Lat. Am. J. Aquat. Res., 46(1): 20-36, 2018
DOI: 10.3856/vol46-issue1-fulltext-4

Research Article

Regionalization in the distribution of larval fish assemblages during winter and autumn in the Gulf of California

Homero Urias-Leyva[1], Gerardo Aceves-Medina[1], Raymundo Avendaño-Ibarra[1]
Ricardo J. Saldierna-Martínez[1], Jaime Gómez-Gutiérrez[1] & Carlos J. Robinson[2]
[1]Instituto Politécnico Nacional, Departamento de Plancton y Ecología Marina
Centro Interdisciplinario de Ciencias Marinas, La Paz, B.C.S., México
[2]Instituto de Ciencias del Mar y Limnología, Laboratorio de Ecología de Pesquerías
Universidad Nacional Autónoma de México, D.F., México
Corresponding author: Gerardo Aceves Medina (gaceves@ipn.mx)

ABSTRACT. Larval fish composition and abundance were analyzed during February-March (winter) and November-December (autumn) of 2005 to investigate which environmental conditions and mesoscale oceanographic processes affect the distribution of larval fish assemblages in the Gulf of California, and if these variables and processes are useful to delimit specific regions of ichthyofaunal distribution. The overall pattern was mostly a latitudinal gradient of the abundance of two faunistic complexes of larval fish assemblages (temperate northern and tropical southern complexes) strongly associated with the spatial distribution of sea surface temperature. The integration of these results, with previous investigations in the region, lets us confirm that the northern and southern larval fish assemblages extend and contract their distribution ranges according to the latitudinal displacement of the 21°C sea surface isotherm. We identified this to be a valuable criterion to establish the southern distribution limit of the temperate larval fish assemblage, and the 18°C as the northern limit of the tropical larval fish assemblage. However, this general pattern is maintained only in absence of mesoscale oceanographic features (upwelling and eddies) that increase larval drift from the coast to the central region of the Gulf, particularly during the November-December period when longitudinal gradients were stronger than in February-March.

Keywords: fish larvae, assemblage, upwelling, eddies, Gulf of California.

INTRODUCTION

In the Gulf of California (GC) previous studies have shown that mesoscale structures such as fronts, upwelling, and eddies influence the larval fish distribution as well as the structure and diversity of their species assemblages (Danell-Jiménez *et al.*, 2009; Contreras-Catala *et al.*, 2012; Avendaño-Ibarra *et al.*, 2013). Understanding the effect of these oceanographic processes on ichthyoplankton assemblages is relevant to characterize both the spawning habitat and the nursery sites of the fishes.

Several studies have explored the coupling between larval fish assemblages and mesoscale structures (Sánchez-Velasco *et al.*, 2013; Apango-Figueroa *et al.*, 2014; Contreras-Catala *et al.*, 2015), including the use of numerical models which compare the fish larval abundance and connectivity among regions of the Gulf of California (Peguero-Icaza *et al.*, 2008, 2011). These studies inherently have a synoptic deterministic approach under specific oceanographic conditions (*i.e.*, conditions prevailing across a specific eddy) and show local distribution patterns imposed by species spawning behavior that result in highly dynamic species assemblages. An alternate, less deterministic approach is to investigate the overall effect of mesoscale structures by comparing distinct seasonal conditions (*e.g.*, intense *vs* weak mesoscale structure activity) which from a biogeographic perspective represent broad multi-specific habitats.

Research on ichthyoplankton in the GC has shown that there are two main larval fish faunistic complexes: the northern complex (formed by temperate and subtropical species assemblages) with its southern distribution limit at the 21°C sea surface isotherm, and the southern complex (formed by tropical and subtropi-

---

Corresponding editor: Guido Plaza

cal species assemblages), with its northern limit approximately at the 18°C isotherm. The area between the 18 and 21°C SST isotherms likely represents a transition zone in the central region of the GC in which both larval fish species complexes coexist during the spring and autumn. These three zoogeographic regions were proposed by Aceves-Medina *et al.* (2004) and roughly match the adult ichthyofaunal bio-regionalization pattern (Walker, 1960). The geographic limits among regions change seasonally, influenced by climate and sea current patterns that modify the surface isotherms positions throughout the year. The original conceptual ichthyoplankton zoogeography scheme proposed by Aceves-Medina *et al.* (2004) only included samples from the area north of 27°N during the winter (late December to March), leaving out much of the central and southern region of the GC during that period. This model seems to work well in absence of coastal upwelling events, since Avalos-García *et al.* (2003) detected similar latitudinal patterns of the larval fish species assemblages in the spring but not during the autumn, when strong wind-forced upwelling events are coupled with mesoscale eddies (Pegau *et al.*, 2002). In the GC predominant northwest winds cause wind-forced upwelling along the continental coast during the cool period from late November to May (Pegau *et al.*, 2002).

To provide additional observational evidence about latitudinal zoogeographic patterns, particularly in the southern region during the winter, to fill the previous knowledge gap, the present study has three goals: 1) to compare larval fish assemblages, in February-March (winter) *vs* November-December (autumn) of 2005, in a large portion of the GC; 2) to test if the regionalization of the Gulf of California, as previously proposed (Aceves-Medina *et al.*, 2004), is seasonally valid, by comparing two cruises carried out in 2005; and 3) to analyze the effect of jets and eddies, coupled with upwelling processes, on the larval fish assemblages observed during November-December 2005.

MATERIALS AND METHODS

Study area

Two oceanographic surveys were carried out in the Gulf of California to collect zooplankton samples and measure environmental conditions of the water column (Fig. 1). The first survey (representative of the cold period) was carried out on board the R/V Alejandro de Humboldt (Secretaría de Marina, Armada de México) between February 25 and March 12, 2005 (Feb-Mar) sampling 39 oceanographic stations (27°42’-23°24’N, 111°57’-107°30’W). The second survey (representative of the short transitional period, with numerous jet and eddies) was carried out between November 15 and December 5, 2005 (Nov-Dec) on board the R/V El Puma (UNAM) sampling 23 oceanographic stations (30°12’-24°48’N, 113°54’-109° 12’W).

Environmental measurement

Seawater temperature and density were measured from the surface to 200 m depth (seafloor depth permitting) at each oceanographic station using a CTD (Seabird SBE 19 SeaCAT and General Oceanics Mark III). Along seven selected longitudinal transects, vertical profiles of temperature and density were obtained to detect the thermocline and pycnocline depth, and confirm where the coastal upwelling likely occurred using further evidence from Aqua MODIS SST and chlorophyll satellite images (https://coastwatch.noaa.gov/cw_html/index.html). Additionally, during Nov-Dec 2005, the near-surface temperature was recorded every 5 s throughout the research vessel path, from seawater pumped from a depth of 4 m to a MicroCAT CTD Seabird. Continuous temperature records were geo-referenced with a GPS Trimbley AG160 using time (hours, minutes and seconds) records.

Water column stability (WCS, density gradient) was estimated as in Peterson *et al.* (1988): WCS = $\Delta\delta$-t/Δz, where $\Delta\delta$-t is the difference of the seawater sigma-t recorded at the surface and in the deepest strata recorded, and Δz is the difference in depth between the surface and the deepest water sampled at each station (the deepest record was 200 m). The variation in vertical density gradient >0.1 was used as a depth index of the mixed layer depth (MLD) (Palomares-García *et al.*, 2013).

Only during the Nov-Dec survey, sea water collected with 20 L Niskin bottles at the surface, 5, 10, 25, 50, and 75 m deep was sampled to measure the dissolved oxygen concentration (mg O_2 L^{-1}) by using a YSI 556 MPS multi-sensor. From each Niskin bottle, 350 mL of seawater was filtered with a GF/F 0.7 µm pore filter, which was immediately frozen in liquid Nitrogen. The filters were used to estimate the chlorophyll-*a* concentration (Chl-*a*) using the standard HPLC (Vidussi *et al.*, 1996). Discrete Chl-*a* concentration values by depth were integrated throughout the water column.

Larval fish composition

Zooplankton samples were collected with oblique tows (maximum depth 210 m, bottom depth permitting), using Bongo nets (505-µm net mesh) and mechanical flowmeters (General Oceanics) to estimate the water volume filtered following the standard method of Smith & Richardson (1977).

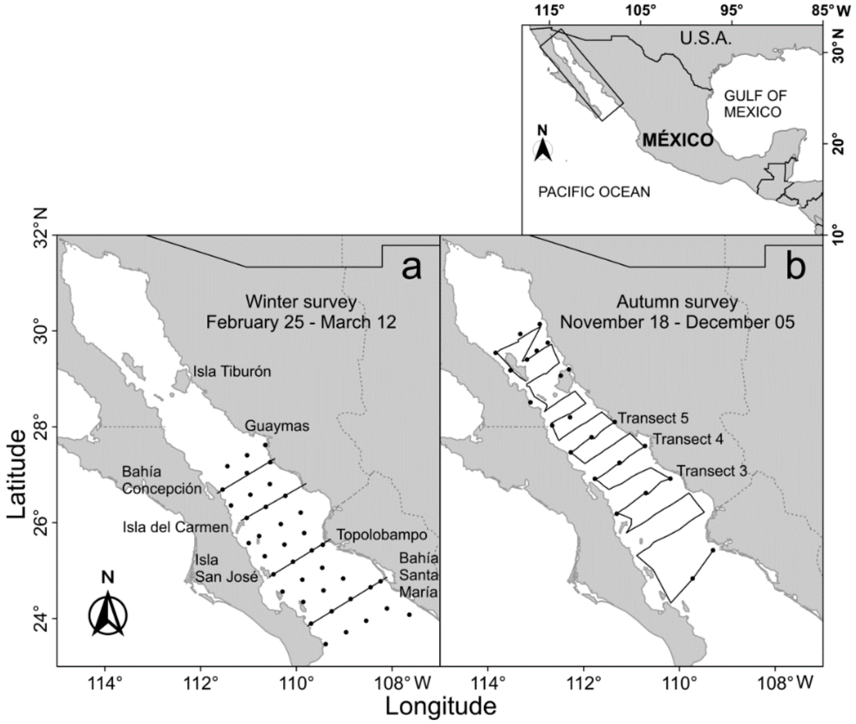

Figure 1. Study area and oceanographic stations sampled (solid circles) during the 2005 cruises: a) February-March cruises. The four straight lines show transects for vertical profiles, and b) November-December cruises. The continuous line shows the ship track where temperature was measured every 5 s.

Zooplankton was preserved with ethanol (96%) and posteriorly fish larvae were sorted out with a Carl Zeiss Stemi SV6 stereomicroscope and identified, usually to species. Those specimens identified only to genus or family level were classified as morphotypes based on their meristic, morphometric and pigmentation patterns (*e.g.*, Gonostomatidae sp. 1 or *Diplectrum* sp. 1). Fish larvae were counted from each sample and their abundance was standardized to the number of organisms per 10 m^2 of sea surface (Smith & Richardson, 1977). Voucher specimens were catalogued and deposited in the Mexican North Pacific Ichthyoplankton Collection at CICIMAR, La Paz, BCS, México (SEMARNAT B.C.S.-INV-196-06-07).

Data analysis

Species richness (R, the number of species in a plankton sample) and Shannon-Weaver Diversity Index (*H*') were estimated using $\log_2$ with the PAST v.2.17c software (Hammer *et al.*, 2001). Larval fish assemblages of each survey were obtained by cluster analyses (CA) using the Bray-Curtis similarity index as well as using the simple average link method with the PAST software, including only those species present at >15% of the zooplankton sampling stations.

Canonical correspondence analysis (CCA) was used to analyze the correlation between environmental variables and larval fish abundance. The environmental matrix included SST, mixed layer depth (MLD), mean dissolved oxygen concentration (O_2) from surface to 75 m depth, and Chl-*a* concentration integrated throughout the water column. The CCA was calculated using the PC-ORD v.4 software (McCune & Mefford, 1999). For all statistical analyses, ichthyoplankton abundance was log (x+1) transformed, where x is the abundance of fish larvae. The CCA was performed using the standard error of each environmental variable ($\sigma_x = \sigma/n^{1/2}$). After this, values of each variable were transformed with (x–X)/σ_x; where *x* is the variable value and *X* is the average value of this particular variable.

A Multi-Response Permutation Procedure (MRPP) with the Bray-Curtis distance measure was calculated with the PC-ORD software to test for statistically significant differences between the groups of oceanographic stations formed in the CCA (McCune *et al.*, 2002). We also tested the hypotheses that there were differences between fish larval assemblages from regions separated by the 21°C sea surface isotherm. When the MRPP tests showed statistical differences, the Indicator Species Analysis (Dufrêne & Legendre,

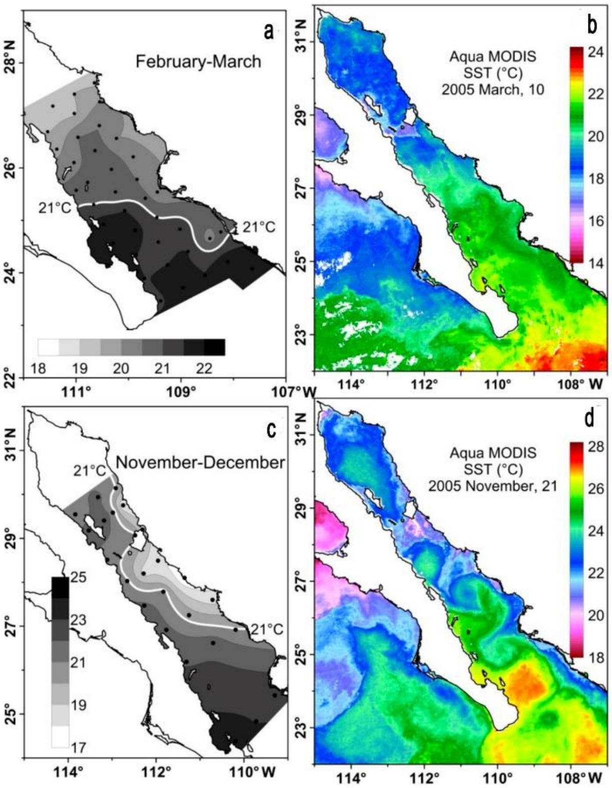

Figure 2. Sea temperature distribution (°C) during Feb-Mar 2005: a) *in situ* SST, b) SST satellite image and during Nov-Dec 2005, c) *in situ* 4 m depth continuous temperature (25 m resolution), d) SST satellite image.

1997) was used to define which species were significantly associated (indicator) to stations with sea surface temperatures <21°C and >21°C. The Indicator Species Analysis index (ISA) ranges between 0 (not an indicator) and 100% (perfect indicator). The ISA was tested for statistical significance using the Monte Carlo method (McCune *et al.*, 2002). Only species with $P \leq 0.01$ were considered indicator species of a particular larval fish assemblage.

RESULTS

Environmental variables

During Feb-Mar, the SST in the Gulf of California (GC) showed a latitudinal gradient, increasing from 19°C in the north to 22°C in the south (Fig. 2a). The SST had a weak longitudinal gradient, with the northeast coast only 1°C cooler than the west coast. The 21°C isotherm was oriented transversally between the north of Isla San Jose and the south of Bahia Santa María. SST satellite imagery (Fig. 2b), vertical profiles of water temperature, and density (Figs. 3a, 3b), as well as dissolved oxygen distribution, and chlorophyll concentration (Figs. 4a-4c) did not show evidence of strong upwellings or eddies processes. However, along with the Isla San José and Bahía Santa María transects, a weak rise of the thermocline and halocline was observed.

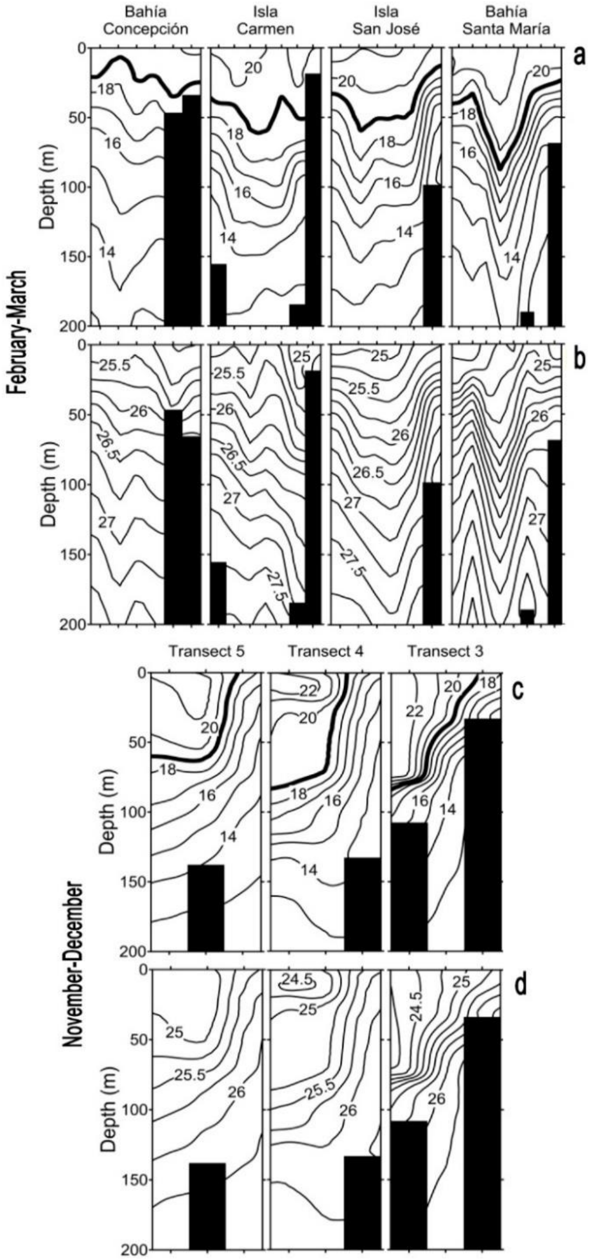

Figure 3. Vertical profiles during February-March (a-b) and November-December (c-d) 2005 from the peninsular coast (left side) toward the continental coast (right side) of the Gulf of California: (a and c) temperature (°C); (b and d) seawater density (kg m^{-3}).

During Nov-Dec, the temperature measured continuously at 4 m depth showed a coastal band of low temperature (<21°C) along the northeast coast that was considerably cooler than the peninsular coast, with a re-

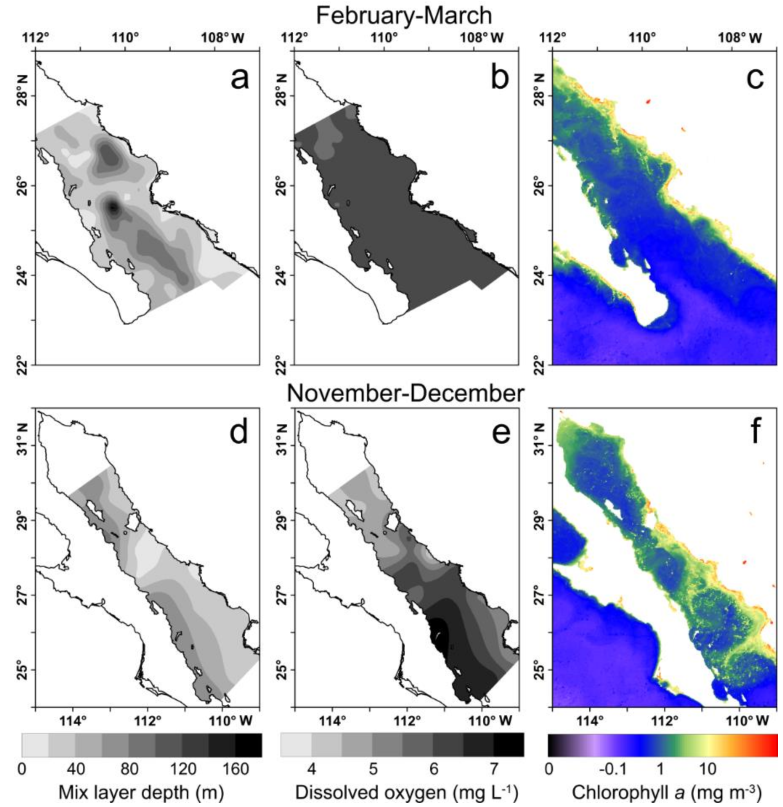

Figure 4. Horizontal distribution of environmental variables during February-March (CGC 0503) and November-December 2005 (GOLCA 0511): a, d) mixed layer depth; b, e) mean dissolved oxygen concentration of the water column <75 m depth; c, f) surface concentration of Chl-*a* from satellite images.

latively pronounced temperature gradient of about 4°C (Fig. 2c). The SST satellite image showed two prominent cold-water filaments extending from the continental coast towards the peninsular coast associated with cyclonic eddies south of Isla Tiburón and north of Topolobampo. The highest SST values (~26°C) were observed in the southwest region of the GC (Fig. 2d). Nov-Dec vertical profiles of temperature and density (Figs. 3c-3d) along transects 3-5 (Fig. 2b) showed additional evidence of upwelling events, with cold and dense water near the surface (<25 m deep) located on the continental coast (~25.75 kg m^{-3}) associated with a shallow MLD (Fig. 4d), lower O_2 (Fig. 4e) and higher Chl-*a* (Fig. 4f).

Larval fish composition

In Feb-Mar 2005, larvae of 74 fish taxa were recognized pertaining to 35 families and 56 genera (50 identified to species level) (Table 1). Eight species accounted for 93% of the total abundance and were present at >30% of the total sampled stations. Only *Vinciguerria lucetia*, *Diogenichthys laternatus*, *Engraulis mordax*, *Benthosema panamense* and *Leuroglossus stilbius* had total relative abundances >5% of the total fish larvae (range 5-35%) (Table 2).

Species richness per sampling station ranged between 1 to 19 taxa (average = 8) showing high R values in the central and southern regions of the GC (Fig. 5a). A similar distribution pattern was found with the *H*' Index, which ranged between 0.03 and 2.5 bits, with two high diversity cores (Fig. 5b).

During Nov-Dec 2005, larvae of 75 fish taxa were recognized pertaining to 34 families and 46 genera (45 were identified to species level) (Table 1). Nineteen species accounted for 86% of the total larval catch, but the most abundant and frequent species were *B. panamense*, *Triphoturus mexicanus*, *E. mordax* and *V. lucetia* which had total abundances >5% (Table 2). Species richness per sampling station ranged between 1 and 28 (Fig. 5c), but the average was similar to that observed in Feb-Mar (R = 9 taxa). The distribution of R, as well as the *H*' index, showed the highest diversity in the southern GC (Fig. 5d).

Larval fish assemblages

During Feb-Mar, the CA showed two groups with similarity values near >50% (Fig. 6a). Temperate and subtropical taxa formed the first winter group (WG1), two dominant species were from the coastal pelagic

Table 1. Larval fish species total standardized abundance in org 10 m^{-2} of sea surface during February-March (W) and November-December (A) 2005. Arranged by Family (F) according to Nelson (2006).

Family/taxa	W	A	Family/taxa	W	A
F. Albulidae			*Benthosema panamense*	1701	6129
Albula spp.	17	27	*Diogenichthys laternatus*	4886	525
F. Ophichthidae			*Hygophum atratum*	731	
Ophichthus zophochir	32		F. Bregmacerotidae		
Ophichthus triserialis		31	*Bregmaceros bathymaster*	32	208
F. Congridae			*Bregmaceros* sp.	51	6
Rhynchoconger nitens	8		F. Macrouridae		
Ariosoma gilberti	17		*Coryphaenoides* sp.	7	
Congridae sp. 1	8		Macrouridae sp. 1		21
F. Clupeidae			*Nezumia* spp.	48	
Etrumeus teres	16	6	F. Moridae		
Opisthonema sp.	7		*Physiculus nematopus*	14	
Sardinops sagax	47	493	F. Ophidiidae		
F. Engraulidae			*Cherublemma emmelas*	16	
Engraulis mordax	1852	1994	*Chilaria taylori*	32	
Engraulidae spp.		121	*Lepophidium negropinna*		81
F. Argentinidae			*Lepophidium stigmatistium*	17	39
Argentina sialis	8	118	*Lepophidium* sp. 1		8
F. Bathylagidae			*Ophidion scrippsae*	36	
Bathylagus pacificus		28	*Ophidion* sp. 1		121
Bathylagoides wesethi	21		Ophidiidae sp. 2		42
Leuroglossus stilbius	1032		Ophidiidae sp. 3		40
Bathylagidae sp.	8		Ophidiidae sp. 4	7	
F. Gonostomatidae			F. Lophiidae		
Cyclothone spp.	17		*Lophiodes caulinaris*		6
Diplophos proximus	15		*Lophiodes spilurus*		7
Gonostomatidae sp. 1	7		F. Melamphaidae		
F. Phosichthyidae			*Scopelogadus bispinosus*	9	
Vinciguerria lucetia	6463	1131	*Melamphaes* sp. 1		40
F. Aulopidae			Melamphaidae spp.	8	
Aulopus bajacali	15		F. Fistulariidae		
F. Scopelarchidae			*Fistularia commersonii*		40
Scopelarchoides nicholsi	14		*Fistularia corneta*		7
F. Synodontidae			F. Scorpaenidae		
Synodus lucioceps	7	41	*Pontinus* sp. 2		66
Synodus sp. 1		6	*Pontinus* sp. 1		31
F. Myctophidae			*Scorpaenodes xyris*	29	214
Diaphus pacificus	16		*Sebastolobus altivelis*		31
Lampanyctus parvicauda	9	16	F. Triglidae		
Nannobrachium idostigma	7		*Prionotus ruscarius*		8
Triphoturus mexicanus	353	2465	Triglidae sp. 1		6
F. Serranidae			*Lytrypnus zebra*	17	24
Diplectrum sp. 1	32	6	Gobiidae sp. 1		137
Diplectrum sp. 2		6	Gobiidae sp. 2		8
Hemanthias signifier		16	Gobiidae sp. 3	8	
Pronotogrammus eos	7		Gobiidae sp. 4	22	
Pronotogrammus multifasciatus	23	23	Gobiidae sp. 6		24
Serranus spp.		77	Gobiidae sp. 7	7	
Serranidae sp. 1	28	8	Gobiidae spp.	7	
F. Apogonidae			F. Scombridae		
Apogon sp. 1		6	*Scomber japonicus*	361	167
F. Carangidae			F. Trichiuridae		
Alectis ciliaris		40	*Lepidopus fitchi*	8	7

Continuation

Family/taxa	W	A	Family/taxa	W	A
Caranx caballus		40	*Trichiurus nitens*		7
Caranx sp. 1	16		F. Nomeidae		
Caranx sp. 2		16	*Cubiceps pauciradiatus*		150
Chloroscombrus orqueta	9		*Psenes pellucidus*	15	
Seriola sp.	20		*Psenes sio*	6	55
Trachurus symmetricus	6		Nomeidae sp. 1	38	
F. Malacanthidae			F. Paralichthyidae		
Caulolatilus princeps	8	38	*Citharichthys fragilis*		252
Caulolatilus sp. 1		47	*Citharichthys gordae*		8
F. Scianidae			*Citharichthys platophrys*		67
Menticirrhus sp. 1		5	*Citharichthys sordidus*		46
Umbrina roncador	8		*Citharichthys xanthostigma*		7
F. Chaetodontidae			*Citharichthys* sp. 1		114
Chaetodon sp. 1		14	*Cyclopsetta* sp. 1	8	
F. Labridae			*Etropus crossotus*	7	
Labridae sp. 1		5	*Etropus* sp.		379
F. Labrisomidae			*Syacium ovale*		8
Labrisomus xanthi	22		F. Bothidae		
Labrisomidae sp.	8		*Bothus leopardinus*	9	121
F. Chaenopsidae			*Monolene asaedai*	15	
Chaenopsidae sp.	31		F. Pleuronectidae		
F. Blennidae			*Pleuronichthys verticallis*	8	
Hypsoblennius jenkinsi		7	F. Cynoglossidae		
Ophioblennius steindachneri	7		*Symphurus atramentatus*	7	772
F. Eleotridae			*Symphurus oligomerus*		252
Eleotridae sp. 1	59	40	*Symphurus williamsi*	15	60
F. Gobiidae			F. Diodontidae		
Coryphopterus nicholsii	16		*Diodon holocanthus*		8
Ilypnus gilberti		8	Unidentified larvae	143	632
			TOTAL	18619	17862

habitat (*E. mordax* and *Scomber japonicus*) and one was mesopelagic (*L. stilbius*). The highest abundance of the WG1 was in the northern sampling area (Fig. 7a). The second group (WG2) was composed of mesopelagic species with a tropical affinity (*D. laternatus*, *V. lucetia*, *B. panamense*, *T. mexicanus*, and *Hygophum atratum*) and was distributed throughout the entire study area, but with highest abundances in the southern region of the GC (Fig. 7b).

The larval fish assemblages collected during Feb-Mar at SST values <21°C were significantly different in species composition and abundance to those collected at SST >21°C (MRPP analysis: A = 0.08; $P < 0.01$). According to the indicator species analysis (ISA), all species belonging to the northern complex could be representative of the area with SST <21°C since they had high fidelity values (53.4 to 65.7%; $P < 0.01$), while for the southern complex only *V. lucetia* could be considered an indicator species of the area with SST >21°C (58.9%; $P < 0.01$) (Table 3).

In Nov-Dec, the CA showed five larval fish groups with similarity values >50% (Fig. 6b). The AG1 was formed by demersal tropical species (*Serranus* spp., *Pontinus* sp. 2, *Symphurus williamsi*, and *Citharichthys platophrys*) while the AG2 representative taxa included *Citharichthys* sp. 1 (demersal, tropical affinity), *Cubiceps pauciradiatus* (epi and mesopelagic, tropical-subtropical affinity), and *Argentina sialis* with *Citharichthys fragilis* (demersal, temperate-subtropical affinity). Both AG1 and AG2 were distributed mainly on the peninsular side, but AG2 had a northernmost distribution (Figs. 8a-8b).

The AG3 group was formed by tropical-subtropical species: *S. atramentatus*, *S. oligomerus*, and *Etropus* spp. (demersal species), and *D. laternatus*, *V. lucetia*, and *T. mexicanus* (mesopelagic species) (Fig. 9a). This group was widely distributed along the study area, although it was mainly concentrated in the central and the southern region of the GC (Fig. 9a).

Table 2. Most abundant larval fish species during February-March and November-December 2005: total standardized abundance in larvae 10 m^{-2} (AB), relative abundance (RA%), and percent of positive samples (PS%).

Taxa	AB	RA%	PS%
February-March			
Vinciguerria lucetia	6463	34.68	84.62
Diogenichthys laternatus	4886	26.22	76.92
Engraulis mordax	1852	9.94	33.33
Benthosema panamense	1701	9.13	66.67
Leuroglossus stilbius	1032	5.54	48.72
Hygophum atratum	624	3.35	35.90
Scomber japonicus	361	1.94	38.46
Triphoturus mexicanus	353	1.90	35.90
November-December			
Benthosema panamense	6129	34.31	86.96
Triphoturus mexicanus	2465	13.80	56.52
Engraulis mordax	1994	11.16	65.22
Vinciguerria lucetia	1131	6.33	39.13
Symphurus atramentatus	772	4.32	34.78
Diogenichthys laternatus	525	2.94	39.13
Sardinops sagax	493	2.76	39.13
Etropus sp. *peruvianus*?	379	2.12	34.78
Symphurus oligomerus	252	1.41	26.09
Citharichthys fragilis	252	1.41	52.17
Scorpaenodes xyris	214	1.20	17.39
Scomber japonicus	167	0.94	26.09
Cubiceps pauciradiatus	150	0.84	17.39
Citharichthys sp. 1	114	0.64	26.09
Argentina sialis	118	0.66	17.39
Serranus spp.	77	0.43	21.74
Citharichthys platophrys	67	0.38	21.74
Pontinus sp. 2	66	0.36	21.74
Symphurus williamsi	60	0.33	17.39

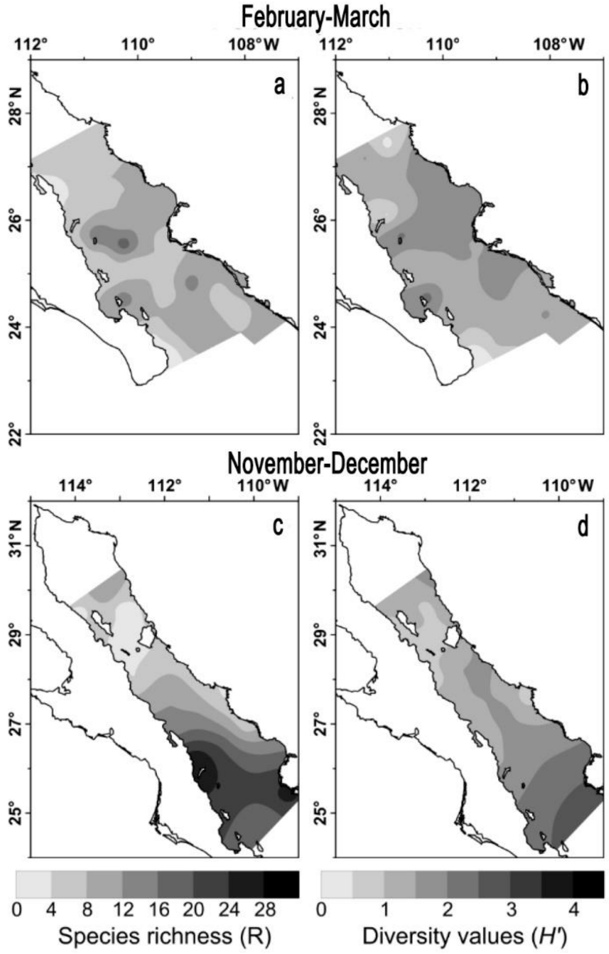

Figure 5. Gulf of California larval fish species richness (a, c), and Shannon's diversity index (b, d), during February-March (a, b), and November-December, 2005 (c, d).

Scomber japonicus (temperate-subtropical) and *Sardinops sagax* (temperate-subarctic) formed AG4 (Fig. 9b) and they were mostly distributed in the northern GC and in the central region close to the peninsular coast. The AG5 had two species, one from a coastal pelagic habitat of temperate affinity (*E. mordax*), and the second from a mesopelagic habitat of tropical affinity (*B. panamense*). This group was distributed throughout most of the study area, although low abundances were found in the northeast of the GC on the continental coast (Fig. 9c).

The explained variance by the CCA using Nov-Dec values was low (26.6 %). Dissolved oxygen concentration (r = 0.57) and SST (r = -0.65) were the variables with the highest correlation to axis 1, which explained 18.7 % of the variance, while MLD was mostly correlated to axis 2 (r = 0.8), which explained 4.9 % of the total variance. Axis 3 explained 3% of the total variance, and O_2 (r = 0.81), as well as SST (r = -0.72), were the variables with the highest correlations (Table 4). The ordination diagram shows two groups of oceanographic stations (Fig 10a). The sampling stations to the right of the dashed line correspond to the continental area from Guaymas to Isla Tiburón (Fig. 10c), characterized by the lower O_2 and SST values, a deeper MLD and higher Chl-*a* concentrations. Stations to the left of the dashed line were located mostly along the peninsula coast with opposite environmental characteristics.

A comparison of the species dispersion diagram in the CCA (Fig. 10b) and the species distribution maps showed that the area with coastal upwelling events contained species with subtropical, temperate, and subarctic affinities, such as *C. fragilis* (demersal), *E. mordax*, *S. japonicus*, and *S. sagax* (coastal pelagic), and *B. panamense* (mesopelagic). The side without upwelling contained species with mainly tropical and subtropical affinities, such as *C. platophrys*, *S. williamsi*, *S. atramentatus*, *Serranus* sp. (demersal), *A. sialis*, *D. laternatus* and *V. lucetia* (mesopelagics).

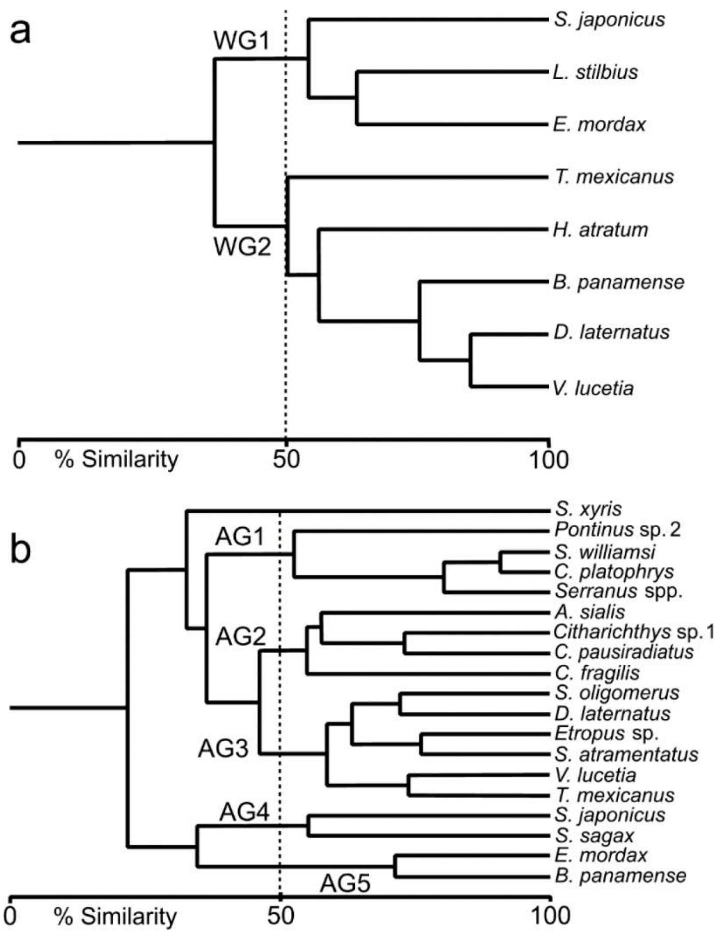

Figure 6. Cluster analysis dendrogram for the most abundant and frequent larval fish species recorded during a) February-March and b) November-December 2005.

The MRPP showed that during Nov-Dec, the taxonomic composition of fish larvae from stations with temperature <21°C was statistically distinguishable from stations with >21°C (A = 0.04; P = 0.02). In addition, the MRPP showed that there were statistically significant differences in the taxonomic composition and abundance between the oceanographic regions shown in Figure 10c and delimited with the CCA (A = 0.11; $P < 0.01$).

The ISA, during autumn, indicated there were significant differences ($P < 0.01$) between the two areas observed in the CCA (Fig. 10c). It shows high percentages of four species from the southern region: *V. lucetia*, *T. mexicanus*, *D. laternatus*, and *S. atramentatus* (Table 3).

DISCUSSION

Satellite imagery showed no evidence of coastal upwelling during winter conditions (Feb-Mar); however, coastal upwelling was detected along the continental coast during Nov-Dec, with a shallow thermocline, halocline, and MLD, as well as low SST and O_2 values. Intensification of upwelling along the continental shelf typically occurs late in the autumn (Lluch-Cota, 2000; Pegau *et al.*, 2002; Lavín & Marinone, 2003). These mesoscale structures caused pronounced gradients with higher Chl-*a* concentration along the continental coast. Previous studies have shown four or five simultaneous eddies throughout the Gulf of California, mostly driven by the thermohaline circulation (Figueroa *et al.*, 2003), but not well represented in 3D numerical models so far (Martínez & Allen, 2004; Zamudio *et al.*, 2008). Satellite imagery from the central and southern region of the Gulf of California show that cyclonic and anticyclonic eddies alternate with high and low Chl-*a* concentrations respectively (Pegau *et al.*, 2002), and that eddies tend to be more evident during the autumn than during the winter.

Although the formation of eddies associated with upwelling processes in the GC is not well understood,

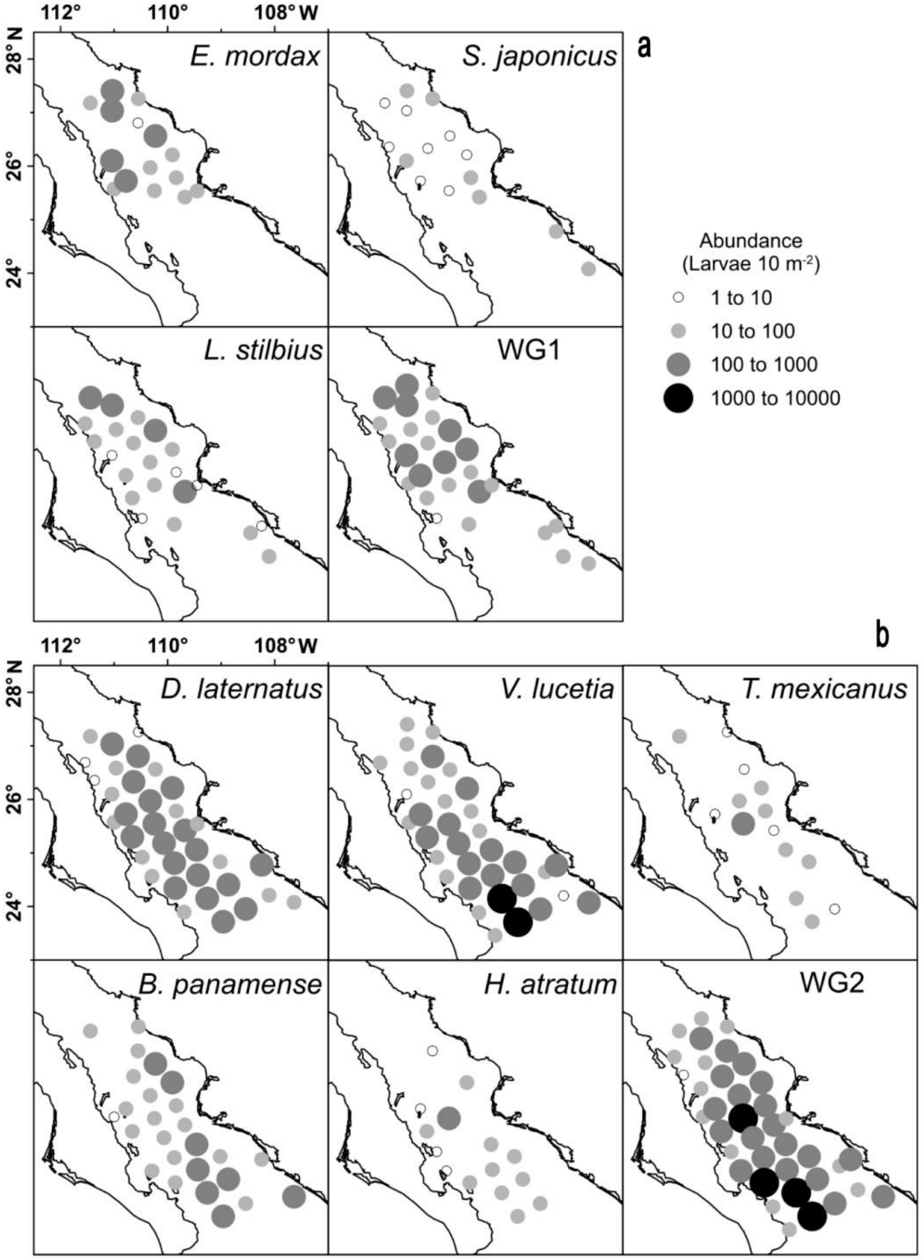

Figure 7. Larval fish species distribution during February-March 2005 included in a) group 1 (WG1), b) group 2 (WG2).

they are known to contribute to the advection of cool water from the mainland towards the peninsular coast (Pegau *et al.*, 2002; Navarro-Olache *et al.*, 2004). These cold plumes have a significant effect on the phytoplankton dispersion from the mainland to the coast of the Baja California Peninsula (Gaxiola-Castro *et al.*, 1999; Pegau *et al.*, 2002); this process explains the high Chl-*a* concentration along the east coast of the GC, which was observed in the Nov-Dec survey.

Previous studies reported that in the winter of 1988 larval fish assemblages consisted of abundant species such as *E. mordax*, *L. stilbius*, *B. panamense*, *S. japonicus*, *T. mexicanus*, *V. lucetia*, *D. laternatus*, *S. sagax*, *Merluccius productus*, *Etrumeus teres*, and *Argentina sialis* (Aceves-Medina *et al.*, 2003). These were the same dominant taxa in the winter of 2005 (Feb-Mar), except for the last four species, which were neither abundant nor frequently sampled (<15%). This was likely because the spawning of adults and core distribution of larvae (at least for *S. sagax* and *E. teres*) extended from the central to the northern region of the GC (Green-Ruiz & Hinojosa-Corona, 1997;

Table 3. Indicator species analysis with the maximum indicator value (IV) observed for each species during in the February-March and November-December surveys. Group column shows: (A21) = temperature above 21°C and (B21) = below 21°C; (hO_2) = high O_2 concentration, and (lowO_2) = low O_2 concentration. Only species with IV >25% are listed. *Indicates those fish larvae with statistically significant *P* values.

Species	Group	IV	Mean	SD	*P*
February-March					
*Vinciguerria lucetia**	A21	58.9	48.5	4.14	0.0105
Diogenichthys laternatus	A21	47.1	45.2	4.95	0.2990
Benthosema panamense	A21	40.1	40.8	5.46	0.4380
Hygophum atratum	A21	35.2	25.7	5.85	0.0840
Triphoturus mexicanus	B21	27	25.9	6.00	0.3740
*Leuroglossus stilbius**	B21	65.7	32.7	6.08	0.0010
*Engraulis mordax**	B21	56.5	24.4	6.37	0.0040
*Scomber japonicus**	B21	53.4	27	6.18	0.0030
November-December					
*Vinciguerria lucetia**	hO_2	68.8	30.6	8.40	0.0020
*Triphoturus mexicanus**	hO_2	66.6	39.2	8.19	0.0040
*Diogenichthys laternatus**	hO_2	68.1	30.5	7.99	0.0010
*Symphurus atramentatus**	hO_2	58.9	28.5	8.35	0.0060
Benthosema panamense	hO_2	58.0	50.5	5.49	0.1110
Serranus spp.	hO_2	45.5	20.9	7.44	0.0330
Citharichthys platophrys	hO_2	45.5	20.7	7.36	0.0330
Pontinus sp. 2	hO_2	45.5	20.9	7.51	0.0380
Symphurus oligomerus	hO_2	40.4	23.3	8.19	0.0580
Symphurus williamsi	hO_2	36.4	17.6	7.65	0.0860
Etropus spp.	hO_2	32.4	28.4	8.40	0.2320
Scorpaenodes xyris	hO_2	27.3	15.4	6.63	0.2190
Sardinops sagax	hO_2	25.1	30.6	8.36	0.6840
Citharichthys fragilis	lowO_2	33.4	37.2	8.40	0.6550
Engraulis mordax	lowO_2	52.3	41.6	8.07	0.1250

Table 4. Axis eigenvalues and explained variance (%) for each axis, with the correlation values for environmental variables of the canonical correspondence analysis for November-December 2005. Variables with the highest correlation values for each axis are in bold.

	Axis 1	Axis 2	Axis 3
Eigenvalue	0.226	0.059	0.037
% of explained variance	18.7	4.9	3.0
% of accumulated variance	18.7	23.6	26.6
Chl-*a*	0.275	0.341	0.051
O_2	**0.569**	-0.060	**-0.813**
MLD	0.261	**0.795**	**-0.540**
SST	**-0.647**	0.029	**-0.719**

Aceves-Medina *et al.*, 2009). Considering those differences, the larval fish assemblages were similar in the winters of 1988 and 2005; this information suggests well-structured larval assemblages in regions with SST values <21°C.

Species cluster analysis indicated that group WG1 of Feb-Mar 2005 was virtually the same as the northern larval fish complex observed in the winter of 1988, and the WG2 group was almost the same as in the southern complex from 1984-1988 (Aceves-Medina *et al.*, 2004). These similarities indicate that independent of the interannual environmental variability, the larval fish assemblages form groups closely associated with the reproductive strategies of the adults and that the larval assemblages have stable recurrent features in the GC. Spatial distribution of group WG1 indicates that the northern species complex was limited along its southern border approximately by the 21°C isotherm (Fig. 8a) and this was statistically confirmed using the MRPP test. The larval fish assemblage north of the 21°C isotherm was significantly different from that in the southern region. Because the SST range in Nov-Dec 2005 was >19.4°C, it was not possible to test the hypothesis that the 18°C isotherm was the northern limit of the southern larval fish assemblages, as suggested by Aceves-Medina *et al.* (2004). The southern species group (WG2) was present throughout the studied area, overlapping distribution with the northern assemblage. The ISA values showed that the northern complex had a significantly high fidelity (<21°C) in relation to the southern complex

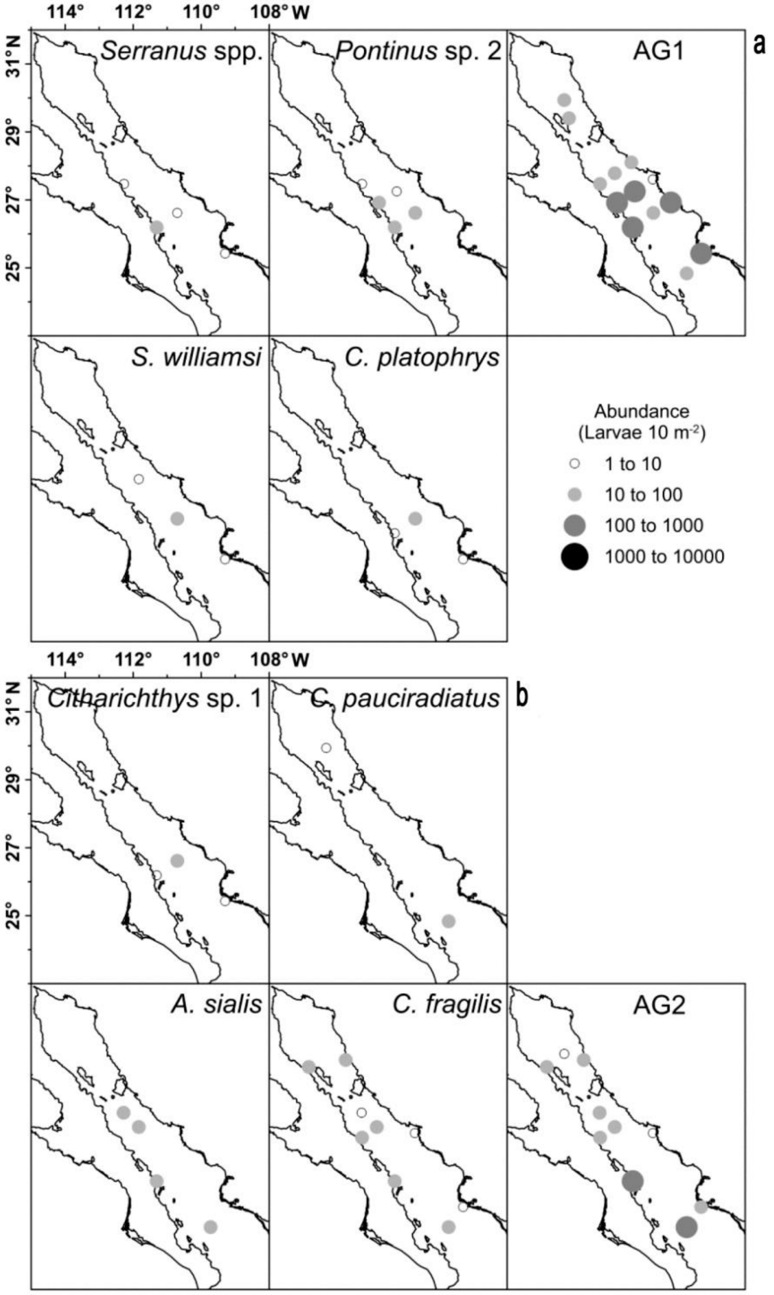

Figure 8. Distribution of larval fish species of November-December 2005 contained in a) group 1 (AG1), b) group 2 (AG2).

(>21°C), which had only one representative species of the warmer habitat in the GC.

The southern limit of the transitional region around the 21°C isotherm was characterized by low values of R and *H'*. We expected to find the highest values of *H'* in the northern part of the transitional region, due to the overlap of the northern and southern complexes. A similar pattern of *H'* values was observed during the spring and autumn periods of 1984-1988 (Aceves-Medina *et al.*, 2004), and during the Nov-Dec 2005 (this study). Considering the similarities of the larval fish assemblages during the winter of 1988 and 2005, we suggest a winter regionalization based on the larval fish assemblages consisting of a pattern in which range limits of the northern and southern assemblages expand and contract as a response to seasonal changes in oceanographic conditions. Thus, the northern complex is delimited to the south by the 21°C isotherm and the southern complex to the north by the 18°C isotherm. A transitional zone is present between these two isotherms, in which both complexes coexist, usually located in the central region of the Gulf of California (Fig. 11a).

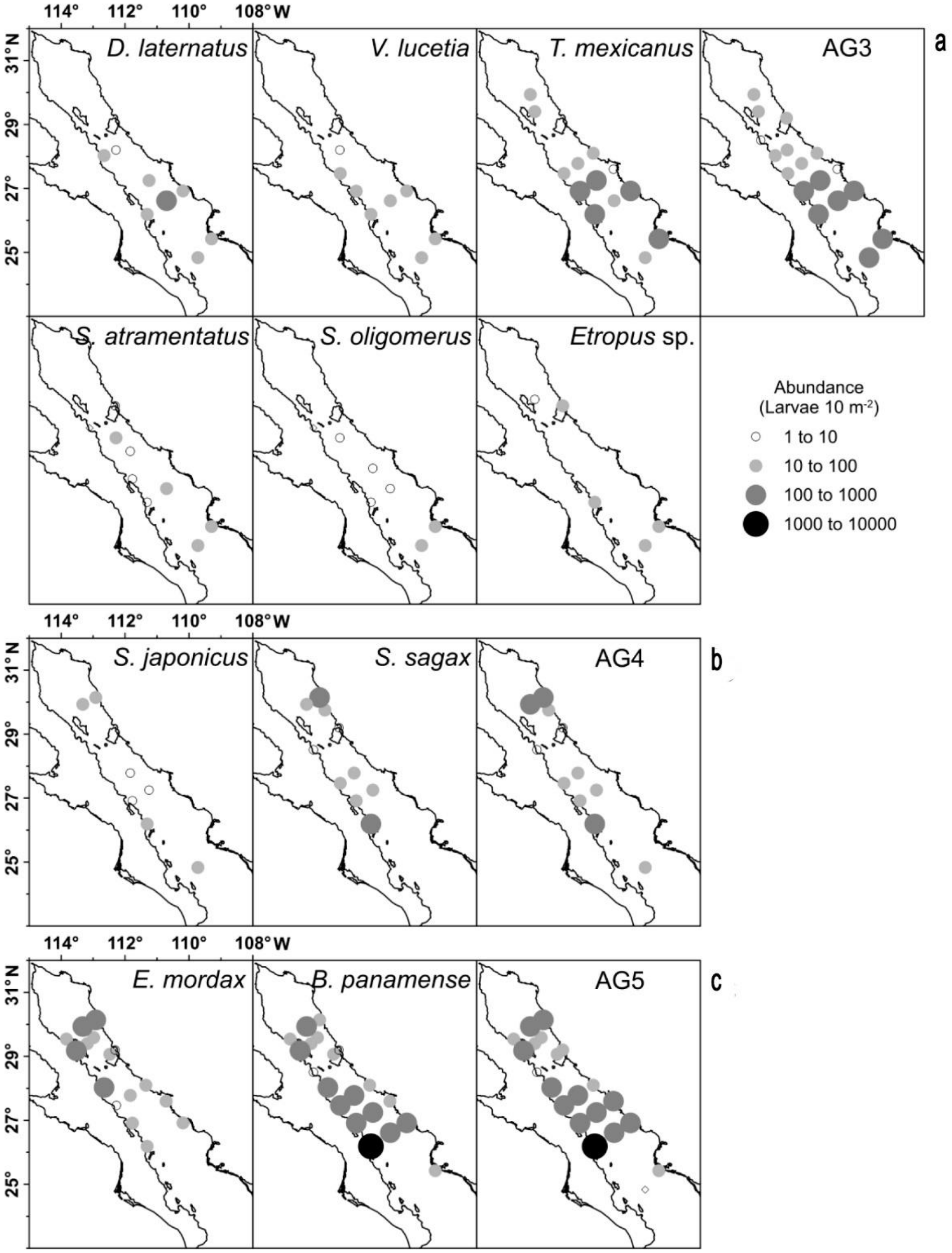

Figure 9. Distribution of larval fish species of November-December 2005 contained in a) group 3 (AG3), b) group 4 (AG4), c) group 5 (AG5).

This general distribution pattern of larval fish assemblages seems to be maintained during periods of water column stability and relatively high stratification. However, during periods of intense upwelling coupled with the circulation (such as those found during Nov-Dec 2005), larval fish assemblages seems to change in both species composition and distribution.

This research shows that 93% of the larval fish abundance in Nov-Dec 2005 was obtained with a higher number of taxa (34), compared to the same season of the 1984-1988 period, in which 95% of the abundance was achieved by eight species (Aceves-Medina *et al*., 2004). Additionally, during the 1984-1988 period upwelling index values were low (Lluch-Cota, 2000) compared to this study in which two new assemblages were found

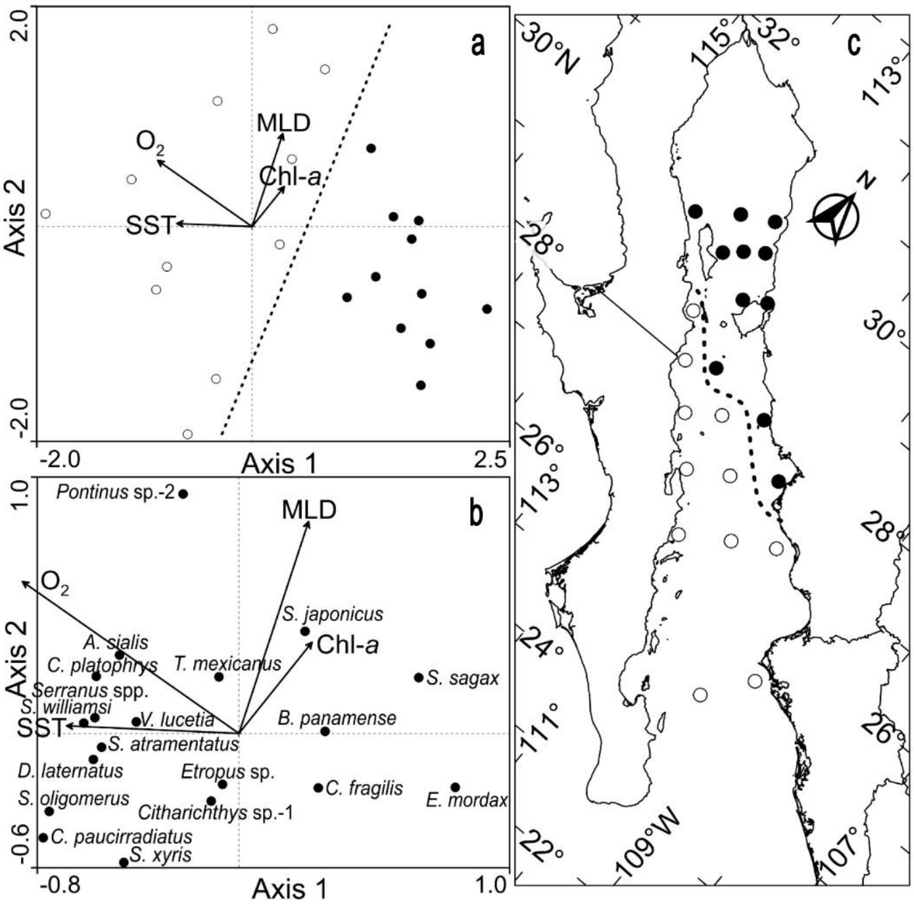

Figure 10. Canonical correspondence analysis for Nov-Dec 2005: a) dispersion diagram, and spatial distribution of the sampling stations, b) dispersion diagram per species, c) regionalization in the distribution of larval fish assemblages based on the dispersion diagram in figure 10a. SST: Sea surface temperature, O_2: average of the oxygen concentration from the surface to 75 m layer, MLD: depth to the mixing layer, and Chl-*a*: integrated Chl-*a* of the water column.

(AG1 and AG2). Similar taxonomic groups were not detected in previous studies in the central and southern area of the GC (Avalos-García *et al*., 2003; Aceves-Medina *et al*., 2004).

During Nov-Dec 2005 the larval fish assemblages were distributed mainly along the western side of the Gulf of California, except for *E. mordax* and *B. panamense*. The coastal environmental conditions caused by upwelling along the continental coast (eastern side) seem to have had a latitudinal effect on the distribution range of the larval fish assemblages since their northern limit coincided with the upwelling area.

A relevant difference between the distributions of the larval fish assemblages observed during the Nov-Dec 2005 and 1998 was that the 21°C isotherm did not match the southern limits of the northern assemblages, which extended into the water with SST >26.6°C. This observation was demonstrated statistically with the results of the MRPP analysis; no significant differences in species composition and abundance between northern and southern assemblages were found, and no indicator species were recorded for any of the areas delimited by the 21°C isotherm during Nov-Dec 2005.

The multivariate ordination of larval fish abundance as a function of in situ environmental variables measured during Nov-Dec 2005 showed two different regions of the GC, primarily distinguished by O_2 concentration gradient and the MLD ($P < 0.05$, MRPP test). The *H'* and R distributions pattern suggest a regionalization of larval fish assemblages similar to that detected in both the CCA and CA analyses (Fig. 11a). The taxa associated with the northern region and the mainland coast north of Guaymas mostly had a subarctic affinity. This distribution pattern results from the advection and retention processes related to upwelling and eddies in the central region of the GC (Aceves-Medina *et al.*, 2009; Avendaño-Ibarra *et al.*, 2013).

We conclude that the regionalization of fish larvae in the GC is primarily latitudinal, coinciding with the distri-

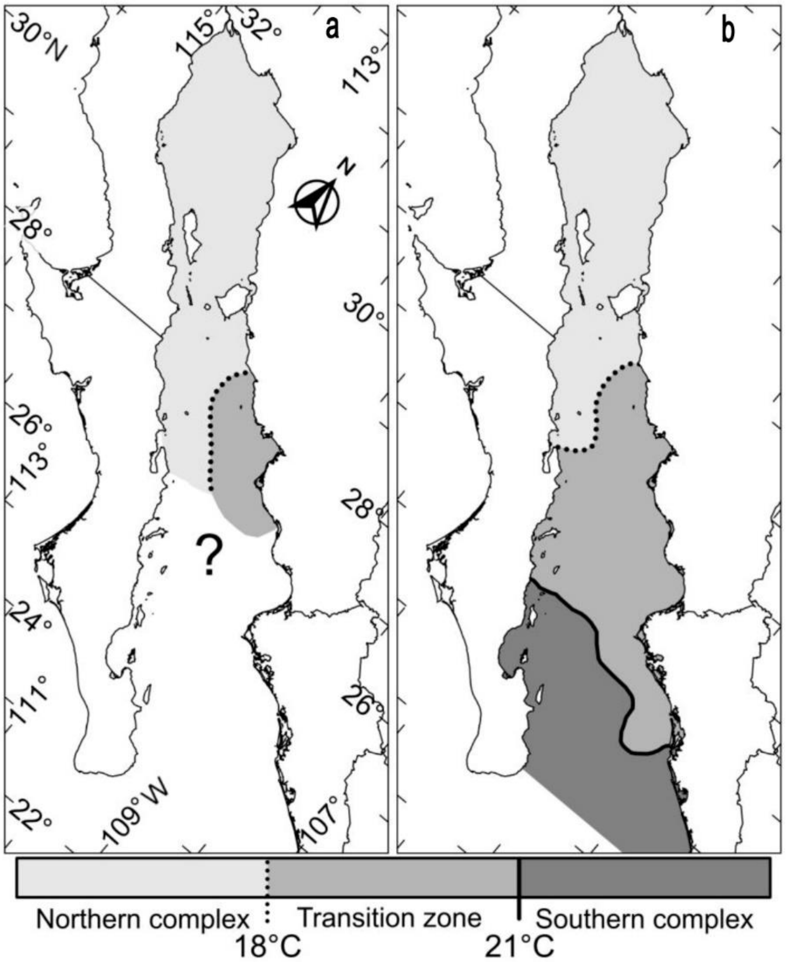

Figure 11. Larval fish assemblage regionalization in the Gulf of California. a) Winter 1988 (Aceves- Medina *et al.*, 2004). b) February-March 2005 (this research).

bution pattern observed in adult rocky fish species (Walker, 1960). However, this basic regionalization can be modified by the magnitude, type, and size of the mesoscale structures, as has been observed in the distribution of larval fish assemblages across local thermohaline fronts and eddies (Danell-Jiménez *et al.*, 2009; Contreras-Catala *et al*., 2012; Sánchez-Velasco *et al*., 2014). The surface isotherm of 21°C is a rough, but a practical and useful indicator of the southern limit of the northern larval fish assemblages during winter periods when mesoscale activity (upwelling, eddies, and fronts) is weak. However, the latitudinal gradient of the predominant larval fish assemblages in the central region of the Gulf weakens during periods with intense mesoscale structures activity (Nov-Dec), when wind stress generates intense upwelling that produces cold filaments and/or eddies; during these events the longitudinal gradient (coast-to-coast) of species assemblages is evident. Under stable conditions, several typical larval fish groups prevail, and during seasons of intense upwelling, they remain present. However, the detection of previously unreported species and groups in this study suggests that the southern limit of the northern larval fish complex (21°C isotherm) is not always valid, due to heterogeneities and offshore advection caused by coastal upwelling along the east coast. The cyclonic and anti-cyclonic eddies seem to be relevant structures that generate heterogeneity in the GC through dispersion and retention of larval fish assemblages. On a narrower geographical scale, several fish species spawn simultaneously and their eggs and larvae distribute inside and outside these structures, indicating high species resilience to cope with changing currents in highly dynamic environments.

ACKNOWLEDGEMENTS

This research was supported by projects of the Centro Interdisciplinario de Ciencias Marinas-Instituto Politécnico Nacional (SIP20050533), CONACYT

(FOSEMARNAT-2004-01-144, SAGARPA S007-2005-1-11717), Instituto de Ciencias del Mar y Limnología-Universidad Nacional Autónoma de México (PAPIIT IN219502, IN210622), and Secretaría de Marina, Armada de México. The authors wish to thank the Beca de Estímulo Institucional de Formación de Investigadores, Estímulo al Desempeño de la Investigación, Comisión de Operación y Fomento de Actividades Académicas, and SNI for the economic support. We thank the crew of the R/V El Puma, R/V Alejandro Humboldt and graduate students and scientists from CICIMAR, ICMyL-UNAM, Universidad Autónoma de Baja California Sur, and Universidad de Occidente for their cooperation in the collection of oceanographic information and zooplankton samples.

REFERENCES

Aceves-Medina, G., R. Palomares-García, J. Gómez-Gutiérrez, C.J. Robinson & R.J. Saldierna-Martínez. 2009. Multivariate characterization of spawning and larval environment of small pelagic fishes in the Gulf of California. J. Plankton Res., 31(10): 1283-1297.

Aceves-Medina, G., S.P.A. Jiménez-Rosenberg, A. Hinojosa-Medina, R. Funes, R.J. Saldierna & P.E. Smith. 2004. Fish larvae assemblages in the Gulf of California. J. Fish Biol., 65(3): 832-847.

Aceves-Medina, G., S.P.A. Jiménez-Rosenberg, A. Hinojosa-Medina, R. Funes, R.J. Saldierna-Martínez & W. Watson. 2003. Fish larvae from the Gulf of California. Sci. Mar., 67(1): 1-11.

Apango-Figueroa, E., L. Sánchez-Velasco, M.F. Lavín, V. Godínez & E.D. Barton. 2014. Larval fish habitats in a dipole eddy-pair in the Gulf of California. Deep-Sea Res. I, 103: 1-112.

Avalos-García, C., L. Sánchez-Velasco & B. Shirasago. 2003. Larval fish assemblages in the Gulf of California and their relation to hydrographic variability (autumn 1997-summer 1998). Bull. Mar. Sci., 72(1): 63-76.

Avendaño-Ibarra, R., E. Godínez-Domínguez, G. Aceves-Medina, E. González-Rodríguez & A. Trasviña. 2013. Fish larvae response to biophysical changes in the Gulf of California, Mexico (Winter-Summer). J. Mar. Biol. [http://www.hindawi.com/journals/jmb/2013/176760/)] Reviewed: 14 April 2016.

Contreras-Catala, F., L. Sánchez-Velasco, M.F. Lavín & V.M. Godínez. 2012. Three-dimensional distribution of larval fish assemblages in an anticyclonic eddy in a semi-enclosed sea (Gulf of California). J. Plankton Res., 34(6): 548-562.

Contreras-Catala, F., L. Sánchez-Velasco, E. Beier & V.M. Godínez. 2015. Efectos de un remolino de mesoescala sobre la distribución de larvas de peces mesopelágicas en el Golfo de California. Rev. Biol. Mar. Oceanogr., 50(3): 575-582.

Danell-Jiménez, A., L. Sánchez-Velasco, M.F. Lavín & S.G. Marinone. 2009. Three-dimensional distribution of larval fish assemblages across a surface thermal/ chlorophyll front in a semi-enclosed sea. Estuar. Coast. Shelf Sci., 85(3): 487-496.

Dufrêne, M. & P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol. Monogr., 67(3): 345-366.

Figueroa, J.M., S.G. Marinone & M.F. Lavín. 2003. A description of geostrophic gyres in the southern Gulf of California. In: O.U. Velasco-Fuentes, J. Sheinbaum & J. Ochoa (eds.). Nonlinear processes in geophysical fluid dynamics Kluwer Academic Publishers. Dordrecht, pp. 237-255.

Gaxiola-Castro, G., S. Álvarez-Borrego, M.F. Lavín, A. Zirino & S. Nájera-Martínez. 1999. Spatial variability of the photosynthetic parameters and biomass of the Gulf of California phytoplankton. J. Plankton Res., 21(2): 231-245.

Green-Ruíz, Y.A. & A. Hinojosa-Corona. 1997. Study of the spawning area of the northern anchovy in the Gulf of California from 1990 to 1994, using satellite images of the sea surface temperatures. J. Plankton Res., 19(8): 957-968.

Hammer, Ø., D.T.A. Harper & P.D. Ryan. 2001. PAST: Paleontological statistics software package for education and data analysis. [http://palaeo-electronica.org/2001_1/past/issue1_01.htm]. Reviewed: 14 April 2016.

Lavín, M.F. & S.G. Marinone. 2003. An overview of the physical oceanography of the Gulf of California. In: O. Velasco-Fuentes, J. Sheinbaum & J. Ochoa (eds.). Nonlinear processes in geophysical fluid dynamics. A tribute to the scientific work of Pedro Ripa. Kluwer Academic, Amsterdam, pp. 173-204.

Lluch-Cota, S.E. 2000. Coastal upwelling in the Eastern Gulf of California. Oceanol. Acta, 23(6): 731-740.

Martínez, J.A. & J.S. Allen. 2004. A modeling study of coastal-trapped wave propagation in the Gulf of California. Part I: response to remote forcing. J. Phys. Oceanogr., 34(6): 1313-1331.

McCune, B. & M.J.M. Mefford. 1999. (CD-ROM) PC-ORD. Multivariate analysis of ecological data. Version 4. MjM Software Design. Gleneden Beach, Oregon, USA.

McCune, B., J.B. Grace & D.L. Urban. 2002. (CDR-ROM) Analysis of ecological communities. MjM Software Design. Gleneden Beach, Oregon, USA.

Navarro-Olache, L.F., M.F. Lavín, L.G. Alvarez-Sánchez & A. Zirino. 2004. Internal structure of SST features in the central Gulf of California. Deep-Sea Res. II, 51(6-9): 673-687.

Nelson, J.S. 2006. Fishes of the world. John Wiley & Sons, New Jersey, 601 pp.

Palomares-García, R., J. Gómez-Gutiérrez & C.J. Robinson. 2013. Winter and summer vertical distribution of epipelagic copepods in the Gulf of California. J. Plankton Res., 5: 1009-1026.

Pegau, W.S., E. Boss & A. Martínez. 2002. Ocean color observation of eddies during the summer in the Gulf of California. Geophys. Res. Lett., 29(9): 1295.

Peguero-Icaza, M., L. Sánchez-Velasco, M.F. Lavín & S.G. Marinone. 2008. Larval fish assemblages, environment, and circulation in a semi-enclosed sea (Gulf of California, Mexico). Estuar. Coast. Shelf Sci., 79(2): 277-288.

Peguero-Icaza, M., L. Sánchez-Velasco, M.F. Lavín, S.G. Marinone & E. Beier. 2011. Seasonal changes in connectivity routes among larval fish assemblages in a semi-enclosed sea (Gulf of California). J. Plankton Res., 33(3): 517-533.

Peterson, W.T., D.F. Arcos, G.B. McManus, H.G. Dam, D. Bellatoni, T. Johnson & P. Tiselius. 1988. The nearshore zone during coastal upwelling: daily variability and coupling between primary and secondary production off central Chile. Prog. Oceanogr., 20(1): 1-40.

Sánchez-Velasco, L., M.F. Lavín, S.P.A. Jimenez-Rosenberg & V.M. Godínez. 2014. Preferred larval fish habitat in a frontal zone of the northern Gulf of California during the early cyclonic phase of the seasonal. J. Mar. Syst., 129: 368-380.

Sánchez-Velasco, L., M.F. Lavín, S.P.A. Jiménez-Rosenberg, V.M. Godínez, E. Santamaría-del-Ángel & D.U. Hernández-Becerril. 2013. Three-dimensional distribution of fish larvae in a cyclonic eddy in the Gulf of California during summer. Deep-Sea Res. I, 75: 39-51.

Smith, P.E. & S.L. Richardson. 1977. Standard techniques for pelagic fish egg and larval surveys. FAO, Roma, 100 pp.

Vidussi, F., H. Claustre, J. Bustillos-Guzman, C. Cailliau & J.C. Marty. 1996. Determination of chlorophylls and carotenoids of marine phytoplankton: separation of chlorophyll a from divinyl chlorophyll-*a* and zeaxanthin from lutein. J. Plankton Res., 18(12): 2377-2382.

Walker, B.W. 1960. The distribution and affinities of the marine fish fauna of the Gulf of California. Syst. Zool., 9(3/4): 123-133.

Zamudio, L., P. Hogan & E.J. Metzger. 2008. Summer generation of the southern Gulf of California eddy train. J. Geophys. Res., 113(C06020): 1-21.

Received: 4 May 2016; Accepted: 14 June 2017