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Research Article

Fish Larvae Response to Biophysical Changes in the Gulf of California, Mexico (Winter-Summer)

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We analyzed the response of fish larvae assemblages to environmental variables and to physical macro- and mesoscale processes in the Gulf of California, during four oceanographic cruises (winter and summer 2005 and 2007). Physical data of the water column obtained through CTD casts, sea surface temperature, and chlorophyll *a* satellite imagery were used to detect mesoscale structures. Zooplankton samples were collected with standard Bongo net tows. Fish larvae assemblages responded to latitudinal and coastal-ocean gradients, related to inflow of water to the gulf, and to biological production. The 19°C and 21°C isotherms during winter, and 29°C and 31°C during summer, limited the distribution of fish larvae at the macroscale. Between types of eddy, the cyclonic (January) registered high abundance, species richness, and zooplankton volume compared to the other anticyclonic (March) and cyclonic (September). Thermal fronts (Big Islands) of January and July affected the species distribution establishing strong differences between sides. At the mesoscale, eddy and fronts coincided with the isotherms mentioned previously, playing an important role in emphasizing the differences among species assemblages. The multivariate analysis indicated that larvae abundance was highly correlated with temperature and salinity and with chlorophyll *a* and zooplankton volume during winter and summer, respectively.

1. Introduction

The biological-physical interactions in the oceans play an important role in determining patterns of horizontal distributions of the plankton communities [1], and these interactions occur at a wide range of temporal and spatial scales [2], being the mesoscale processes such as fronts, eddy, and upwelling, the most determinant factors in the spatial distribution and structure of the zooplankton communities on basin and local scales [3]. Mesoscale oceanographic structures such as eddy and fronts can work as mechanisms of retention and concentration of fish larvae [4–11], and upwelling filaments, including eddy, may work as mechanisms of dispersion [12–17].

The Gulf of California is a semienclosed dynamic sea where strong changes in temperature, salinity, and currents [18] are related to the seasonal flux of the Gulf of California and to tropical surface water masses which provide a unique environment where the southern tropical, subtropical, and northern temperate marine biota develops [19, 20]. The northern region has an anticyclonic circulation most of the year, while in June and September it reverses to a cyclonic eddy [21]. Strong winter upwelling is present in the continental coast, while during the summer it is weak at the peninsular coast [18]. Three to five alternated eddy and jet streams [22, 23] have been registered from south of the Big Islands to the south o the gulf with a markedly seasonal component. All these dynamic features may promote a wide diversity of responses of the fish larvae community to the environment.

It has been shown that the ichthyofauna distribution in the Gulf of California responds to a latitudinal gradient: (a) temperate species are more abundant to the north, (b) tropical affinity species are more abundant to the south, and

(c) an apparent mixture of temperate-tropical fauna has been found in the central zone. Besides these, the abundance is directly related to the thermal gradient [24] in a portion of the Gulf of California. In the same area, several spatially limited studies had shown that oceanographic processes such as fronts, filaments, jets, upwelling, and cyclonic eddy determine local differential ontogenetic distribution patterns in small pelagic fishes [25, 26], maintain differentiated horizontal patterns of the fish larvae assemblages [27–30], and promote retention or eggs and larval drift [24].

In spite of the useful information generated in these previous works, gaps still remain in the knowledge of the effects of oceanographic mesoscale structures on larval fish communities in a broad spatial and seasonal scale. These gaps lead to several questions that remain unsolved such as (a) are the mesoscale structures relevant in the formation of regional patterns of the fish larvae assemblages? Or (b) are the 18°C and 21°C isotherms [24] the most influential factors to explain the spatial and seasonal patterns of the fish larvae assemblages? And (c) what other large spatial gradients, besides latitudinal gradient, are evidenced in the gulf?

In this paper we study the relationship between the macro- and mesoscale oceanographic processes and fish larvae assemblages in a semi-enclosed sea with strong seasonal variability using remotely sensed data sets, field oceanographic measurements, and fish larvae species abundance in the entire area of the Gulf of California, under the two most contrasting seasonal conditions (winter and summer).

2. Methods

Environmental and zooplankton data were collected during four oceanographic cruises made in the winter and summer seasons in the Gulf of California, Mexico. Winter cruises were conducted from February 25 to March 12, 2005 (CGC0503) and from January 13 to 27, 2007 (GOLCA0701), while summer cruises were conducted from September 7 to 19, 2005 (CGC0509) and from July 20 to August 2, 2007 (GOLCA0707) (Figure 1).

Daily high resolution satellite images of sea surface temperature (SST) and chlorophyll *a* were obtained from MODIS on Aqua (http://oceancolor.gsfc.nasa.gov/), level 2 (1 Km resolution). The level 2 satellite imagery was only georeferenced but not orthorectified. To transform all the images into a Cartesian plane projection, the GRI program (http://gri.sourceforge.net/) was used. Once transformed, the resulting images were averaged for the corresponding days of each survey and used to detect mesoscale processes. To obtain a representative value, the chlorophyll *a* concentration for each sampling station was calculated from the satellite images using the average value of the following pixels: one corresponding to the location of each station, plus left, right, up, and down respect to the former station. Weekly satellite images composites prior to and after the sampling dates (not showed here) were also generated and analyzed to register the time lag of the eddy observed.

A total of 160 CTD casts (77 in CGC0503, 17 in GOLCA0701, 49 in CGC0509, and 17 in GOLCA0707) were made using calibrated SBE 19, Sea-Bird Electronics and a Mark III, General Oceanics. These data were used to construct temperature profiles from longitudinal transects of the cruises, to calculate the maximum stability depth [31] and to identify water types according to Torres-Orozco [32].

A total of 143 zooplankton samples were collected (39 samples in CGC0503, 26 in GOLCA0701, 43 in CGC0509, and 35 in GOLCA0707). Except for those from CGC0509, all zooplankton samples were obtained with oblique tows using Bongo nets with 505 μm mesh (0.6 m diameter) equipped with a digital flow meter. Oblique tows were made to a maximum depth of 200 m [33]. During CGC0509, samples were collected with a simple conical CalCOFI net at surface (0.6 m diameter, 505 μm mesh). All samples were fixed in 96% ethyl alcohol. Zooplankton volumes were obtained using the displacement volume method [34]. The ichthyoplankton fraction was sorted, and fish larvae were counted and identified to species level [35–40]. Abundance was standardized to number of larvae 10 m^{-2} [33], and species richness was estimated as number of species. Since zooplankton samples during the September survey were taken using surface tows, we only used these data to analyze the relationship of the locations of mesoscale structure. Comparative zooplankton and fish larvae abundance analyses were done only among those surveys in which zooplankton samples were taken with oblique tows.

Canonical ordination methods were used to explore the relationship between the distribution and abundance of fish larvae and the environmental variables for each survey. The larval fish abundance was transformed to the fourth root, and seven environmental variables were used as independent variables: temperature (T10), salinity (S10), density (D10), water type (WM10), maximum stability depth (MSD), sea surface chlorophyll *a* concentration (CHL), and zooplankton volumes (ZV); the first four were obtained from 10 m depth. To select the most robust canonical analysis, a detrended canonical correspondence analysis (DCA) was performed to obtain the length of the environmental gradients [41]. In DCA, D10 had high orthogonal values so it was not used in further analysis. The species-environment relationship was explored using a redundancy analysis (RDA) [42]. In both statistical analyses, scaling was focused on the interspecies correlations. Species scores were divided by their corresponding standard deviation and centered by species. Further selection of environmental variables was performed automatically and statistical significance was calculated using unrestricted Monte Carlo permutation tests. Only those variables that significantly explained the species variability were included in the final analysis; therefore, water mass variable was also eliminated from the results. Biplots were used for the representation of the biological variables ordination in the environmental multidimensional space [42]. All the statistical multivariate analyses were done with the Canonical Community Ordination (CANOCO) for Windows software ver. 4.56. The naming convention for the groups obtained was to use the first two letters of the month and the number of the group analyzed, for example, Group1 of January = JaG1. A one way analysis of variance (ANOVA) test for significant differences between ZV during each cruise was performed using the STATISTICA V.8 software. CHL and ZV were used

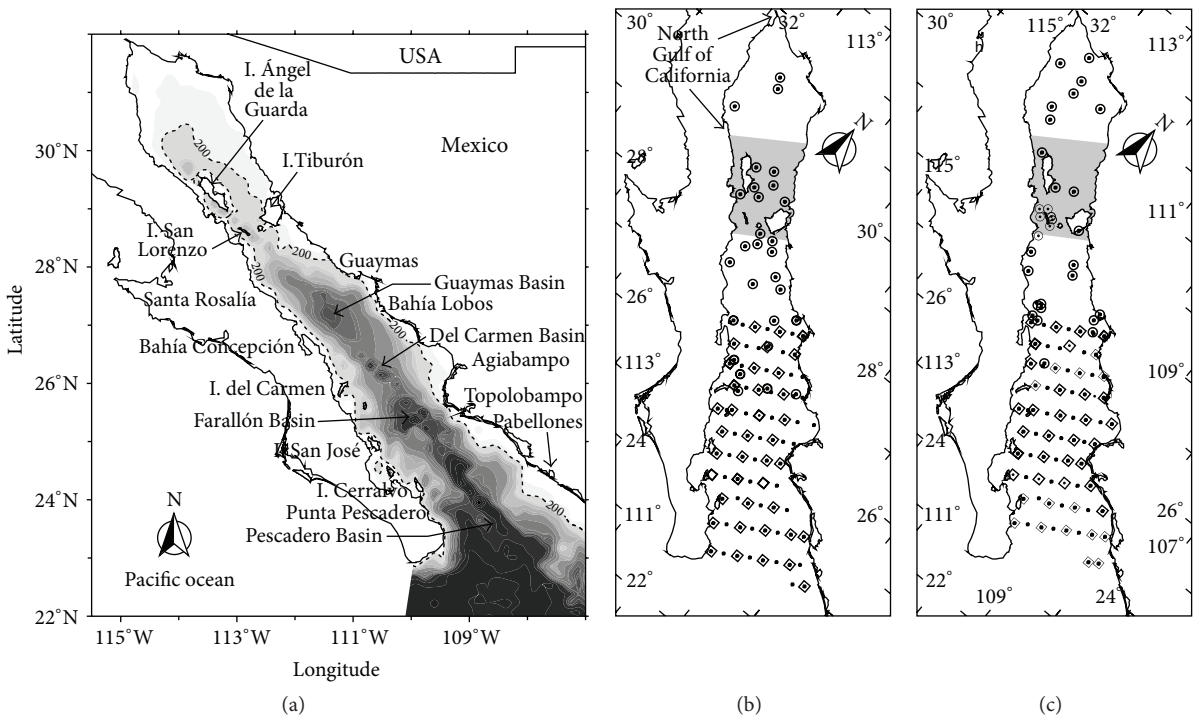

Figure 1: Study area and sampling grid stations in the Gulf of California, Mexico. (a) Localities, some basins, and 200 m isobath. Grid stations during (b) winter and (c) summer. Shaded area indicates the Big Islands Archipelago region. Open circles: GOLCA0701 and GOLCA0707 cruises. Open squares: CGC0503 and CGC0509 cruises. Solid circles: CTD casts.

as gross indicators for the biological production and the amount of available food in the environment.

3. Results

3.1. Environmental Conditions. In both winter months (January 2007, Figure 2(a), and March 2005, Figure 3(a)), a north-south gradient of SST observed in satellite images was found in the Gulf of California (mean SST = 16.5°C in January and 20.6°C in March). The 21°C isotherm, used as the limit of recurrent groups on ichthyoplankton [24], and related to the entrance of warm water to the gulf, was registered south of Isla Cerralvo in January, while in March, its position was far north from Bahía Concepción to Topolobampo. During the summer months, an east-west gradient of SST with low values was recorded at the peninsular coast and high values at the continental coast. During July, mean SST was 27.2°C, while during September it was 30.4°C (Figures 4(a) and 5(a)).

The MSD was deeper during the winter months than in the summer when it was very shallow along the gulf (Table 1). During January, a shallow MSD at the continental coast progressively deepened toward the peninsular coast reaching 180 m depth north of Santa Rosalía (Figure 2(b)). During March, MSD was relatively shallow in both coasts and deeper at the most oceanic area. The maximum depth (150 m) was recorded northeast of Isla San José (Figure 3(b)). During July, MSD was shallow at the peninsular coast (Figure 4(b)), and deeper northeast of Isla Tiburón (70 m). In September, MSD was the shallowest of the analyzed cruises reaching 42 m depth south of Bahía Lobos and Isla San José (Figure 5(b)).

3.2. Sea Surface Chlorophyll a. During winter cruises, CHL showed a latitudinal gradient with higher concentrations to the north and lower to the south (Figures 2(d) and 3(d)). In all cruises, high CHL values (>1.0 mg m^{-3}) were recorded in the coastal zone of the gulf, particularly at the continental coast and at the Big Islands region. CHL concentration was higher in the winter than in the summer (mean = 1.147 mg m^{-3} and 0.786 mg m^{-3}, Table 1). During January, high CHL values were distributed from Isla Tiburón to Pabellones in the continental coast (Figure 2(d)), while during March high CHL values were observed covering a wider area along the coasts as well as practically in all the northern gulf's area (Figure 3(d)). During July and September, CHL concentrations were low (<0.2 mg m^{-3}) in almost all the gulf (Figures 4(c) and 5(d)).

3.3. Zooplankton Volumes. Low values of ZV (<200 mL 1000 m^{-3}) were observed in a large area of the gulf in all the oceanographic cruises, with some isolated cores of high ZV (>500 mL 1000 m^{-3}). For those samples taken with oblique trawls, no significant differences in ZV were recorded in both seasons ($F_{7.240} = 10.3$, $P < 0.001$), being slightly higher in the winter (197 mL 1000 m^{-3}) than in the summer (167 mL 1000 m^{-3}). In January, high ZV were found south of Isla Tiburón (841 mL 1000 m^{-3}) and medium ZV (200–500 mL 1000 m^{-3}) in two cores southwest of Guaymas and north of Santa Rosalía (Figure 2(e)). During March, high ZV (729 mL 1000 m^{-3}) were registered southeast of Isla del Carmen and at the continental side of the gulf (Figure 3(e)). In July, high ZV (527 mL 1000 m^{-3}) were found north of Bahía Concepción,

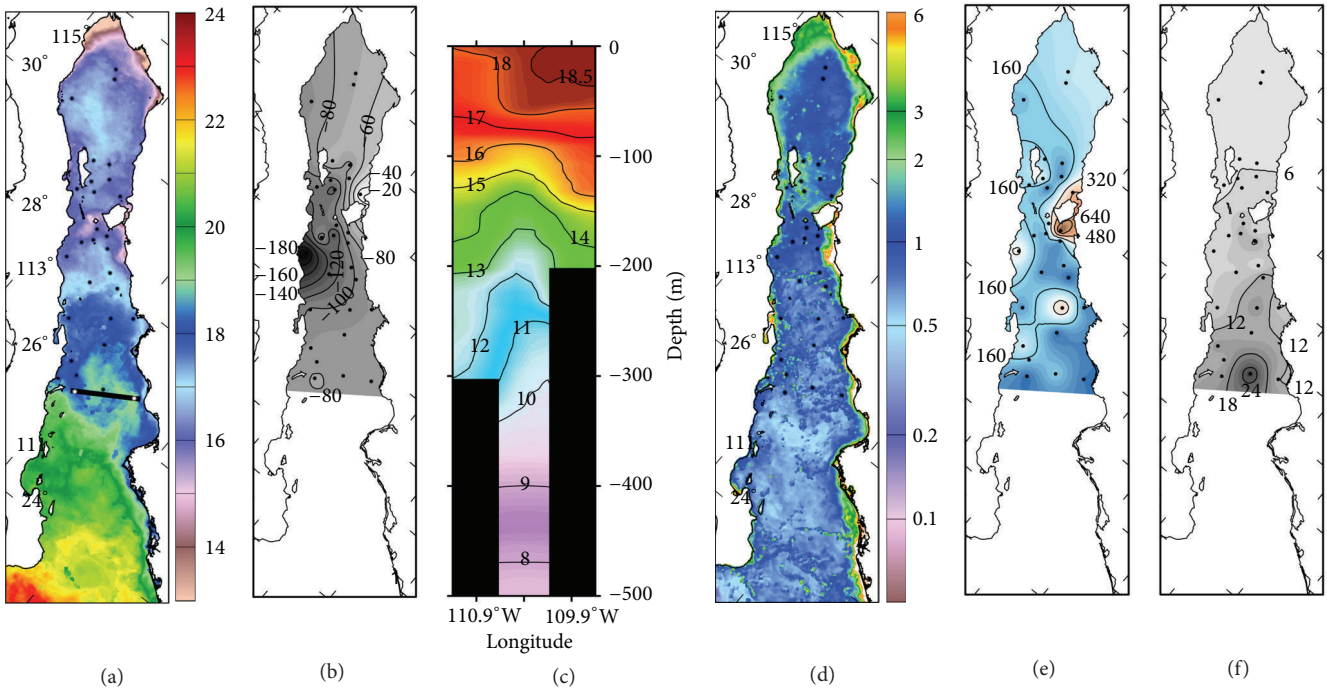

Figure 2: Biophysical characteristics during January. Composite of (a) SST (°C) and (d) CHL (mg m^{-3}) satellite images of the Gulf of California. Black line in (a) indicates transect analyzed for water column profile. (c) Temperature profile (°C). Distribution of (b) maximum stability depth (MSD), (e) zooplankton volumes, and (f) species richness.

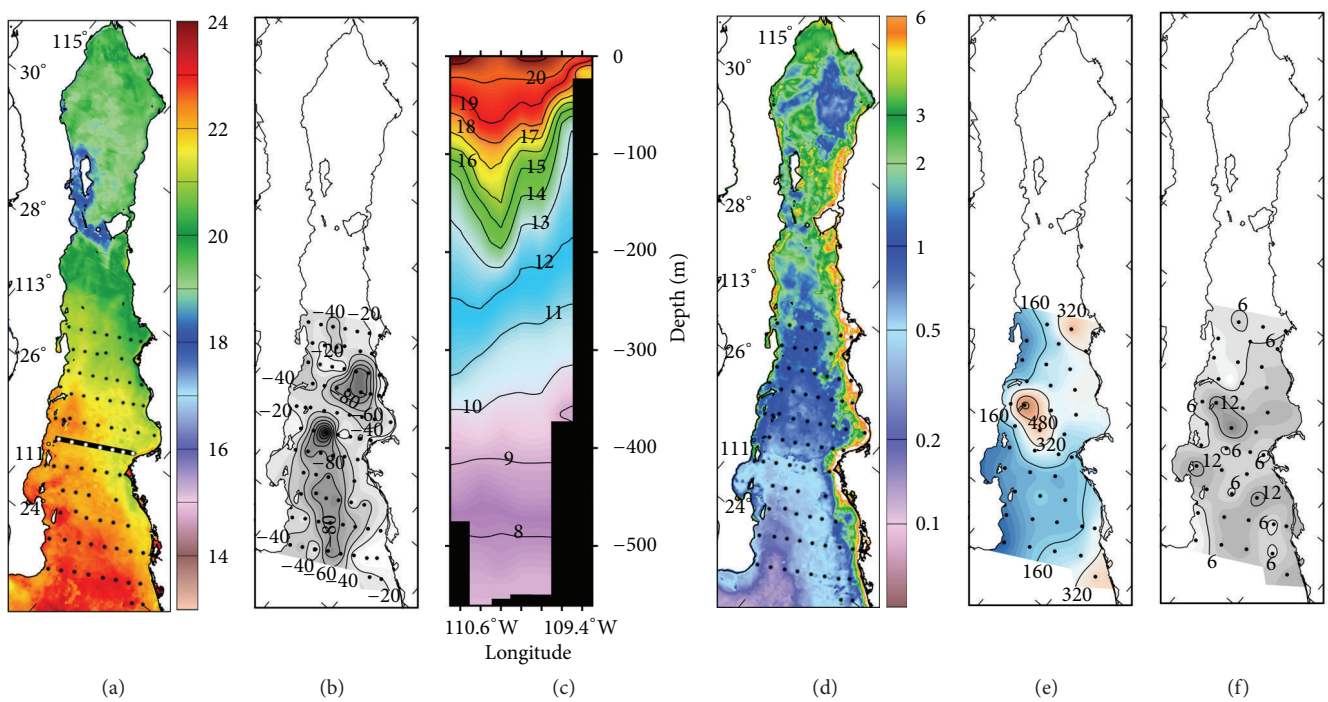

Figure 3: Biophysical characteristics during March. Composite of (a) SST (°C) and (d) CHL (mg m^{-3}) satellite images of the Gulf of California. Black line in (a) indicates transect analyzed for water column profile. (c) Temperature profile (°C). Distribution of (b) maximum stability depth (MSD), (e) zooplankton volumes, and (f) species richness.

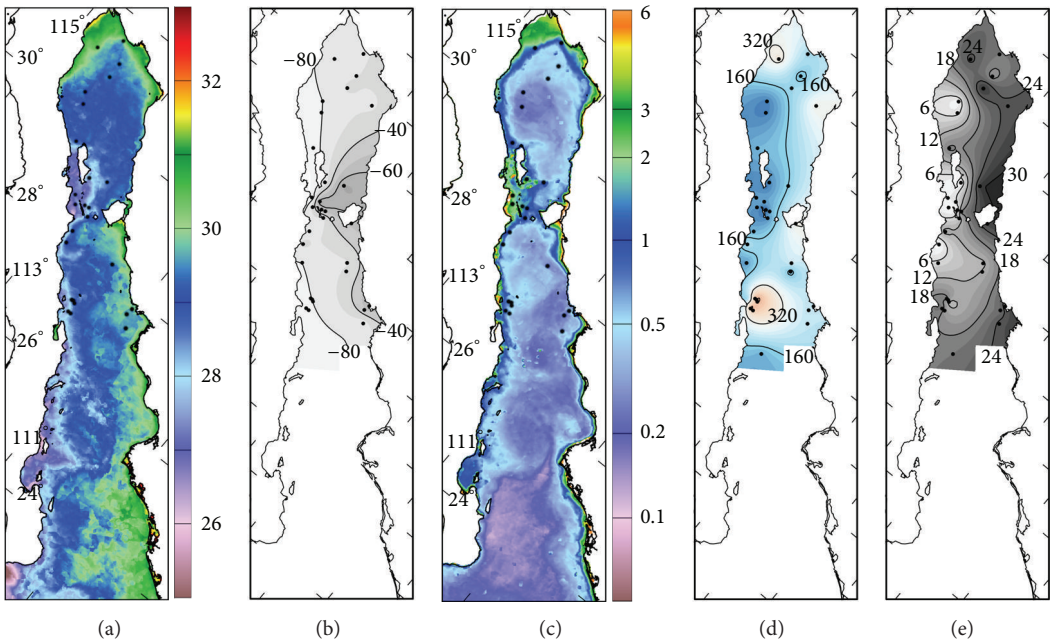

Figure 4: Biophysical characteristics during July. Composite of (a) SST (°C) and (c) CHL (mg m^{-3}) satellite images of the Gulf of California. Distribution of (b) maximum stability depth (MSD), (d) zooplankton volumes, and (e) species richness.

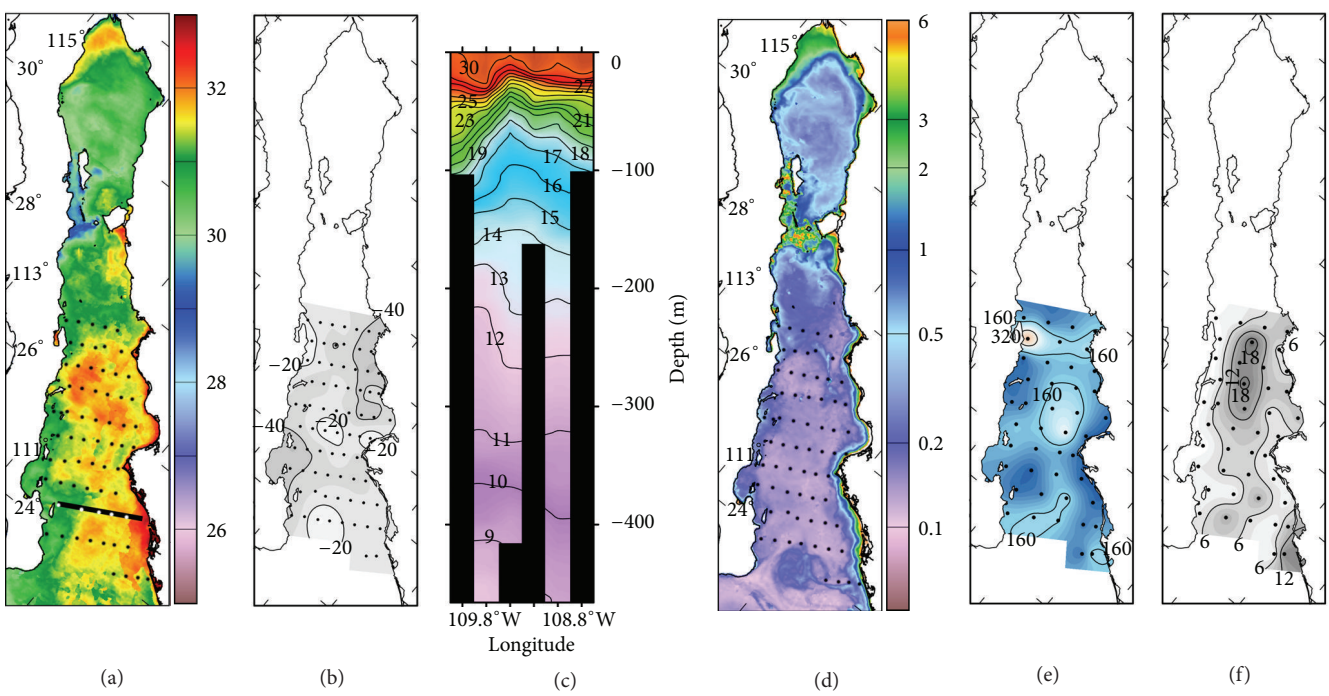

Figure 5: Biophysical characteristics during September. Composite of (a) SST (°C) and (d) CHL (mg m^{-3}) satellite images of the Gulf of California. Black line in (a) indicates transect analyzed for water column profile. (c) Temperature profile (°C). Distribution of (b) maximum stability depth (MSD), (e) zooplankton volumes, and (f) species richness.

with medium ZV associated to the continental coast southeast of Isla Tiburón and at the north gulf (Figure 4(d)). During September, only two small cores of medium ZV were registered, one in front of Bahía Concepción and the other southwest of Agiabampo (Figure 5(e)).

3.4. Oceanographic Processes. During January, a frontal thermal zone was observed south of San Lorenzo and Tiburón Islands with 15°C to 16°C, also the curling of a warm water filament located in the oceanic area off Isla del Carmen suggested the presence of a cyclonic eddy about 127 km in

Table 1: Larval abundance by faunistic affinity and habitat registered in the Gulf of California, Mexico (winter and summer of 2005 and 2007). Values are given as the average of winter (January 2007 and March 2005) and summer (July 2007 and September 2005) cruises.

	Winter	Summer
Larval abundance		
Average per sample (larvae 10 m^{-2})	1064	4273
Faunistic affinity (%)		
Temperate	7.5	1.8
Tropical	41.8	55.5
Subtropical	49.2	40
Wide distribution	1.5	2.7
Habitat (%)		
Mesopelagic	17.1	6.1
Coastal-pelagic	12.2	20.9
Oceanic-pelagic	2.4	6.8
Shallow-demersal	56.1	60.1
Deep-demersal	6.1	2.7
Bathypelagic	6.1	3.4

diameter (Figure 2(a)). The temperature profile along the transect in Figure 2(a) showed presence of water >18°C in the first 50 m in the continental side and at the center, with lower values in the peninsular side (Figure 2(c)), followed by a relatively homogeneous layer of cold water (17°C to 15°C) down to about 125 m. The isotherms at the center of the transect showed a dome shape with the 16°C isotherm at 90 m, while it was at 100 m in the west and at 140 m in the east. The rising of the isotherms was observed from 90 m to 300 m in depth (Figure 2(c)). In March, the SST satellite image showed also a front from northwest of Isla Ángel de la Guarda to south of Isla Tiburón (Figure 3(a)), and an anticyclonic eddy northeast Isla San José was observed in the CHL satellite image of this month (Figure 3(d)). The temperature profile along the transect in Figure 3(a) showed a warmer water column than in January, with 21.2°C at surface, and 18°C at 90 m depth. A shallow 16°C isotherm (90 m depth in the west and 50 m in the east) was found in this month, and isotherms at the center of the transect were strongly valley shaped between 70 m to 215 m depth (Figure 3(c)). Although the sampling grid station during July did not allow us to generate longitudinal transects profiles, both satellite images for this month showed a front close to the peninsular coast from northwest of Isla Ángel de la Guarda to the south of Isla San Lorenzo. The presence of three eddies, one located in front of Santa Rosalía, the second southeast of Bahía Concepción, and the third northeast of Isla San José were also observed in both images (Figures 4(a) and 4(c)). During September, satellite images did not show mesoscale features in the region where the zooplankton sampling was done (Bahía Concepción to Punta Pescadero). However, the temperature profile (Figure 5(c)) along the transect in Figure 5(a) showed a strongly stratified water column with the highest temperatures (30.7°C) and shallower thermocline at the continental side, dome shaped isotherms at the center of the transect (cyclonic eddy), and a more spread out isotherm at the peninsular side. The dome shaped isotherms showed that the 16°C isotherm deepened at about 120 m in both coasts, while it reached 95 m at the center of the dome. The rising of the isotherms can be observed at 150 m depth to the surface (Figure 5(c)).

3.5. Fish Larvae Composition and Abundance. A total of 73 families were identified from the four cruises analyzed, with the highest species richness during the summer. During the winter, 41 families, 70 genera, and 98 species were registered, while in the summer, 60 families, 96 genera, and 183 species were identified. See also Supplementary Material available online at http://dx.doi.org/10.1155/2013/176760 for details of species abundance by cruise, by season, and faunistic affinity and habitat.

The main seasonal differences in the larval fish community besides species richness (Table 1) were related to (a) lower total fish larvae abundance during the winter (average per sample 1064 larvae 10 m^{-2}) than in the summer (average per sample 4273 larvae 10 m^{-2}) in samples taken with oblique trawls, (b) about 4.2 times more temperate species in the winter, (c) lower relative abundance of shallow-demersal, coastal-pelagic, and oceanic-pelagic species (56.1%, 12.2%, and 2.4%, resp.) and more abundant mesopelagic species (17.1%) in the winter than in the summer (60.1%, 20.9%, 6.8%, and 6.1% resp.) and (d) a change in the community structure which included eight species: *E. mordax*, *Vinciguerria lucetia*, *Diogenichthys laternatus*, *Leuroglossus stilbius*, *S. sagax*, *Benthosema panamense*, *Citharichthys fragilis*, and *Scomber japonicus* during the winter and 13 species: *Cetengraulis mysticetus*, *Opisthonema libertate*, *Benthosema panamense*, *Triphoturus mexicanus*, Gobiidae sp. 3, *Oligoplites saurus*, *Auxis* sp. 2, *Scomberomorus sierra*, *V. lucetia*, Sciaenidae sp. 1, *Thunnus* sp. 1, *Eucinostomus dowii*, and *Balistes polylepis* during the summer, accounting for 90% of the relative abundance in each season. The species *V. lucetia* and *B. panamense* were present in both seasons; however, *V. lucetia* was more abundant in the winter while *B. panamense* in the summer.

3.6. Species Richness. Distribution patterns of the species richness showed a southward gradient during January, with low values north of the Big Islands and high richness in the south (Figure 2(f)) related to the cyclonic eddy, while species richness had no pattern during March (Figure 3(f)). During July, sampling stations near the continental coast had the highest species richness of the study with a maximum (30 species) registered in one sampling station north of Isla Tiburón (Figure 4(e)), and during September, high values were recorded only at the oceanic central and southeast gulf (Figure 5(f)). In all months, high values of species richness were coincident with high SST values.

3.7. Data Analyses. During January, the first two RDA canonical axes explained 87.9% of the total variance of the species-environment relationships (Table 2). The first RDA axis was explained by T10 and CHL with negative and positive correlation, respectively, while the second axis was associated with positive correlation values for S10 and negative for MSD

Table 2: Summary of the redundancy analysis (RDA) applied to fish larvae abundance and environmental variables in each cruise.

	January		March		July		September	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Var S-E	67.4	87.9	69.1	91.2	44.3	78.3	53.8	85.9
T10	**−0.689**	0.6294	**0.914**	−0.2303	0.5118	**−0.5589**	0.7056	0.178
S10	0.5016	**0.7568**	−0.4443	0.0594	−0.0723	−0.2364	0.5531	0.0403
CHL	**0.5506**	0.4591	**−0.4807**	**−0.3429**	**−0.2869**	−0.1223	**0.7882**	−0.0744
ZV	0.0871	0.0607	−0.1282	**0.867**	**0.6975**	**0.7093**	−0.2496	**0.9036**
MSD	−0.1975	**−0.7277**	0.3368	0.5255	−0.084	−0.2908	**−0.7622**	−0.0677

Bold numbers are the highest correlation values for each axis. Var S-E: cumulative percentage variance of species-environment relation; T10: temperature 10 m depth; S10: salinity 10 m depth; CHL: sea surface chlorophyll *a* concentration; ZV: zooplankton volumes; MSD: maximum stability depth.

(Table 2). The RDA biplot showed three sampling stations groups in three different environments. The first group (JaG1) was related to high CHL and S10 values (Figure 6(a)) and was located from the Big Islands to the north (Figure 6(b)). Shallow and deep-demersal species of temperate and tropical affinity such as *Prionotus ruscarius*, *Hippoglossina stomata*, and *Merlucius productus* were included in this group (Figure 6(c)). A second group of stations (JaG2) shared an environment where the deepest values of MSD were found (Figure 6(a)), located between the southern part of Isla Tiburón to Bahía Concepción (Figure 6(b)). In this group, we found contrasting distribution among species. Coastal-pelagic (*E. mordax*) and shallow-demersal species (*Citharichthys fragilis* and *Sebastes* sp.) were distributed at the frontal zone near Ángel de la Guarda and San Lorenzo Islands, while species of deep habitats such as mesopelagic (*Triphoturus mexicanus* and *Diogenichtys laternatus*), deep-demersal tropical (*Argentina sialis*), and bathypelagic temperate species (*Leuroglossus stilbius*), as well as oceanic-pelagic (*Trachurus symmetricus*), were registered south, out of the frontal area (Figure 6(c)). In these two groups, fish larvae abundance values were from medium to high (100–999 larvae $10\,m^{-2}$ and 1000–9999 larvae $10\,m^{-2}$, resp.), particularly off Isla Ángel de la Guarda and south of Isla Tiburón. The third group (JaG3) was related to the highest T10 values in this cruise (Figure 6(a)), located from Guaymas to the south (Figure 6(b)). Almost all the coastal-pelagic species (*Bregmaceros bathymaster*, *Etrumeus teres*, *Sardinops sagax*, and *Scomber japonicus*) except temperate *E. mordax*, the most abundant mesopelagic (*Benthosema panamense* and *Vinciguerria lucetia*), and bathypelagic (*Stomias atriventer*) species of tropical and subtropical affinity were found in this group (Figure 6(c)). The maximum abundance in this southern group found in station 72 was related to the maximum species richness (Figure 2(f)) and to the center of the mesoscale eddy observed in the SST satellite image for this month (Figure 2(a)).

In March, the first two axes of the RDA explained 91.2% of the variance being T10 and CHL in the first axis, and ZV in the second, the best correlated variables (Table 2). In this month, RDA biplot showed a first group (MaG1) which included sampling stations where T10 had lower values but higher CHL, and higher S10 than in the second group, located from Bahía Concepción to the northern part of Topolobampo (Figures 7(a) and 7(b)). Fish larvae abundance was medium and homogeneous along the area, with a maximum of 842 larvae $10\,m^{-2}$ by station. The second group (MaG2) distributed from Isla San José to the south at the highest T10. In this MaG2, station T3 was located at the center of the cyclonic eddy where highest MSD, ZV, fish larvae abundance (1854 larvae $10\,m^{-2}$), and species richness were registered in this month. The RDA biplot of species-environment showed three species groups, the first related with high S10 and low T10 values, and relatively high ZV, and included two temperate (*E. mordax* and *L. stilbius*) and one subtropical species (*S. japonicus*). The second group gathered most of the species with different affinity and habitat (Gobiidae spp., *Bregmaceros bathymaster*, *Chilara taylori*, and *Diplophos taenia*) related with the highest T10, while the third group included the most abundant tropical mesopelagic (*B. panamense*, *V. lucetia*, *D. laternatus*, and *Hygophum atratum*) and coastal-pelagic species (*S. sagax*) at high T10, and MSD values (Figure 7(c)). This last species were also found at the center of the eddy.

During the summer, the first two RDA canonical axes explained 78.3% in July and 85.9% in September of the total variance of the species-environment relationships (Table 2). In July, ZV and T10 were the best correlated variables in both axes (Table 2). RDA biplot of stations environment showed three groups of stations, JuG1 sharing the coldest and saltiest environment with high CHL values but low ZV (Figure 8(a)), located at the peninsular coast from the northwestern part of Isla Ángel de la Guarda to the southern part of Isla San Lorenzo (Figure 8(b)) in the frontal area observed at the satellite images for this month. In this group, tropical mesopelagic species *B. panamense* and tropical shallow-demersal species *Scorpaenodes xyris*, *Lepophidium negropinna*, and *Abudefduf troschelii* were found (Figure 8(c)). Five stations formed the second group (JuG2) and were related to high ZV (Figure 8(a)) north of Bahía Concepción (Figure 8(b)) with tropical and subtropical mesopelagic (*T. mexicanus*, *V. lucetia*), coastal-pelagic (*O. libertate*, *Caranx caballus*), oceanic-pelagic (*Thunnus* sp. 1), and shallow-demersal species (*Synodus lucioceps*, *Stegastes rectifraenum*) (Figure 8(c)). The third group was related primarily to the highest T10 (Figure 8(a)) observed at the continental coast and northern gulf (Figure 8(b)) and included most of the tropical, subtropical, and temperate affinity species, with coastal-pelagic (*Cetengraulis mysticetus*, *Scomberomorus sierra*, *O. saurus*, and *B. bathymaster*), oceanic-pelagic (*Auxis* sp. 2), and shallow-demersal

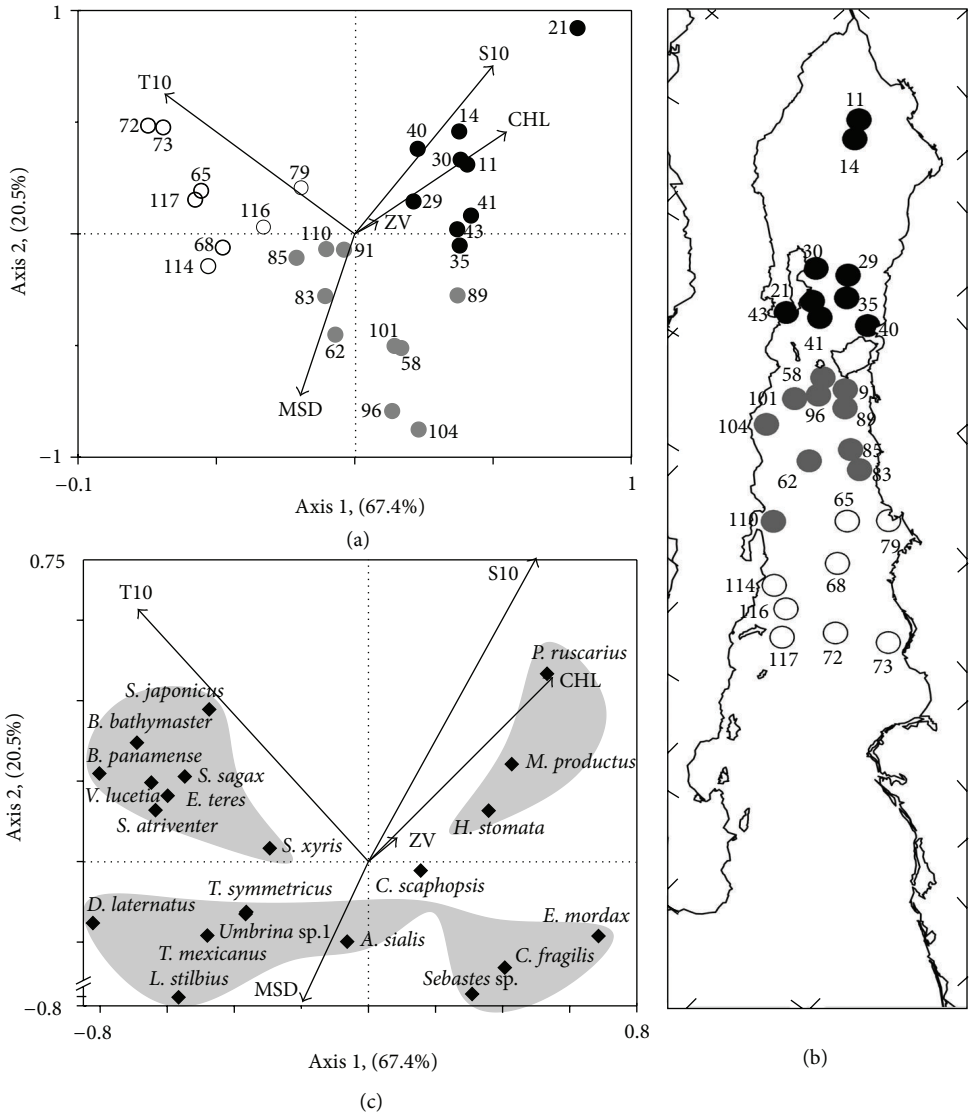

Figure 6: Classification and ordination analysis: January. (a) RDA biplot of sampling stations environment, black circles = JaG1; grey circles = JaG2; open circles = JaG3. (b) Distribution of stations groups resulting from RDA. (c) RDA biplot species environment.

species (*Eucinostomus dowii*, *Balistes polylepis*, *Symphurus williamsi*, and *Scorpaena guttata*) (Figure 8(c)). Fish larvae abundance in the three groups was high, but at the northernmost gulf in the third group, we registered the highest fish larvae abundance in this study (59751 larvae 10 m^{-2} and 16818 larvae 10 m^{-2}).

The canonical axes for September's RDA had the highest positive correlation to CHL and negative to MSD, while the second axis had a high correlation to ZV (Table 2). In the RDA stations-environment biplot, the first group (SeG1) represented mainly coastal stations of both sides of the gulf (Figure 9(b)) with very low fish larvae abundance (maximum of 46 larvae 10 m^{-2} by station) related to areas with high CHL values and shallow MSD, in a warm environment (Figure 9(a)), in which tropical species of coastal-pelagic (*Opisthonema* spp., *Anchoa* spp., *Oligoplites saurus*, and *Hirundichthys* spp.) and shallow-demersal habitat (Gerreidae spp. and Mullidae spp.) were found (Figure 9(c)). In this group, station W3 located at the center of the gulf and of the cyclonic eddy registered only 0.14 larvae 10 m^{-2} contrasting with stations at the edge of the eddy that reached from 5 to 50 times more abundance. The second group was distributed at many oceanic stations of the center of the gulf, where high ZV and medium to high MSD values were registered during this month (Figures 9(a) and 9(b)). Abundance was also low in this group (maximum of 59 larvae 10 m^{-2} by station). Here, tropical and subtropical species of oceanic-pelagic (*Auxis* spp., *Katsuwonus pelamis*, and *Cheilopogon heterurus*) and shallow-demersal habitat (*S. ovale*, *Lutjanus* spp., and *Pristigenys serrula*) and the only mesopelagic species *B. panamense* were registered (Figure 9(c)). No temperate species were found in this month.

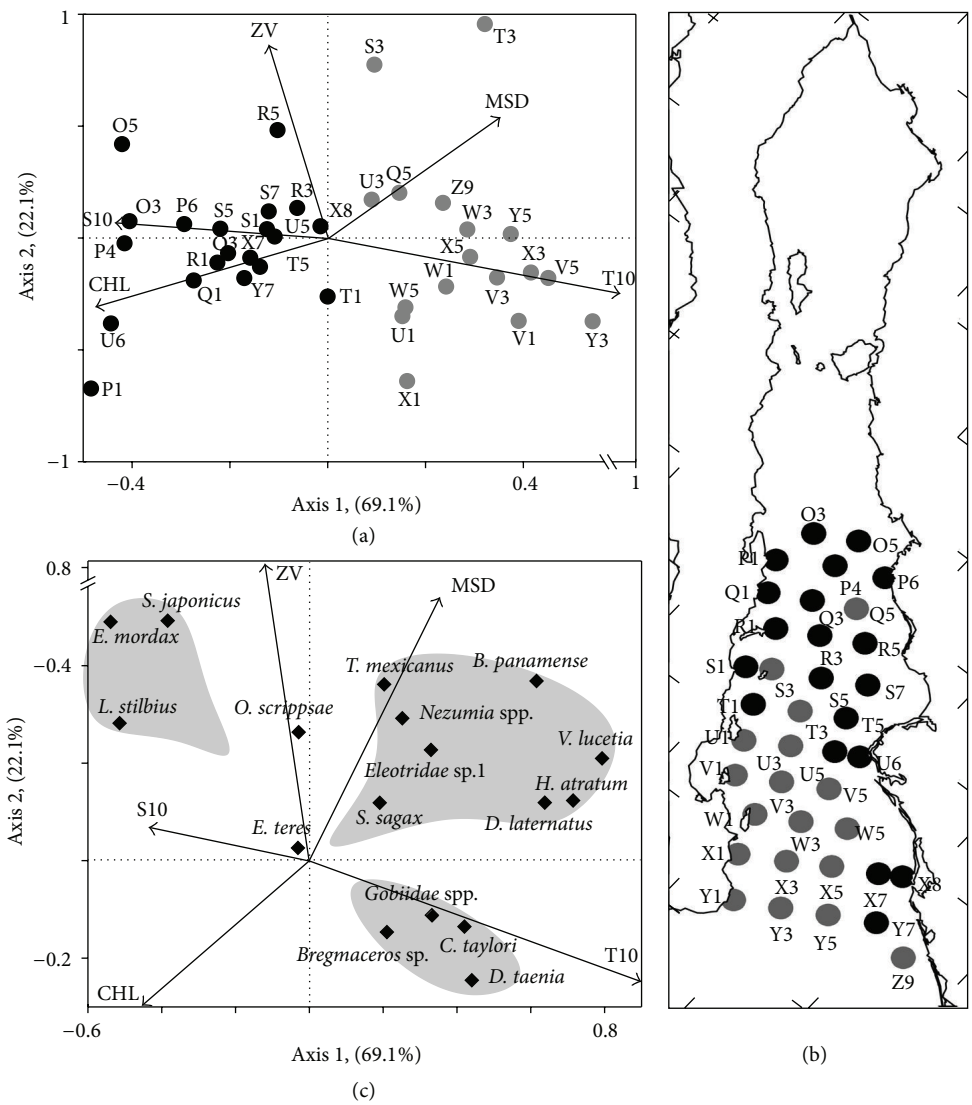

Figure 7: Classification and ordination analysis: March. (a) RDA biplot of stations environment, black circles = MaG1; grey circles = MaG2. (b) Distribution of stations groups resulting from RDA. (c) RDA biplot species environment.

4. Discussion

This is the first study that focused on the understanding of the composition, distribution, and abundance of fish larvae assemblages and their relationships with the physical environment in a macroscale analysis, which includes mesoscale processes, such as fronts and eddy structures in the Gulf of California, Mexico, covering the two most important seasons of the year.

The results of this study showed a close relationship between fish larvae abundance and environmental gradients present along the Gulf of California, particularly those of T10, S10, CHL, and ZV present during each season of the year. These relationships were also influenced by the local biophysical gradients related to the mesoscale processes such as fronts and eddy found in this area. In general terms, the responses of the ichthyoplanktonic community were observed as changes in the fish larvae assemblages promoted by north-south and coastal-ocean gradients and accumulation or dispersion effects of the eddy according to their type and stage of formation, and by strong abundance and composition differences among fish larvae assemblages separated by thermal frontal barriers.

In seasonal terms, we found differences in abundance, composition, distribution, and biogeographic affinity between winter and summer fish larvae assemblages observed in the Gulf of California. These differences were related to major seasonal changes and to interannual variability in the oceanographic conditions of the Gulf of California.

4.1. Winter Season. The winter (January and March) mean environmental conditions in the Gulf of California included the presence of a north-south SST gradient, low temperature, high S10 related to the presence of Gulf of California Water (GCW), and a deep MSD in practically all the sampling

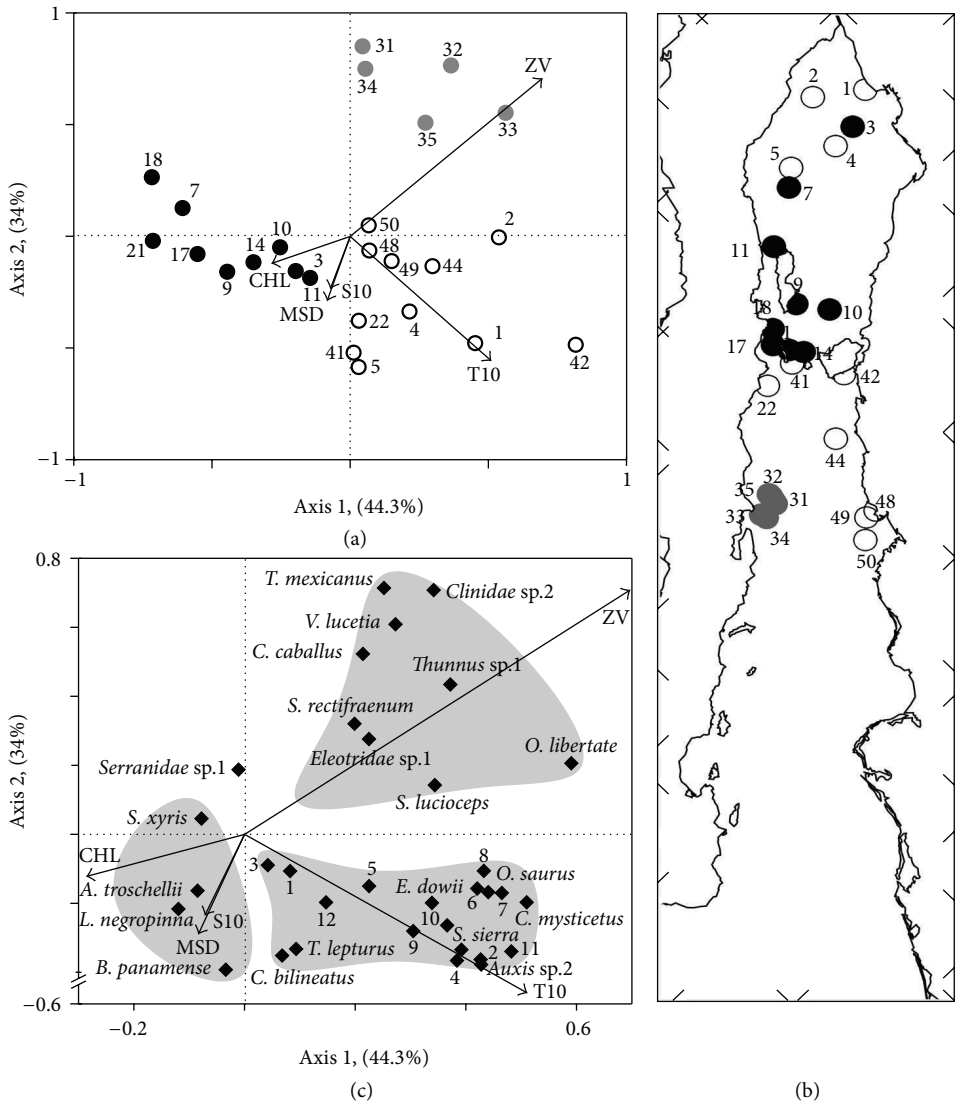

Figure 8: Classification and ordination analysis: July. (a) RDA biplot of sampling stations environment, black circles = JuG1; grey circles = JuG2; open circles = JuG3. (b) Distribution of stations groups resulting from RDA. (c) RDA biplot species environment. 1 = *Bregmaceros bathymaster*, 2 = *Balistes polylepis*, 3 = *Epinephelus* sp. 1, 4 = Gobiidae sp. 2, 5 = Gobiidae sp. 3, 6 = *Ophichthus zophochir*; 7 = Sciaenidae sp. 1, 8 = Sciaenidae sp. 2, 9 = *Scorpaena guttata*, 10 = *Syacium ovale*, 11 = *Symphurus williamsi*, 12 = Angiliforme sp. 1.

stations in agreement with winter conditions [18, 43]. In terms of biomass, CHL mean was 1.147 mg m^{-3} and high values found at the Big Islands region and at the peninsular coastal zone were both mostly related to the strong tidal mixing [44, 45] and to coastal upwelling events [46] present in this season, respectively. Also, medium to high ZV (181 mL 1000 m^{-3} and 218 mL 1000 m^{-3}) indicated a productive environment. Fish larvae assemblages in these conditions were primarily correlated to T10 and S10, but also to ZV (Table 2).

Tropical-subtropical and shallow-demersal species dominated the fish larvae composition of the Gulf of California during winter (91% and 56.1%, resp.). This dominance of tropical-subtropical species could be explained by an increased sea surface temperature related to a weak El Niño registered as positive anomalies in the multivariate ENSO index (http://www.esrl.noaa.gov/psd/enso/mei/table.html), and could be the result of more sampling efforts and a larger sampling area at the southern gulf region if compared with previous studies. A very similar species composition by biogeographic affinity was found during March 2005 by Avendaño-Ibarra et al. [47], but the mesopelagic component dominated. In contrast, Aceves-Medina et al. [20] registered 96% of total larval abundance of temperate affinity during winter season and coastal-pelagic species (63%) as the most abundant.

High relative abundance of fish larvae of small pelagic fishes (*S. sagax*, *E. mordax*, *T. symmetricus*, *S. japonicus*, and *E. teres*) registered in January could be related to the high productivity in terms of CHL and ZV that may have enhanced the reproductive activity of the adults present in the gulf

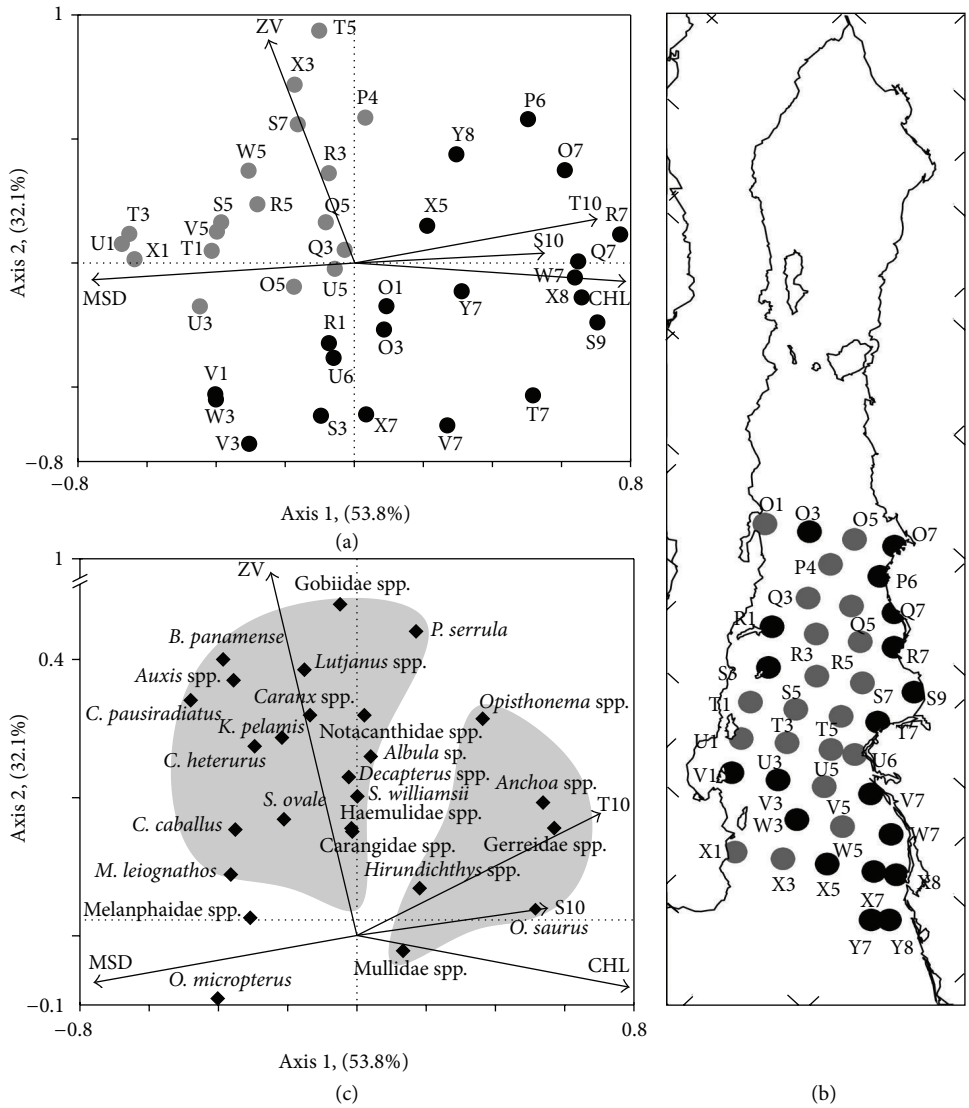

Figure 9: Classification and ordination analysis: September. (a) RDA biplot of sampling stations-environment, black circles = SeG1; grey circles = SeG2. (b) Distribution of stations groups resulting from RDA. (c) RDA biplot species-environment.

during the winter. Tidal mixing is important in the north of the Gulf of California and in the archipelago and the shelf south of Isla Tiburón that show conditions for strong internal mixing and upwelling over the sills and in the surrounding area [18, 48, 49]. These features promote the presence of lower temperatures in this area compared to those in the rest of the gulf during almost all the year. These conditions allowed us to detect fronts in this area in all the SST satellite images during our study.

In January, fish larvae of JaG1 were located to the north of the front where an intense water column mix due to strong tidal currents promoted the incorporation and availability of nutrients to the phytoplankton [48] resulting in the highest CHL concentrations of the cruise in a cold environment. Survival of Pacific hake larvae (*Merluccius productus*), an abundant component of this group, is strongly influenced by the environmental conditions (such as upwelling, advection, and water temperature) experienced during the first few months after spawning at the California Current System [50] and fed upon a wide range of prey particularly on copepod eggs, filter feeding nauplii and copepodites [51]. The enhanced productivity present in the JaG1 area is likely a base for the development of a favorable feeding area for this species inside the Gulf of California.

The JaG2 was distributed over and south of the front in this month. Thermal frontal zones have been recognized as high CHL and ZV areas [52–54]. The high abundance of filter feeding *E. mordax* larvae that characterized JaG2, suggests the presence of an important food supply in the area and also that adults of this species may be spawning at or near this frontal zone. Highest abundance of *E. mordax* and *T. symmetricus* in this region contrasts with *S. sagax* low abundance coinciding with previous reports of spatial segregation between these species [24, 25], and also differences in abundance and composition between the sides of the front line [27, 28]. Surface connectivity in the Gulf of California studied by Marinone

[55] indicates that the export of particles during January is notably large from the north to the south and that particles in the Tiburón and Angel de la Guarda Islands are retained there only 2-3 months because of the strong currents produced by bathymetric restrictions. This southward connectivity and the strong gradient found in this month may limit the degree of connectivity between the north and south sides of the front, affecting the JaG1 and JaG2 species composition (only 44% of the species were present in both regions), in spite of the large connectivity mentioned before.

In January, the cyclonic eddy had low intensity since the isotherms did not reach the surface of the water column probably indicating an early stage of eddy formation [56, 57], it was almost as wide as the gulf extension at the center of the gulf, and was closely related to the Del Carmen Basin [58]. Cyclonic eddy are related to divergence and upwelling at the centers. In these types of eddy, high concentrations of phytoplankton as well as low abundance of zooplankton [59, 60], and fish larvae [11], have been registered [61]. However, the ichthyoplankton sampling made in January allowed us to register the shape of a cold core eddy and the warm jet surrounding it, also observed in the Gulf of Alaska [62]. In this characteristic eddy, coastal surface water is segregated while the deeper water portion of eddy core maintains its physical and biological characteristics resulting in a mix of communities. The response of fish larvae to this oceanographic process resulted in JaG3 being the group with highest species richness [24] and the highest values of ZV (154 mL 1000 m^{-3}) at the center of the eddy at ~18.4°C. Also, the lowest ZV (~45 mL 1000 m^{-3}) was associated with water coming from the southern gulf (~19°C), and with the second highest abundance of fish larvae of the cruise at the center of the eddy. This group had a fish larvae community formed by coastal pelagic species and high abundance of the most important mesopelagic species (*Benthosema panamense* and *Vinciguerria lucetia*). The 19°C isotherm coincided with the northern edge of the cyclonic eddy establishing the boundary between the JaG2 and JaG3 group.

The 21°C isotherm observed in the SST satellite image from March crossing from Bahía Concepción at the peninsular coast to Topolobampo at the continental coast of the gulf showed an apparent inverse circulation of the water with inflow by the peninsular side and outflow at the continental side. This hydrodynamic feature has been observed particularly in this month when a weakening of the poleward eastern coastal current is found, favoring the outflow of water very close to the continental coast of the gulf [23]. This isotherm indicates the boundary in the distribution of larvae fish assemblages MaG1 to the northern portion of the study area (low T10, high CHL and ZV) from MaG2 (high T10) at the south associated to the inflow of warmer and low productive water.

The anticyclonic eddy registered in March was at least 79 km wide and was located over the Farallón Basin, very close to the boundary between the MaG1 and MaG2 groups. It seems to be a recurrent oceanographic process [58]. In spite of the low productivity associated to MaG2, the center of the eddy registered a ZV of 460 mL 1000 m^{-3}, more than twice the ZV found at the center of the cyclonic eddy of January. Anticyclonic eddy are related to convergence and downwelling at the centers and are also known as warm core eddy. Biophysical conditions registered at the center of the eddy observed in this month indicated a suitable environment for mesopelagic species dominated by *V. lucetia*, *D. laternatus*, *H. atratum*, *T. mexicanus*, and *B. panamense* but not for the coastal pelagic species *E. mordax* and *S. sagax* that distributed at lower T10 than mesopelagic species in the eddy. High concentrations of zooplankton and fish larvae abundance in the March anticyclonic eddy coincide with the same type of eddy [11, 60]. The inflow of warm and low productive water delimited by the 21°C isotherm in a large extension of the southern study area contributed also to a more complex community in MaG2 (high species richness) and was the main factor delimiting larvae fish assemblages in the Gulf of California.

The fish larvae assemblages showed a latitudinal gradient related to SST. Also, the distribution of the 18°C and 21°C isotherms, in January and March, respectively, proposed by Aceves-Medina et al. [24] as the limit of the fish larvae recurrent groups matched the eddy structures edges in these months. The warmer environment registered during our winter cruises, particularly during March, displaced the 18°C isotherm to the north determining the presence of the frontal zone of the Big Islands. Thus, interannual variability may also be playing an important role in the distribution of the fish larvae assemblages at the macroscale.

4.2. Summer Season. July and September conditions included a coastal-ocean gradient, with high T10 and lower S10 resulting from the presence of tropical surface water (TSW) entering the gulf along the continental coast [63]. Also, a stratified water column, lower CHL and ZV, but fish larvae abundance higher than in winter season was present. Assemblages were primarily correlated to the ZV and CHL gradients (Table 2) and the tropical-subtropical species dominated the community (95.5%) coinciding with Aceves-Medina et al. [20], although shallow-demersal species dominated over the mesopelagic component registered by these authors. Epipelagic species (*O. libertate*, *Opisthonema* spp., *Anchoa* spp., *C. mysticetus*, *C. caballus*, *O. saurus*, *S. sierra*, *Thunnus* sp. 1, *Kajikia audax*, and *Katsuwonus pelamis*) replaced the species registered during the winter. A very similar well-mixed water column, highly productive, and cold environment related to the tidal mixing and upwelling process was occupied by mesopelagic and shallow-demersal species present in January and in July (JuG1) in the Big Islands area.

The grouping of species in JuG2 located outside of Bahía Concepción was related to high ZV. Bays, and coastal lagoons are recognized as organic carbon [64] and particulate organic matter [65] exportation zones particularly in summer conditions. These exported organic compounds can be used by mesozooplankton, increasing phytoplankton productivity of the coastal and adjacent oceanic systems [66], providing a suitable environment for the feeding and development of fish larvae.

A very disperse group of sampling station formed JuG3. It was found in shallow and warmer sampling stations located at the continental coast, south of the Big Islands, and at

the continental shelf of the northern area of the Gulf of California. In this last zone, extraordinary abundance of larvae of *O. libertate* (24,252 larvae 10 m^{-2}) and *C. mysticetus* (40,149 larvae 10 m^{-2}) filter-feeding coastal-pelagic species evidenced a spawning event of their adults. These larvae were distributed in the northern boundary of the eddy generated by the cyclonic circulation present during the summer in the northern gulf [18, 21, 67, 68], while at the center of the eddy the larvae were scarce. The adults of *O. libertate* and *C. mysticetus* may be spawning at the edge of the cyclonic eddy, as observed in other species (*E. mordax* and *S. sagax*) [26] selecting a very productive area in terms of CHL. Such selection may increase survival of fish larvae at early stages. The thermal front of this month did not influence the formation of groups.

During September, most of the gulf had high temperatures, but the coastal-ocean gradient was lower than in July. The limit between the coastal and oceanic groups (SeG1 and SeG2) formed in this month was independent of T10 and was related to high CHL. The SeG1 was found at the coastal productive environment in both continental and peninsular areas, while the oceanic group (SeG2) at the center of the gulf was correlated with the highest ZV in this cruise. We found a cyclonic low intensity eddy of only ~48 km, located at the northern portion of the Pescadero Basin. The biological component response to the presence of this oceanographic feature was contrary to that observed in the cyclonic and anticyclonic eddy structures observed in the winter. At the center of the September cyclonic eddy, we recorded the lowest ZV, species richness, and fish larvae abundance of the cruise according to eddy records in other areas [11, 59, 60]. The few larvae present at the center of the eddy belonged to one coastal-pelagic (*O. micropterus*) and one shallow-demersal (Gerreidae spp.) species.

Besides the effect of dispersion of this cyclonic eddy, surface tows made in this month influenced the composition and low abundance recorded in this eddy. Methodology of surface tows versus Bongo tows resulted in lower filtering efficiency and collections of mostly surface fish larvae assemblages. Also, few shallow-demersal and meso-bathy pelagic species were found. However, tropical-subtropical biogeographic affinity of the fish larvae registered during surface tows in September was representative of the summer season. Filter efficiency and similar ZV collections in other zooplankton groups have been found [69, 70]. These differences (surface versus oblique tows) may also be important to explain mesoscale effects. However, the analysis of the distribution patterns of fish larvae from surface and oblique tows demonstrates that even with the differences associated to the methodology, the relationships between abundance and environmental variables are similar in both cases. Also, when sampling is not extensively made in time and space over eddy and/or front structures, the oceanographic and biological data may limit some inferences related to its evolution through time, giving only a quick look of the processes present at that moment.

During July and September, the 29°C and 31°C isotherms observed in the corresponding SST satellite images ran across the gulf from the south of the Big Islands to the mouth of the gulf, dividing the gulf in two. The edges of the eddy structures in July coincide with the 29°C isotherm, while the 31°C isotherm registered in September coincided with the west edge of the cyclonic eddy of this month. The similarity in the fish larvae assemblages of both coasts during this last month may be related to transport mechanisms through eddy movement from one coast to the other.

The use of physical and biological variables to understand fish larvae abundance and distribution in the Gulf of California provided a wider overview of their relationships. Satellite imagery not always showed mesoscale processes, as we observed during March and September cruises. This may be explained by the fact that the signal of the dome or valley shape of the water column did not reach the surface. However, water column profiles did show the eddy signals allowing us to confirm their presence and therefore to relate these oceanographic processes to the biological information.

Although most of the previous records in this area established that temperature and physical mesoscale processes are responsible for the presence and distribution of fish larvae assemblages at different scales [24, 30, 71], we found that besides T10 and S10, CHL and ZV gradients used as gross indicators of the biological production and of the amount of available food in the environment were also highly correlated with the fish larvae abundance (Table 2) in the Gulf of California, particularly during summer months.

It is known that spawning activity in fishes is stimulated by environmental gradients, and among them, temperature ones seem to be the most important [26, 72]. Therefore distribution and abundance of fish larvae are highly related to those environmental gradients in large regions because of the physiological requirements of each species, as observed along the Gulf of California. However, in a local scale, mesoscale processes seem to be the main force driving not only the distribution of species but also the biophysical gradients. Eddy structures that retain fish larvae, also affect the distribution of physical variables increasing, for example, the temperature in the cores. In this way, the relationships observed between fish larvae abundance and T10, S10, CHL, and ZV could be the effect of two possibilities. The first is that the coincidence of the distribution of all variables is the result of their dependence on the mesoscale process; the second is that the mesoscale process promotes suitable physical environments that stimulate adults to spawn.

The SST difference between winter and summer in our study was about 10°C and was wide enough to establish low fish larvae abundance and the presence of more temperate (7.5%) species in colder winter conditions than in the summer. The change of T10 and S10 as the main factors affecting fish larvae assemblages during the winter to CHL and ZV during the summer reflects different biophysical conditions for fish larvae inside the gulf related to the seasonal environmental changes. In a not limited food supply environment, because of the presence of a high production originated from strong upwelling during winter [18], the T10 north-south gradients observed in the gulf strongly influenced the formation of fish larvae groups that also distributed in a north-south pattern. In contrast, high T10 along the gulf,

but strong food limitation during the summer, related to weak upwelling at the peninsular coast and inflow of low productive TSW with a high-coastal low-ocean gradient, promoted fish larvae groups to distribute according to this pattern.

It is known that the formation and composition of fish larvae assemblages are first determined by the location of the spawning areas of the adults, by timing in spawning, and subsequently by interspecific differences in mortality and development rates associated to larvae behavior, among others [73–75]. In terms of reproductive strategies, Aceves-Medina et al. [26] propose the hypothesis that *E. mordax* fish larvae are abundant when those of *S. sagax* are scarce indicating that the species occupies different positions in the water column, with *S. sagax* mostly above the thermocline while *E. mordax* distributes deeper, and that the adults spawn at different places, not only at the mainland coast.

The cyclonic and anticyclonic eddy registered in our study during winter retain pacific sardine larvae at the center of the gulf, while presence of *E. mordax* in the frontal zone may indicate that the species use these highly productive but different oceanographic processes as nursery areas.

5. Conclusions

The results obtained in this study provide a more comprehensive explanation of the response of the fish larvae community to the environmental complexity of macro, and mesoscale processes in the Gulf of California.

Strong differences between winter (latitudinal gradient) and summer (coast-ocean gradient) environmental conditions as well as in the composition, abundance, biogeographic affinity, and habitat of the fish larvae assemblages were found in the area. In the macroscale, fish larvae abundance was highly related to environmental variables with seasonal changes in the main factors, T10 and S10 during the winter, and CHL and ZV during the summer, affecting the formation of groups. Besides S10, CHL, and ZV, 19°C and 21°C isotherms during the winter, and 29°C and 31°C isotherms during the summer, seemed to be related to the distributional limits between fish larvae assemblages at the macroscale. Changes in location of these limits were related to interannual variability associated to the El Niño, which also represents a major source of variability in the formation of the fish larvae assemblages.

The center of the winter eddy had more abundance than the summer eddy. Among types of eddy, the cyclonic of January recorded the highest abundances of mesopelagic (*V. lucetia*, *D. laternatus*, and *B. panamense*) and coastal-pelagic species (*S. sagax*, *S. japonicus*, and *E. teres*) than in the anticyclonic of March and cyclonic eddy of September, indicating that the evolution of the eddy over the time scale may be important to understand the complexity of the fish larvae community. Eddy structures have an important impact on larval fish assemblages, but these impacts can change depending on the type, size, age, source water mass, dynamics within the eddy and interactions with the surrounding waters, generation time of the organisms, and even by the time and type of sampling. At the mesoscale, eddy and fronts coincided with these isotherms, playing an important role in emphasizing the differences among species assemblages.

Future research on fish larvae ecology on a similar or more complete data base set basis and high resolution sampling of both eddy types and frontal zones, following them over time should be encouraged in order to provide a better understanding of the species-environment relationships. Also, interannual analysis should be attempted in order to understand the macroscale changes in fish larvae assemblages.

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