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Article

Influence of hydrographic conditions on larval fish assemblage structure in the northern Gulf of California

Influencia de las condiciones hidrográficas en la estructura de los ensambles de larvas de peces en el norte del Golfo de California

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Resumen.- Se analiza la variabilidad estacional de los ensambles de larvas de peces en relación con las condiciones hidrográficas, durante 4 cruceros en la región norte del Golfo de California (GC). De acuerdo a las propiedades termohalinas y fauna asociada se identificaron 2 periodos: un periodo frío, cuando la temperatura disminuye y la corriente costera fluye en dirección al ecuador en invierno y primavera (circulación anticiclónica), dominado por especies de afinidad templada y subtropical (*e.g., Engraulis mordax* y *Merluccius productus*); y un periodo cálido, caracterizado por la intrusión de agua tropical superficial en verano y otoño (circulación ciclónica), con alta diversidad de especies de afinidad subtropical-tropical (*e.g.*, *Benthosema panamense* y *Anchoa* spp.). La variabilidad estacional se identifica como el elemento principal en la estructuración de los ensambles de larvas de peces. Sin embargo, la hidrodinámica incide en los patrones de agregación y el predominio de la biota pelágico costera, demersal y mesopelágica a lo largo del año.

Palabras clave: Larvas de peces, masas de agua, hidrografía, Golfo de California

Abstract.- This paper analyzes the seasonal variability on larval fish assemblage structure and the relationships to hydrographic conditions during 4 seasonal surveys in the northern Gulf of California. Two periods were identified according to thermohaline properties and associated fauna: a cold period, when temperature drops and the coastal current flows equatorward in winter and spring (anticyclonic circulation), dominated by species of temperate and subtropical affinity (*e.g., Engraulis mordax* and *Merluccius productus*); and a warm period, characterized by poleward intrusion of Tropical Surface Water in summer and autumn (cyclonic circulation), with a high diversity of tropical-subtropical species (*e.g.*, *Benthosema panamense* and *Anchoa* spp.). Cluster analysis defined 2 groups of stations and associated taxa: a Northern Group, located in the Delfín Basin, including mainly demersal taxa; and a Mainland-Insular group, of species with various affinities (demersal, coastal-pelagic, mesopelagic). Seasonal variability is identified as the main element in the structuring of larval fish assemblages. However, hydrodynamic changes influence the aggregation patterns and the prevalence of the coastal pelagic, demersal and mesopelagic biota throughout the year.

Key words: Fish larvae, water masses, hydrography, Gulf California

Introduction

The larval fish assemblages resulting from adaptive convergence within the life history of the species, common strategies may converge influenced by reproductive strategies, hydrographic processes, or use of the same resources (McGowen 1993). Larval assemblages may change in time and space, and in general, are flexible and sensitive to external perturbations; the degree of distortion varies in time and space, in small-scale disturbances such as local variations of turbulence, upwelling, or currents instabilities have short-lived impacts on assemblages, briefly disrupting them, but allowing their constituents to re-form relatively quickly after the perturbation has passed (Duffy *et al*. 2006). However, these associations tend to be distinct within oceanographic regions (*e.g.*, water masses) and have differential responses to environmental changes. Thus larval assemblages have been used to predict their spatial and temporal distributions related to the environment (Lluch-Belda *et al.* 1991, Ibaibarriaga *et al.* 2007), and also as indicators of environmental characteristics (Moser *et al.* 1987, Kane & Neira 2008).

The fish larval assemblages all along the Gulf of California (GC) indicated 2 main seasonal stages (winter and summer), and 2 transitional periods related with strong latitudinal temperature gradients (spring and autumn), where temperate and subarctic species spawn from autumn to spring in the north GC, and tropical and subtropical species dominate the southern region (Aceves-Medina *et al.* 2004). In northern GC, identifying the causes of the larval assemblages have been linked to specific hydrographic features such as eddies and currents and their seasonal evolution (Sánchez-Velasco *et al.* 2009, Peguero-Icaza *et al.* 2011).

The GC is unique for being a major evaporation basin, characterized by a broad seasonal variability in temperature, ocean circulation, winds, upwelling and productivity (Lavín *et al.* 1997, Lavín & Marinone 2003). Due to its high primary productivity with exceptionally high rates of primary productivity (Zeitzschel 1969, Gaxiola-Castro *et al.* 1995) and fish diversity (Thomson *et al.* 2000, Aceves-Medina *et al.* 2003), the Gulf of California is considered a conservation priority area in Mexico. In the GC, strong winds dominate from the NW in autumn and winter, with weak winds from the SE in late spring and summer (Bordoni *et al.* 2004, Lavín *et al.* 2009). The autumn and winter winds give rise to strong upwelling areas along the mainland coast. Sea surface temperature displays significant variations, with minimum temperatures in January and February that peak in August (18-32°C) (Lavín *et al.* 1997, Soto-Mardones *et al.* 1999).

The seasonal surface circulation of the GC is forced mainly by the geostrophic coastal circulation of the Eastern Tropical Pacific (Ripa 1997, Marinone 2003, Zamudio *et al.* 2008) and to a lesser degree by the surface winds, with a small contribution from buoyancy flux (Beier 1997, Ripa 1997). Direct observations of currents (Lagrangian and Eulerian) (Lavín *et al.* 1997, Palacios-Hernández *et al.* 2002), and numerical models (Beier 1997, Ripa 1997, Marinone 2003, Zamudio *et al.* 2008) have established that the surface circulation in the entire GC is anticyclonic from late autumn to early spring and cyclonic in summer. The poleward coastal current is associated with the intrusion of the Mexican Coastal Current into the Gulf of California as far as the GC entrance in summer (Marinone 2003, Zamudio *et al.* 2008, Lavín *et al.* 2009).

Two inter-related phenomena of the seasonally reversing circulation in the northern GC are an eddy in the center of the basin and a coastal current on the mainland shelf. Direct observations show that the central eddy is 150 m deep, cyclonic from June to September and anticyclonic from November to April (Palacios-Hernández *et al.* 2002, Carrillo *et al.* 2002). This eddy implies high potential for the recruitment of larvae in this province (Marinone 2012, Sánchez-Velasco *et al.* 2009, Peguero-Icaza *et al.* 2011), while coastal areas with strong currents on the continental side (low recruitment) could facilitate the connectivity and increase larval dispersal to different areas depending on the direction of flow (Marinone 2003, Marinone 2006, 2012; Marinone *et al.* 2011, Peguero-Icaza *et al.* 2011).

Environments characterized by distinctive ocean dynamics leads to complex fish larval associations that are often used as indicators of change between different assemblages (Moser *et al.* 1987, Aceves-Medina *et al.* 2004, Bernal *et al.* 2007, Keane & Neira 2008, Funes-Rodríguez *et al.* 2011). Larvae are vulnerable to different mortality sources, with their specific requirements and the characteristics of spawning grounds as important components in the development and survival. Processes that promote the enrichment and concentration of particles (*e.g.*, convergence, water column stability, mixing), along with retention processes, often result in favorable spawning conditions and good larval survival (Lasker 1978, Bakun 1996, Logerwell & Smith 2001, Agostini & Bakun 2002, Lynn 2003, McClatchie *et al.* 2007).

In the GC the main fisheries (in capture volume) are centered in the small pelagic fishes and therefore many ichthyoplankton studies has been focused to cold period of the year (December-April), and the rest of the year is not well represented. Most fish species in the GC have well-defined spawning periods and areas: temperate species spawn primarily in winter, while subtropical-tropical species spawn in summer (Moser *et al.* 1974, Green-Ruiz & Hinojosa-Corona 1997, Hammann *et al.* 1998, Aceves-Medina *et al.* 2004, Dannel-Jiménez *et al.* 2009, Sánchez-Velasco *et al.* 2009). According with this in many studies has been described several associations or recurrent groups of fish larvae. Our objective was to investigate temporal and spatial trends of fish larval species assemblages in function of the hydrographic conditions in the north region of the GC. We approached this goal by investigating trends in the species abundance, richness and diversity, and seasonal trends of species dominance and abundance.

Materials and Methods

Sampling and schedule

Zooplankton samples were collected in 4 cruises between the large islands (Tiburón and Ángel de la Guarda) and the northern Gulf of California (28°15'N 30°58'N and 111°50'W 114°30'W) in March (26 stations) and July 2005 (16), November 2006 (12) and April 2007 (12) (Fig. 1). Cruises were conducted to investigate the distribution and abundance of the Pacific hake (*Merluccius productus*) in the GC, following school's of this species on-board the research vessel INAPESCA BIP XI-Guaymas, Sonora. During each cruise, vertical plankton tows were conducted using a Bongo net (0.6 m in mouth diameter, 505-µm mesh) at a constant speed (1 m s^{-1}) through the water from near the bottom (~200 m depth) to the surface; vertical tows were made at an average of 137 m depth. Samples were preserved with 4% sodium borate-buffered formalin. Plankton biomass was measured using the displaced volume technique (Beers 1976). Fish eggs and larvae were removed from samples and identified to the lowest taxonomic level possible according to Moser (1996). Fish-larvae and zooplankton-biomass data were converted to 1000 m^3 of filtered water. Filtered water volume was calculated by multiplying the area of the net mouth by sampling distance. Temperature, pressure and conductivity were recorded with a CTD (Seabird 19) to a maximum depth of 200 m. All the depths from the hydrographic cast were used to elaborate T-S diagrams, in order to visualize water masses according to the intervals proposed by Lavín & Marinone (2003) and Castro *et al.* (2006). Chlorophyll-*a* 30-day composite image from Seawifs-Modis Aqua / Terra-Meris sensors and 30-day composite SST images are from Modis Aqua / Terra sensors were obtained from Scripps Institution of Oceanography and merged to increase coverage (reduced missing data due to clouds). These high resolution (1.1 km. in the nadir), type HRPT (High Resolution Picture Transmission) HDF format (Hierarchical Data Format) images were manipulated with the software WIM (Windows Image Manager) and ERMapper Image Processing System.

Statistical analyses

Larval abundance per taxon (90) and station (71) was organized in a matrix of species as rows and station as columns. To determine assemblage structure, the Shannon-Wiener diversity index (*H'*), Evenness (*J*) and dominance *k* were calculated. A Canonical Correspondence Analysis (McCune & Mefford 1999) was applied to each

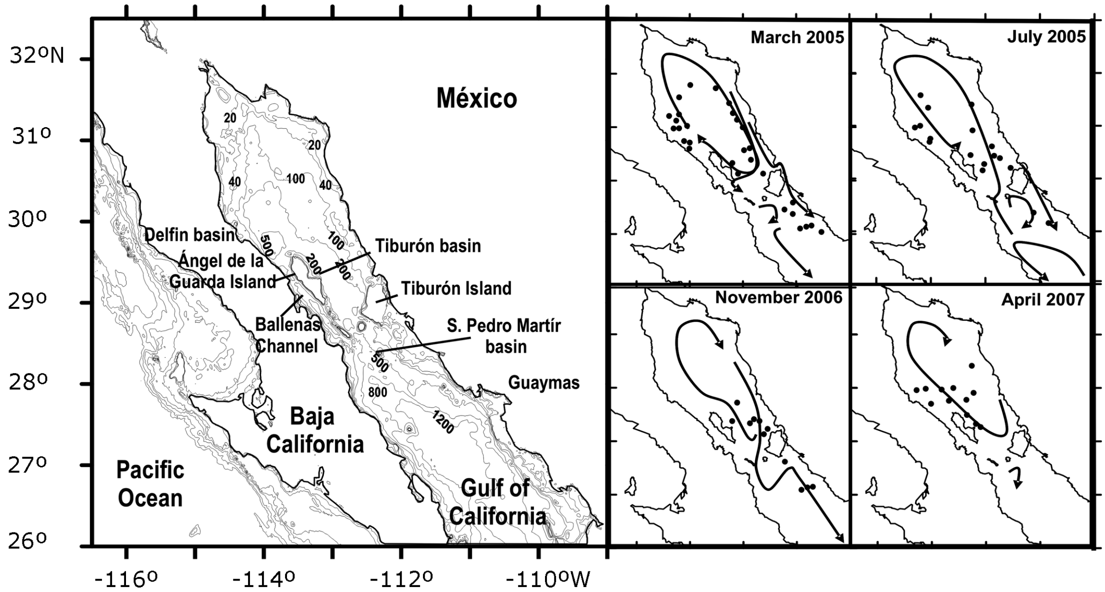

Figure 1. Study area and stations sampled in the northern Gulf of California, Mexico. Arrows, approximate schematization of the seasonal circulation of the northern Gulf of California for the depth range 0-60 m redraw from Marinone (2003) / Área de estudio y estaciones muestreadas en el norte del Golfo de California, México. Las flechas indican la esquematización aproximada de la circulación estacional entre 0-60 m de profundidad al norte del Golfo de California, redibujada de Marinone (2003)

cruise (999 permutations) for correlating larval abundance with hydrographyc conditions (temperature and salinity: 0, 10 and 50 m depth), including zooplankton biomass and maximum sampling depth. Additionally, unweighted pair-group method using arithmetic averages (UPGMA) based on Bray Curtis distance was used to construct dendrograms for describing the classification of groups of stations in each cruise. Similarity levels (cut-off limits) were defined by comparisons with distribution (faunal association) and information on spawning season (Moser 1996, Froese & Pauly 2013). Taxa that occurred at fewer than 5% of stations in each cruise were removed. All abundance data were log-transformed (x+1). Distribution and fish faunal association are given for adults based on Moser (1996) and Froese & Pauly (2013).

Quotient analysis was used to explore the relationship between larval distribution and temperature for the main species of each group derived of the CCA. In this method, the temperature was divided into classes (equally sized bins) and the percentage of stations and the percentage of total abundances per class were compared (*e.g.*, Van der Lingen *et al.* 2005). This technique is commonly used to identify the preference or avoidance of organisms, by evaluating their distribution in relation to variables of interest (Emmett *et al.* 2005, Bernal *et al.* 2007, Ibaibarriaga *et al.* 2007). Quotient analysis was performed using data from all surveys combined. *E. mordax* larvae were compared with the sea surface temperature, and *M. productus* and *B. panamense* larvae with temperature at the 50 m depth. Previous works of the vertical distributions of pelagic fish larvae in the California Current and Gulf of California indicated that *E. mordax* occurs mostly in the upper 23 m level and *M. productus* in greatest abundance within and below the thermocline (Ahlstrom 1959), similar to *B. panamense* generally at depths < 50 m (Danell-Jimenéz *et al.* 2009).

Results

Water masses properties

The Gulf of California Water (GCW) prevailed in all cruises and, to a lesser extent, the Subtropical Subsurface Water (StSsW) in November, March and April (Fig. 2). In July, GCW was the only water mass present, while in November

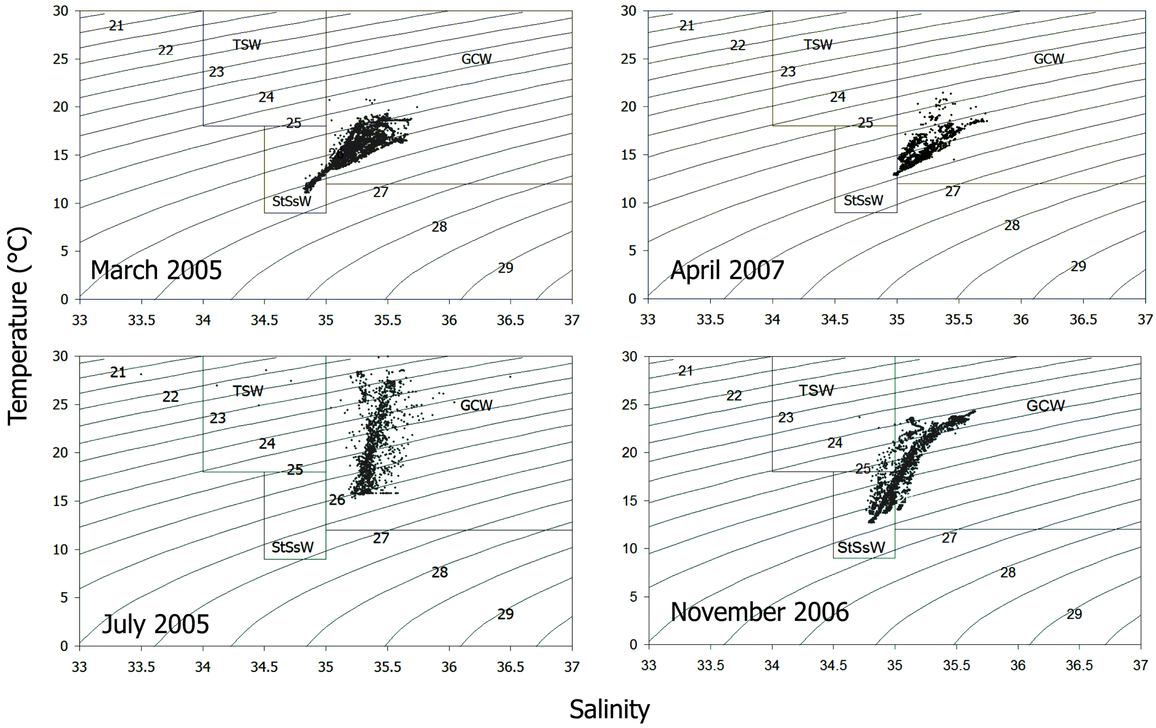

Figure 2. T-S diagram for water masses in the northern Gulf of California during March and July 2005, November 2006 and April 2007. GCW (Gulf of California water); StSsW (subtropical subsurface water); and TSW (tropical surface water) / Diagrama T-S para definir las masas de agua en el norte del Golfo de California durante marzo y julio 2005, noviembre 2006 y abril 2007. GCW (agua del Golfo de California); StSsW (agua subtropical subsuperficial); y TSW (agua tropical superficial)

Tropical Surface Water (TSW) was also observed, indicating the advance of tropical water flow. During March and April (cold season) the temperature was relatively low, suggesting mixing processes and little atmospheric warming. Satellite SST images revealed an area of lower temperature from the northern GC to south of the large islands (17-20°C, 17-19°C, respectively in March and April), with a higher SST farther south (21-23°C and 24°C, respectively) (Fig. 3). In contrast, during the warm season a high SST prevailed along the GC in July (~ 29°C) and the southern Gulf of California in November: however SST decreased slightly in northern GC (21-24°C), indicating an environmental transition in November (Fig. 3). During the cold period the highest chlorophyll *a* concentration (Chl *a*) was located primarily in the northern and eastern GC (Fig. 3), decreasing (≤ 1 mg m^{-3}) during the warm season, except for an increase in a narrow coastal strip at the mainland side of the GC and south of the large islands, mostly in November (Fig. 3). Additionally, mesoscale cyclonic eddies were observed, which were more evident in July in the northern and central GC Chl *a* images (Fig. 3).

Assemblage structure

Fish larvae belonged to 90 taxa in 41 families (Table 1). There was a remarkable difference in species composition with seasonality, with only some species occurring in 3

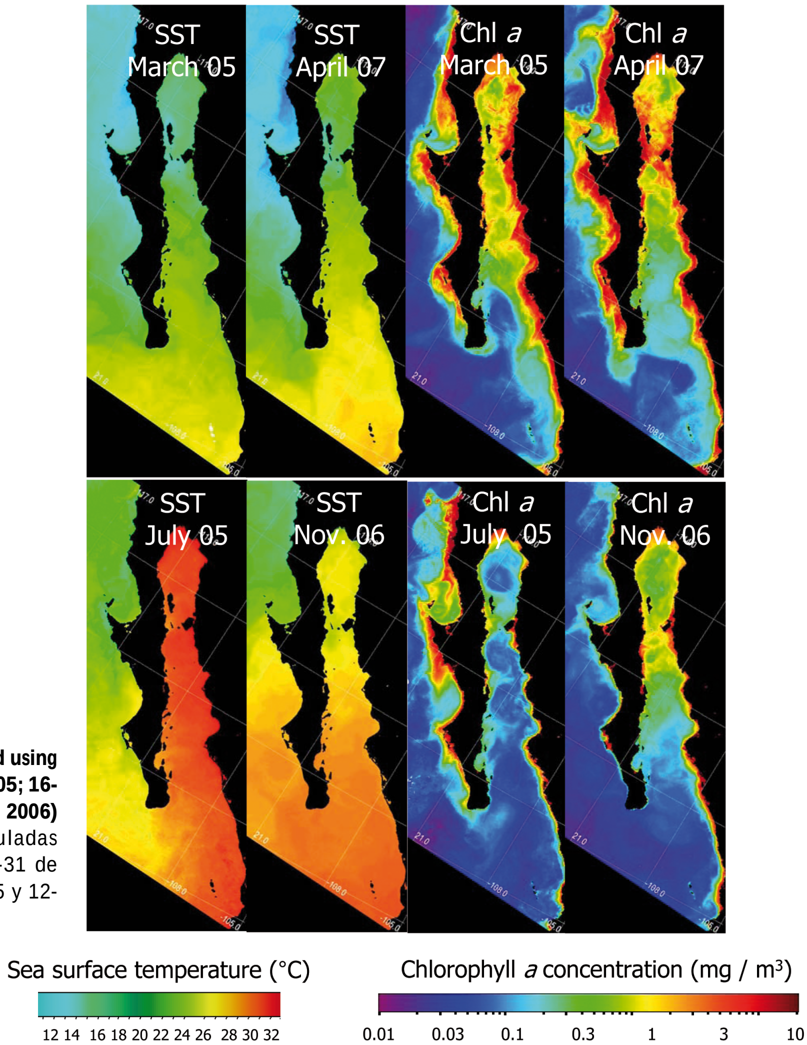

Figure 3. Composite images of SST and Chl *a* calculated using MODIS data in the Gulf of California (17-31 March 2005; 16-30 April 2007; 15-29 July 2005; and 12-26 November 2006) / Composición de imágenes de SST y Chl *a* calculadas usando datos MODIS en el Golfo de California (17-31 de marzo 2005; 16-30 de abril 2007; 15-29 de julio 2005 y 12-26 de noviembre 2006)

Table 1. Taxonomic composition, distribution, faunal association and average abundance (1000 m^3) of fish larvae in the northern Gulf of California during March and July 2005, November 2006 and April 2007 / Composición taxonómica, distribución, asociación faunística y abundancia promedio de larvas de peces (1000 m^3) en el norte del Golfo de California durante marzo y julio 2005, noviembre 2006 y abril 2007

Family	Code	Species	Distribution	Faunal association	Average abundance (AA) Standard deviation (SD)							
					March		July		November		April	
					AA	SD	AA	SD	AA	SD	AA	SD
Albulidae	Albusp	*Albula* sp.	Demersal	Tropical	34	9						
Ophichthidae	Otrise	*Ophichthus triserialis* (Kaup, 1856)	Demersal	Subtropical	37							
	OphichI	Ophichtidae I	Demersal				119	98				
Congridae	Rniten	*Rhynchoconger nitens* (Jordan & Bollman, 1890)	Demersal	Tropical	21							
Clupeidae	Eteres	*Etrumeus teres* (De Kay 1842)	Coastal pelagic	Subtropical	62				198		263	
	Oliber	*Opisthonema libertate* (Günther 1867)	Coastal pelagic	Tropical			79	31				
	Ssagax	*Sardinops sagax* (Jenyns 1842)	Coastal pelagic	Subtropical			54					
Engraulidae	Emord	*Engraulis mordax* (Girard 1854)	Coastal pelagic	Subtropical	2686	7189					928	1903
	Anchsp	*Anchoa* sp.	Coastal pelagic				381	349	350	607		
Argentinidae	Asialis	*Argentina sialis* (Gilbert 1890)	Demersal	Temperate	74	41						
Bathylagidae	Lstilb	*Leuroglossus stilbius* (Gilber, 1890)	Mesopelagic	Temperate	43	17						
Phosichthyidae	Vlucet	*Vinciguerria lucetia* (Garman 1899)	Mesopelagic	Tropical	21		503		29			
Synodontidae	Slucio	*Synodus lucioceps* (Ayres 1855)	Reef asociated	Subtropical			60	15	200	264		
Bregmacerotidae	Brbathy	*Bregmaceros bathymaster* (Jordan & Bollman, 1890)	Demersal	Subtropical					95	52		
Macrouridae	Cscaph	*Caelorinchus scaphopsis* (Gilbert, 1890)	Benthopelagic	Temperate	67	10						
	Clepto	*Coryphaenoides leptolepis* (Günther, 1877)	Bathydemersal	Deep-water	69							
Merlucciidae	Mprodu	*Merluccius productus* (Ayres, 1855)	Demersal	Temperate	92	62					39	
Moridae	Moridae	Moridae	Demersal						56			
	Pnemat	*Physiculus nematopus* (Gilbert, 1890)	Demersal	Tropical	27							
Myctophidae	Dlater	*Diogenichthys laternatus* (Garman, 1899)	Mesopelagic	Subtropical	37				175	123		
	Tmexic	*Triphoturus mexicanus* (Gilbert 1890)	Mesopelagic	Subtropical	21		473	576	63	60		
	Bpanam	*Benthosema panamense* (Tåning 1932)	Mesopelagic	Tropical	215	316	498	634	606	900		
Bythitidae	Crubri	*Cataetyx rubrirostris* (Gilbert, 1890)	Mesopelagic	Temperate	26							
Ophidiidae	Cemme	*Cherublemma emmelas* (Gilbert, 1890)	Bathydemersal	Tropical					56			
	Lnegro	*Lepophidium negropinna* (Hildebrand & Barton, 1949)	Demersal	Tropical			51					
	Lstigm	*Lepophidium stigmatistium* (Gilbert, 1890)	Demersal	Subtropical					56			
Carapidae	Edubi	*Encheliophis dubius* (Putnam 1874)	Demersal	Tropical			49					
Antennariidae	Antensp	*Antennarius* sp.					43					
Scorpaenidae	Sgutt	*Scorpaena guttata* (Girard, 1854)	Demersal	Subtropical			43					
	Scorp	Scorpaena	Demersal	Tropical			49					
	Pontsp	*Pontinus* sp.	Demersal	Tropical			54					
Sebastinae	Sebsp	*Sebastes* sp.	Demersal		28							
	SebspI	*Sebastes* I	Demersal		64							
	SebspII	*Sebastes* II	Demersal		21							
	SebspIII	*Sebastes* III	Demersal		42							
	SebspIV	*Sebastes* IV	Demersal		26							
	SebspV	*Sebastes* V	Demersal				59	2				
Triglidae	Prusca	*Prionotus ruscarius* (Gilbert & Starks, 1904)	Demersal	Tropical			102	83	224			
Serranidae	Pclath	*Paralabrax clathratus* (Girard, 1854)	Benthopelagic	Subtropical	27		54				44	
	Pnebul	*Paralabrax nebulifer* (Girard, 1854)	Reef asociated	Subtropical	64						60	
	Spsit	*Serranus psittacinus* (Valenciennes, 1846)	Reef asociated	Tropical			100	2				
	Sersp	*Serranus* sp.	Reef asociated	Tropical			62	12				
Apogonidae	Aretro	*Apogon retrosella* (Gill 1863)	Reef asociated	Tropical			54					
Carangidae	Corqu	*Chloroscombrus orqueta* (Jordan y Gilbert 1833)	Benthopelagic	Subtropical			82	36	66			
	DecapspI	*Decapterus* I	Reef asociated						56			
	DecapspII	*Decapterus* II	Reef asociated						336			
	Oinorn	*Oligoplites saurus inornatus* (Bloch & Schneider, 1801)	Reef asociated	Subtropical			121					
	Scrume	*Selar crumenophthalmus* (Bloch, 1793)	Reef asociated	Subtropical			49					
Gerreidae	Gerreidae	Gerreidae I	Demersal				61					
	Dperuv	*Diapterus peruvianus* (Cuvier, 1830)	Demersal	Subtropical			198					
	EucinosI	*Eucinostomus* I	Demersal				214					
Haemulidae	Haemul	Haemulidae	Demersal				49					
	HaemulI	Haemulidae I	Demersal				322					
	Xcalifor	*Xenistius californiensis* (Steindachner, 1876)	Demersal	Subtropical			88					
Kyphosidae	Hazurea	*Hermosilla azurea* (Jenkins y Evermann 1889)	Benthopelagic	Subtropical	59		88	36	29			
Pomacentridae	Atrosch	*Abudefduf troschelii* (Gill 1862)	Reef asociated	Tropical			54					
	Srecti	*Stegastes rectifraenum* (Gill 1862)	Reef asociated	Subtropical			63					
Labrisomidae	LabrisI	*Labrisomidae* I	Reef asociated				57					
Blenniidae	Hjenk	*Hypsoblennius jenkinsi* (Jordan & Evermann, 1896)	Demersal	Subtropical	70						32	

Table 1. Continued / Continuación

Gobiidae	GobidaeI	Gobidae I	Demersal		37		161				
	Gcresce	*Gobulus crescentalis* (Gilbert, 1892)	Demersal	Subtropical	31		214	166	56		25
	Igilber	*Ilypnus gilberti* (Eigenmann & Eigenmann, 1889)	Demersal	Subtropical			99	39			
	Qycauda	*Quietula y-cauda* (Jenkins & Evermann, 1889)	Demersal	Subtropical			206	59			
	Ldalli	*Lythrypnus dalli* (Gilbert,1890)	Demersal	Subtropical			144	172			
	Lzebra	*Lythrypnus zebra* (Gilbert, 1890)	Demersal	Subtropical			144	1			
Microdesmidae	Maffin	*Microdesmus affinis* (Meek & Hildebrand, 1928)	Demersal	Tropical			98				
Scombridae	Auxissp	*Auxis* sp.	Epipelagic				161		59		
	Sjapon	*Scomber japonicus* (Houttuyn, 1782)	Coastal pelagic	Subtropical	67				56		
Sciaenidae	Bicist	*Bairdiella icistia* (Jordan & Gilbert, 1882)	Demersal	Tropical			51				
	Rstearn	*Roncador stearnsii* (Steindachner, 1876)	Demersal	Subtropical			44				
	LarspII	*Larimus* II	Demersal						85	40	
Latilinae	Cprince	*Caulolatilus princeps* (Jenyns, 1840)	Reef asociated	Subtropical	27						
Eleotridae	Earmi	*Erotelis armiger* (Jordan & Richardson, 1895)	Demersal	Tropical	75				56		
Labridae	Hsemic	*Halichoeres semicinctus* (Ayres, 1859)	Reef asociated	Subtropical			43				
Trichiuridae	Tnitens	*Trichiurus nitens* (Garman, 1899)	Benthopelagic	Subtropical					56		
Paralichthyidae	Sovale	*Syacium ovale* (Günther 1864)	Demersal	Tropical			75	28			
	Cithasp	*Citharichthys* sp.	Demersal				51				
	Cfrag	*Citharichthys fragilis* (Gilbert, 1890)	Demersal	Subtropical	106	128			33		
	Ecross	*Etropus crossotus* (Jordan & Gilbert, 1882)	Demersal	Subtropical	42	20	92	65	112		
	Xliole	*Xystreurys liolepis* (Jordan & Gilbert, 1880)	Demersal	Subtropical							25
	Parasp	*Paralichthys* sp.	Demersal		37						
Pleuronectidae	PleuroI	*Pleuronectidae* I			70						
	PleuroII	*Pleuronectidae* II			140						
	PleuroIV	*Pleuronectidae* IV			33						
	Pvertic	*Pleuronichthys verticalis* (Jordan & Gilbert, 1880)	Demersal	Subtropical							20
Cynoglossidae	Satric	*Symphurus atricaudus* (Jordan y Gilbert 1880)	Demersal	Subtropical	83		89	26	189	107	
	Satram	*Symphurus atramentatus* (Jordan y Bollman 1890)	Reef asociated	Tropical	62				112		
	Sgorg	*Symphurus gorgonae* (Chabanaud, 1948)	Demersal	Tropical	37						
	Swilli	*Symphurus williamsi* (Jordan & Culver, 1895)	Demersal	Tropical			78	30	234	252	

of the 4 cruises (*Etrumeus teres, Vinciguerria lucetia, Triphoturus mexicanus, Benthosema panamense, Paralabrax clathratus, Hermosilla azurea, Etropus crossotus, Symphurus atricaudus*) and *Gobulus crescentalis* in 4. Both diversity (*H'*) and species number (*S*) were highest in July (mean 1.17 bits ind.$^{-1}$, 49 species); similar, intermediate *H'* values were observed in March and November (mean ~0.8 bits ind.$^{-1}$; 39 and 27 species, respectively), while the lowest occurred in April (mean 0.22 bits ind.$^{-1}$, 9 species) (Fig. 4a). The dominance *k* curves (Fig. 4b) clearly differentiate the cold season (dominated by *E. mordax*) from the warm season with its higher abundances of mesopelagic and demersal species and more equitable distribution of abundances overall (Table 1).

Cold season

The Cluster and Canonical Correspondence Analysis (CCA) identified 2 groups of stations in March (26 stations/10 taxa matrix) (Fig. 5a, b). The Northern Group was located in the Delfín Basin and comprised demersal species (*M. productus, Citharichthys fragilis, Physiculus nematopus, Albula* sp.). These species were positively related to higher salinities (Fig. 5a, b). The opposite was true of the Mainland-Insular Group composed mostly of mesopelagic and demersal species, including *E. mordax* larvae as dominant species in the Mainland-Insular group (*B. panamense, Leuroglossus stilbius,* and *Argentina sialis, E. crossotus, Caelorinchus scaphopsis*). Axes 1 and 2 accounted for 30.2% of the cumulative variance; the highest correlations for species axis 1 were 0.76-0.81 (salinity at 0, 10, 50 m depth), and for axis 2 was 0.75 (depth) (Fig. 5b, Table 2). Only the Northern Group was identified in April (12 stations and 10 species) because the southern stations were no sampled (Fig. 6a, b). *E. mordax* and demersal species (*e.g.*, *M. productus*,

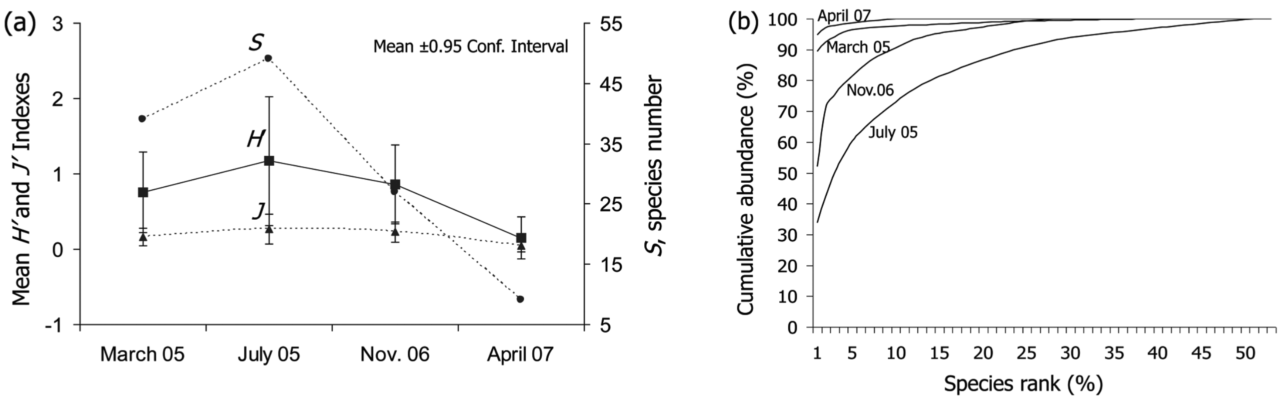

Figure 4. (a) Temporal changes in the assemblage structure of fish larvae: diversity (*H'*); equitability (*J'*); number of species (*S*) and (b) dominance *k* Index in the northern Gulf of California / (a) Cambios temporales de la estructura del ensamble de larvas de peces: diversidad (*H'*); equitatividad (*J'*); número de especies (*S*) y (b) dominancia *k* en el norte del Golfo de California

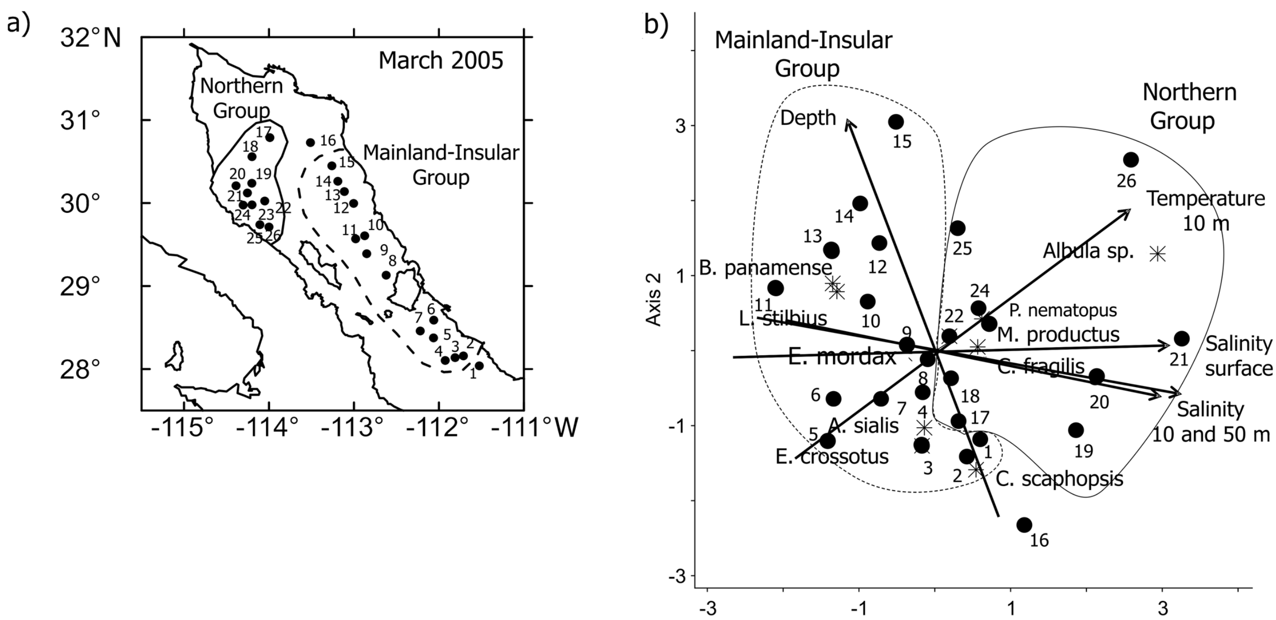

Figure 5. (a) Station Groups determined from Cluster analysis, based on the summed abundance of each taxon (10 taxa and 26 stations) and (b) CCA ordination diagram using the same similarity matrix during March 2005. Temperatures, and salinities (0, 10, 50 m depth), zooplankton biomass and sampling depth (arrows). Clusters are indicated in the ordination. Mainland-Insular Group and Northern Group / (a) Grupos de estaciones determinados por el análisis de agrupamientos, basados en la sumatoria de la abundancia de cada taxón (10 taxones y 25 estaciones) y (b) ordenación de CCA usando la misma matriz de similitud durante marzo 2005. Temperaturas y salinidades (0, 10, 50 m de profundidad), biomasa del zooplancton y profundidad del muestreo (flechas). Los agrupamientos son indicados en la ordenación. Grupo Continental-Insular y Grupo Norteño

Paralabrax nebulifer, Pleuronichthys verticalis) were related to lower temperatures and salinities, and to higher zooplankton biomass, but *E. teres* and *Paralabrax clathratus* were related to higher salinities. The variance accounted for axes 1 and 2 was 46.5%; the highest correlations for species axis 1 were 0.70 (temperature at 50 m depth) and 0.50 (SST and salinity at 50 m); for axis 2, these were 0.52 and -0.52 (zooplankton and SST, respectively) (Fig. 6b, Table 2).

WARM SEASON

Two groups of stations (16 stations/49 taxa matrix) were identified in July (Fig. 8a). The Northern Group, was located in the Delfín basin (Fig. 7a) and larvae of *Anchoa* sp. and demersal species (*e.g.*, *Citharichtys* sp., *Bairdiella icistia*, Gerreidae) were related to higher SST, and the Mainland-Insular Group, broadly distributed from the vicinity of Guaymas to north of the large islands, dominated by *B. panamense* and including mainly

Table 2. Axis eigenvalues and explained variance (%) Canonical Correspondence Analysis using larval fish abundance and environmental parameters during in March and July 2005, November 2006 and April 2007 in the northern Gulf of California / Eigenvalores y varianza explicada (%) del Análisis de Correspondencia Canónica (CCA) usando la abundancia de larvas y parámetros ambientales durante marzo y julio 2005, noviembre 2006 y abril 2007 en el norte del Golfo de California

	March 2005			April 2007		
	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
Eigenvalue	0.04	0.27	0.13	0.83	0.59	0.43
Explained variance (%)	14.40	10.50	5.30	27.00	19.40	14.10
Accumulated variance (%)	14.40	24.90	30.20	27.00	46.50	60.50
	Correlation values			Correlation values		
Maximum sampling depth	-0.32	**0.75**	-0.19	-0.20	**0.46**	0.35
Zoop	0.22	0.02	-0.17	-0.16	**0.52**	-0.13
T-0	0.29	0.20	-0.22	**0.50**	0.03	-0.05
T-10	0.48	0.30	0.29	0.12	0.13	-0.20
T-50	-0.27	-0.07	0.15	**0.70**	-0.38	0.02
S-0	**0.76**	0.00	**-0.56**	0.06	**-0.52**	-0.01
S-10	**0.81**	-0.13	-0.32	0.36	-0.39	0.38
S-50	**0.80**	-0.10	-0.07	**0.50**	-0.41	-0.08

	July 2005			November 2006		
	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
Eigenvalue	0.60	0.55	0.47	0.58	0.52	0.39
Explained variance (%)	12.70	11.70	9.90	20.00	17.80	13.40
Accumulated variance (%)	12.70	24.40	34.30	20.00	37.80	51.10
	Correlation values			Correlation values		
Depth	-0.28	0.22	**-0.52**	-0.13	**0.46**	**0.77**
Zoop	**0.73**	0.38	-0.09	-0.50	0.23	0.04
T-0	-0.43	-0.18	**0.82**	**0.85**	0.02	0.46
T-10	0.43	0.27	**0.66**	**0.85**	0.03	0.46
T-50	**0.56**	0.42	0.18	**0.89**	0.28	0.02
S-0	0.30	0.06	**0.91**	-0.15	0.31	-0.04
S-10	-0.44	-0.41	-0.01	**0.69**	0.00	**0.56**
S-50	**-0.57**	0.36	0.05	**0.60**	0.44	-0.15

Selected variables are those that were significant in Monte Carlo tests of F-ratios ($P < 0.05$), and so were used to constrain the CCA ordination. Bold values denote those variables that were considered to be biologically meaningful for that CCA axis (*i.e., $r \geq 0.5$*)

demersal species (*e.g.*, *Symphurus williamsi*, *Scyacium ovale*) were related to increasing zooplankton biomass and temperature at 50 m deep. Mesopelagic species in the Mainland-insular group (*V. lucetia*, *Triphoturus mexicanus*) were associated with less saline water at 50 m deep, south of the study area. Axes 1 and 2 accounted for 24.4% of cumulative variance; the highest correlations for species axis 1 were 0.73 (zooplankton), and 0.56 and -0.57 (temperature and salinity at 50 m, respectively) (Fig. 7b, Table 2). In November, only the Mainland-Insular Group was clearly defined (12 stations and 27 taxa) because the north was no sampled, except by one isolated station (Fig. 8a). Some mesopelagic and demersal species (*V. lucetia*, *T. mexicanus*, *Diogenichthys laternatus* and *B. bathymaster*) were inversely related to temperature and salinity, in contrast positive relationships for *B. panamense*, *Anchoa* spp., *Auxis* sp., *H. azurea* and *S. williamsi*. Axes 1 and 2 accounted for 37.8% of cumulative variance; the highest correlations for species axis 1 were 0.85-0.89 (temperature at 0, 50 and 100 m depth) and 0.69 and 0.60 (salinity at 10 and 50 m depth, respectively) (Fig. 8a, Table 2).

The quotient analysis conducted to identify the preferred temperature intervals of fish larvae (Fig. 9) revealed that *E. mordax* larvae occurred between 16° and 19°C SST, with a peak abundance at 16°C. This species was most abundant in March in the Tiburón Basin and south of Tiburón Island (> 30.000 larvae per 1000 m^3), and in April in the Delfín Basin (> 6.500 larvae per 1000 m^3). *Merluccius productus* prevailed in the range of 15° to 17°C (peak at 16°C, 50 m depth) and was most abundant in March in the Delfín and Tiburón basins (~ 500 larvae per 1000 m^3), but was scarce in April (~50 larvae). *B. panamense* was collected in a broad temperature range (15° to 24°C, 50 m depth) with a peak at 18°C. This species was most abundant in July and in November in the Tiburón basin and near Guaymas (500-1500 larvae per 1000 m^3) (Fig. 9).

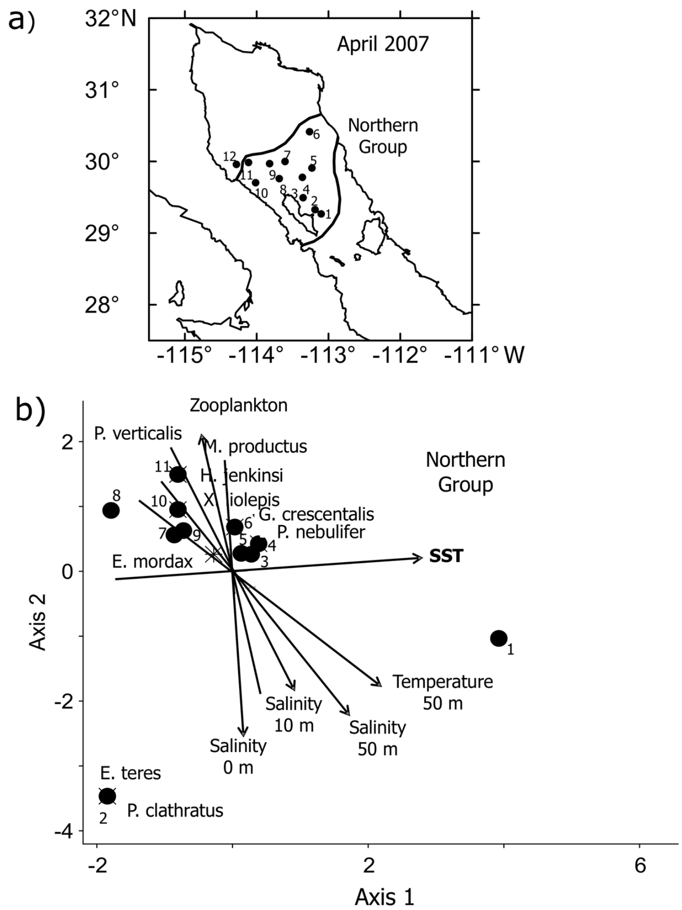

Figure 6. (a) Station Groups determined from Cluster analysis, based on the summed abundance of each taxon (10 taxa and 12 stations) and (b) CCA ordination diagram using the same similarity matrix during April 2007. Temperatures and salinities (0, 10, 50 m depth), zooplankton biomass and sampling depth (arrows). Clusters are indicated in the ordination. Northern Group / (a) Grupos de estaciones determinados por el análisis de agrupamientos, basados en la sumatoria de la abundancia de cada taxón (10 taxones y 12 estaciones) y (b) ordenación de CCA usando la misma matriz de similitud durante abril 2007. Temperaturas y salinidades (0, 10, 50 m de profundidad), biomasa del zooplancton y profundidad del muestreo (flechas). Los agrupamientos son indicados en la ordenación. Grupo Norteño

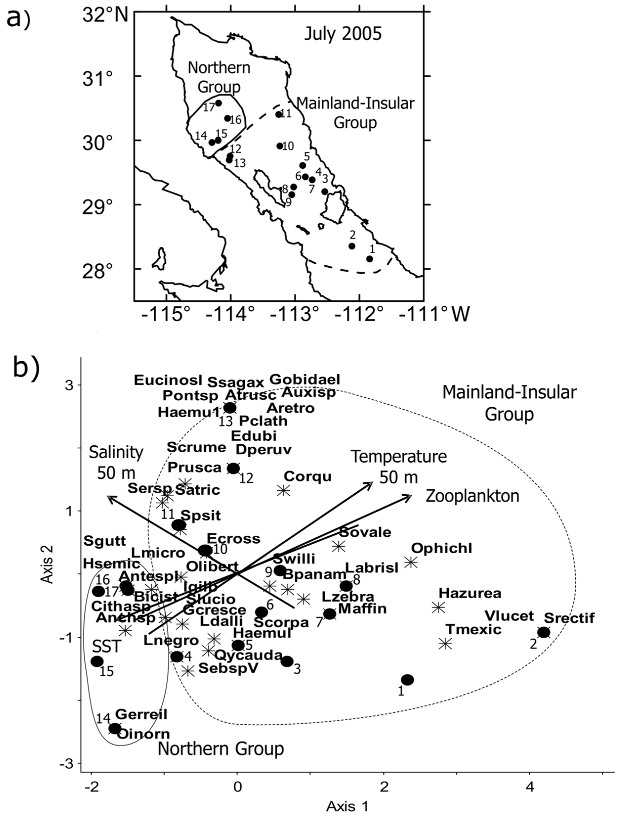

Figure 7. (a) Station Groups determined from Cluster analysis, based on the summed abundance of each taxon (49 taxa and 17 stations) and (b) CCA ordination diagram using the same similarity matrix during July 2005. Temperatures and salinities (0, 10, 50 m depth), zooplankton biomass and sampling depth (arrows). Clusters are indicated in the ordination. Mainland-Insular Group and Northern Group. Acronyms are listed in Table 1 / (a) Grupos de estaciones determinados por el análisis de agrupamientos, basados en la sumatoria de la abundancia de cada taxón (49 taxones y 17 estaciones) y (b) ordenación de CCA usando la misma matriz de similitud durante julio 2005. Temperaturas y salinidades (0, 10, 50 m de profundidad), biomasa del zooplancton y profundidad del muestreo (flechas). Los agrupamientos son indicados en la ordenación. Grupo Continental-Insular y Grupo Norteño. Abreviaturas se muestran en Tabla 1

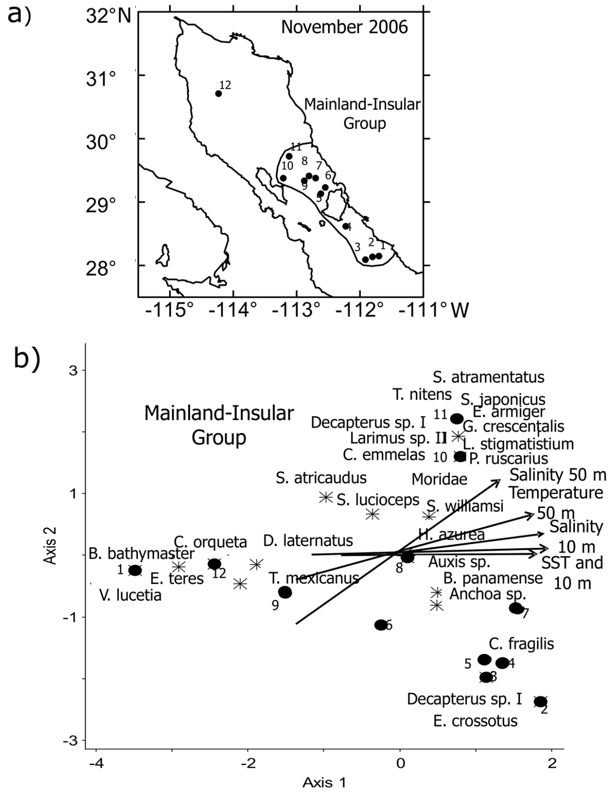

Figure 8. (a) Station Groups determined from Cluster analysis, based on the summed abundance of each taxon (27 taxa and 12 stations) and (b) CCA ordination diagram using the same similarity matrix during November 2006. Temperatures and salinities (0, 10, 50 m depth), zooplankton biomass and sampling depth (arrows). Clusters are indicated in the ordination. Mainland-Insular Group / (a) Grupos de estaciones determinados por el análisis de agrupamientos, basados en la sumatoria de la abundancia de cada taxón (27 taxones y 12 estaciones) y (b) ordenación de CCA usando la misma matriz de similitud durante noviembre 2006. Temperaturas y salinidades (0, 10, 50 m de profundidad), biomasa del zooplancton y profundidad del muestreo (flechas). Los agrupamientos son indicados en la ordenación. Grupo Continental-Insular

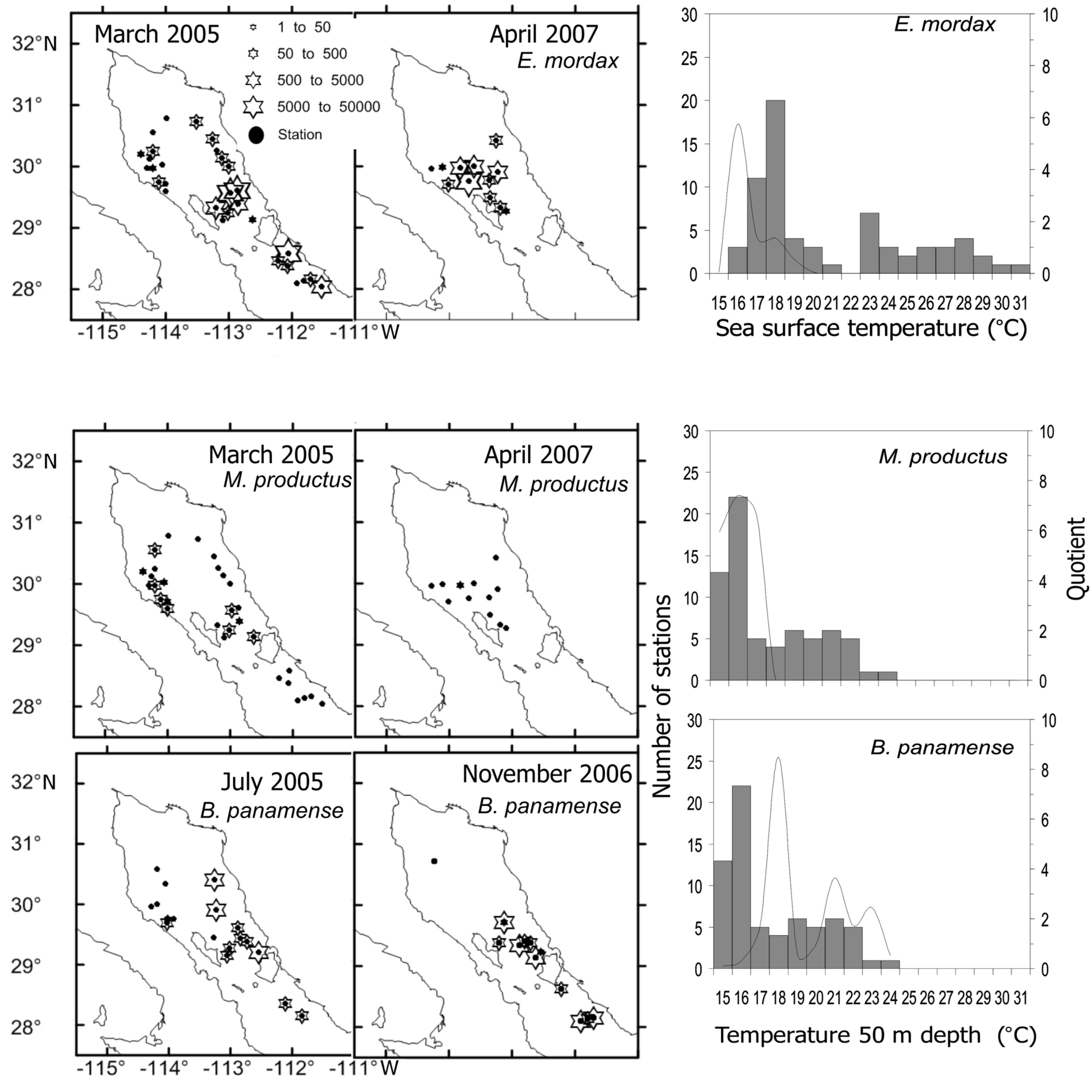

Figure 9. Distribution of the most abundant fish larvae (abundance per 1000 m³) and Quotient lines of larvae abundance (dark line) of *Engraulis mordax* in relation to the sea surface temperature and *Merluccius productus* and *Benthosema panamense* to temperature at 50 m depth. Histograms indicate the number of samples taken in each class interval in the northern Gulf of California / Distribución de las larvas de peces más abundantes (abundancia por 1000 m³) y líneas de cocientes de la abundancia de larvas (línea obscura) de *Engraulis mordax* en relación la temperatura superficial del mar y *Merluccius productus* y *Benthosema panamense* a la temperatura de 50 m de profundidad. Los histogramas indican el número de muestras recolectadas en cada intervalo de clase en el norte del Golfo de California

Discussion

Seasonal variation

The variability in the composition, distribution and assemblage structure of fish larvae displayed a seasonal pattern that closely matched the variability in temperature and salinity in northern GC. Distinctive features in the cold season (March and April) included the Gulf of California Water (GCW) and the Subtropical Subsurface Water (SsStW), the latter with its maximum intrusion into the northern Gulf in autumn and winter (Lavín *et al.* 1997). However, the seasonal variability in SST depends on the intensity of the atmospheric warming, especially in the northern GC where strong tidal currents and wind cause vertical mixing that cool the surface waters (Marinone 2003). This was confirmed by the decrease in SST during the cold season, which suggests mixing processes with the prevalence of NW winds and the increase in Chl-*a* values between the northern GC and large islands. During winter, high surface Chl-*a* (2-4 mg m^{-3}) associated with the lowest SST is reported by Gaxiola-Castro *et al.* (1995).

The cold season displayed a marked dominance of *Engraulis mordax*. Its larvae were collected from 16° to 20°C SST, and peaked at 17°C, similar to previous reports, from late autumn to early spring, mainly in areas adjacent to the large islands (Green-Ruíz & Hinojosa-Corona, 1997, Aceves-Medina *et al.* 2009, Inda-Díaz *et al.* 2010), even with El Niño warming (Sánchez-Velasco *et al.* 2002). However, those findings contrast with those observed by Sánchez-Velasco *et al.* (2009) who found *E. mordax* larvae among the more abundant taxa in summer, when SST reach peaks values (~27°C) in the northern GC. *Merluccius productus* occurred in an environment of lower SST as confirmed by the CCA and it was taken only during winter in the Sánchez-Velasco *et al.* (2009) study.

E. mordax and *M. productus* are related to lower water temperature and salinity, except for *M. productus* in March in the Northern Group, when it was related to more saline water suggested by the CCA. Although both species are adapted to living in the Gulf of California, as judged by their larval densities (Moser *et al.* 1974, Green-Ruiz *et al.* 1994, Aceves-Medina *et al.* 2004, this study), both are more abundant in the California Current area (Bailey *et al.* 1982, Lluch-Belda *et al.* 1991, Moser *et al.* 1993, Moser *et al.* 1997, Funes-Rodríguez *et al.* 2009), and their relationships with the temperature are similar between the GC and California Current. *E. mordax* eggs and larvae are collected between 15° and 18°C SST in the GC (Green-Ruiz *et al.* 1994, this study) and California Current (12 to 18.9°C) (Ahlstrom 1966). *M. productus* larvae prevalence temperature range are comparable to the Southern Baja California (15-17°C at 50 m depth), but relatively cold with peak concentrations of larvae in Ensenada waters at 14°C (Funes-Rodríguez *et al.* 2009) and in the California Current (11.5-14.3°C) (Ahlstrom & Counts 1955).

Warming induces a marked stratification but is the cyclonic circulation that results in isopycnal dome-shaped structure in the northern GC (Marinone 2006, Lavín *et al.* 1997, Beier & Ripa 1999, Lavín & Marinone 2003). This season was dominated by GCW due to the predominance of evaporation over precipitation; hence, GCW can be classified as subtropical water for its high salinity. Tropical Surface Water (salinity < 35, temperature ≥ 18°C) displays its maximum intrusion in the summer; the opposite occurs in the winter (Lavín *et al.* 1997). The rise in SST, coupled with a lower concentration in Chl-*a*, characterized the warm season (July and November). During warm season, Chl-*a* values are low (< 1 mg m^{-3}) along the GC, except for some stations with subsurface maximum (10 m depth) near Tiburón Island in autumn (Gaxiola-Castro *et al.* 1999). During the warm season, *Benthosema panamense* larvae dominated along with the increase in the diversity of species of tropical-subtropical affinity, in accordance with a greater stability of the water column which favors high-diversity centers, as pointed out by other authors (Avalos-Garcia *et al.* 2003, Aceves-Medina *et al.* 2004, Dannell-Jiménez *et al.* 2009, Sánchez-Velasco *et al.* 2009).

Spatial variation

Stations and associated species groups formed a Northern Group near the Delfín basin, composed mainly of demersal species, and a Mainland-Insular Group, stretching from the large islands to south of Tiburón Island to the central GC, with a higher diversity of larvae whose adults belongs to various habitat affinities (demersal, coastal pelagic and mesopelagic). Station groups and dominant species in the larval assemblages were comparable with those described by other authors (Sánchez-Velasco *et al.* 2009, Peguero-Icaza *et al.* 2011), and are probably related to seasonal fluctuations in hydrodynamic conditions.

The interface and connectivity between both groups (Northern and Mainland-Insular) can be related to tidal currents affecting the northern Gulf from San Pedro Mártir basin, where strong tidal currents are recorded (50-100 cm s^{-1}) (Badan-Dangon *et al.* 1991, Marinone 2003). An important vertical migration of larvae takes place in this threshold that separates deep southern waters from shallower northern waters (Marinone *et al.* 2011). Larvae of the Mainland-Insular group (*e.g.*, *V. lucetia, B. panamense, T. mexicanus*), with peak population densities in deep waters (mesopelagic zone) south of San Pedro Mártir basin, could eventually advected upward in the water column and then be redistributed by surface currents to the northern Gulf, particularly in the warm season when a northward flow prevails both at the surface and in deep water (Marinone 2003, 2006, Marinone *et al.* 2011); resulting in a high retention of particles in the northern GC (Marinone 2012, Peguero-Icaza *et al.* 2011) and the expansion of the Mainland-Insular group from the central GC.

The circulation in the northern GC is cyclonic from June to September and anticyclonic from November to March (Lavín *et al.* 1997, Lavín & Marinone, 2003, Marinone 2003, López-Calderón *et al.* 2008). Along the mainland coast, the northern GC includes a wide continental shelf and strong currents, so that particles can travel 50 km in just 10-20 days; however, their final destination will be at the continental side in winter anticyclone gyre (Marinone 2003). This is consistent with the horizontal expansion of *E. mordax* spawning area along mainland coast and to the south of the large islands (Mainland-Insular group), with a peak of viteline larvae in the Tiburón basin in the winter anticyclonic gyre. This distribution of *E. mordax* also was observed in other studies (Moser *et al.* 1974, Cotero-Altamirano & Green-Ruiz 1997) and can be related to dispersal from breeding grounds due to equatorward currents.

However, other species of the Northern group (demersal species) could be retained in the vicinity of the Delfin basin and eventually be dispersed towards the Tiburón basin. This is possible because particles remain near the center of gyre and along the peninsula's coast (Delfín basin) for two or more months (Marinone 2006); moreover, small larvae could remain at medium depths (50-100 m), as in the case of *M. gayi* which does not migrate vertically until the caudal fin is fully developed (Landaeta & Castro 2012), or *M. productus* larvae complete the notochord flexion in ~7-8 weeks in the California Current (Butler & Nishimoto, 1997). Additionally, it is known that vertical excursion of particles in the gyre area is slight (< 45 m in winter, < 25 m in summer) relative to the average depth in the area (130 m) (Marinone 2006). Nevertheless, *M. productus* viteline and flexión larvae were found in the Delfín and Tiburón basins in winter, suggesting the maximum expansion of the spawning area, whereas their viteline larvae were scarce and restricted to the Delfín basis in April.

The dominant species of temperate and subarctic affinity (*E. mordax* and *M. productus*) and tropical (*B. panamense*) were consistent with those reported in other studies in northern GC, including a low diversity during the cold period, and an increase during the warm period (Aceves-Medina *et al.* 2004, Danell-Jiménez *et al.* 2009, Sánchez-Velasco *et al.* 2009, Peguero-Icaza *et al.* 2011). Dominant species had remarkable changes in distribution, but still greater were the monthly differences in taxa composition in the fish larval assemblages with respect to previous studies. Some species named here as indicator species coincided into the Northern Group assemblage (*M. productus* and *C. fragilis* in winter; *E. mordax*, *P. nebulifer* and *G. crescentalis* in spring; and *Anchoa* sp. in summer); and other species coincided in the Mainland Group (*E. mordax*, *E. teres*, *L. stilbius*, *D. laternatus* and *E. crossotus* in winter; *Opisthonema libertate*, *V. lucetia*, *B. panamense*, *T. mexicanus, Selar crumenophthalmus*, *Auxis* sp. and *S. ovale* in summer; and *B. panamense, T. mexicanus* and *C. fragilis* in autumn). Thus the wide seasonal changes drive the diversity and structure of the fish larvae assemblage in function to ambient variability, that imply monthly changes in surface circulation in the northern Gulf of California, and the incursion of tropical fauna associated with the seasonal advancement or retreat of tropical water inside the gulf.

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