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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, Ibaíbarriaga 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 dominate 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 higher 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 m³ 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 Lavin & 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

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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 hydrographic 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-Jimenez 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

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**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
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

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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, *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

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<th>March 2005</th>
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<td>Axis 1</td>
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<tr>
<td>Eigenvalue</td>
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<td>Explained variance (%)</td>
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<td>Accumulated variance (%)</td>
<td>14.40</td>
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**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**

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 ≥ 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 m²), and in April in the Delfín Basin (> 6,500 larvae per 1000 m²). 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 m²), 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 m²) (Fig. 9).
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.

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.
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 oscura) 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 (SSSW), 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-Ruíz 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-Ruíz 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-García 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 advection 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 anticyclone 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 Delfín 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 (Landaela & 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 basin 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 Anchos sp. in summer); and other species coincided in the Mainland Group (E. mordax, E. teres, L. stilbius, D. latexnatus and E. crosstus in winter; Opisthomena libertata, 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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**LITERATURE CITED**


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