

Cephalopod paralarval assemblages in the Gulf of California during 2004–2007

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ABSTRACT: The responses of cephalopod paralarvae to environmental and hydrodynamic variability were analyzed using data collected during 8 oceanographic cruises (2004–2007) carried out in the entire Gulf of California. Redundancy analysis showed that temperature and salinity at 10 m depth (on the first axis), and zooplankton volumes and chlorophyll *a* concentration (on the second axis) were the main environmental variables influencing paralarval abundance. Relatively high correlations with the first axis were found in paralarvae of *Pterygioteuthis hoylei* (–0.5126), in the SD complex (*Sthenoteuthis oualaniensis* and *Dosidicus gigas*, 0.4526), and in *Gonatus pyros* (–0.3350). We observed 3 recurrent cephalopod paralarval assemblages related to the seasonal flux of water masses. The Gulf and Shallow assemblages were distributed mostly in Gulf of California water (salinity ≥ 35.0) located in the most productive environment. The Tropical assemblage was distributed in tropical surface water, associated with high temperatures and a less productive environment. During the spring, species richness and diversity in the assemblages were high in response to northward advection of tropical surface water into the gulf. The lowest richness values were recorded during summer, associated with the southward flow of Gulf of California water, and the highest temperatures of the year. The assemblages included mostly pelagic, tropical–subtropical taxa and few temperate and cosmopolitan taxa. Paralarval abundance in the gulf was numerically dominated by a few species, but each assemblage had a significantly different community structure and seasonal latitudinal boundaries, suggesting assemblages can be used as biological indicators of the distribution of water masses in the gulf.

KEY WORDS: Cephalopod · Paralarval assemblages · ENSO · Gulf of California

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INTRODUCTION

The collapse of several industrial-scale fisheries targeting small pelagic fishes (sardine, herring, and anchovy) and cod in the last 50 yr (Hauge et al. 2009) coincided with an increase in the market for cephalopods and a rapid expansion of cephalopod

fisheries to new target species, fishing areas, and depths. As a consequence, annual catches of cephalopods (mainly squids) have increased dramatically in recent decades (Caddy & Rodhouse 1998, FAO 2013). Cephalopod fisheries target relatively few species but for many of these species, the life-cycle characteristics are not well known,

particularly for the paralarval stage (Young & Harman 1988).

Paralarval abundance and distribution respond strongly to the environmental changes caused by ocean dynamics. Temperature is one of the most influential factors determining paralarval development rates (Boyle & Rodhouse 2005). Variations in salinity and in the concentrations of ions in the water also have significant effects on embryo survival and hatching rates, while the abundance of food strongly influences survival following hatching (D'Aniello et al. 1989, Rodhouse et al. 1998, Boyle & Rodhouse 2005, Vidal et al. 2010). Paralarval distribution is highly dependent on ocean circulation (Yamamoto et al. 2007, Pierce et al. 2008), which includes multi-scale oceanographic processes such as upwelling, coastal currents, and thermohaline fronts, among others (Anderson & Rodhouse 2001, Diekmann & Piatkowski 2002, Haimovici et al. 2002). These oceanographic processes influence the distribution of adults, which often show a close relationship to regional bathymetry and ocean water masses (Anderson & Rodhouse 2002, Nesis 2003, Moreno et al. 2009).

Thermohaline fronts may place boundaries that influence the dispersion of cephalopod paralarvae of different biogeographic affinities or, conversely, the seasonal flow of currents or water masses in a region can transport or mix fauna of different biogeographic affinities, leading to higher regional biological diversity. These features have been documented in other regions around the world, including the Scotian Sea, the Sargasso Sea, and in the western Iberian region (Anderson & Rodhouse 2002, Diekmann & Piatkowski 2002, Moreno et al. 2009).

In an oceanic area off the west coast of the Baja California Peninsula, Granados-Amores et al. (2010) found paralarvae of tropical–subtropical affinity during the winter of 1998, when anomalous northward advection of the warm surface transitional–subtropical water mass occurred due to the strong 1997–1998 El Niño Southern Oscillation (ENSO). They also reported a predominance of subarctic–temperate species of the family Gonatidae in the southward flow of the subarctic water mass during the 1999–2001 La Niña. The 1997–2001 ENSO caused considerable changes in the paralarval assemblages in this region.

The Gulf of California is a narrow semi-enclosed sea (~150 to 200 km wide, ~1400 km long), located in northwestern Mexico. The atmospheric and oceanographic forcing from the Pacific Ocean influence its environmental conditions. In this area, upwelling processes caused by seasonal wind patterns and

local topography are common (Lavín & Marinone 2003), promoting high primary productivity along the east coast of the gulf during the winter and moderate primary productivity along the west side of the gulf during summer (Álvarez-Borrego 2012). Two surface water masses are found in the epipelagic zone, with seasonally changing distributional boundaries. Tropical Surface Water (TSW) enters the gulf during summer, causing an increase in plankton diversity and abundance of tropical and subtropical species (tropicalization), and retreats during winter to over the Mazatlán Basin. Fewer temperate species are present in the gulf in summer than in winter (Brinton et al. 1986, Lavaniegos-Espejo & Lara-Lara 1990). The Gulf of California Water mass (GCW) has a complementary distribution to the TSW, being typically present to the north of the TSW throughout the year (Lavín & Marinone 2003). In this area, mesoscale physical processes, such as eddies and jets, also contribute to the environmental spatio-temporal variability (Zamudio et al. 2008, Avendaño-Ibarra et al. 2013).

Climatic variability in the gulf is mainly seasonal, and strong latitudinal or longitudinal gradients in environmental factors are reflected in the planktonic biota of the area. Gaxiola Castro et al. (1999) found a strong significant linear relationship between surface temperature with nutrients and phytoplankton abundance (>8 µm) in the Gulf of California. The composition and distribution of euphausiid species (Brinton & Townsend 1980, Lavaniegos-Espejo et al. 1989), and the distributional diversity and assemblages of fish larvae change seasonally according to the water masses present in the gulf (Avendaño-Ibarra et al. 2013). Fish larval assemblages inside the Gulf of California are dominated by subtropical and temperate–subarctic species during winter and by tropical species during summer. In spring and autumn, there are strong latitudinal gradients that also allow the presence of regional differences in this zooplanktonic group (Aceves-Medina et al. 2004). The abundance of fish larvae has also been observed to be closely related to sea-surface temperature, salinity, chlorophyll *a* (chl *a*) concentration, and zooplanktonic volume gradients in the gulf (Aceves-Medina et al. 2003, 2004, Avendaño-Ibarra et al. 2013).

Cephalopod paralarval distribution patterns as a function of the oceanographic conditions are poorly documented in the Gulf of California. Most ecological studies of paralarvae in the gulf have focused on *Dosidicus gigas* (Staaf et al. 2008, Camarillo-Coop et al. 2011), a commercially important species, and on *Pterygioteuthis hoylei*, the most abundant species

collected with oblique plankton tows (De Silva-Dávila et al. 2013). A pelagic egg mass of *D. gigas* was found in warm water (25–27°C) at a depth of 16 m in the center of the Gulf of California (Staaf et al. 2008), while paralarvae considered *D. gigas* were collected near chl *a* fronts, where potential prey are likely to concentrate (Camarillo-Coop et al. 2011). Recent research in the eastern tropical Pacific suggests that surface manta net tows are more efficient than oblique tows in collecting *Sthenoteuthis oualaniensis* and *D. gigas* paralarvae (SD complex) of the family Ommastrephidae (Staaf et al. 2013). However, there have been no ecological studies of the comprehensive cephalopod paralarval assemblage in the Gulf of California and its relation to environmental conditions in the water column.

Our goal was to analyze the seasonal and inter-annual distribution patterns and changes in community structure of cephalopod paralarvae collected during 8 oceanographic cruises covering the extensive region from Bahía de Banderas (20°N) to the

northern Gulf of California (31°N), in order to explore species responses to spatial and seasonal environmental and hydrodynamic variability using multivariate statistical analysis. We intended to determine the most relevant environmental variables influencing cephalopod paralarval assemblages (defined as groups of species having a common response to environmental variables and therefore high similarity values) in the entire Gulf of California.

MATERIALS AND METHODS

A total of 241 zooplankton samples were collected during 8 oceanographic cruises from November 2004 to July 2007 covering virtually the entire Gulf of California (from Bahía de Banderas to the northern Gulf of California, 20° to 31°N), Mexico (Fig. 1). The cruises were conducted during November of 2004 (S-195), 2005 (CAPEGOLCA0511), and 2006 (S-207); March, May, and September 2005 (CGC0503,

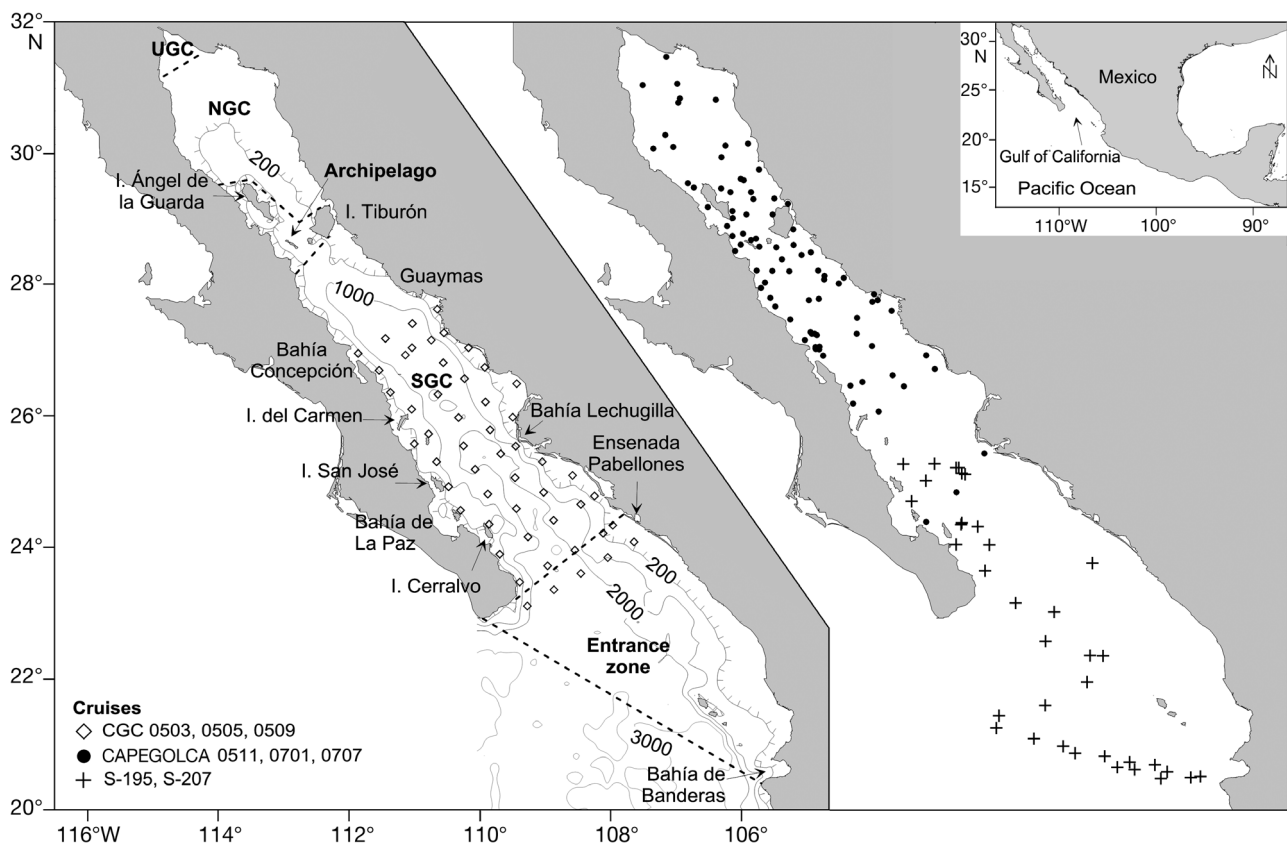


Fig. 1. Mexico and the Gulf of California (inset) and map of sampling grid stations of 8 oceanographic surveys carried out between 2004 and 2007 in the Gulf of California, Mexico. Cruises CGC0503, 0505 and 0509 are shown on the left; the other cruises are shown on the right. Local toponimy and bathymetry (in meters) are also shown. Dotted lines indicate divisions of the gulf (Lavín & Marinone 2003): UGC, upper Gulf of California; NGC, northern Gulf of California; archipelago; SGC, southern Gulf of California; and entrance zone

CGC0505, and CGC0509), and January and July 2007 (CAPEGOLCA0701 and CAPEGOLCA0707). Zooplankton samples (184) from 7 cruises were obtained from oblique tows using standard bongo nets (0.6 m mouth diameter) or a conical net (1.0 m mouth diameter) both equipped with 505 μm mesh. Maximum sampling depth in oblique tows was 210 m at most sampling stations; at shallower stations, sampling was conducted to within 10 m of the seafloor (Smith & Richardson 1979). Surface plankton tows (57) lasting 30 min were also done in November 2004 and 2006 using a neuston net (0.5 m², 335 μm mesh), while in September 2005 we only used a conical net (0.6 m mouth diameter, 505 μm mesh). Each net was equipped with a calibrated flowmeter (General Oceanics). All zooplankton samples were fixed in 96% non-denatured ethanol.

Zooplankton volumes were measured on board before chemical fixation using the displaced volume method (Beers 1976), and all cephalopod paralarvae were sorted and removed from the samples. Identification was done to the most precise taxonomic level possible (Okutani & McGowan 1969, Sweeney et al. 1992, Wakabayashi et al. 2002). Paralarval abundances per taxon were standardized to number of paralarvae per 1000 m⁻³ of filtered seawater (Postel et al. 2000).

We identified the water mass at each sampling station through data recorded with calibrated CTD casts. The 35.0 isohaline was used to delimit the boundary between GCW and the TSW (Lavín & Marinone 2003), allowing us to prepare maps of the seasonal distribution of the surface-water masses in the gulf. We used the criteria of Lavín & Marinone (2003) to divide the study area into 5 zones: upper Gulf of California, northern Gulf of California, archipelago, southern Gulf of California, and entrance zone (Fig. 1). No sampling was done in the upper Gulf of California where the average depth is 15 m. Sea-surface temperature (SST) data and surface chl *a* concentrations during each oceanographic cruise were derived from the average of daily high-resolution satellite images MODIS on Aqua, Level 2 (1 km resolution; <http://oceancolor.gsfc.nasa.gov/>) obtained for the days of each cruise. Bathymetry data (General Bathymetric Chart of the Oceans; www.gebco.net) and monthly satellite QuikScat wind intensity data (Easier Access to Scientific Data, ERDDAP) in the Gulf of California were used to complement the on-site environmental analyses. The zooplankton volume maps were done with Surfer 11 software using kriging as the interpolation method (Golden Software).

One-way ANOVA analyses and post hoc Tukey tests were calculated using Statistica 8.0 software (Stat-Soft) to test for significant differences in mean chl *a*, zooplankton volume, and total paralarval abundance recorded among oceanographic cruises. Data were previously log-transformed [$\log(x + 1)$] to fulfill ANOVA statistical assumptions (Zar 2010).

Agglomerative hierarchical 2-way cluster analyses were conducted to identify spatio-temporal presence-absence patterns of cephalopod taxa collected with oblique and surface net tow datasets. For these analyses we applied the Bray-Curtis distance measure and a flexible beta ($\beta = -0.25$) clustering algorithm using PC-ORD software 6.0 (MjM Software Design).

To explore the relationships between the distribution and abundance of paralarvae and environmental gradients recorded in the cruises, we used canonical ordination. The paralarval abundance dataset (including the 8 cruises) was screened, excluding all taxa with only 1 organism and sampling stations with only 1 species. Then it was log transformed [$\log_{10}(x + 1)$]. Eight environmental variables were used as independent variables: temperature at 10 m depth (T10), salinity at 10 m depth (S10), density at 10 m depth (D10), seafloor depth at the sampling station (DEP), sea-surface chl *a* concentration (CHL), zooplankton volume (ZV), and the sampling station's latitude (LAT) and longitude (LON). To select the most robust canonical analysis, detrended canonical correspondence analysis (DCA) was used to obtain the length of the environmental gradient (Ter Braak & Prentice 2004). In this first DCA, D10 was highly correlated with T10 and S10; then, it was excluded from further statistical analysis. A second DCA showed a small gradient length (2.6); we, thus, inferred a linear response of the cephalopod taxa to the environmental gradients. To support this inference, we plotted the paralarval abundance per taxon as a function of each environmental variable measured using Statistica 8.0 software. Correlations and pair-plots (not shown) indicated significant ($\alpha > 0.05$) linear relationships in a high proportion of taxa (~69%). Then, the species-environment relationship was examined using redundancy analysis (RDA) (Legendre & Legendre 1998). In all canonical statistical analyses (DCA and RDA), scaling focused on inter-species correlations. Species scores were divided by the corresponding standard deviation and centered for each species. Further selection of environmental variables was performed automatically, and statistical significance was calculated using unrestricted Monte Carlo permutation tests. Only

Table 1. Average, minimum, maximum, and standard deviation (StDev) of temperature (T10) and salinity (S10) at 10 m, surface chlorophyll *a* concentrations (CHL), and zooplanktonic volume (ZV), recorded during 8 cruises (2004–2007) in the Gulf of California. **Bold** numbers indicate minimum and maximum values during the study period

Date of oceanographic cruise	T10 (°C)		S10		CHL (mg m ⁻³)		ZV (ml 1000 m ⁻³)	
	Mean (StDev)	Min.–max.	Mean (StDev)	Min.–max.	Mean (StDev)	Min.–max.	Mean (StDev)	Min.–max.
Jan 2007	16.7 (1.0)	15.2 –18.5	35.469 (0.112)	35.348–35.789	0.869 (0.257)	0.584–1.345	138.5 (119.2)	10.2 –446.8
Mar 2005	20.6 (0.7)	19.2–22.2	35.409 (0.327)	34.630– 36.010	1.001 (0.857)	0.207– 3.976	230.4 (142.3)	45.6–728.6
May 2005	24.5 (1.2)	20.2–25.9	35.002 (0.387)	34.354–35.790	0.421 (0.219)	0.121–1.098	165.9 (89.3)	65.5–570.7
Jul 2007	27.0 (1.7)	23.9–29.3	35.352 (0.254)	34.989–35.887	1.060 (0.727)	0.336–3.241	214.6 (155.5)	48.8–515.1
Sep 2005	30.3 (0.7)	29.2– 31.7	34.909 (0.158)	34.536–35.132	0.226 (0.156)	0.135–0.670	139.3 (52.8)	10.3–207.3
Nov 2004	27.2 (0.7)	25.7–28.6	34.519 (0.231)	34.200–35.150	0.147 (0.058)	0.099 –0.270	81.7 (51.0)	18.0–229.1
Nov 2005	21.7 (2.2)	16.4–24.1	35.294 (0.140)	35.025–35.531	1.818 (1.039)	0.575–3.745	541.4 (523.0)	201.0– 1944.4
Nov 2006	28.1 (0.7)	27.3–29.4	34.729 (0.482)	33.970 –35.750	0.251 (0.086)	0.130–0.390	102.7 (68.0)	30.1–271.4

those variables that significantly explained paralarval taxon abundance variability were included in the final RDA analysis. Two biplots were used for the representation of the biological variables' ordination in the environmental multi-dimensional space. All statistical multidimensional analyses were done using Canonical Community Ordination (CANOCO) Software 4.56. We explored the resulting RDA using attribute plots with the CANOCO software. The results of this exploration and of the 2-way cluster analysis showed that the water type factor (GCW and TSW) allowed us to segregate sampling stations of each cruise in 1 or 2 main groups, while zooplankton volume (high values) was the environmental variable that distinguished the third group in the RDA. Once the sampling stations corresponding to each group were identified in each cruise, we plotted their geographic position on maps to identify the seasonal boundaries of the groups using Surfer 11 software (Golden Software).

A similarity percentage analysis that calculated the contribution of each taxon to the similarity within and the dissimilarity between assemblages obtained from the RDA was conducted using Primer 6 software (Primer-E). Rarefaction curves of species richness (*S*) and diversity (Shannon's index, *H'*) were also seasonally estimated for each RDA assemblage using Ecosim 7.71 software (Acquired Intelligence Inc. & Kesey-Bear). This data analysis provides comparative estimates, regardless of differences in the sample sizes of the groups compared (Gotelli & Graves 1996). Abundance levels for simulation were established using the group with the lowest values of abundance to allow comparisons among all sample groups. We used the Monte Carlo method and 1000 replicates in the simulation for each estimate. Samples were randomly selected without replacement,

and this procedure was repeated 1000 times to estimate an average value and 95 % confidence intervals for various levels of abundance.

RESULTS

Environmental variables

The environmental variables T10, S10, CHL, and ZV showed high variability during each cruise (Table 1). T10 showed a continuous increase from January (coldest month, 15.2°C) to September, when the maximum mean temperature was recorded (31.7°C). SST satellite images showed that the northern and upper gulf had high thermal variability and the archipelago zone had lower SSTs than the rest of the gulf throughout the study period (Fig. 2A). A consistent latitudinal thermal gradient (low SST at the archipelago and high SST at Bahía Banderas) occurred during winter–spring (January–May). The thermal gradient changed from east to west (longitudinal) during summer (Fig. 2A; July–September), with higher SSTs along the continental coast (east side of the gulf), and the lowest SSTs along the peninsular coast (west side of the gulf). During November 2005, the SST thermal gradient was reversed (west to east), with higher SSTs toward the peninsular coast and low SSTs at the continental coast. The distribution of T10 showed a pattern similar to that observed in SSTs from satellite imagery.

During January, all salinity values recorded were >35.0, indicating the presence of GCW throughout the area in the upper 200 m of the water column (Fig. 2A). A low salinity core at the tip of the Baja California Peninsula recorded during March 2005 indicated northward advection of TSW into the gulf

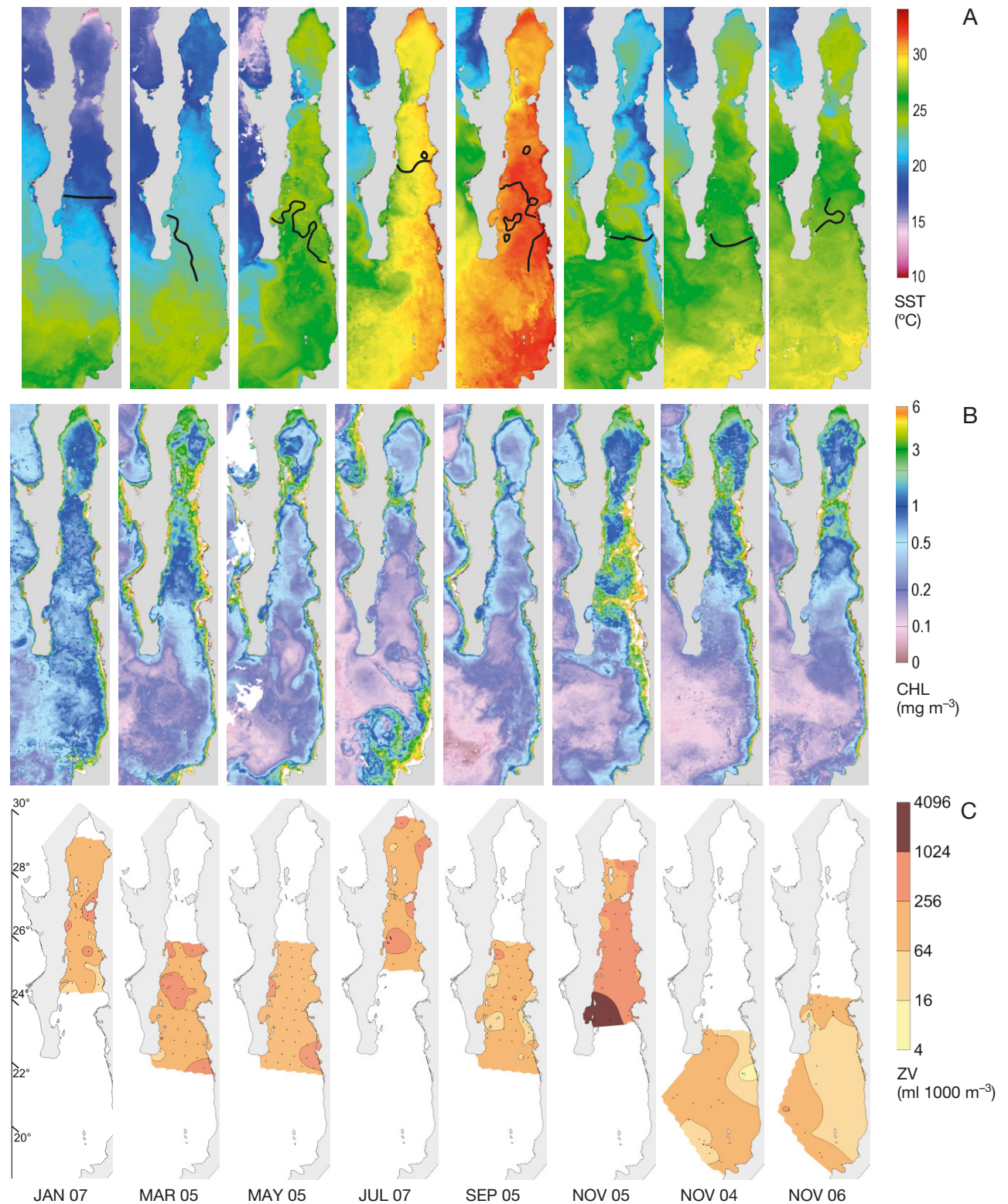


Fig. 2. Composite of satellite images: (A) sea-surface temperature (SST; °C), (B) surface concentration of chlorophyll a (CHL; mg m^{-3}), and (C) zooplankton volumes (ZV; $\text{ml } 1000 \text{ m}^{-3}$) in the Gulf of California during 8 cruises conducted during November 2004 (S-195), 2005 (CAPEGOLCA0511), and 2006 (S-207); March, May, and September 2005 (CGC0503, CGC0505, and CGC0509); and January and July 2007 (CAPEGOLCA0701 and CAPEGOLCA0707). Black lines in the SST images indicate the 35.0 isohaline as the boundary between surface water masses in the Gulf of California during each oceanographic cruise

along the peninsular coast, nearly reaching Bahía de La Paz (Fig. 2A). During May 2005, TSW reached the area between Islas San José and del Carmen. In July and September 2005, a small core of low salinity (<35.0) water reached its maximum northern distribution off Guaymas (Fig. 2A). In November 2004, 2005, and 2006, the GCW reached its maximum extension to the south, covering the entire gulf southward to Bahía de La Paz and even further south.

The monthly CHL average did not show a clear seasonal pattern. However, the distribution of CHL had a consistent pattern during all samplings, with a clear cross-shelf gradient (coastal to ocean). CHL was high along the continental coast, in the archipelago, and in the northern gulf from January through May (Fig. 2B), and low from July through September. The highest CHL (>3.0 mg m⁻³) occurred during November 2005. The oceanic region of the central part of the gulf had a latitudinal gradient, with high CHL in the center and low CHL (<0.25 mg m⁻³) at the entrance zone of the gulf (Fig. 2B).

In most of the study area, ZV generally ranged from 64 to 256 ml 1000 m⁻³, except in a few scattered areas with high ZV ranging from 256 to 1024 ml 1000 m⁻³ (Fig. 2C). In November 2005, ZV was generally high in most of the gulf, with extremely high values (1024–4096 ml 1000 m⁻³) near Bahía de La Paz. Low ZV (16–64 ml 1000 m⁻³) occurred in November 2004 and 2006 at the entrance to the gulf, where oligotrophic surface waters typically prevail (Fig. 2C).

ANOVA analyses and post hoc Tukey tests indicate significant differences in CHL ($F_{7,242} = 26.9$, $\alpha > 0.05$) and ZV ($F_{7,240} = 10.3$, $\alpha > 0.05$) among cruises particularly for November 2005, when both biological variables were unusually high. They also indicate significant differences between summer cruises that sampled in the region from the northern gulf to Isla del Carmen (July) and the southern Gulf of California (September), with higher values recorded in the north (Fig. S1A,B in the supplement at www.int-res.com/articles/suppl/m520p123_supp.pdf). There were no significant differences in total paralarval abundance ($F_{7,159} = 6.3$, $\alpha = 0.05$) among cruises (Fig. S1C in the Supplement).

Paralarval abundance

A total of 3357 paralarvae were collected from 241 samples, of which 69% contained at least 1 paralarva. They included 37 taxa, belonging to 12 families, 17 genera, and 32 species. We also recorded 2

species complexes from the family Ommastrephidae (Table S1 in the Supplement). The families Pyroteuthidae (accounting for 24 to 84% of the total paralarval abundance in the gulf) and Ommastrephidae (4 to 65%) were the most abundant taxa throughout the study period. Other frequently sampled families included the Enoploteuthidae, recorded with a high frequency but low relative abundance (<12%); the Gonatidae, collected only during winter (January 2007 and March 2005, 3 to 7%), and the Argonautidae (37%) and Octopodidae (15%), which were abundant during spring and summer, respectively.

In the oblique tows, 7 taxa composed 90% of the paralarvae collected: *Pterygioteuthis hoylei* (51.6%), *Argonauta* cf. *böttgeri* (14.1%), the SD complex (12.4%), *Abraliopsis* sp. 1 (4.8%), *Argonauta* cf. *argo* (3.9%), *Abraliopsis* sp. 2 (1.7%), and *Argonauta* sp. 4 (1.4%). The SD complex of the family Ommastrephidae, formed by paralarvae of *Sthenoteuthis oualaniensis* and/or *Dosidicus gigas* (≤ 3.0 – 4.0 mm mantle length [ML]) that cannot be identified morphologically at this size, was the most abundant taxon (95.4%) in surface tows, followed by *Abraliopsis* sp. 1 (2%).

Statistical analysis

Two-way cluster analysis applied to abundance data of specimens collected in oblique tows showed the presence of 2 main groups of species. The first consisted of the dominant and frequent taxa (*P. hoylei*, SD complex, *Abraliopsis* sp. 1, and *Abraliopsis* sp. 2) present throughout the study area in either GCW or TSW, together with argonauts found mainly during spring and *D. gigas* paralarvae (Fig. 3A). The second group was formed by species present mostly in TSW from spring to autumn (*Drechselia danae*, *Japetella heathi*, *Euaxoctopus panamensis*, and *Octopus rubescens* among others). Gonatids, 2 octopods, and 2 enoploteuthids formed 3 independent small groups found exclusively in GCW in winter–spring. The second dendrogram obtained from the surface paralarval abundance dataset showed a pattern related to seasonality rather than to water masses, because TSW was observed to be present at all sampling stations in September and November. The presence–absence patterns of surface cephalopod taxa were similar to those observed from oblique tows, with dominant and frequent taxa present in summer and autumn throughout the area (Fig. 3B) and 2 other groups of taxa collected exclusively during autumn cruises in the entrance zone of the Gulf of California.

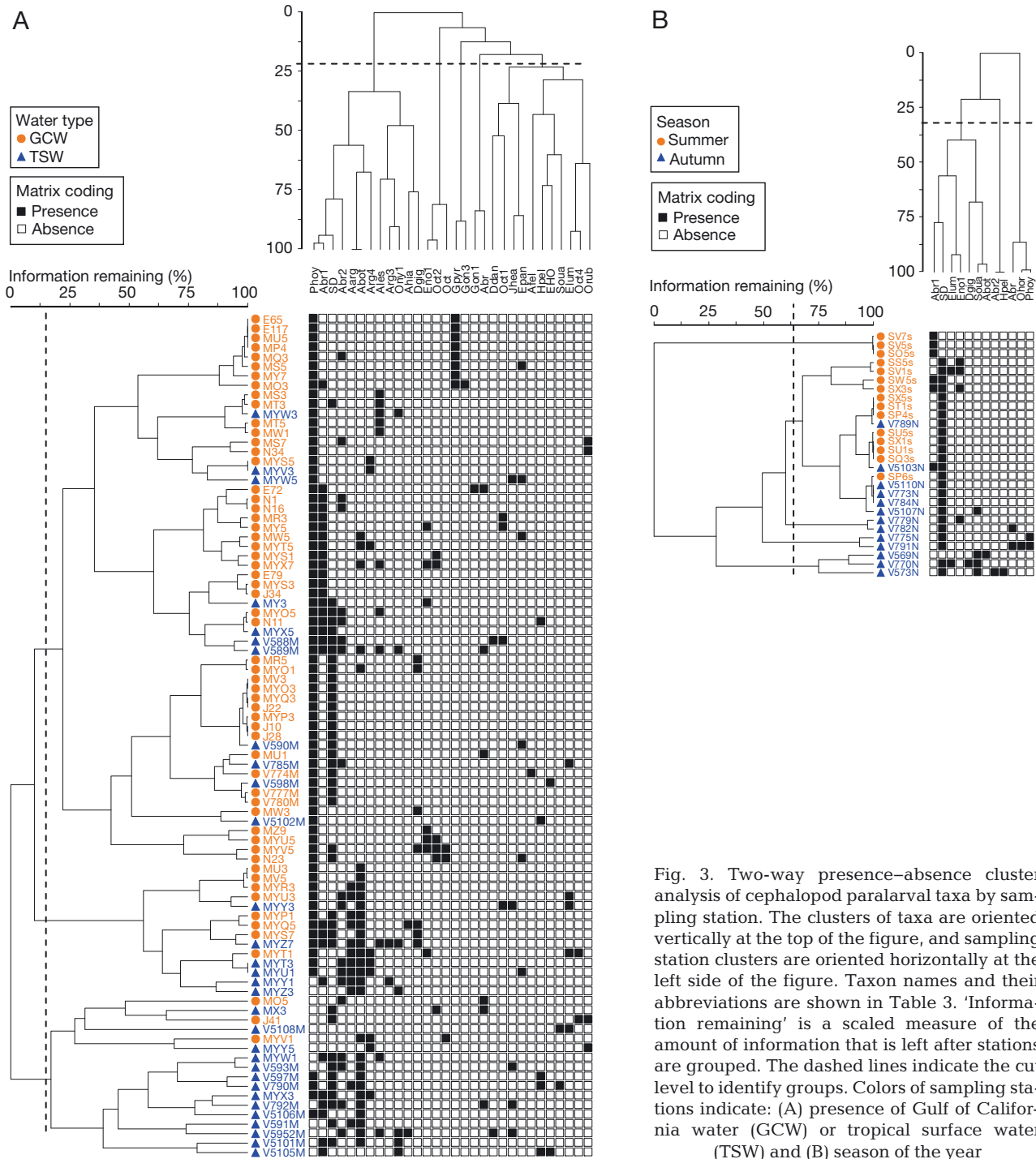


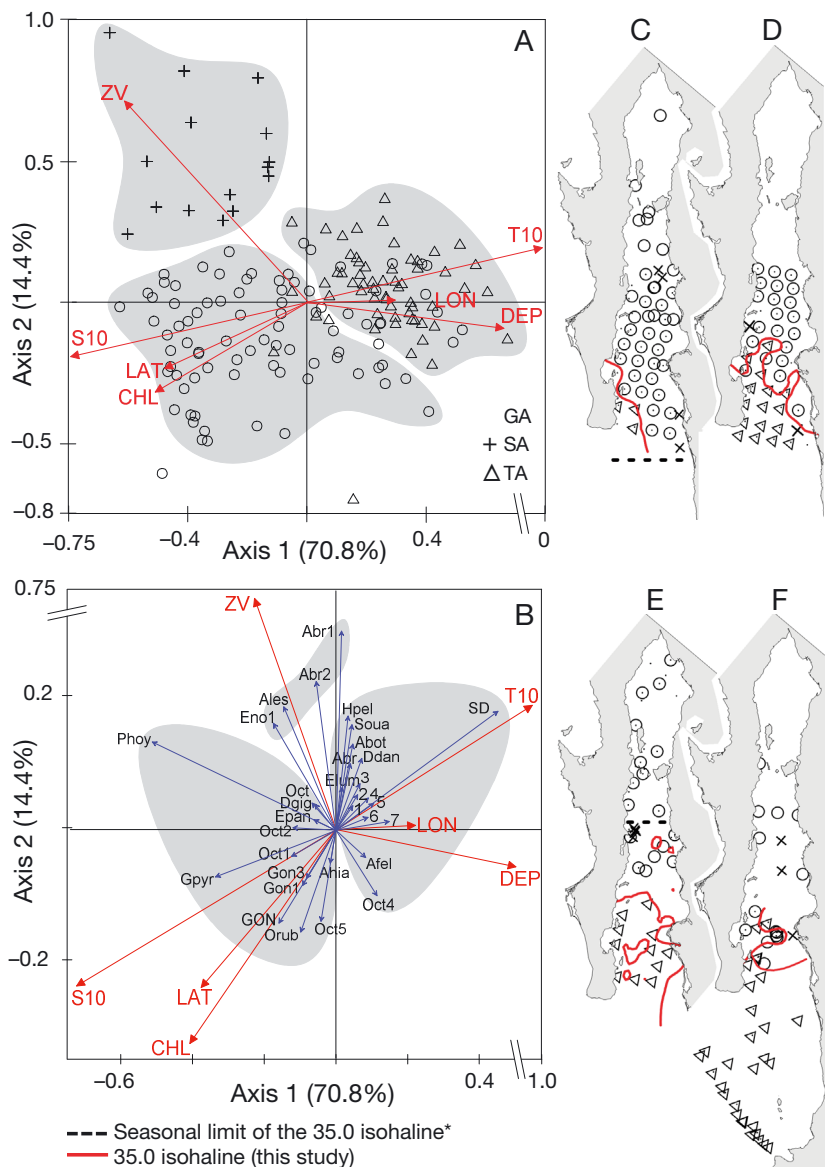
Fig. 3. Two-way presence-absence cluster analysis of cephalopod paralarval taxa by sampling station. The clusters of taxa are oriented vertically at the top of the figure, and sampling station clusters are oriented horizontally at the left side of the figure. Taxon names and their abbreviations are shown in Table 3. 'Information remaining' is a scaled measure of the amount of information that is left after stations are grouped. The dashed lines indicate the cut level to identify groups. Colors of sampling stations indicate: (A) presence of Gulf of California water (GCW) or tropical surface water (TSW) and (B) season of the year

The RDA showed that the first 2 canonical axes explained 85.2% of the accumulated variance in species-environment multidimensional space (Table 2), with significant correlations on Axis 1 ($F = 4.7, p < 0.030$) and on the other axes ($F = 2.06, p < 0.016$). The T10 (0.8853) and S10 (-0.7224) values significantly correlated with Axis 1, while ZV (0.7089) and CHL (-0.3229) values were significantly correlated with

Axis 2 (Table 2). A biplot of the RDA stations-environment showed the presence of 3 groups of sampling stations associated with different environments. Data exploration in CANOCO software indicated 1 group was formed at sampling stations where S10 was ≥ 35.0 corresponding to GCW. The second group observed in the opposite direction along Axis 1 was formed with sampling stations where S10 was

Table 2. Summary of the redundancy analysis of cephalopod paralarval abundance and environmental variables. **Bold** numbers indicate the highest significant correlations ($\alpha = 0.05$) on the respective axis

	Ordination axis			
	1	2	3	4
Cumulative variance (%)				
Species data	12.4	14.9	16.6	16.9
Species–environment relationships	70.8	85.2	94.8	97.0
Longitude (LON)	0.2223	0.0063	-0.0513	-0.0905
Latitude (LAT)	-0.3757	-0.2384	-0.4189	0.2196
Seafloor depth (DEP)	0.5085	-0.0906	0.0053	-0.6656
Temperature at 10 m depth (T10)	0.8853	0.2808	-0.2045	0.1121
Salinity at 10 m depth (S10)	-0.7224	-0.2360	-0.5067	0.1619
Chlorophyll <i>a</i> concentration (CHL)	-0.4066	-0.3229	-0.2271	0.5778
Zooplankton volume (ZV)	-0.4702	0.7089	-0.3293	0.1297



<35.0, corresponding to TSW, while the third group was related to the highest ZV (Fig. 4A). Cephalopod paralarval assemblages defined as groups of species having a similar response to environmental variables then emerged from the biplot of species–environment (Fig. 4B) supported by the information from cluster analysis. Consequently, paralarval assemblages were named according to the water mass where they were found.

The first assemblage, here designated the Gulf assemblage, was present at stations with the highest S10 (≥ 35.0) and relatively high T10 (mean: 23.0°C), which corresponds to the GCW. It was also present at stations with high CHL (mean: 0.859 mg m⁻³) and ZV (mean: 194 ml 1000 m⁻³). During winter, the Gulf assemblage was distributed throughout the gulf, except at the tip of the Baja California Peninsula (Fig. 4C). During spring, it occurred in the northern part of the gulf, roughly delimited by a diagonal line crossing from north of Isla San Jose to Ensenada Pabellones, Sinaloa (Fig. 4D). During summer, the Gulf assemblage was distributed from the northern gulf to south of Isla del Carmen and Bahía de Lobos, Sonora (Fig. 4E). In autumn, it was present throughout the study area south of Isla Espíritu Santo (Fig. 4F). In all seasons, the southern limit of the Gulf assemblage was near the 35.0 isohaline. The assemblage comprised 13

Fig. 4. Ordination analysis: (A) biplot of sampling stations–environment (GA: Gulf assemblage; SA: Shallow assemblage; TA: Tropical assemblage; T10: temperature at 10 m depth; S10: salinity at 10 m depth; DEP: seafloor depth of the sampling station; CHL: surface concentration of chlorophyll *a*; ZV: zooplankton volume; LAT: latitude; LON: longitude). (B) Biplot of species–environment. Abbreviations of taxon names or numbers are shown in Table 3. Shaded areas help distinguish assemblages. Distribution of paralarval assemblages in the gulf during: (C) winter, (D) spring, (E) summer, and (F) autumn. *: taken from Lavín & Marinone (2003)

Table 3. Species composition of the cephalopod paralarval assemblages obtained from the redundancy analysis in the Gulf of California to Bahía de Banderas, Jalisco, 2004–2007. Abbr.: Abbreviations for the corresponding taxa. Numbers in parentheses are related to the names of the taxa in Fig. 4B. SD complex: *Sthenoteuthis oualaniensis* and/or *Dosidicus gigas*; EHO complex: *Euclideanoteuthis luminosa*, *Hyaloteuthis pelagica*, and/or *Ommastrephes bartramii*

Gulf assemblage		Tropical assemblage		Shallow assemblage	
Abbr.	Taxon	Abbr.	Taxon	Abbr.	Taxon
<i>Phoy</i>	<i>Pterygioteuthis hoylei</i>	SD	SD complex	<i>Abr1</i>	<i>Abraliopsis</i> sp. 1
<i>Gpyr</i>	<i>Gonatus pyros</i>	<i>EHO</i>	EHO complex (6)	<i>Abr2</i>	<i>Abraliopsis</i> sp. 2
<i>Gon1</i>	<i>Gonatus</i> sp. 1	<i>Hpel</i>	<i>Hyaloteuthis pelagica</i>	<i>Eno1</i>	<i>Enoploteuthis</i> sp. 1
<i>Gon3</i>	<i>Gonatus</i> sp. 3	<i>Soua</i>	<i>Sthenoteuthis oualaniensis</i>	<i>Ales</i>	<i>Ancistrocheirus</i> cf. <i>lesueuri</i>
GON	Gonatidae	<i>Elum</i>	<i>Euclideanoteuthis luminosa</i>		
<i>Orub</i>	<i>Octopus rubescens</i>	<i>Ddan</i>	<i>Drechselia danae</i>		
<i>Oct1</i>	<i>Octopus</i> sp. 1	<i>Afel</i>	<i>Abraliopsis felis</i>		
<i>Oct2</i>	<i>Octopus</i> sp. 2	<i>Abr</i>	<i>Abraliopsis</i> spp.		
<i>Oct5</i>	<i>Octopus</i> sp. 5	<i>Ohor</i>	<i>Onychoteuthis horstkottei</i> (7)		
<i>Oct</i>	<i>Octopus</i> spp.	<i>Ony1</i>	<i>Onychoteuthis</i> sp. 1 (4)		
<i>Epan</i>	<i>Euaxoctopus panamensis</i>	<i>Jhea</i>	<i>Japetella heathi</i> (5)		
<i>Dgig</i>	<i>Dosidicus gigas</i>	<i>Abot</i>	<i>Argonauta</i> cf. <i>böttgeri</i>		
<i>Ahia</i>	<i>Argonauta</i> cf. <i>hians</i>	<i>Aarg</i>	<i>Argonauta</i> cf. <i>argo</i> (1)		
		<i>Arg3</i>	<i>Argonauta</i> sp. 3 (3)		
		<i>Arg4</i>	<i>Argonauta</i> sp. 4 (2)		
		<i>Oct4</i>	<i>Octopus</i> sp. 4		

taxa, which included *Pterygioteuthis hoylei*, the most abundant species collected in the oblique tows, all of the collected gonatid species, 5 of the 6 sampled octopodid species, *Dosidicus gigas*, and *Argonauta* cf. *hians* (Fig. 4B, Table 3).

The second assemblage, here designated the Tropical assemblage, was present at stations with the highest T10 (mean: 27.0°C) and S10 <35.0, which correspond to TSW. This assemblage was also present at low CHL (mean: 0.271 mg m⁻³) and ZV (mean: 111 ml 1000 m⁻³), and at the deepest sampling stations of the southern and entrance zones of the gulf. The Tropical assemblage, distributed south of the Gulf assemblage, was practically the only assemblage recorded in November 2004 and 2006 in the oceanic region from the tip of the Baja California Peninsula to Bahía de Banderas, Jalisco (Fig. 4F). The assemblage comprised 16 taxa, including 3 species and 2 species complexes in the family Ommastrephidae (the EHO complex comprising *Euclideanoteuthis luminosa*, *Hyaloteuthis pelagica*, and/or *Ommastrephes bartramii* that cannot be identified morphologically at ≤2.0 mm ML, and the SD complex), 5 species from the Cranchiidae, Enoploteuthidae, and the Onychoteuthidae families, and the pelagic octopus *Japetella heathi* (Bolitaenidae). These species were not found in the Gulf assemblage. The Tropical assemblage also included 4 of 5 taxa of the family Argonautidae, and 1 *Octopus* species (Fig. 4B, Table 3).

The third assemblage, here designated the Shallow assemblage, was found only in January, March, May,

July, and November 2005. This assemblage included a few shallow, nearshore sampling stations (<100 m seafloor depth) with the highest ZV (mean: 469 ml 1000 m⁻³) (Fig. 4A), which explains the segregation of this assemblage from the other 2 (Fig. 4B). This assemblage included only 4 taxa: *Abraliopsis* sp. 1, *Abraliopsis* sp. 2, *Enoploteuthis* sp. 1, and *Ancistrocheirus* cf. *lesueuri* (Table 3).

The relatively low correlations of the dominant taxa *Pterygioteuthis hoylei* (−0.5126) and the SD complex (0.4526) with the first axis were probably related to their widespread distribution patterns covering wide latitudinal and seasonal ranges of temperature. The low correlation values found in *Gonatus pyros* (−0.3350) and in *Argonauta* cf. *böttgeri* (0.0478) indicate they are more likely to be related to the reproductive activity of adults in the region.

Only a few species determined the similarity among assemblages. The numerically dominant *P. hoylei* (87.4%) and the SD complex (6.9%) typified the Gulf assemblage, while 4 taxa typified the Tropical assemblage: SD complex (43.3%), *P. hoylei* (26.0%), *A. cf. böttgeri* (14.8%), and *Abraliopsis* sp. 1 (8.2%). In the Shallow assemblage, *P. hoylei* (82.5%) and the SD complex (10.2%) accounted for >92% of the similarity (Table 4A). Differences in relative abundance of the dominant *P. hoylei* and SD complex paralarvae and the presence of a different composition of taxa with low relative abundance discriminated the assemblages, showing high percentages of dissimilarity between them (Table 4B). In particular,

Gonatus pyros, *Ancistrocheirus* cf. *lesueuri*, and *Dosidicus gigas*, occurred only in the Gulf assemblage, *Abraliopsis* sp. 2 occurred mainly in the Tropical assemblage, and *Enoplo-teuthis* sp. 1 was more abundant in the Shallow assemblage, contributing to the differences among them.

Paralarval species richness was low during winter (9 taxa in January 2007 and 19 in March 2005) and increased during spring (23 taxa). During summer, we recorded the lowest species richness which increased again in autumn (Fig. S1C in the Supplement). The results obtained from the rarefaction curves showed significant differences in species richness among the 3 paralarval assemblages. The Gulf assemblage showed the highest species richness throughout the study, with relatively low values only during summer. The Shallow assemblage showed the lowest species richness during most of the year, while the Tropical assemblage had a significant increase in species richness during spring (Fig. 5A). The 3 assemblages were most diverse in spring and least diverse in autumn, with no significant differences among assemblages during each of those seasons (Fig. 5B).

DISCUSSION

This is the first systematic and comprehensive ecological study of oceanic cephalopod paralarval

Table 4. Similarity percentage analysis of cephalopod paralarval assemblages obtained from the redundancy analysis showing only the taxa that contributed >90% on average to: (A) similarity and (B) dissimilarity analyses. GA: Gulf assemblage; TA: Tropical assemblage; SA: Shallow assemblage; n: number of taxa; \bar{S} : average similarity; $\bar{\delta}$: average dissimilarity; % Acc: accumulated contribution (percentage) of taxa to similarity or dissimilarity. Nominal keys for the taxa are given in Table 3

(A) Similarity within:								
GA = 30.3%, n = 19			TA = 14.5%, n = 21			SA = 25.9%, n = 4		
Taxon	\bar{S}	% Acc	Taxon	\bar{S}	% Acc	Taxon	\bar{S}	% Acc
<i>Phoy</i>	26.5	87.4	<i>SD</i>	6.3	43.3	<i>Phoy</i>	21.3	82.5
<i>SD</i>	2.3	94.3	<i>Phoy</i>	3.8	69.3	<i>Abr1</i>	2.6	92.7
			<i>Abot</i>	2.1	84.1			
			<i>Abr1</i>	1.2	92.3			
(B) Dissimilarity between:								
GA vs. TA = 84.0%, n = 11			TA vs. SA = 85.4%, n = 8			GA vs. SA = 72.3%, n = 8		
Taxon	$\bar{\delta}$	% Acc	Taxon	$\bar{\delta}$	% Acc	Taxon	$\bar{\delta}$	% Acc
<i>Phoy</i>	33.2	36.1	<i>Phoy</i>	31.7	37.1	<i>Phoy</i>	32.4	44.8
<i>SD</i>	17.2	62.5	<i>SD</i>	16.4	56.3	<i>Abr1</i>	9.3	57.6
<i>Abot</i>	10.2	71.7	<i>Abr1</i>	9.2	67.0	<i>SD</i>	7.8	68.4
<i>Abr1</i>	3.6	77.1	<i>Abot</i>	9.2	77.8	<i>Abot</i>	5.4	75.8
<i>Aarg</i>	2.8	79.5	<i>Eno1</i>	3.3	81.6	<i>Eno1</i>	3.5	80.6
<i>Arg4</i>	1.9	81.9	<i>Abr2</i>	3.1	85.3	<i>Abr2</i>	2.9	84.7
<i>Abr2</i>	1.6	85.3	<i>Aarg</i>	1.8	89.9	<i>Gpyr</i>	1.7	89.7
<i>Gpyr</i>	1.5	86.9	<i>Abr</i>	1.8	92.1	<i>Abr</i>	1.7	92.0
<i>Ales</i>	1.0	88.2						
<i>Dgig</i>	1.0	89.4						
<i>Soua</i>	0.8	90.5						

assemblages covering virtually the entire Gulf of California, from the northern region to Bahía de Banderas, Mexico. It focused on the relationship between paralarval distribution and abundance patterns as a function of several oceanographic environmental variables using multivariate statistical analysis. The collection of zooplankton samples during 8 oceanographic cruises provided a broad perspective of the environmental changes that influence the spatio-

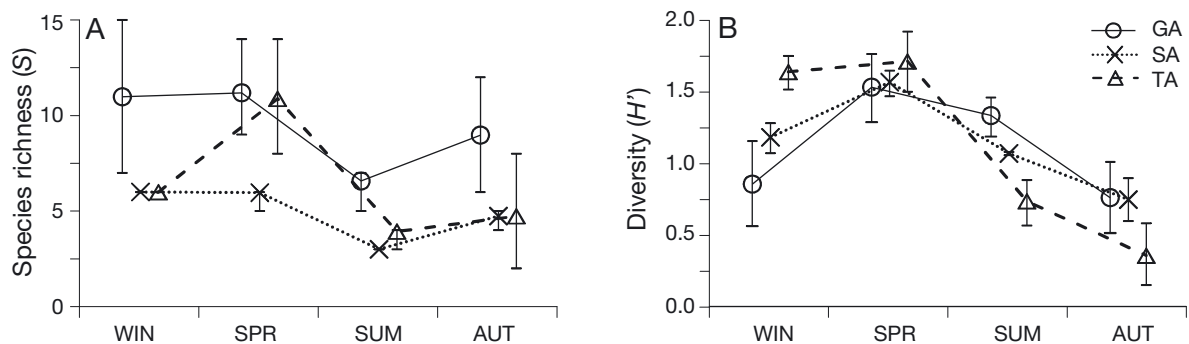


Fig. 5. Rarefaction curves of redundancy analysis groups based on (A) seasonal species richness (S) and (B) Shannon diversity (H'). Symbols and vertical lines indicate averages, and minima and maxima of the indexes analyzed, respectively. WIN: winter; SPR: spring; SUM: summer; AUT: autumn; GA: Gulf assemblage; SA: Shallow assemblage; TA: Tropical assemblage

temporal distribution of the cephalopod paralarval assemblages, and of their faunistic boundaries in the Gulf of California.

Environmental conditions during 2004–2007

Changes in the Ocean El Niño Index (www.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ensoyears.shtml) and Multivariate El Niño Southern Oscillation Index (MEI; www.esrl.noaa.gov/psd/enso/mei/) revealed high inter-annual variability in environmental conditions during 2004–2007 because the period included 2 consecutive ENSO events. The first ENSO (considered weak) lasted from the second half of 2004 through January 2005, with positive anomalies, followed by a La Niña (November 2005 through March 2006, with negative anomalies). A new cycle started with a weak El Niño (second half of 2006) followed by a weak to moderate La Niña during the second half of 2007 through June 2008 (www.cpc.ncep.noaa.gov/products/CDB/CDB_Archive_html/CDB_archive.shtml).

McPhaden (2004) showed that the previous 2002–2003 El Niño event in the Equatorial Pacific Ocean was moderate, with anomalies higher than those recorded during 2004 and 2006. Durazo et al. (2005) found that the influence of this event was weak in the southern region of the California Current System (along the west coast of the Baja California Peninsula), where the biological response (CHL and ZV) was not adversely affected, compared with the 1997–1998 El Niño event in this region. The Gulf of California seems to respond with less intensity to ENSO events than the west coast of the Baja California peninsula.

According to Farfán & Álvarez-Borrego (1992), the 1972–1973 ENSO did not affect the zooplankton biomass in the northernmost region of the Gulf of California. No significant effects on primary productivity in the central gulf region during the strong 1982–1983 El Niño were found (Valdéz-Holguín & Lara-Lara 1987), and no significant differences were found in zooplankton biomass, although changes were found in the structure of the copepod community in the gulf (Jiménez-Pérez & Lara-Lara 1988). Furthermore, Lavaniegos-Espejo et al. (1989) found no significant differences in abundance or distribution of euphausiids during 2 successive spring seasons (March 1982 and March 1983). These studies suggest that local processes of enrichment within the gulf diminish the negative effects of warming events associated with El Niño conditions. All these data

were gathered during considerably higher positive anomalies (stronger El Niño events) than those we recorded during the period from 2004 through 2007.

Significant differences, with extremely high CHL and ZV, occurred in November 2005, at the beginning of the 2005 La Niña event, when low SST and cool conditions were observed in satellite images. This cooling event was likely related to higher wind speeds in November 2005 (QuikSCAT, <http://coastwatch.pfeg.noaa.gov/erddap/index.html>), which promoted regional enriching effects from coastal upwelling. The wind intensity was higher in this month than during the other cruises, even in winter and spring, when the highest biological production of the year, in terms of surface CHL, occurs (Espinosa-Carreón & Valdez-Holguín 2007). In November 2005, the gulf environment was enriched. This coincided with the start of northerly winds, which lead to the cooling of surface waters and a breakdown of the summer thermocline, resulting in a shift in zooplankton groups in the water column and generating high secondary biological productivity (Thunell et al. 1996, Gómez-Gutiérrez et al. 2012). Average ZV from 2004 to 2007 (139–439 ml 1000 m⁻³) was of the same magnitude as the volumes recorded during 10 previous cruises in the gulf (Brinton et al. 1986, Jiménez-Pérez & Lara-Lara 1988, Lavaniegos-Espejo & Lara-Lara 1990, Palomares-García et al. 2013). All were comparable to ZV values in the productive California Current region (Brinton et al. 1986) and were even higher than the values recorded during the 1999 La Niña (52–103 ml 1000 m⁻³; Lavaniegos et al. 2002).

Correlation between CHL (from satellite imagery) and MEI over 10 yr (1997–2006), indicates that the effects of ENSO events are not homogeneous in the gulf, with a more detectable influence (low CHL) along the continental coast and the archipelago region than in the rest of the gulf (Herrera-Cervantes et al. 2010). The degree of association or connection between different areas regarding the flux of nutrients, contaminants, or early larval stages of marine animals based on the trajectories of modeled particles in the Gulf of California has been considered as connectivity. Modeled particles at the surface layer indicate retention during most of the year (9–12 mo) in the northern gulf, along the peninsular side, and in the south gulf (Marinone 2012). In the narrow gulf, productive water that originated from mixing and upwelling along the archipelago and continental coasts remains trapped, contributing to an increase in the production per unit area (Gaxiola-Castro et al. 1995). The additional effects of mesoscale eddy

trains, the bi-directional current flow inside the gulf, and the occurrence of jets in summer (Pegau et al. 2002, Zamudio et al. 2008, Avendaño-Ibarra et al. 2013) contribute to the maintenance of a food supply for cephalopod paralarvae and other larval stages and zooplankton throughout the year. All these studies, suggest a high synergistic effect of several physical processes contributing to high biological production inside the gulf.

This background and the environmental results recorded in this study showed no evidence of a decrease in biological productivity caused by El Niño events during the analyzed period. We assumed that biological variables and cephalopod paralarval assemblages in the gulf responded typically, showing no effect from the relatively weak ENSO events recorded from 2004 through 2007.

Paralarval assemblages

The multidimensional statistical analysis indicated that the 3 distinct paralarval assemblages responded to seasonal and interannual variability and to the environmental gradient present in the Gulf of California. During winter, the formation of assemblages was related to cold temperatures (<21°C), when paralarvae in the Gulf assemblage and Shallow assemblage were linked with the GCW. Synergistic effects of different mesoscale physical processes, such as topographic and seasonal wind-induced upwellings along the continental and peninsular coasts (Gaxiola-Castro et al. 1995, Álvarez-Borrego 2012), strong tidal currents, particularly in the northern gulf (Lavín & Marinone 2003), thermal fronts in the archipelago region, and eddies (Avendaño-Ibarra et al. 2013) may have caused the high CHL observed in satellite images.

Species richness was higher throughout the year, particularly during spring, in the well-defined Gulf assemblage. The incorporation of additional taxa related to the northward advection of the TSW carrying tropical biota into the gulf (Brinton et al. 1986, Palomares-García et al. 2013) caused a tropicalization effect in the Gulf and Tropical assemblages. The paralarval abundance increased in spring in the dominant species *Pterygioteuthis hoylei*, *Argonauta* cf. *böttgeri*, and the SD complex as a response to the reproductive activity of the adults of each species (De Silva-Dávila 2013, De Silva-Dávila et al. 2013). This response is probably supported by the high ZV recorded in this season, suggesting a suitable environment with high food

availability for the paralarvae during both winter and spring.

In summer (July and September) the 3 paralarval assemblages remained well separated, although paralarval abundance, species richness, and diversity strongly decreased, despite the maximum intrusion of TSW into the gulf. This decrease may have been related to high temperatures due to the net solar radiation increases in this season (Brinton & Townsend 1980). We recorded T10 values ranging from 29.2 to 31.7°C in September, but CHL and ZV values were not significantly different from those in the previous seasons. The decrease in ecological indexes in summer could also be related to the lack of oblique sampling in the water column, because only surface tows were done during September. Paralarvae of the dominant species, *P. hoylei*, drastically decreased at the end of the winter–spring reproductive period of the species (De Silva-Dávila et al. 2013), as did those of *Argonauta* cf. *böttgeri*, resulting in a lower abundance of total paralarvae in summer.

During autumn (November 2005), the retreat of TSW to the entrance zone of the gulf led to a predominance of GCW throughout most of the gulf. Abundance and species richness in the assemblages increased again, but did not reach the high values observed during the spring, likely in response to the highly productive environment and low temperatures, but with a maximum decrease in diversity. *P. hoylei* showed a coupling to high winter–spring productivity, but also to high autumn productivity periods in the gulf (De Silva-Dávila et al. 2013). A similar coupling has been recorded in other upwelling areas, where coastal or local species were linked to productivity pulses observed as high paralarval abundances immediately after upwellings (Rocha et al. 1999, González et al. 2005, Moreno et al. 2009).

Two oceanographic cruises in autumn (November 2004 and 2006) surveyed the entrance zone of the gulf. This area is a highly complex oceanic region, where several water masses (TSW, California Current water, and the GCW) converge (Lavín & Marinone 2003). Mesoscale processes (thermohaline fronts, eddies, and filaments related to coastal wind-induced and topographic upwelling throughout the year) and submarine canyons influence the circulation patterns in this region (Torres-Orozco et al. 2005, Zamudio et al. 2008). In this area, only the Tropical assemblage was present, likely because of our limited seasonal sampling effort, which did not allow the observation of the seasonal effect of the southward flow of the GCW that reaches the Mazatlan Basin during winter (Lavín & Marinone 2003) and carries

planktonic biota from the Gulf of California to the eastern tropical Pacific Ocean. The high paralarval abundance recorded during November 2006 was composed primarily of SD complex paralarvae. The presence of this complex, comprised of recently hatched paralarvae of *Sthenoteuthis oualaniensis* and/or *Dosidicus gigas* (≤ 2.0 mm ML), indicated that spawning occurred in the area. The significant, but low correlation between SD complex paralarvae and the first axis in RDA (0.4526) indicated that, although these paralarvae are distributed throughout the entire Gulf of California (De Silva-Dávila 2013), the greatest abundance (in oblique and in surface tows) was related to the higher temperatures found in the southern gulf, particularly near Bahía de La Paz and the entrance zone, in accordance with the findings of Staaf et al. (2013) in the eastern tropical Pacific. The presence of *D. gigas* paralarvae (> 3.0 – 4.0 mm ML, Gulf assemblage) distributed at northern localities inside the gulf indicated, together with previous findings, that paralarvae that hatched in November in the southern portion of the study area may be carried toward higher latitudes inside the gulf during winter, when the water circulation pattern changes again, flowing to the north mainly on the peninsular side of the gulf. Once inside the gulf, paralarvae may take advantage of an optimal long-lasting (winter–spring) physical–biological environment to rapidly develop and grow. Paralarvae spawned inside the gulf may also be retained in this productive environment.

Combining data on paralarval abundance from different types of sampling gear, from areas that do not completely overlap, and from different seasons into a multivariate analysis may lead to unclear paralarval abundance–environmental patterns, due to considerable variability in the data. Surface nets are more effective than oblique nets at sampling the top 50 cm of the water column (depending on the type of net used), where ommastrephid paralarvae, particularly those of the SD complex, seem to occur at a higher abundance (Vecchione 1999, De Silva-Dávila 2013, Staaf et al. 2013). However, in our study area, species richness in this surface layer was low when compared to that obtained by oblique tows (De Silva-Dávila 2013). In contrast, studies of vertical distribution indicate that the abundance of paralarvae is generally high in the upper 50–100 m (Harman & Young 1985, Röpke et al. 1993, Bower & Takagi 2004, Miyahara et al. 2005). In addition, paralarvae show a stronger association with subsurface than surface conditions, through the greater likelihood of capture in oblique compared to surface tows (Staaf et al. 2013). A representative data base of the cephalopod

community of the epipelagic zone, comprising paralarvae of species of commercial interest in the SD complex better represented on surface samples, together with paralarvae distributed in the rest of the water column (0–200 m, oblique tows) could be used as a good source of data for the analysis of assemblages of planktonic paralarvae. Both communities, having similar abundance patterns as indicated by clustering analysis, showed a spatial response consistent with the environment present in the surface water masses of the Gulf of California.

In our study area, the strong latitudinal, cross-shelf, and seasonal environmental gradients, coupled with the seasonal flux of the surface water masses carrying planktonic biota, represent the driving force in the formation of the species assemblages of several planktonic groups at this scale. Phytoplankton cells (Gaxiola-Castro et al. 1999), euphausiids (Brinton & Townsend 1980, Brinton et al. 1986), and larval fish assemblages in the Gulf of California (Aceves-Medina et al. 2003, 2004, Avendaño-Ibarra et al. 2013) show direct relationships with environmental gradients, as we also found for cephalopod paralarval assemblages. The RDA reported here summarizes the findings we obtained by previous independent analyses of separate parts of the data base (oblique, surface, CAPEGOLCA, GCG, and S cruises), indicating statistical coherence of the data and a robust exploratory analysis that includes a wide range of environmental variables in the studied area and the response of well-represented cephalopod paralarval assemblages to this environment.

Similarity percentage analysis and rarefaction curves applied to RDA groups confirmed that the 3 paralarval assemblages differed significantly, because they responded differently to the environment in their patterns of abundance, distribution, species richness, and diversity.

According to De Silva-Dávila (2013), the species composition of paralarvae collected in the Gulf of California during 2004–2007 differed from that in other tropical and temperate regions around the world (Piatkowski et al. 1993, Diekmann & Piatkowski 2002, Granados-Amores et al. 2010). In this study, paralarvae collected in the gulf were dominated by pelagic–mesopelagic, tropical–subtropical oceanic species, but also included subarctic (Gonatidae family), temperate (*Abraliopsis* [*Boreabraliopsis*] *felis*), and cosmopolitan (*Ancistrocheirus* cf. *lesueurii*) species, as well as 1 loliginid (*Lolliguncula* sp. 1) specimen.

The family Gonatidae has a bipolar distribution (Arkhipkin et al. 2010), and, in the North Pacific

Ocean, it ranges from the subarctic zone to the temperate waters of the California Current system. The vast subtropical–tropical regions of the world's oceans are thought to be devoid of gonatids (Roper et al. 2010), but the record of a new species not yet described in the Gulf of California (F. G. Hochberg pers. obs.) indicates that other species may also be present far from their typical zoogeographic regions. Paralarvae of *Gonatus pyros*, *Gonatus* sp. 1, and *Gonatus* sp. 3 (included in the Gulf assemblage, 4.5–15.7 mm ML) were identified mainly by their distinctive head and mantle chromatophore patterns and ocular photophores (Jorgensen 2007, De Silva Dávila 2013). These records together with paralarval presence only during winter with distribution at the central region of the gulf above the deep (1000–3000 m) basins, may indicate a suitable habitat for hatching of paralarvae. Paralarvae could survive in a productive environment (high CHL and ZV) and at the lowest T10 of the year in epipelagic waters. At the same time, meso-bathypelagic subarctic–temperate adults of this family could be present in cold and deep waters of the Gulf of California. The occurrence of these morphologically distinct paralarvae suggests that at least 3 gonatid species likely spawn in the Gulf of California.

Adult specimens of *Abraliopsis* (*Boreabraliopsis*) *felis* (Young 1972), a temperate species thought endemic to the California Current (Okutani & McGowan 1969), have been reported from northern California, USA, to the oceanic area off San Quintín (27°N), Baja California, Mexico (Roper & Jereb 2010). Their paralarvae have been recorded near Cabo San Lucas (23°N) (Okutani & McGowan 1969). We collected this species near Bahía de La Paz and Isla Cerralvo (24.5°N) in winter. Paralarvae (5.0–7.8 mm ML) were identified from sibling species (*Abraliopsis* [*Pfefferiteuthis*] *affinis* and *Abraliopsis* [*Pfefferiteuthis*] *falco*) using, among other morphological characteristics, the distinctive shapes of the larger hook from Arm III and of the largest club hook from the tentacles (Young 1972). These records suggest that the distributional range of adults, and therefore their paralarvae, may be located further south than previously recorded. Another less likely explanation is passive transport or drift of hatched paralarvae from the southern region of the California Current into the gulf.

Enoploteuthid species, in particular *Abraliopsis* sp. 1 and *Abraliopsis* sp. 2, were frequently present as low-abundance species in the study area. Significant morphological differences in paralarvae (number of photophores on the head and mantle and num-

ber of hooks on the manus of the tentacles) of the same size range indicate that differences could indicate the presence of 2 species: *A. falco* and *A. affinis*. Adults of these species have overlapping distributional ranges in the Pacific Ocean off the coast of Mexico (Roper & Jereb 2010), and at least *A. affinis* is present inside the gulf as indicated by the collection of 1 adult specimen in our oblique samples.

Ancistrocheirus lesueurii occurs throughout the tropical and subtropical oceans of the world. In this study, very similar paralarvae (2.0–4.6 mm ML) of this species were recorded in all seasons except summer in both Tropical and Gulf assemblages. The morphology of the 4.6 mm ML specimens is similar to that of paralarvae found along the west coast of the Baja California Peninsula (Granados-Amores 2008) and in the Northwest Atlantic Ocean (Vecchione et al. 2001), but it is different from the specimen collected near Hawaii (Vecchione & Young 2008) and the specimens collected by Young et al. (1992). This suggests that there are at least 2 species of *Ancistrocheirus* in the eastern Pacific Ocean.

The paralarvae of the families Octopodidae and Argonautidae formed a very relevant component of the fauna in the Gulf of California during the spring season and had an important role in the definition of the assemblages. Octopus paralarvae in the gulf were collected at either oceanic or nearshore sampling stations, but almost all specimens were found in GCW. Paralarvae of *Octopus rubescens* were the only ones that coincided with the morphology and chromatophore patterns described for *Octopus* paralarvae by Hochberg et al. (1992). The observation of 5 other *Octopus* morphotypes (De Silva-Dávila 2013) suggests the presence of adults of species that had not previously been described in the Gulf of California, or of a few species with paralarvae with high morphological variance. In contrast, sampling stations with a high abundance of argonautid paralarvae, especially of *Argonauta* cf. *argo* and *Argonauta* cf. *böttgeri*, were associated with nearshore areas of the Baja California peninsula in TSW.

Although we made a significant zooplankton sampling effort, the lack of sampling at stations where seafloor depths were <100 m resulted in the collection of only 1 paralarva of the coastal species *Lolliguncula* sp. 1 (1.3 mm ML), over the continental shelf off Bahía Lechuguilla. The strong overlap in distribution of at least 3 species of this genus in the gulf: *Lolliguncula* (*Loliolopsis*) *diomedae* Hoyle, 1904, *Lolliguncula* (*Lolliguncula*) *panamensis* Berry, 1911, and *Lolliguncula argus* Brakonietcki & Roper 1985, recently proposed as *Doryteuthis argus* by Grana-

dos-Amores (2013), and the lack of morphological descriptions of their paralarvae prevent specific identification and inferences about their distribution patterns in the gulf. Nearshore sampling to obtain coastal species may improve our knowledge of the abundance, species richness, and diversity, as well as the nature of cephalopod coastal assemblages present in the Gulf of California.

The number of families, species richness, diversity, geographical limits, and structure of the cephalopod paralarval assemblages from the Gulf of California to Bahía de Banderas found in this study were observed to be related to typical environmental conditions as discussed earlier for cephalopods and other taxa. However, the response of the assemblages may be different in future ENSO events, because these events could incorporate additional tropical or temperate species in the gulf and modify their abundance and composition. The coupling of cephalopod paralarvae with changes in the flow of water masses has been recorded around the world, whereby thermohaline fronts occurring between water masses usually restrict the distribution of tropical and temperate species, establishing differences in paralarval abundance, diversity, and community structure on either side of the thermohaline fronts (Anderson & Rodhouse 2001, Diekmann & Piatkoski 2002, Granados-Amores 2008).

Conclusions

The warm ENSO phases recorded in 2004–2007 did not significantly influence the analyzed indicators of biological biomass (CHL and ZV) in the Gulf of California. During November 2005 (at the beginning of the ENSO cold phase), there was a decrease in temperature (SST and T10), a high wind speed, and a significant increase in upwelling, leading to high CHL and ZV.

Paralarvae responded to the effect and heterogeneities of environmental gradients of T10, S10, ZV, and CHL in the Gulf of California by forming 3 assemblages—Gulf, Tropical, and Shallow—associated with the seasonally dynamic flow and geographic boundaries of the surface water masses (GCW and TSW) delimited by the ≥ 35.0 isohaline.

The cephalopod paralarvae collected in this study were mostly tropical, pelagic species. A few temperate species were collected, but only during winter and spring, as well as 1 cosmopolitan and 1 coastal species. The effect of the seasonal tropicalization of the planktonic fauna reported in other zooplanktonic

groups (Brinton et al. 1986, Palomares-García et al. 2013) was also observed in cephalopod paralarval assemblages.

Although a few species dominated the overall abundance of paralarvae, the community structure differed significantly between assemblages, suggesting they can be used as biological indicators of water masses and their distributional patterns in the Gulf of California.

The present study represents a base for understanding the environment–abundance relationships of cephalopod paralarval assemblages in the Gulf of California that will be useful for future planktonic ecological research on this zooplanktonic group.

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