2000\text{ mL}/1000\text{ m}^3$  (Fig. 6). The highest values of zooplankton biomass ( $> 650\text{ mL}/1000\text{ m}^3$ ) were found in the surface level, mainly in

the eastern coastal zone, from south of Golfo de Santa Clara to San Jorge Bay. Biomass decreased with depth, with values between  $100$  and  $350\text{ mL}/1000\text{ m}^3$  below  $5\text{ m}$  depth. In the western shallow plain, surface zooplankton biomass values tended to be low, and ranged from  $100$  to  $650\text{ mL}/1000\text{ m}^3$ , and decreased with depth.



**Fig. 4.** Vertical distribution of hydrographic variables along the across-gulf "Line D" (stations D01–D06, marked in blue in Fig. 1): (a) temperature ( $^{\circ}\text{C}$ ), (b) salinity, (c) dissolved oxygen ( $\text{mL/L}$ ) and (d) chlorophyll *a* from fluorescence ( $\mu\text{g/L}$ ).

### 3.4. Fish larvae composition

The mean proportion of fish larvae in relation to total abundance of zooplankton was more than 50%, which is the highest proportion of fish larvae observed in zooplankton samples in the entire Gulf of California.

There were no statistically significant differences in the total larval abundance between day and night hours in all cases ( $P > 0.05$ ). Total larval abundance was the highest in the surface stratum and lowest in the deep stratum (see Sánchez-Velasco et al., 2011); however, the differences among the four strata were not statistically significant ( $P > 0.05$ ).

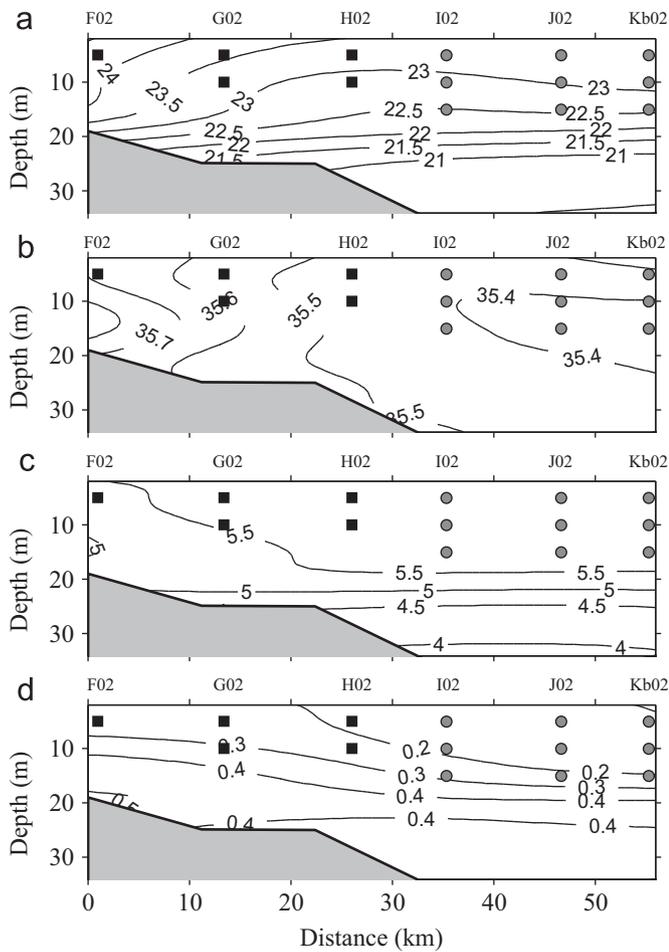
A total of 29,505 fish larvae were collected with mean larval abundance (per stratum) of 1253, which were included in 99 taxa belonging to 32 families of demersal, coastal pelagic and epipelagic

fish. Of the 99 taxa, 43 were identified to species level, 16 to genus and 40 to family and suborder levels. There were taxonomic difficulties in identifying larvae, mostly due to: (i) the large number of larvae (more than 85%) that were in preflexion stage and (ii) the relatively few larvae (only  $\sim 10\%$ ) of all the fish species that inhabit the Gulf of California that have been described (see Moser, 1996).

The most abundant species were *Anchoa* spp. (52%), *Opisthonema* sp. 1 (27%) and Scianidae type 1 (4%), which comprise more than 80% of the total larval abundance. These species were mostly in the surface stratum (see Sánchez-Velasco et al., 2011).

### 3.5. Larval fish habitats

The Bray–Curtis dissimilarity index clearly defined four larval fish habitats, with differences in composition and abundance at a

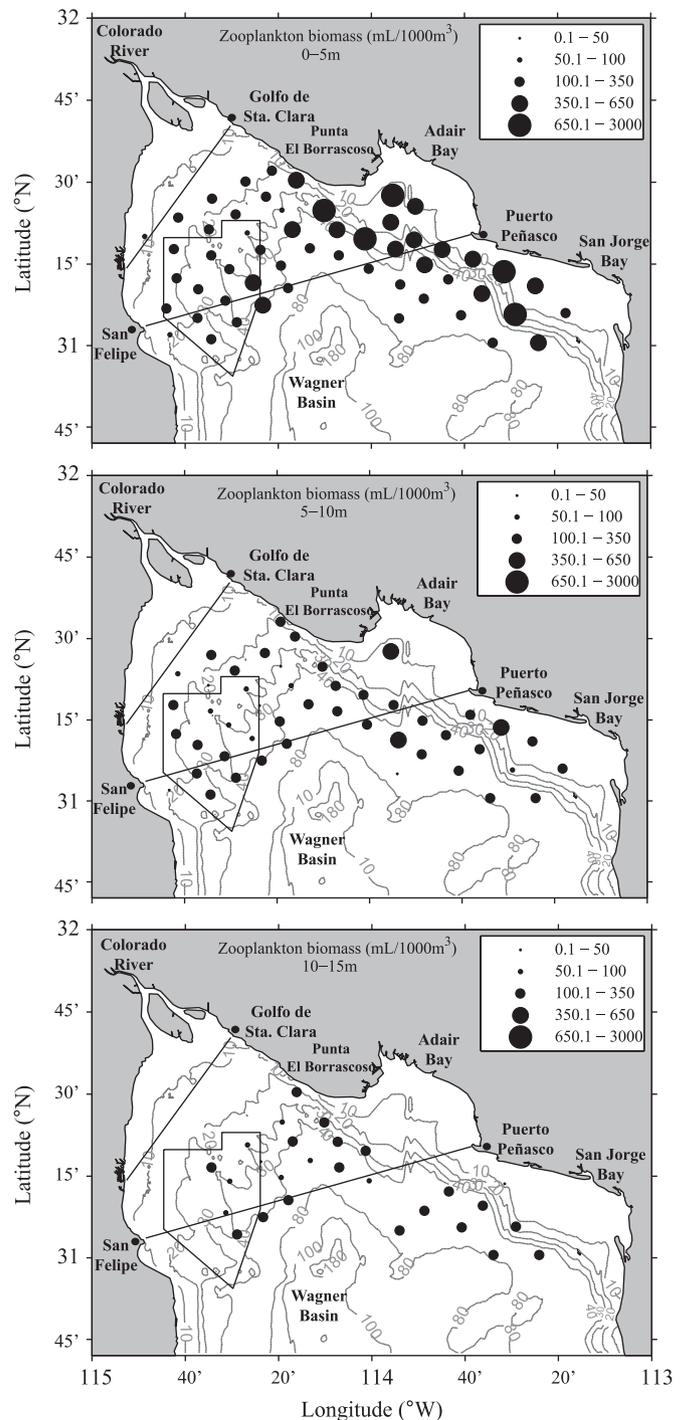


**Fig. 5.** Vertical distribution of hydrographic variables along “Line L” (stations F02, G02, H02, I02, J02 and Kb02, marked in blue in Fig. 1): (a) temperature (°C), (b) salinity, (c) dissolved oxygen (mL/L) and (d) chlorophyll *a* from fluorescence (µg/L).

level > 41 (see dendrogram in Supplementary material 1). The MRPP test showed that the four larval habitats were significantly different ( $T = -19.8613$ ,  $A = 0.1080$ ,  $P < 0.0001$ ). These larval habitats, whose distribution is shown in Figs. 2 and 7, were named as follows: (i) “Mixed”, (ii) “Front”, (iii) “Shelf” and (iv) “Delta”. The habitats covered from 15 m depth to the surface, and the largest abundance was found in the surface stratum (0–5 m).

The “Mixed” habitat, formed by 20 samples, was located in the shallow (bottom depth < 30 m) vertically mixed area to the north, and included the Vaquita Refuge (Figs. 2 and 7) but extended to the NE. The habitat was positioned over the weak temperature and salinity gradients on the vertically mixed, warm, salty side of the tidal-mixing front (Fig. 2a and b) and on the low side of the oxygen front and high side of the chlorophyll front (Fig. 2c and d). It had 36 taxa and a mean abundance of 554 larvae/10 m<sup>2</sup> of sea surface, the lowest diversity of the study (not counting the Delta habitat). The coastal pelagic *Anchoa* spp. presented high abundance in this habitat, associated with demersal species such as *Gobulus crescentalis* and Scianidae type 1 (Table 1).

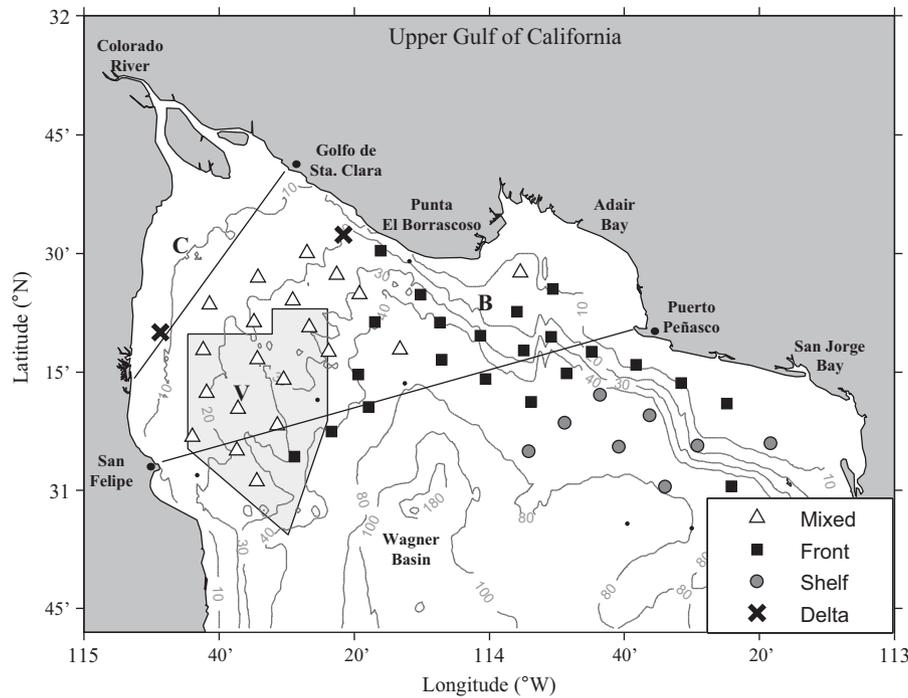
The “Front” habitat, defined by 22 samples, was mostly located on the central and eastern sectors of the Buffer Zone of the Reserve (10–50 m depth) and extended to the southeast (~10 m depth) parallel to the mainland coast (Figs. 2 and 7). This habitat was located mostly in the cool side and close to the tidal-mixing front, which is the fresh side of the haline front (Fig. 2a and b). This habitat was located on the high-values side of the oxygen



**Fig. 6.** Zooplankton biomass (mL/1000 m<sup>3</sup>) in the three sampled strata: (a) 0–5 m, (b) 5–10 m and (c) 10–15 m.

front, and was completely excluded from the shallow UGC (Fig. 2c). It was found in relatively low chlorophyll waters to the south and on the strong chlorophyll front itself (Figs. 2d and 3b). It had the highest specific richness (85 taxa) and mean abundance (1355 larvae/10 m<sup>2</sup>). Epipelagic species such as *Anchoa* spp. and *Opisthonema* sp 1. dominated this habitat, and their dominance was associated with larvae of demersal species such as *Anisotremus davidsoni* and *Eucinostomus dowii* (Table 1).

The “Shelf” larval habitat (8 samples) was found only in the southeastern sector of the study area, in bottom depths between 20 and 80 m (mostly ~60 m; Figs. 2 and 7). Given its offshore location, this habitat was characterized by cool fresher water



**Fig. 7.** Distribution of the four fish larval habitats observed in June 2008, overlaid on the bathymetry (m) of the Upper Gulf of California. Symbols indicate fish larval habitats (see text). White triangles: “Mixed” habitat. Black squares: “Front” habitat. Gray circles: “Shelf” habitat. Black crosses: “Delta” habitat.

**Table 1**

Dominant taxa per fish larval habitat in the Upper Gulf of California (June 2008). Abundance is expressed as number of larvae per 10 m<sup>2</sup> of sea surface. X: mean abundance; %F: percentage of occurrence.

| Taxa                                     | Mixed habitat |     | Front habitat |      | Shelf habitat |     | Delta habitat |     |
|--|---------------|-----|---------------|------|---------------|-----|---------------|-----|
|  | X             | %F  | X             | %F   | X             | %F  | X             | %F  |
| <i>Opisthonema</i> sp 1                  | 35            | 70  | 258           | 98   | 180           | 91  |               |     |
| <i>Anchoa</i> spp.                       | 291           | 98  | 384           | 98   | 138           | 77  | 28            | 100 |
| <i>Synodus</i> sp. 1                     |               |     |               |      | 18            | 32  |               |     |
| <i>Serranus</i> sp. 1                    |               |     |               |      | 36            | 64  |               |     |
| <i>Diapterus peruvianus</i>              |               |     | 39            | 23   |               |     |               |     |
| <i>Eucinostomus dowii</i>                |               |     | 41            | 46   |               |     |               |     |
| <i>Anidotremus davidsoni</i>             |               |     | 34            | 60   |               |     |               |     |
| <i>Xenistius californiensis</i>          |               |     | 24            | 48   |               |     |               |     |
| Sciaenidae type 1                        | 30            | 77  | 40            | 67   |               |     | 22            | 67  |
| <i>Gobulus crescentalis</i>              | 72            | 64  |               |      |               |     |               |     |
| <i>Auxis</i> sp. 1 <sup>a</sup>          |               |     |               |      | 4             | 14  |               |     |
| <i>Scomber japonicus</i> <sup>a</sup>    |               |     |               |      | 7             | 55  |               |     |
| <i>Scomberomerus sierra</i> <sup>a</sup> |               |     |               |      | 9             | 9   |               |     |
| <i>Etopus crossotus</i>                  |               |     |               |      |               |     |               |     |
| Total mean abundance                     |               | 554 |               | 1355 |               | 640 |               | 85  |
| Number of species                        |               | 36  |               | 85   |               | 37  |               | 9   |
| Number of stations                       |               | 20  |               | 22   |               | 8   |               | 2   |

<sup>a</sup> Scombridae species that occurred in the region.

(Fig. 2a and b). The distribution of this habitat in relation to surface dissolved oxygen and chlorophyll (Fig. 2c and d) suggests that it was located on the eastward intrusion of offshore water mentioned before. This habitat was represented by 37 taxa and a mean larval abundance of 640 larvae/10 m<sup>2</sup> of sea surface. It was dominated by *Opisthonema* sp 1. and demersal species such as *Synodus* sp 1. and *Serranus* sp 1. Epipelagic species like the Scombridae (e.g., *Scomber japonicus*, *Auxis* spp., *Scomberomerus sierra*) were also recorded in this habitat (Table 1).

The “Delta” habitat consisted of only the two shallowest sampling stations A01 (8 m depth) off the mainland coast and A05 (10 m) off the peninsula coast (Fig. 6). Larval abundance

(~85 larvae/10 m<sup>2</sup>) and number of species (nine) were very low. Since this habitat consisted of only two stations, one at each side of the UGC, it is probably undersampled, and will not be considered further.

### 3.6. Three-dimensional distribution of the larval fish habitats

The three-dimensional distribution of the larval habitats obtained by the Bray–Curtis Index is presented overlaid on the vertical distribution of physical and chemical variables across the transversal transect (Line D) in Fig. 4. It is observed that the “Mixed” habitat (marked by white triangles) was found from 15 m depth to surface from station D06 in the west to station D03 at the center of the section. The latter station was located right at the tidal-mixing front, so that the “Front” stations D02 and D01 were in the warm, less salty, well oxygenated surface layer on the stratified side of the front.

The habitats present in Line L (Fig. 5) were “Front” in water with bottom depths < 30 m and “Shelf” in the deeper stations in the south. The boundary between the two habitats was between stations H02 and I02, where a weak front was found in most physical–chemical variables, in agreement with Fig. 2.

### 3.7. Relations between larval fish habitats and environmental variables

The larval fish habitats were also detected by the canonical correspondence analysis (Fig. 8). The “Mixed” habitat was clearly separated from the others, and correlated significantly with the highest salinity, temperature and chlorophyll concentration, and with the lowest dissolved oxygen. The “Front” and “Shelf” habitats showed a wide interval of environmental variables, although the “Shelf” habitat was more associated with the highest dissolved oxygen and depth.

Correlation among the environmental indicators showed them to be virtually independent. Most of the variation was explained by the first axis (Tables 2 and 3), although only 15.9% of the total

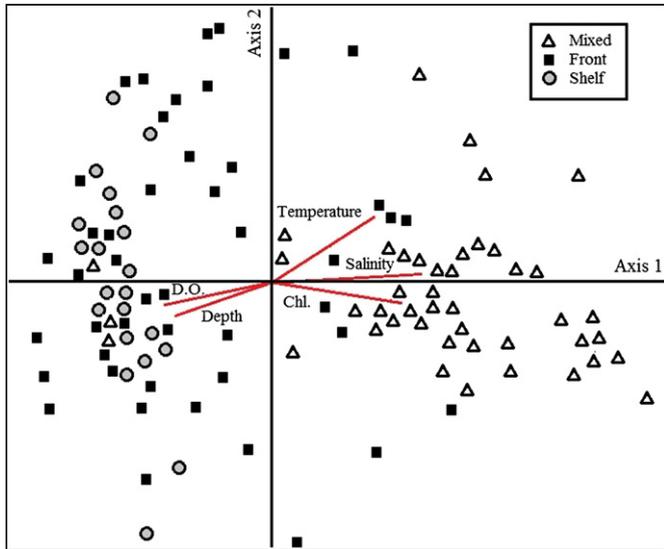


Fig. 8. Graphic of the canonical correspondence analysis in the Upper Gulf of California (June 2008).

Table 2

Variance explained by depth and environmental indicators from the canonical correspondence analysis in the Upper Gulf of California (June 2008).

|                                      | Axis 1 | Axis 2 | Axis 3 |
|--------------------------------------|--------|--------|--------|
| Eigenvalue                           | 0.216  | 0.070  | 0.026  |
| Variance in species data             |        |        |        |
| % of variance explained              | 11.0   | 3.6    | 1.3    |
| Cumulative % explained               | 11.0   | 14.6   | 15.9   |
| Pearson Correlation, Spp-Envt        | 0.765  | 0.612  | 0.431  |
| Kendall (rank) Correlation, Spp-Envt | 0.553  | 0.317  | 0.350  |

Table 3

Multiple regression results between depth and environmental indicators from the canonical correspondence analysis in the Upper Gulf of California (June 2008).

| Variable    | Correlations |        |        | Biplot scores |        |        |
|-------------|--------------|--------|--------|---------------|--------|--------|
|             | Axis 1       | Axis 2 | Axis 3 | Axis 1        | Axis 2 | Axis 3 |
| Temperature | 0.630        | 0.705  | 0.071  | 0.292         | 0.187  | 0.011  |
| Salinity    | 0.935        | 0.087  | -0.047 | 0.434         | 0.023  | -0.007 |
| D.O.        | -0.806       | -0.290 | 0.071  | -0.374        | -0.077 | 0.011  |
| Chlorophyll | 0.810        | -0.229 | -0.074 | 0.376         | -0.061 | -0.012 |
| Depth       | 0.677        | -0.406 | -0.577 | -0.314        | -0.108 | -0.092 |

variance was explained; salinity was the most strongly related environmental indicator with this axis, and temperature the least related. The Monte Carlo Test results showed significant difference among the four habitats (Table 4). The eigenvalue for the first axis is higher than the range expected by chance.

#### 4. Discussion

The composition and abundance of fish larvae in the UGC are reported for the first time, based on intensive horizontal and vertical sampling carried out in June 2008. The high species richness (99 taxa) and great larval abundance (mean of 1253 fish larvae per 5-m stratum) recorded in this study (Table 1) indicate that despite its human-induced change from brackish-water

Table 4

Monte Carlo Test results from the canonical correspondence analysis in the Upper Gulf of California (June 2008).

| Axis | Eigenvalue            | Randomized data |         |         | p      |
|------|-----------------------|-----------------|---------|---------|--------|
|      |                       | Mean            | Minimum | Maximum |        |
| 1    | 0.216                 | 0.052           | 0.021   | 0.140   | 0.0100 |
| 2    | 0.070                 | 0.028           | 0.013   | 0.048   | 0.0100 |
| 3    | 0.026                 | 0.017           | 0.007   | 0.034   | 0.0400 |
|      | Spp-Event Correlation |                 |         |         |        |
| 1    | 0.765                 | 0.470           | 0.325   | 0.777   | 0.0300 |
| 2    | 0.612                 | 0.399           | 0.250   | 0.549   | 0.0100 |
| 3    | 0.431                 | 0.360           | 0.182   | 0.494   | 0.0800 |

estuary (Lavín and Sánchez, 1999) to hypersaline inverse estuary (Alvarez-Borrego and Galindo-Bect 1974; Alvarez-Borrego et al., 1975; Lavín et al., 1988; Figs. 2b, 4b and 5b), the UGC remains an important fish spawning zone and nursery area.

The specific richness and larval abundance recorded in this study is very high in relation to the fish larvae records for the Northern Gulf of California for the same month, where Sánchez-Velasco et al. (2009) found fish larvae of 29 taxa with mean larval abundance < 516 during June 2003. However, in August (high summer), Sánchez-Velasco et al. (2009) recorded 52 taxa with mean larval abundance > 1260. This indicates that the highest specific richness during the annual cycle occurs during high summer in the Northern Gulf. Therefore, it is very likely that specific richness and larval abundance in the UGC also increase in high summer, which would add fish larvae to the seasonality of the UGC, in addition to circulation and hydrography (Lavín et al., 1998).

Although there is no record of what fish larvae species were present in the former estuary, nor of the distribution of their habitats, there is a growing body of evidence indicating that post-dam conditions (extremely high salinity and turbidity) have impacted some life history parameters of fish species. Slowed growth of the endangered *T. macdonaldii* (Rowell et al., 2005), reduction of nursery habitat for *C. othonopterus* (Rowell et al., 2008) and drastic decline in abundance of the delta clam, *Mulinex coloradoensis* (Rodríguez et al., 2001), have been associated with increased salinity in the UGC. The striking coincidence found in this study between hydrographic conditions and larval habitats suggests that either seasonal or anthropogenic hydrographic changes (pre- and post-dam) in the UGC would present distinct larval habitats with variations in composition and abundance. We detected that the "Mixed" larval habitat, which had the lowest diversity in the study, was correlated with the hypersaline conditions; this may indicate that the area of some species has shrunk since river damming.

As expected, in view of the strong tidal mixing in the UGC (Argote et al., 1995; Lavín et al., 1998), zooplankton biomass and larval fish abundance were found to be vertically well mixed in the first 15 m of the water column (differences among strata were not statistically significant); however, in the deeper part, there was a thermocline at 20 m depth, below which a different larval habitat may be present. We found fish larvae habitats with well-marked horizontal limits coinciding with physical-chemical boundaries (salinity, temperature, chlorophyll, oxygen), as seen in the horizontal distributions shown in Fig. 2. Environmental limits for fish larvae habitats have been recorded in deeper regions of the Gulf of California, where mesoscale hydrographic structures such as fronts and eddies were found to function as zooplankton boundaries (e.g., Sánchez-Velasco et al., 2009; Danell-Jiménez et al., 2009; Inda-Díaz et al., 2010). The definition

of larval fish habitats in the UGC reveals a planktonic zonation in the ecosystem, which must control the first level of the trophic webs in the region.

The “Mixed” habitat, the least diverse and with the lowest abundance of the UGC (Table 1), was dominated by *Anchoa* spp. larvae, which presented high concentration in this habitat, associated with larvae of demersal species like Scianidae type 1 and *G. crescentalis*, the latter almost restricted to this habitat. The larvae of these species, which correlated statistically with the highest salinity, inhabit the saltiest water of the entire Gulf, and they may be examples of those that adapted to the new inverse-estuary conditions. In studies of the entire Gulf, *Anchoa* spp. were recorded (Sánchez-Velasco et al., 2009) as dominant only in the northern extreme of the mainland shelf of the Northern Gulf of California during high summer (August 2003); however, its frequency was much lower than that recorded here, which suggests that the UGC is its preferred spawning ground in the Gulf of California. This idea is congruent with the diet composition recorded for the Vaquita (Brownell, 1983), which includes adult *Anchoa* spp. (*Anchoa helleri*, *Anchoa ischana*, *Anchoa macrolepidota*, *Anchoa nasus*) and some demersal fish (Scianidae such as *Bairdiella icistia*, *M. megalops*, *C. othonopterus*) among others.

The summer “Mixed” habitat described here includes the known distribution of Vaquita (Fig. 7) at the time the Refuge was established (Rojas-Bracho et al., 2006). However, a fall 2008 visual and acoustic survey of the Vaquita population indicates that 50% of the population occurs outside the Refuge (Gerrodette and Rojas-Bracho, 2011). Understanding the seasonal changes in larval habitat and distribution of the Vaquita’s prey may offer insights on the Vaquita’s seasonal use of the UGC, with important implications for management (Gerrodette et al., 2011).

The “Front” habitat (Fig. 7) had the highest specific richness, larval abundance (Table 1) and zooplankton biomass values of the sampled area. This is the habitat representative of the physical-chemical frontal region between the UGC and the Northern Gulf (Figs. 2 and 3); the position of the front is determined by the balance between bottom mixing and irradiance-induced stratification (Argote et al., 1995). Coastal pelagic species such as *Anchoa* spp. and *Opisthonema* sp. 1 dominated the habitat but the distribution of the latter was apparently limited by the frontal zone (not shown; see Sánchez-Velasco et al., 2011). Since *Opisthonema* sp. 1 has been reported as abundant in the Northern Gulf of California mainland shelf during summer (Moser et al., 1974; Sánchez-Velasco et al., 2009), and since it was absent from the “Mixed” habitat, the front might represent the northernmost limit of its distribution in the Gulf of California.

The “Front” habitat environmental conditions are highly favorable for the zooplanktonic community as evidenced by the coincidence of the highest abundance of larvae of coastal pelagic fish species in the UGC study area, the highest zooplankton biomass, and the presence of the preferential spawning zone of blue shrimp *L. stylirostris* (Calderón-Aguilera et al., 2002; Galindo-Bect et al., 2010).

The “Shelf” larval habitat was less diverse and abundant than the “Front” habitat, dominated by *Opisthonema* sp. 1 larvae, with the presence of epipelagic species such as the Scombridae *S. japonicus*, *Auxis* spp. and *S. sierra*, probably representing an extension of their spawning area in deeper adjacent areas to the south. In the Northern Gulf of California Moser et al. (1974) and Sánchez-Velasco et al. (2009) also found larvae of *Auxis* spp. and *S. sierra* in summer, and of *S. japonicus* in winter. Their presence indicates the influence of Northern Gulf water on the eastern side of the UGC. This is probably linked to the late spring–summer cyclonic circulation proposed by Lavín and Marinone (2003), which flows northward on the mainland shelf. Satellite images also show the presence of eddies from the Northern Gulf affecting

the UGC (Lopez-Calderon et al., 2008), probably carrying plankton organisms, including eggs of pelagic fishes.

More ecological studies are necessary in the UGC because it is a complex ecosystem with extreme environmental conditions and strong seasonality (Lavín et al., 1998; Sánchez-Velasco et al., 2009), and its socio-economic importance offers many management challenges. The “no net-fishing” policy in the Vaquita Refuge (Gerrodette and Rojas-Bracho, 2011) is expected to have a beneficial impact on Vaquita, on the ecosystem and on fisheries. If the abundance of resident adults and spawning fish increases, the availability of food for top predators (including the Vaquita) will also increase in this zone. However with the lack of knowledge about the temporal and spatial distribution of fish spawning strategies (some may spawn all year with peaks of reproduction in a particular area and/or season of year; others may restrict spawning to an area and/or season) it is very difficult to predict the possible impact of such management actions on the UGC ecosystem. It is probable that the impact would be observed at the species level, following connectivity routes (dispersion/retention) of the planktonic phases of the fish species that inhabit the region, such as has been observed previously in the Northern Gulf of California (Sánchez-Velasco et al., 2009; Peguero-Icaza et al., 2011).

## 5. Conclusions

The UGC remains an important spawning area and nursery ground despite the human-induced change from estuary to inverse estuary; 29,505 fish larvae were collected, and classified in 99 taxa.

Larval fish habitats with statically significant well-defined limits that coincided with marked environmental gradients were found, despite the large tidal excursions and strong tidal mixing associated with the macrotidal character of the UGC.

The “Mixed” larval habitat, which included the Vaquita Refuge, was the saltiest and the one with the lowest larval diversity, which suggests that the human-induced shift to hypersaline conditions may have reduced the area for some species, at least during early summer.

## Supplementary material 1

Dendrogram of groups of sampling strata, defined by the Bray-Curtis dissimilarity index and the flexible agglomerative method, from fish larvae data collected in the Upper Gulf of California during June 2008.

## Acknowledgments

This study was financed by Consejo Nacional de Ciencia y Tecnología de México (Contract 2009-105922), and by the David and Lucile Packard Foundation (Contract 2009-34967) through the University of Arizona PANGAS project (<http://pangas.arizona.edu>). Additional support was received from CICESE and CICI-MAR-IPN internal budgets. We thank the scientific participants, skipper and crew of the *R/V Francisco de Ulloa* for their support during the cruise. Special thanks to two anonymous referees for helping improve this article.

## Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.csr.2011.11.009](https://doi.org/10.1016/j.csr.2011.11.009).

## References

- Álvarez-Borrego, S., Galindo-Bect, L.A., 1974. Hidrología del Alto Golfo de California-I. Condiciones durante otoño. *Ciencias Marinas* 1, 46–64.
- Álvarez-Borrego, S., Flores-Báez, B.P., Galindo-Bect, L.A., 1975. Hidrología del Alto Golfo de California II. Condiciones durante invierno, primavera y verano. *Ciencias Marinas* 2, 21–36.
- Alvarez, L.G., Jones, S.E., 2002. Factors influencing suspended sediment flux in the Upper Gulf of California. *Estuarine, Coastal and Shelf Science* 54, 747–759.
- Argote, M.L., Amador, A., Lavín, M.F., Hunter, J.R., 1995. Tidal dissipation and stratification in the Gulf of California. *Journal of Geophysical Research* 100, 16103–16118.
- Beers, J.R., 1976. Volumetric methods. In: Steedmann, H.F. (Ed.), *Zooplankton Fixation and Preservation. Monographs of Oceanic Methods*. UNESCO.
- Borguez, R., Vaz, J., Serrão, E.A., Gonçalves, E.J., 2009. Short-term temporal fluctuation of very-nearshore larval fish assemblages at the Arrábida Marine Park (Portugal). *Journal of Coastal Research* 56, 376–380.
- Bray, J.R., Curtis, J.T., 1957. An ordination of the upland forest communities of Southern Wisconsin. *Ecological Monographs* 7, 325–349.
- Brownell, R., 1983. Distribution of the vaquita *Phocoena sinus* in Mexican waters. *Marine Mammal Science* 2 (4), 299–305.
- Calderón-Aguilera, L.E., Aragón-Noriega, E.A., Licón, H.A., Castillo-Moreno, G., Maciel-Gómez, A., 2002. Abundance and composition of penaeid postlarvae in the Upper Gulf of California. In: Hendrickx, M.E. (Ed.), *Contribution to the study of East Pacific crustaceans*. Mexico City. Universidad Nacional Autónoma de México.
- Carriquiry, J.D., Sánchez, A., 1999. Sedimentation in the Colorado River delta and Upper Gulf of California after nearly a century of discharge loss. *Marine Geology* 158, 125–145.
- Cudney-Bueno, R., Lavín, M.F., Marinone, S.G., Raimondi, P.T., Shaw, W.W., 2009. Rapid effects of marine reserves via larval dispersal. *Public Library of Science ONE* 4 (1), e4140. doi:10.1371/journal.pone.0004140 (eISSN-1932-6203).
- Danell-Jiménez, A., Sánchez-Velasco, L., Lavín, M.F., Marinone, S.G., 2009. Three-dimensional distribution of larval fish assemblages across a surface thermal/chlorophyll front. *Estuarine, Coastal and Shelf Science* 85, 487–496.
- De La Cruz-Aguero, G., 1994. ANACOM: Sistema para el análisis de comunidades. Ver 3.0. Manual el Usuario. CICIMAR-IPN, La Paz, Baja California Sur, México, 99 p.
- Espinosa-Fuentes, M.L., Flores-Coto, C., 2004. Cross-shelf and vertical structure of ichthyoplankton assemblages in continental shelf waters of the southern Gulf of México. *Estuarine, Coastal and Shelf Science* 59, 333–352.
- Felger, R., Broyles, B., 2007. *Dry Borders: Great Natural Reserves of the Sonoran Desert*. University of Utah Press, Salt Lake City.
- Field, J.G., Clarke, K.R., Warwick, R.M., 1982. A practical strategy for analyzing multispecies distribution patterns. *Marine Ecology Progress Series* 8, 37–52.
- Galindo-Bect, M.S., Aragón-Noriega, E.A., Hernández-Ayón, J.M., Lavín, M.F., Huerta-Díaz, M.A., Delgadillo-Hinojosa, F., Segovia-Zavala, J.A., 2010. Distribution of penaeid shrimp larvae and postlarvae in the Upper Gulf of California. *Crustaceana* 83 (7), 809–819.
- García-Córdoba, J., Galindo-Bect, M.S., Sánchez-Velasco, L., Inda-Díaz, E., Godínez, V.M., Lavín, M.F., Ocampo-Torres, A., Cabrera-Ramos, C., 2008. Datos hidrográficos en el Golfo de California durante junio de 2008. Campaña GOLCA 0806. B/O Francisco de Ulloa. Informe Técnico 84911. Departamento de Oceanografía Física, CICESE, Ensenada, Mexico.
- Gerrodette, T., Rojas-Bracho, L., 2011. Estimating the success of protected areas for the vaquita, *Phocoena sinus*. *Marine Mammal Science* 27 (2), E101–E125. doi:10.1111/j.1748-7692.2010.00449.x.
- Gerrodette, T., Taylor, B., Swift, R., Rankin, S., Jaramillo-Legorreta, A., Rojas-Bracho, L., 2011. A combined visual and acoustic estimate of 2008 abundance, and change in abundance since 1997, for the vaquita, *Phocoena sinus*. *Marine Mammal Science* 27 (2), E79–E100. doi:10.1111/j.1748-7692.2010.00438.x.
- Hastings, P., Findley, L., 2007. Marine fishers of the Upper Gulf Biosphere Reserve, Northern Gulf of California. In: Felger, R., Broyles, B. (Eds.), *Dry Borders: Great Natural Reserves of the Sonoran Desert*. University of Utah Press, Salt Lake City, pp. 364–382.
- Inda-Díaz, E.A., Sánchez-Velasco, L., Lavín, M.F., 2010. Three-dimensional distribution of small pelagic fish larvae (*Sardinops sagax* and *Engraulis mordax*) in a tidal-mixing front and surrounding waters (Gulf of California). *Journal of Plankton Research* 32, 1241–1254.
- Jaramillo-Legorreta, A., Rojas-Bracho, L., Gerrodette, T., 1999. A new abundance estimate for vaquitas: first step for recovery. *Marine Mammal Science* 15, 957–973.
- Jaramillo-Legorreta, A., Rojas-Bracho, L., Urbán-Ramírez, J., 2005. A Review of Acoustic Surveys and Conservation Actions for the Vaquita. Scientific Committee Document SC/SM/10, International Whaling Commission, Cambridge, UK.
- Jiménez-Rosenberg, S.P.A., González-Navarro, E.A., Saldierna-Martínez, R.J., 2006. Larval, prejuvenile and juvenile development of *Eucinostomus currani*. *Journal of Fish Biology* 69 (28–37).
- Lavín, M.F., Organista, S., 1988. Surface heat flux in the northern Gulf of California. *Journal of Geophysical Research* 93, 14033–14038.
- Lavín, M.F., Godínez, V., Alvarez, L.G., 1998. Inverse-estuarine features of the Upper Gulf of California. *Estuarine, Coastal and Shelf Science* 46, 769–795.
- Lavín, M.F., Sánchez, S., 1999. On how the Colorado River affected the hydrography of the Upper Gulf of California. *Continental Shelf Research* 19, 1545–1560.
- Lavín, M.F., Marinone, S.G., 2003. An overview of the Physical Oceanography of the Gulf of California. In: Velasco-Fuentes, O.U., Sheinbaum, J., Ochoa de la Torre, J.L. (Eds.), *Nonlinear Processes in Geophysical Fluid Dynamics*. Kluwer Academic Publishers, Dordrecht, Netherlands, pp. 173–204.
- Lopez-Calderon, J., Martinez, A., Gonzalez-Silvera, A., Santamaria-del Angel, E., Millan-Núñez, R., 2008. Mesoscale eddies and wind variability in the northern Gulf of California. *Journal of Geophysical Research* 113, C10001. doi:10.1029/2007JC004630.
- McCune, B., Grace, J.B., 2002. *Analysis of Ecological Communities*. MjM Software Design, Gleneden Beach, Oregon.
- Moser, H.G., 1996. The early stages of the fishes in the California Current region. *California Cooperative Oceanic Fisheries Investigation Atlas No. 33*. Allen Press, Inc., Lawrence, Kansas.
- Moser, H.G., Ahlstrom, E.H., Kramer, D., Stevens, E.G. 1974. Distribution and abundance of fish eggs and larvae in the Gulf of California. *California Cooperative Oceanic Fisheries Investigation Report* 17, pp.112–128.
- Nowlis, J.S., Friedlander, A., 2005. Marine Reserve function and design for fisheries management. In: Norse, E.A., Crowder, L.B. (Eds.), *Marine Conservation Biology: The Science of Maintaining the Sea's Biodiversity*. Island Press, Washington, DC, USA.
- Pollnac, R.B., Christie, P., Cinner, J., Dalton, T., Daw, T.M., Forrester, G.E., Graham, N.A.J., McClanahan, T.R., 2010. Marine reserves as linked social-ecological systems. *Proceedings of the National Academy of Sciences*.
- Peguero-Icaza, M., Sánchez-Velasco, L., Lavín, M.F., Marinone, S.G., Beier, E., 2011. Seasonal changes in connectivity routes among larval fish assemblages in a semi-enclosed sea (Gulf of California). *Journal of Plankton Research* 33 (3), 517–533.
- Rodríguez, C., Flessa, K., Dettman, D., 2001. Effects of upstream diversion of Colorado River water on the estuarine valve Mollusc *Mulinia coloradoensis*. *Conservation Biology* 15 (1), 249–258.
- Rojas-Bracho, L., Reeves, R., Jaramillo-Legorreta, A., 2006. Conservation of the vaquita *Phocoena sinus*. *Mammal Review* 36 (3), 179–216.
- Rowell, K., Flessa, K., Dettman, D., Roman, M., 2005. The importance of Colorado River flow to nursery habitats of the Gulf corvina (*Cynoscion othonopterus*). *Canadian Journal of Fisheries and Aquatic Sciences* 62 (12), 2874–2885.
- Rowell, K., Flessa, K., Dettman, D., Roman, M., Gerber, L., Findley, L., 2008. Diverting the Colorado River leads to a dramatic life history shift in an endangered marine fish. *Biological Conservation* 131, 1138–1148.
- Sánchez-Velasco, L., Lavín, M.F., Peguero-Icaza, M., León-Chávez, C.A., Contreras-Catala, F., Marinone, S.G., Gutiérrez-Palacios, I.V., Godínez, V.M., 2009. Seasonal changes in larval fish assemblages in a semi-enclosed sea (Gulf of California). *Continental Shelf Research* 29, 1697–1710.
- Sánchez-Velasco, L., Jiménez-Rosenberg, S.P.A., Sánchez-Uvera, A., Lavín, M.F., Pacheco-Chávez, M., del, R., 2011. Fish larvae from the Upper Gulf of California: Cruise GOLCA-0806 (June 2–17, 2008). Informe Técnico 100281. Departamento de Oceanografía Física, CICESE, Ensenada, Mexico.
- Smith, P.E., Richardson, S.L., 1979. Técnicas modelo para la prospección de huevos y larvas de peces pelágicos. Documentos Técnicos de Pesca Núm. 175. FAO.
- Sokal, R.R., Rohlf, F.J. 1985. *Biometry*. Glume Barcelona, Spain.
- Sokal, R.R., Sneath, P.H.A., 1963. *Principles of Numerical Taxonomy*. Freeman.
- Ter Braak, C.J.F., 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67 (5), 60–71.