

Research Article

Influence of the oceanographic dynamic in size distribution of cephalopod paralarvae in the southern Mexican Pacific Ocean (rainy seasons 2007 and 2008)

**Gerardo Aceves-Medina¹, Roxana De Silva-Dávila¹, Iván Cruz-Estudillo^{1†}
Reginaldo Durazo^{1,2} & Raymundo Avendaño-Ibarra¹**

¹Instituto Politécnico Nacional, Centro Interdisciplinario de Ciencias Marinas
La Paz, Baja California Sur, México

²Facultad de Ciencias Marinas, Universidad Autónoma de Baja California
Carretera Ensenada-Tijuana, Ensenada, Baja California, México

Corresponding author: Roxana De Silva-Dávila (rdesilva@ipn.mx)

ABSTRACT. The southern Mexican Pacific Ocean presents seasonal changes related to the rainy season and Tehuano winds, which generate mesoscale processes affecting biological productivity and marine biodiversity. Size distributions of squid paralarvae collected in this region during the rainy season (July 2007 and May-June 2008) were analyzed in relation to regional oceanography. Samples were collected through oblique hauls, and CTD casts were used to determine the structure of the water column. Between surveyed periods, there were no significant changes in the water temperature at 10 m, but there were significant variations in the mixed layer depth (MLD). The number of taxa, community composition and total abundance of paralarvae were similar between periods. However, in July paralarvae ≤ 2.0 mm were distributed along the margins of cyclonic and anticyclonic eddies associated with high temperatures. In May-June, the MLD and high concentrations of chlorophyll-*a* (Chl-*a*) determined the presence of a group of oceanic paralarvae and another of coastal paralarvae, separated by an upwelling front. The percentage of recently spawned paralarvae (≤ 2.0) nearly doubled during this period as a result of increased coastal sampling and high concentrations of Chl-*a*, indicating a coupling of adult reproduction with regional productivity. In the absence of winds, the mesoscale oceanographic complexity generates gradients and a differential effect on the distribution, transport and survival of cephalopod paralarvae.

Keywords: eddies, paralarvae, hatching areas, squid, Gulf of Tehuantepec.

INTRODUCTION

The ecological and fishing relevance of squid in marine ecosystems has encouraged their study in the principal fishing regions of the world over the last three decades (Gilly *et al.*, 2006; Jereb & Roper, 2010). In Mexico, studies of adults have been fundamental for fisheries (Morales-Bojórquez *et al.*, 2001; Nigmatullin *et al.*, 2001; Markaida *et al.*, 2004), while those of paralarvae have been useful for determining species richness and its relationship with diverse environmental factors and oceanographic processes at various scales (Granados-Amores *et al.*, 2010; De Silva-Dávila *et al.*, 2015; Sánchez-Velasco *et al.*, 2016) which affect survival, distribution and abundance (Diekman *et al.*, 2002;

Vega *et al.*, 2002; Moreno *et al.*, 2009). Size analysis also allows for the detection of reproductive areas and periods (Bower *et al.*, 1999).

Squid diversity in the micronekton of the Eastern Tropical Pacific is low, with only 15 species reported from the families Eupoloteuthidae, Onychoteuthidae, Cranchiidae, Histioteuthidae and Ommastrephidae (Blackburn, 1968). In this region, the squid paralarval community is dominated by *Dosidicus gigas* (D'Orbigny, 1835) and *Sthenoteuthis oualaniensis* (Lesson, 1830), which is amplified through the effect of El Niño-Southern Oscillation (ENSO) and the proximity of the Costa Rica Dome (Vecchione, 1999; Staaf *et al.*, 2013).

In the oceanic zone of northwestern Mexico (including the Gulf of California), paralarval distribution has been associated with the seasonal and interannual advance and retreat of latitudinal distributions of water masses, the northward transport of warm waters by El Niño-Southern Oscillation, the convergence and front formation of surface water masses, retention through mesoscale eddies, and with adult spawning habitats (Granados-Amores *et al.*, 2010; De Silva-Dávila *et al.*, 2013; Staaf *et al.*, 2013; Sánchez-Velasco *et al.*, 2016). The spawning season, area and environment of *Pterygioteuthis hoylei* (Pfeffer, 1912), one of the most abundant species in the Gulf of California, has also been characterized based on paralarvae size analysis (De Silva-Dávila *et al.*, 2013).

In the Gulf of Tehuantepec, there is only one antecedent that established the taxonomic composition and abundance of paralarval and juvenile cephalopods during summer and autumn of 2001 (Alejo-Plata *et al.*, 2013), meanwhile the relation of this paralarval community to regional oceanography remains unknown.

The Gulf of Tehuantepec and the nearby Pacific maintain a high biological diversity due to strong environmental contrasts and high primary productivity (Lara-Lara *et al.*, 2008). The continental platform of the western gulf is narrow and rocky, but in the east it is wide and muddy-sandy, with important lagoon systems and freshwater inputs (Morales de la Garza & Carranza-Edwards, 1995). From October to April (dry period) intense northerly winds known as Nortes or Tehuanos ($\sim 20 \text{ m s}^{-1}$ for up to 10 days) flow from the Gulf of Mexico toward the Pacific Ocean across the Isthmus of Tehuantepec, provoking intense upwelling, mesoscale eddies and divergence zones in the Gulf and nearby regions (Zamudio *et al.*, 2006; Barton *et al.*, 2008; Trasviña & Barton, 2008). In May the rainy period begins, and from May to September upwelling and eddies occur. During this period the Tehuano winds are not present or are very weak (Velázquez-Muñoz *et al.*, 2014).

The eddies establish the formation of thermal and saline fronts and gradients as well as depth of the thermocline and mixed layer (Trasviña *et al.*, 2003; Zamudio *et al.*, 2006; Trasviña & Barton, 2008), which represent physical borders or advective mechanisms that shape and modify spatial patterns of species abundance (Moreno *et al.*, 2009).

The objective of this work was to analyze the effects of environmental variables and regional oceanography on the abundance and size distribution of squid paralarvae registered in the Gulf of Tehuantepec and the surrounding southern Mexican Pacific during the rainy period in absence of Tehuano winds.

MATERIALS AND METHODS

The survey area is located in the Eastern Tropical Pacific in the southern region of the Mexican Pacific Ocean, demarcated to the north by the coasts of Puerto Escondido, Oaxaca ($15^{\circ}55' \text{N}$, $97^{\circ}10' \text{W}$) and Puerto Madero, Chiapas ($15^{\circ}30' \text{N}$, $93^{\circ}00' \text{W}$), and to the south by the coordinates $12^{\circ}12' \text{N}$, $98^{\circ}12' \text{W}$ y $13^{\circ}04' \text{N}$, $93^{\circ}51' \text{W}$ (Fig. 1). Two oceanographic campaigns were conducted aboard the R/V Altair BI-03 of the Secretaría de Marina, Armada de México (Secretariat of Navy-Mexican Navy) from 3 to 12 July 2007, and 26 May to 8 June 2008, corresponding to the rainy period in absence of Tehuano winds. Three perpendicular transects to the coast were surveyed, obtaining 32 zooplankton samples in July and 36 in May-June. Additional stations were included on the continental shelf in May-June (Fig. 1).

The sampling method was described by Smith & Richardson (1979), comprising oblique tows of paired 0.6 m diameter Bongo nets with 303 μm and 505 μm mesh and flexible cod-ends. Flowmeters were fitted to the center of the mouth of each net to estimate the water volume filtered in each tow. Tow speed was from 1.5 to 2 knots. Samples analyzed in this study were caught in the 505 μm net, and were fixed in 96% alcohol.

At each station a CTD (Seabird) was cast to a maximum depth of 600 m was conducted. For each CTD cast the mixed layer depth (MLD), defined as the depth where the temperature differed by 1°C from the temperature at 10 m was calculated. In each transect the stations were separated by 35-40 km, except for the most oceanic stations of transects 1 and 2 during July 2007, which were separated by distances between 70-80 km and 50-60 km, respectively. Maps of sea level anomalies (MSLA, in cm) relative to the average altimetry from images during the period 1993-2013 (<http://www.avisio.altimetry.fr>) were used. Surface chlorophyll-*a* (Chl-*a*) data were used to generate distributional maps, obtained from Aquamodis satellite images (<http://ocean.color.gsfc.nasa.gov/>).

In the laboratory, the displaced volume of each zooplankton sample was measured (Beers, 1976) and the values were standardized to $\text{mL } 1000 \text{ m}^{-3}$ of filtered water (Postel *et al.*, 2000). The paralarvae were separated under a stereoscope and identified to the lowest possible taxonomic level following Sweeney *et al.* (1992), Diekmann & Piatkowski (2002), Wakabayashi *et al.* (2002), and Bolstad (2010). The dorsal mantle length (ML) of all paralarvae was measured (Roper & Voss, 1983) with a calibrated ocular micrometer. Paralarval abundance and distribution were analyzed by taxon at species level and were grouped into two size classes: recently spawned charac-

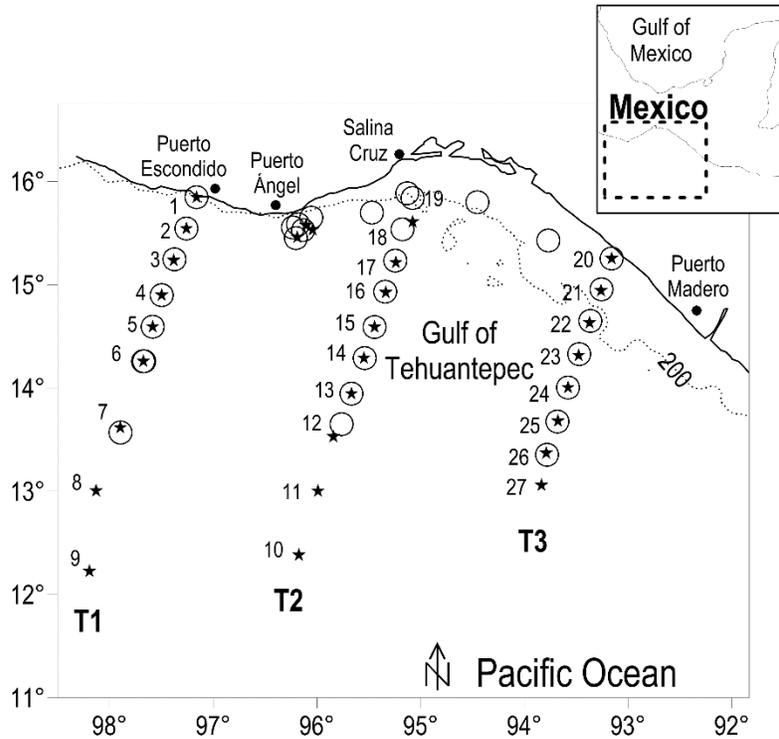


Figure 1. Study area, transects (T1, T2, T3), and sampling stations for cruises during July 2007 (★) and May-June 2008 (○). Dashed line: 200 m depth isobath.

terized by $ML \leq 2.0$ mm (Bower *et al.*, 1999; Vecchione, 1999; Goto, 2002; Shimura *et al.*, 2005), and sizes of $ML > 2.0$ mm. Abundance by taxon and size was standardized for each station to number of paralarvae (PL) in 1000 m³ of filtered water (PL 1000 m⁻³) (Postel *et al.*, 2000).

A canonical correspondence analysis (CCA, Ter Braak & Prentice, 2004) was used to explore the relation between environmental variables and paralarval abundance for each cruise. Seven environmental variables were used: temperature at 10 m depth (T10), mixed layer depth (MLD), average temperature, density and salinity at the base of the mixed layer (TMLD, DMLD and SMLD respectively), surface Chl-*a* concentration and zooplankton volume (ZV). To determine the most robust canonical analysis for the species-stations group, a detrended correspondence analysis (DCA) (Ter Braak & Prentice, 2004) was applied which permitted the determination of the environmental gradient length in both periods and the redundancy between variables. A Monte Carlo test (499 permutations) was used to test significance of the analysis. The main matrix (species abundance) of the CCA was refined by eliminating sampling stations and taxa with only one individual. Paralarval abundance values were transformed to $[\log(x_{ij}+1)]$, where x is the abundance of species i in station j . The values of

environmental variables in the second matrix were transformed to standard error ($SE = X - \mu / \sigma (\sqrt{n-1})$) in each of the analyzed periods, where X = value of the environmental variable analyzed, μ = mean value of X , σ = standard value of X , and n = number of data.

RESULTS

Temperature in the first 10 m of the water column was homogenous over all transects during July (Fig. 2a). Average T10 was 30.2°C, with the lowest value of 29.8°C in the most coastal stations of transects 1 and 2, and the highest of 31.0°C across the entire transect 3. Average MLD was 28 m, but was deepest in transect 2, where the thermocline profiles dropped to 42 m in the middle stations.

During May-June the T10 had a barely perceptible gradient (28.1-29.5°C, Fig. 2b) and the average (28.9°C) was 1.3°C lower than during July 2007. The highest values were found in the coastal zone between transects 1 and 2. Temperature profiles showed an elevation of the thermocline in the middle stations of the three transects, and 32 m average MLD depth, 4 m deeper than that observed the year before.

In July, geostrophic surface currents showed three eddies. One cyclonic in the extreme western region of

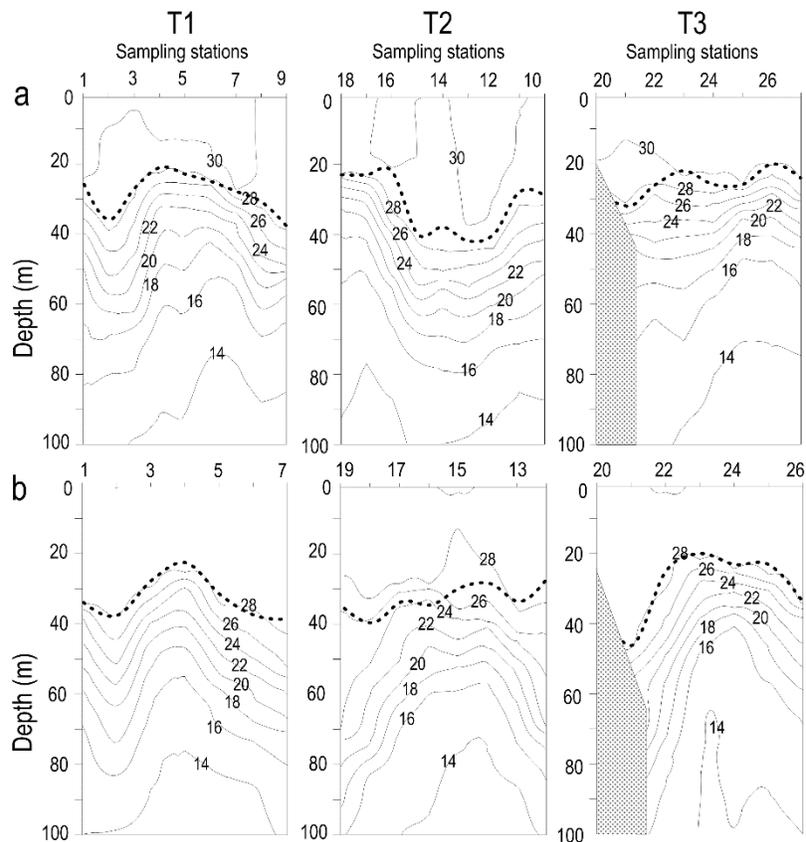


Figure 2. Temperature profiles of transects T1, T2, and T3 for a) July 2007 and b) May-June 2008. Dashed line indicates the mixed layer depth.

the surveyed area, an anticyclonic in front of Salina Cruz (transect 2) and a third cyclonic eddy of smaller magnitude to the east of the surveyed area (Fig. 3a).

The western cyclonic eddy circulation explains the elevation of the thermocline and the cold water core in the middle stations of transect 1 (Figs. 2a, 3c) through seawater elevation as well as increased Chl-*a* concentrations (Fig. 3d) in the same stations. The anticyclonic eddy induced a deepening of the MLD in transect 2 (Fig. 2a) due to the accumulation of warm water in its core (Fig. 3c) and a reduction of Chl-*a* concentrations (Fig. 3d). Transect 3 was located in the front zone between the anticyclonic eddy and the smaller eastern cyclonic eddy (Fig. 3a). The highest concentrations of zooplankton were distributed along the oceanic border of the western eddy and the coastal region of transect 3 (Fig. 3e).

The highest abundance of recently spawned paralarvae (≤ 2 mm ML) was collected at the eddy margins (Fig. 3a), while the highest abundance of paralarvae ≥ 2 mm ML was found in the center of the anticyclonic eddy and in the center of transect 3, where flow intensity was relatively lower (Fig. 3b). Regar-

dless of size, paralarvae were distributed at the highest temperatures.

Geostrophic currents during May-June (Fig. 4a) showed circulation patterns similar to July, with a cyclonic eddy over transect T1, next to an anticyclonic eddy in transect T2 and a third cyclonic eddy with lower flow velocity to the east (Fig. 4a). Temperature at the MLD (32 m) was higher in the coastal and oceanic zones (26–30°C), which were separated by a relatively cold intermediate zone (21–25°C, Fig. 4c) and circulation showed a westerly flow of warm water along the coast (Fig. 4a). Higher values of Chl-*a* (Fig. 4d) and zooplankton volume (Fig. 4e) were associated with coastal stations and the middle stations of the three transects, where MLD was shallower (Fig. 2b).

Abundance of recently spawned paralarvae was higher in the coastal zone and the cyclonic eddy to the west of Puerto Ángel (Fig. 4a), while the larger paralarvae showed low abundances in the western coastal zone and at the eddy margins (Fig. 4b).

From 68 samples collected in July 2007 and May-June 2008 in the Gulf of Tehuantepec, 376 squid paralarvae were recorded. At least one paralarvae was

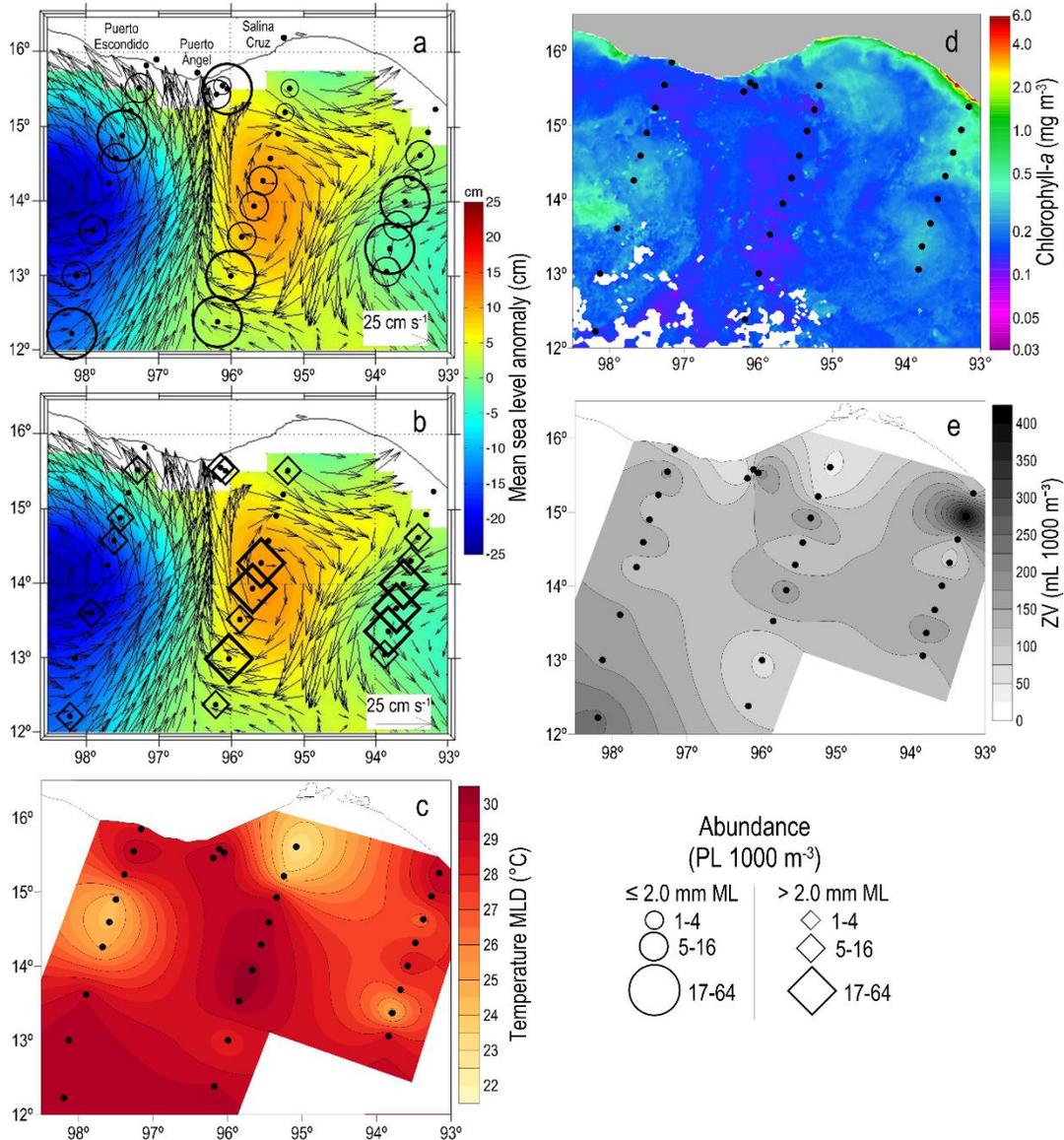


Figure 3. July 2007. Horizontal distribution of a) paralarvae abundance ≤ 2.0 mm ML (circles), mean sea surface level anomaly (cm, colors), and vectors of associated geostrophic currents, b) paralarvae abundance ≥ 2.0 mm ML (diamonds), mean sea surface level anomaly (cm, colors), and vectors of associated geostrophic currents, c) temperature at the mixed layer depth (MLD), d) chlorophyll-*a* concentration, e) zooplankton volume (ZV).

present in 73.5% of the samples. Fifteen taxa were identified, classified in seven families and nine genera (ITIS, 2015). Seven taxa were identified to species level, and three more were assigned a type (sp. 1 or sp. 2), which allowed for their inclusion as entities equivalent to species in the analysis. Four taxa were identified only to genera and one species complex (Table 1). Of the 15 taxa, eight (53.3%) were registered in both surveyed seasons and seven (46.7%) in only one (Table 1). The most abundant families were Enoplateuthidae, Ommastrephidae, Cranchiidae and Onychoteu-

thidae, with slightly different values between periods (Table 2). Total paralarval abundance was similar in both cruises (544 and 535 PL 1000 m⁻³), as well as number of taxa (12 and 11), and average paralarval abundance per sampling station (20.6 and 22.3 PL 1000 m⁻³).

The paralarval community was similar in both periods, with slight differences in dominant taxa. In July, the six taxa that contributed to 90% of abundance were: *Abraliopsis* sp. 2 (21.8%), the *Sthenoteuthis oualaniensis-Dosidicus gigas* complex (SD complex,

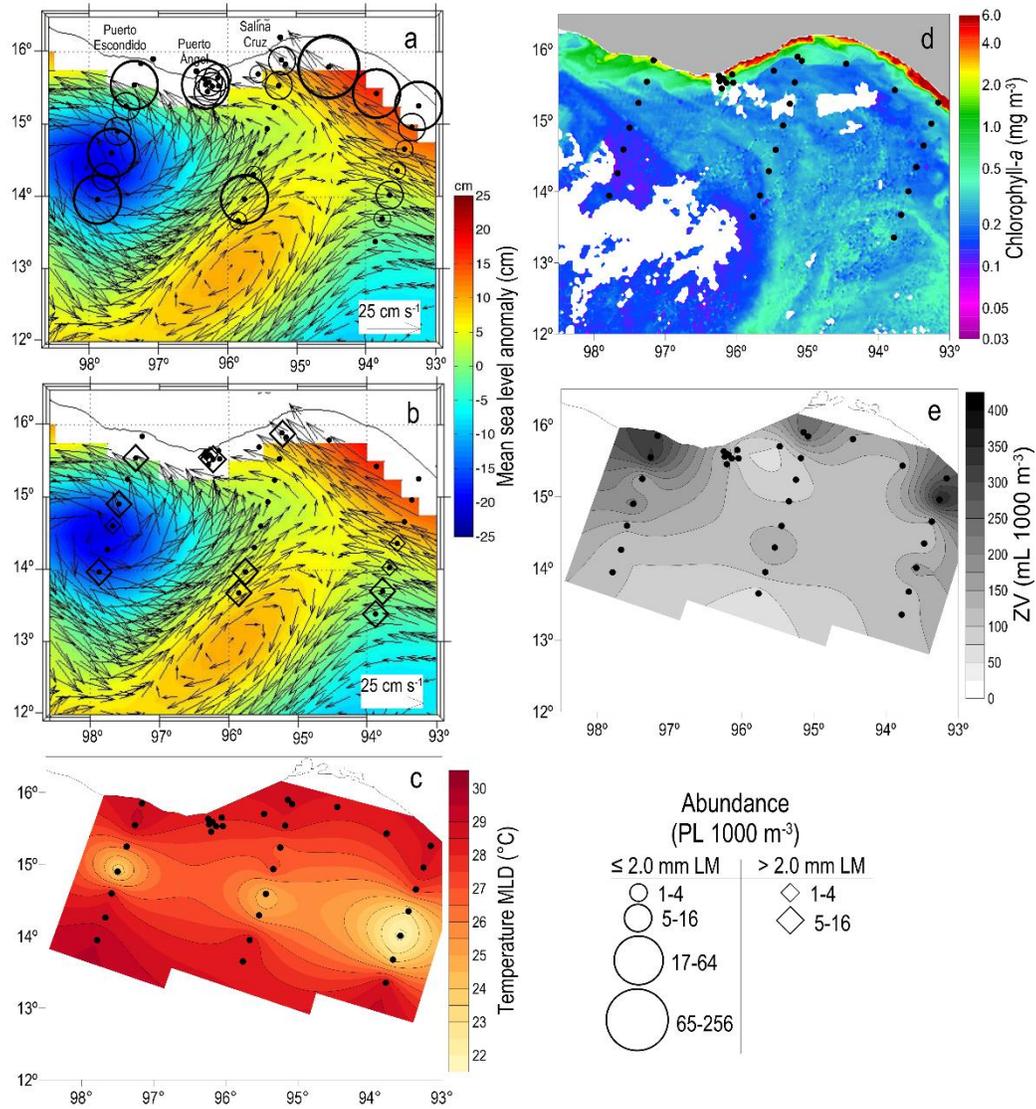


Figure 4. May-June 2008. Horizontal distribution of: a) paralarvae abundance ≤ 2.0 mm ML (circles), mean sea surface level anomaly (cm, colors), and vectors of associated geostrophic currents, b) paralarvae abundance ≥ 2.0 mm ML (diamonds), mean sea surface level anomaly (cm, colors), and vectors of associated geostrophic currents, c) temperature at the mixed layer depth (MLD), d) chlorophyll-*a* concentration, e) zooplankton volume (ZV).

comprising morphologically indistinguishable paralarvae < 3.0 mm ML) (18.2%), *Onychoteuthis horstkottei* (17.4%), *Drechselia danae* (16.2%), *Abraliopsis* sp. 1 (14.3%) and *Sthenoteuthis oualaniensis* (4.6%) (Table 2).

In May-June the most abundant taxa were: the SD complex (32.5%), two species of *Abraliopsis*, *Leachia* spp. and *Onychoteuthis horstkottei*. The species *Lolliguncula* sp. 1, *Pterygioteuthis hoylei* and *Abraliopsis falco* were registered only during this period (Table 2). Due to damage or incompleteness, 1.1% of paralarvae were not measured. Of the remaining paralarvae, 45.3%

were ≤ 2.0 mm ML in July, and this percentage almost doubled in May-June to 83.8% (Table 2), suggesting higher reproductive activity at the beginning of summer.

In comparative terms, paralarvae ≤ 2.0 mm ML of the two *Abraliopsis* species, the SD complex, and *Leachia* spp. were most abundant in May-June. Paralarvae ≤ 2.0 mm ML of *Lolliguncula* sp. 1 were only registered in May-June, while all paralarvae of *Drechselia danae*, *Sthenoteuthis oualaniensis*, *Chiroteuthis calyx*, *Hyaloteuthis pelagica* and *Abraliopsis falco* were > 2.0 mm ML (Table 2).

Table 1. Systematic list of squid paralarvae collected during July 2007 (JUL) and May-June 2008 (MAY-JUN) in the southern Mexican Pacific Ocean. Abbreviations of species names for Figure 5, in parentheses.

Taxonomic list		JUL	MAY-JUN
Order Teuthida			
Suborder Myopsina			
Family Loliginidae	<i>Lolliguncula</i> sp. 1		X
Suborder Oegopsida			
Family Chiroteuthidae	<i>Chiroteuthis calyx</i> (Young, 1972) (Chical)	X	X
	<i>Chiroteuthis</i> spp. (Chir)	X	
Family Cranchiidae	<i>Drechselia danae</i> (Joubin, 1931) (Dredan)	X	X
	<i>Leachia</i> spp. (Leachia, Lea)	X	X
Family Enoploteuthidae	<i>Abraliopsis falco</i> (Young, 1972) (Abrfal)		X
	<i>Abraliopsis</i> sp. 1 (Abr1)	X	X
	<i>Abraliopsis</i> sp. 2 (Abr2)	X	X
	<i>Abraliopsis</i> spp. (Abr)	X	
Family Ommastrephidae	<i>Hyaloteuthis pelagica</i> (Bosc, 1802) (Hyapel)	X	
	<i>Sthenoteuthis oualaniensis</i> (Lesson, 1830) (Sthoua)	X	X
	Complejo SD (SD)	X	X
Family Onychoteuthidae	<i>Onychoteuthis horstkottei</i> Bolstad, 2010 (Onyhor)	X	X
	<i>Onychoteuthis</i> spp. (Ony)	X	
Family Pyroteuthidae	<i>Pterygioteuthis hoylei</i> (Lindgren, 2010) (Pte)		X

Table 2. Total abundance (Ab, PL 1000 m⁻³) and relative abundance (%) of squid paralarvae. Relative abundance of paralarvae by size class (≤ 2.0 mm and > 2.0 mm LM), from July 2007 and May-June 2008. Shaded area: taxa contributing to 90% of abundance.

Taxa	July 2007			May-June 2008		
	Ab (%)	≤ 2.0	> 2.0	Ab	≤ 2.0	> 2.0
Enoploteuthidae	198 (36.4)			217 (40.5)		
<i>Abraliopsis falco</i>		--	--	2 (0.4)	0.0	100
<i>Abraliopsis</i> sp. 1	78 (14.3)	80.9	19.1	56 (10.4)	100	0.0
<i>Abraliopsis</i> sp. 2	119 (21.8)	41.2	58.8	159 (29.7)	91.5	8.5
<i>Abraliopsis</i> spp.	2 (0.3)	100	0.0	--	--	--
Ommastrephidae	131 (24.1)			187 (35)		
<i>Hyaloteuthis pelagica</i>	5 (0.9)	0.0	100	--	--	--
<i>Sthenoteuthis oualaniensis</i>	25 (4.6)	0.0	100	8 (1.4)	0.0	100
Complejo SD	99 (18.2)	86.9	13.1	174 (32.5)	100	0.0
Cranchiidae	100 (18.4)			68 (12.7)		
<i>Drechselia danae</i>	88 (16.2)	0.0	100	3 (0.5)	0.0	100
<i>Leachia</i> spp.	12 (2.2)	0.0	100	65 (12.2)	80.2	19.8
Onychoteuthidae	99 (18.1)			42 (7.8)		
<i>Onychoteuthis horstkottei</i>	95 (17.4)	42.8	57.2	41 (7.8)	0.0	100
<i>Onychoteuthis</i> spp.	4 (0.7)	50.0	50.0	--	--	--
Loliginidae	--			13 (2.4)		
<i>Lolliguncula</i> sp. 1		--	--	13 (2.4)	100	0.0
Chiroteuthidae	16 (3.0)			6 (1.0)		
<i>Chiroteuthis calix</i>	9 (1.6)	0.0	100	6 (1.0)	0.0	100
<i>Chiroteuthis</i> spp.	8 (1.4)	25.9	74.1	--	--	--
Pyroteuthidae	--			3 (0.5)		
<i>Pterygioteuthis hoylei</i>		--	--	2 (0.5)	100	0.0
Total paralarvae	544	45.3	54.7	535	83.8	16.2
Paralarvae by positive station +	20.6			22.3		

In July the majority of paralarvae had an oceanic distribution regardless of size (Figs. 3a-3b), but in May-June more than 70% of paralarvae ≤ 2.0 mm ML (SD complex *Abraliopsis* sp. 2, *Abraliopsis* sp. 1, *Leachia* spp. and *Lolliguncula* sp. 1), were distributed along the shelf and continental margin of the Gulf of Tehuantepec and in the oceanic zone of transect 1 (Fig. 4a). In this period almost all paralarvae >2.0 mm ML had an oceanic distribution (Fig. 4b).

The detrended canonical correspondence analysis showed that S10, D10 and DMLD were redundant in both periods, therefore they were eliminated from the CCA. The July CCA showed that the environmental variables explained 62.8% of variance in the species-environment correlation (Table 3). Axis 1 explained 37.0% of the variance and had a significant negative correlation (-0.74) with T10, while axis 2 was correlated with ZV (-0.55) explaining 25.8% of variance. The distribution diagram of the July CCA (Fig. 5a) shows an ordination in which the species to the extreme left of axis 1 (*Leachia* spp. and *Chiroteuthis calyx*), were distributed exclusively in the eastern transect of the surveyed area (Fig. 6d), in stations with lower temperatures than nearby stations. The diagram also shows that *Abraliopsis* sp. 2 and *Onychoteuthis horstkottei*, which were present in all transects (Figs. 6a-6b) did not present any particular relation with the environmental variables. The SD complex *Drechselia danae* and *Sthenoteuthis oualaniensis* (Figs. 6e-6g), as well as less abundant and frequent species (Fig. 6h) which in conjunction represented 57% of total paralarvae abundance, were located in stations with higher T10 and low Chl-*a* and ZV.

The May-June CCA explained 75.2% of species-environment variance (Table 3). The MLD was significantly correlated to the first axis (51.1% explained variance, -0.68), and concentration of Chl-*a* (0.77) in the second axis (Table 3). The distribution diagram of the May-June CCA (Fig. 5b) shows a clear association between *Abraliopsis* sp. 1, which was only distributed in the coastal region of transect 1 (Fig. 7f), and high concentrations of Chl-*a*. At the positive end of axis 1, *Lolliguncula* sp. 1 was recorded in the most coastal station of transect 3 (Fig. 7g) with the shallowest MLD and high ZV. Paralarvae of the most abundant taxa such as the SD complex, *Leachia* spp., *Onychoteuthis horstkottei* and *Abraliopsis* sp. 2 either were not registered in the middle stations of transects 2 and 3 or were present in very low abundances (Figs. 7a, 7c, 7e). The two first taxa were associated with large Chl-*a* values and the highest temperatures (T10 and TMLD), while the others had a more oceanic distribution associated with low values of Chl-*a* and relatively lower temperatures.

DISCUSSION

The Gulf of Tehuantepec is one of the regions of the world with the least amount of information on marine communities and environmental variability (Ortega-García *et al.*, 2000), which is reflected in the limited information on the cephalopod community. In this region, adults of 45-50 species of squid have been registered (Jereb & Roper, 2010) but only 11 of paralarvae (Alejo-Plata *et al.*, 2013). The present study adds five new identifications based on paralarvae of *Lolliguncula* sp. 1, *Chiroteuthis calyx*, *Abraliopsis falco*, *Onychoteuthis hostkottei* and *Pterygioteuthis hoylei*.

Ibáñez & Cifuentes-Bustamante (2016) mention that historically, the most commonly reported name for the *Onychoteuthis* genera around the world is *Onychoteuthis banksii*. Based on the studies by Bolstad (2008, 2010), these authors establish that the previous records of *O. banksii* in the southeast Pacific Ocean are probably *O. aequimanus*. A review of available literature and the previous records of *Onychoteuthis banksii* sp. 1 and *O. banksii* sp. 2 in the Gulf of Tehuantepec (Alejo-Plata *et al.*, 2013), suggests that these species probably belong to *O. compacta* (Berry, 1913), *O. borealijaponica* (Okada, 1927) or *O. horstkottei* which are distributed in Mexican Pacific waters between 90°-120°W. Morphological and systematic analyses of the family performed by Bolstad (2008, 2010) demonstrated that *O. banksii* is only distributed in the Atlantic Ocean. Verification is also required of *Leachia dislocata* (Young, 1972) (R. Young, *com. pers.*), which appears to be a junior synonym of *Leachia pacifica* (Issel, 1908) (ITIS, 2015). It is also important to specify that the valid name of *Leachia danae* is *Drechselia danae* (ITIS, 2015). Taking this into account we can conclude that to date, the cephalopod paralarval community of the Gulf of Tehuantepec includes at least 16 species, which represent 32 to 36% of adults registered in the zone.

The squid paralarval community was practically the same in July 2007 and May-June 2008, sharing 72% of the same species, which together accounted for 98% of abundance. This community was primarily oceanic with a tropical affinity, whose adults distribute in the epi-mesopelagic zone (*Abraliopsis falco*, *Dosidicus gigas*), epi-bathypelagic (*Hyaloteuthis pelagica* (Bosc, 1802), *Sthenoteuthis oualaniensis*), mesopelagic (*Pterygioteuthis hoylei*), meso-bathypelagic (*Chiroteuthis calyx*, *Leachia pacifica*), and bathypelagic (*Drechselia danae*) (Jereb & Roper, 2010). The presence of *Lolliguncula* paralarvae over the continental shelf reflected the coastal-demersal habitat of their adults.

Table 3. Canonical correspondence analysis results and correlation values of: T10: temperature at 10 m, MLD: mixed layer depth, TMLD and SMLD: temperature and salinity at the mixed layer depth respectively, ZV: zooplankton volume, and Chl-*a*: chlorophyll-*a* concentration. Shaded numbers: significant correlation values.

Cumulative variance (%)	July 2007			May-June 2008		
	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
Species abundance	8.50	14.40	18.20	26.10	38.50	44.60
Species-environment relation	37.00	62.80	79.30	51.10	75.20	87.10
T10	-0.74	-0.32	0.55	-0.30	0.56	-0.30
MLD	0.50	-0.17	-0.03	-0.68	0.25	-0.49
TMLD	0.05	0.09	-0.15	0.10	0.49	-0.78
SMLD	-0.54	0.13	-0.03	-0.54	0.08	0.26
Chl- <i>a</i>	-0.02	-0.05	0.55	-0.05	0.77	0.61
ZV	-0.18	-0.55	-0.18	0.43	0.44	0.30

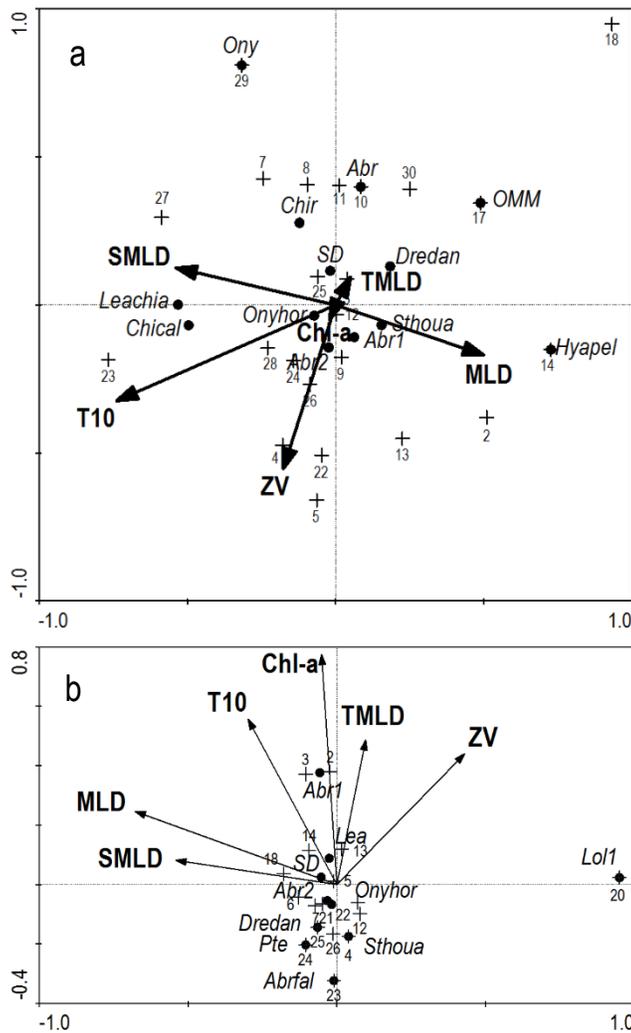


Figure 5. Dispersion diagrams of the canonical correspondence analyses for: a) July 2007 and b) May-June 2008. T10: temperature at 10 m depth, MLD: mixed layer depth, TMLD and SMLD: temperature and salinity at the mixed layer depth respectively, ZV: zooplankton volume, Chl-*a*: chlorophyll-*a* concentration. OMM: Ommastrephidae. Names of taxa in a) and b), in Table 1.

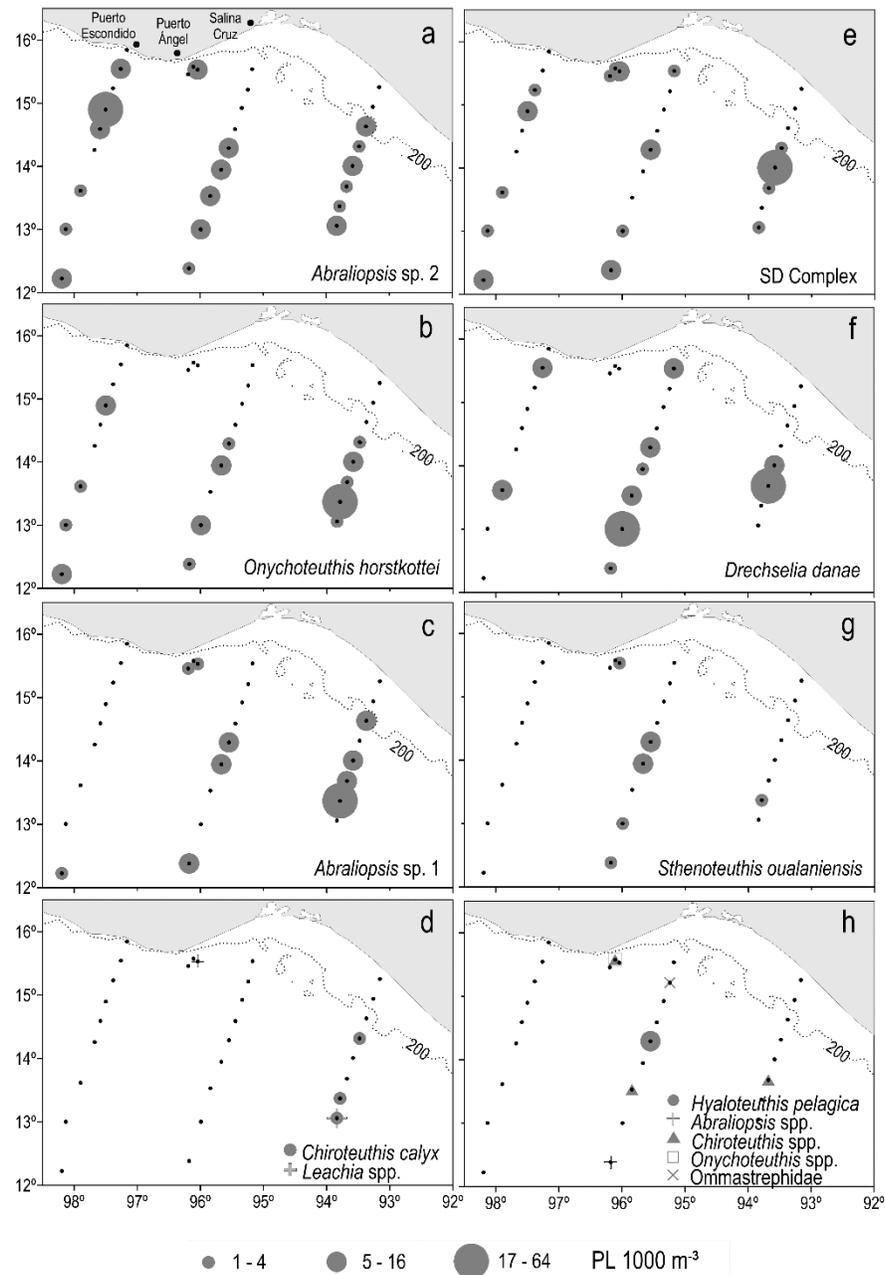


Figure 6. Horizontal distribution of squid paralarvae in the southern Mexican Pacific Ocean during July 2007.

During the analyzed cruises variation in T10 was barely perceptible, coinciding with the previously reported thermal regime for this tropical zone (Barton *et al.*, 1993). Both periods also showed a marked similarity between values of physical variables, circulation patterns which showed cyclonic and anticyclonic eddies in practically the same position and similar paralarval communities. This allows for the conclusion that the surveys conducted in July 2007 and May-June 2008 can be considered comparable and corresponding to the summer rainy season with no

Tehuano winds, characterizing this scarcely studied period of the year.

The circulation pattern in both periods was defined primarily by the pair of eddies (dipole), cyclonic to the west and anticyclonic at the center of the survey area. The anticyclonic eddies last longer (6-7 weeks) and propagate towards the southwest (Trasviña & Barton, 2008), therefore they can function as a mechanism of zooplankton retention and transport towards the ocean.

In July, the dipole hydrodynamics played an important role in the coupling of the paralarvae with the envi-

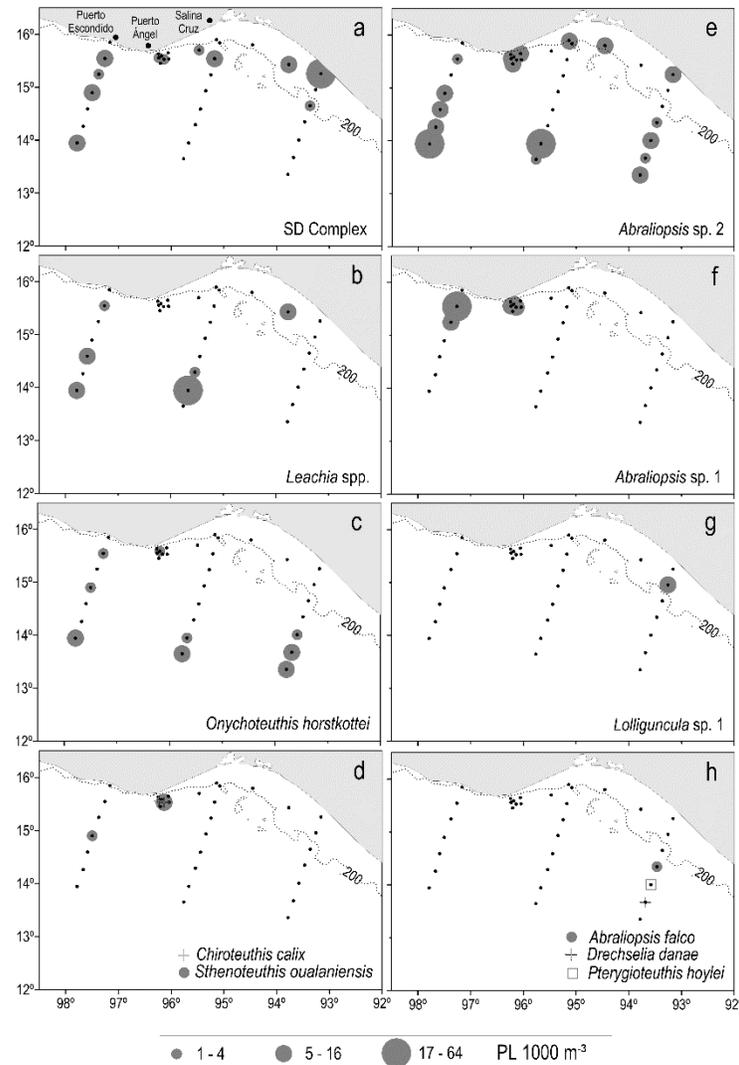


Figure 7. Horizontal distribution of squid paralarvae in the southern Mexican Pacific Ocean during May-June 2008.

ronment. The results suggest a spawning event, or at least a hatching area, in the influence zone of the western cyclonic eddy (T1). Some of these small paralarvae and those that were found along the southern margin of this eddy could be drawn toward the center of the anticyclonic eddy. The slight increase in ZV in the middle station of transect 2, together with the higher abundance of large paralarvae, suggests an initial stage in the evolution of the eddy with an incipient retention of organisms at the center. The abundance of small paralarvae along the margin of the eastern anticyclonic eddy (T3) indicates another hatching event. Paralarval dispersion in this part of the surveyed area appears to be non-significant, since the paralarvae (small and large) were maintained in the same stations, probably due to the lower velocity of the current. In addition, all paralarvae were distributed in high temperature zones within the dipole; hatching sites (small paralarvae)

were associated with higher Chl-*a* concentrations, and the majority abundance of large paralarvae with higher zooplankton volume.

According to the July CCA, along axis 1 the strongest correlation between abundance and environmental variables was with T10. However, at this depth the thermal conditions were different than those at MLD, where the eddy effect on paralarval distribution was evident. Given that most paralarval abundance is found in the first 50 m of the water column (Sánchez-Velasco *et al.*, 2016), both T10 and the hydrodynamics determined the distribution of hatching areas. In the second axis, ZV was correlated with greater concentrations of large paralarvae. However, failure to monitor the evolution of the eddy in time and space makes it difficult to know if this is what actually happens and for how long.

The circulation during May-June also presented a dipole with a cyclonic eddy in the western portion and an anticyclonic in the middle transect (T2), the latter weaker and located to the south of the area. Thermocline elevation in the center of the cyclonic eddy and along the margins of the anticyclonic eddy generated a cold water fringe in the center of the three transects. In this case, two main hatching areas were detected under different environmental conditions, consistent with CCA results showing MLD and Chl-*a* as the most important variables influencing paralarval distribution. One of the areas was located in the cold-core cyclonic eddy, and the other in the neritic zone with warmer waters but higher concentrations of Chl-*a*, where the highest abundances of the SD complex, *Abraliopsis* sp. 2, *Leachia* spp. and *Lolliguncula* sp. 1 were found. Unlike the July survey, the notably low abundance of large paralarvae (>2 mm ML) found within the influence zone of the cyclonic eddy and the similar distribution range of the small paralarvae, suggests the start of hatching, assuming a non-significant dispersion process. This was more evident in the eastern coastal zone of the survey area, where the abundance of small paralarvae was highest and the large paralarvae were absent.

According to the results obtained, there is intense reproductive activity of squid from May to June in the Gulf of Tehuantepec and the adjacent oceanic zone, with spawning and/or hatching grounds preferentially located in the high Chl-*a* concentration areas of cyclonic eddies, front zones and coastal areas with high primary production. As the paralarvae grow, they are transported by advection toward the center of the anticyclonic eddies that are common features in the Gulf of Tehuantepec and nearby areas.

As in other regions of the Mexican Pacific (off the western coast of the Baja California Peninsula, in the Gulf of California and the rest of the Eastern Tropical Pacific), in July the paralarvae showed predominantly oceanic distribution (Granados-Amores *et al.*, 2010; Alejo-Plata *et al.*, 2013; Staaf *et al.*, 2013). However, the May-June survey included a larger number of stations over the continental shelf of the Gulf of Tehuantepec, and revealed the importance of including the neritic zone in sampling designs of cephalopod paralarvae. The large abundance of small paralarvae over the shelf indicates that *Dosidicus gigas* and *Sthenoteuthis oualaniensis* (SD complex) spawned in both the oceanic zone and on the continental shelf of the Gulf of Tehuantepec, as has been reported for other areas (Nigmatullin *et al.*, 2001; Jereb & Roper, 2010). Likewise, the presence of small paralarvae of *Abraliopsis* sp. 1 and *Abraliopsis* sp. 2 (probably *A. falco* and *A. affinis*), whose adult form are distributed

in the Mexican Pacific (Jereb & Roper, 2010) suggests that these species also reproduce in both, neritic and oceanic regions.

In both periods, the horizontal distribution of Chl-*a* inferred from satellite images showed a coastal-oceanic gradient with highest concentrations over the eastern continental shelf of the gulf. The high abundance of recently hatched paralarvae (≤ 2.0 mm ML) in this same area suggests a coupling of reproduction with mesoscale processes and biological production.

Adults of most of the species analyzed perform extensive vertical and horizontal migrations, tolerating strong changes in temperature and density, such as variations in the pycnocline and the mixed layer depth. Paralarvae are instead dependent on oceanic currents (Jereb & Roper, 2010) and their distribution is more restricted. Our results lead us to propose that the paralarvae distributed over the continental shelf, particularly those of the SD complex, develop in a more productive environment while transported along the coast in a northwesterly direction by the coastal current that regularly flows over the shelf, until around Salina Cruz. Posteriorly, they are returned by the coastal current associated with the margin of the anticyclonic eddies in the western gulf (Barton *et al.*, 2008), creating a retention cell over the continental shelf. The paralarvae trapped in the center of the anticyclonic eddies can be transported through advection toward the oceanic zone and to the southwest out of the coast.

Despite the primarily oceanic and tropical affinity of the regional paralarval community, the presence of high abundances of small sized paralarvae of the SD complex and the *Abraliopsis* genera on the continental shelf evidenced recent spawns by their adults in both periods, but with greater intensity during May-June. This suggests that adults that reproduce in the neritic zone present a coupling of reproduction with pulses of productivity and retention associated with the hydrodynamics of the mesoscale eddies and the primary production induced by mixing of currents and runoff of rivers on the continental shelf, which promote increased food availability for the paralarvae.

The mesoscale oceanographic complexity in absence of winds as recorded in this study, as well as the productivity pulses associated with Tehuanos that occur in the Gulf of Tehuantepec, promote the generation of gradients and a differential effect of these processes over the distribution, retention, transport and survival of cephalopod paralarvae and can determine the recruitment of species such as *Dosidicus gigas*, which is captured regionally in the productive waters of the Costa Rica Dome (Nigmatullin *et al.*, 2001).

Given its importance as one of the few sources of nutrient enrichment through mesoscale processes in the entire Pacific coast of Central America, as well as the presence of high paralarval abundances, the Gulf of Tehuantepec and the adjacent oceanic zone should be considered a key reproductive region for adults of the species analyzed.

ACKNOWLEDGEMENTS

Funding for this study was provided by CONACyT and the Instituto Politécnico Nacional through the projects No I0013-90331 y SIP 20150609, 20151160, 20151175 and 20160625 respectively. The altimeter products were processed by Ssalto/Duacs and distributed by Aviso, with support of Cnes (<http://www.aviso.altimetry.fr/>). Thanks to the Secretaría de Marina, Estación de Investigación Oceanográfica of Salina Cruz, Oaxaca, for use of the research vessel for cruises. Thanks to the exclusivity grant system (COFAA-IPN) and to the incentives for researcher performance program (EDI-IPN). The authors GAM, RSD, RD, and RAI are members of the national system of researchers (SNI). RDA is a visiting professor in CICIMAR-IPN. †We dedicate this publication to the family of the author Iván Cruz Estudillo, who obtained part of the results presented here while studying for a Masters in Marine Sciences with specialty in Marine Resource Management at CICIMAR-IPN. Unfortunately he could not win his battle against cancer.

REFERENCES

- Alejo-Plata, M.C., R. García-Guillén & J. Herrera-Galindo. 2013. Paralarvas y juveniles de cefalópodos en el Pacífico sur de México. *Hidrobiológica*, 23(2): 250-264.
- Barton, E.D., M. Lavín & A. Trasviña. 2008. Coastal circulation and hydrography in the Gulf of Tehuantepec, Mexico, during winter. *Cont. Shelf Res.*, 29(2): 485-500.
- Barton, D.E., M.L. Argote, J. Brown, M.P. Kosro, M. Lavín, J.M. Robles, R.L. Smith, A. Trasviña & H.S. Vélez. 1993. Supersquirt: dynamics of the Gulf of Tehuantepec, Mexico. *Oceanography*, 6: 23-30.
- Beers, J.R. 1976. Determination of zooplankton biomass. In: H.F. Steedman (ed.). *Zooplankton fixation and preservation. Monographs on Oceanographic Methodology*. UNESCO Press, Paris, pp. 35-84.
- Blackburn, M. 1968. Micronekton of the eastern tropical Pacific Ocean: family composition, distribution, abundance, and relations to tuna. *Fish. Bull.*, 67(1): 71-115.
- Bolstad, K.S. 2008. Two new species and a review of the squid genus *Onychoteuthis* Lichtenstein, 1818 (Oegopsida: Onychoteuthidae) from the Pacific Ocean. *Bull. Mar. Sci.*, 83: 481-529.
- Bolstad, K.S.R. 2010. Systematics of the Onychoteuthidae Gray, 1847 (Cephalopoda: Oegopsida). *Zootaxa*, 2696: 1-186.
- Bower, J.R., Y. Nakamura, K. Mori, J. Yamamoto, Y. Isoda & Y. Sakurai. 1999. Distribution of *Todarodes pacificus* (Cephalopoda: Ommastrephidae) paralarvae near the Kuroshio off southern Kyushu, Japan. *Mar. Biol.*, 135: 99-106.
- De Silva-Dávila, R., F.G. Hochberg, A.R. Lindgren & C. Franco-Gordo. 2013. Paralarval development, abundance, and distribution of *Pterygioteuthis hoylei* (Cephalopoda: Oegopsida: Pyroteuthidae) in the Gulf of California, México. *Molluscan Res.*, 33: 50-64.
- De Silva-Dávila, R., C. Franco-Gordo, F.G. Hochberg, E. Godínez-Domínguez, R. Avendaño-Ibarra, J. Gómez-Gutiérrez & C.J. Robinson. 2015. Cephalopod paralarval assemblages in the Gulf of California during 2004-2007. *Mar. Ecol. Prog. Ser.*, 520: 123-141.
- Diekmann, R. & U. Piatkowski. 2002. Early life stages of cephalopods in the Sargasso Sea: distribution and diversity relative to hydrographic conditions. *Mar. Biol.*, 141: 123-130.
- Gilly, W.F., C.A. Elliger, C.A. Salinas, S. Camarillo-Coop, G. Bazzino & M. Beman. 2006. Spawning by jumbo squid (*Dosidicus gigas*) in the San Pedro Mártir basin, Gulf of California, Mexico. *Mar. Ecol. Prog. Ser.*, 313: 125-133.
- Goto, T. 2002. Paralarval distribution of the ommastrephid squid *Todarodes pacificus* during fall in the southern Sea of Japan, and its implication for locating spawning grounds. *Bull. Mar. Sci.*, 71(1): 299-312.
- Granados-Amores, J., R. De Silva-Dávila, S. Camarillo-Coop, F.G. Hochberg, R. Durazo & R. Avendaño-Ibarra. 2010. Composición de especies y patrones de distribución de paralarvas de calamar, 1996-1999. In: G. Gaxiola-Castro & R. Durazo. (eds.). *Dinámica del ecosistema pelágico frente a Baja California 1997-2007. Diez años de investigaciones mexicanas de la Corriente de California*. SEMARNAT-INE-CICESE-UABC, México, pp. 453-467.
- Ibáñez, C.M. & A.F. Cifuentes-Bustamante. 2016. Squids of the family Onychoteuthidae Gray, 1847 in the southeastern Pacific Ocean. *Lat. Am. J. Aquat. Res.*, 44(2): 416-421.
- Integrated Taxonomic Information System (ITIS). 2015. Sistema de información taxonómica integrado. [<http://www.itis.gov>]. Reviewed: 15 May 2016.
- Jereb, P. & C.F. E. Roper. 2010. Cephalopods of the world. An annotated and illustrated catalogue of

- cephalopod species known to date. Volume 2. Myopsid and Oegopsid squids. FAO Sp. Cat. Fish. Purp., 2(4), Rome, 605 pp.
- Lara-Lara, J.R., V. Arenas-Fuentes, C. Bazán-Guzmán, V. Díaz-Castañeda, E. Escobar-Briones, M.C. García-Abad, G. Gaxiola-Castro, G. Robles-Jarero, R. Sosa-Ávalos, L.A. Soto-González, M. Tapia-García & J.E. Valdez-Holguín. 2008. Los ecosistemas marinos. In: J. Soberón, G. Halffter & J. Llorente-Bousquets (eds.). Capital natural de México. Vol. I. Conocimiento actual de la biodiversidad. CONABIO, México, pp. 135-159.
- Markaida, U., C. Quiñonez-Velázquez & O. Sosa-Nishizaki. 2004. Age, growth and maturation of jumbo squid *Dosidicus gigas* (Cephalopoda: Ommastrephidae) from the Gulf of California, Mexico. Fish. Res., 66: 31-47.
- Morales-Bojórquez, E., M.A. Cisneros-Mata, M.O. Nevárez-Martínez & A. Hernández-Herrera. 2001. Review of stock assessment and fishery biology of *Dosidicus gigas* in the Gulf of California, Mexico. Fish. Res., 54: 83-94.
- Morales de la Garza, E.A. & A. Carranza-Edwards. 1995. Sedimentos fosfatados en el Golfo de Tehuantepec. Hidrobiológica, 5(1-2): 25-36.
- Moreno, A., A. Dos Santos, U. Piatkowski, M.P. Santos & H. Cabral. 2009. Distribution of cephalopod paralarvae in relation to the regional oceanography of the western Iberia. J. Plankton Res., 31(1): 73-91.
- Nigmatullin, C.M., K.K. Nesis & A.I. Arkhipkin. 2001. A review of the biology of the jumbo squid *Dosidicus gigas* (Cephalopoda: Ommastrephidae). Fish. Res., 54: 9-19.
- Ortega-García, S., J.A. Trigueros-Salmerón, R. Rodríguez-Sánchez, S. Lluch-Cota & H. Villalobos. 2000. El Golfo de Tehuantepec como un centro de actividad biológica y su importancia en las pesquerías. In: D. Lluch-Belda, J. Elorduy-Garay, S.E. Lluch-Cota & G. Ponce-Días (eds.). BAC: Centros de actividad biológica del Pacífico mexicano. CIBNOR, CICIMAR-IPN, CONACYT, México, pp. 335-356.
- Postel, L., H. Fock & W. Hagen. 2000. Biomass and abundance. In: R.P. Harris, P.H. Wiebe, J. Lenz, H.R. Skjoldal & M. Huntley (eds.). Zooplankton methodology manual. Academic Press, San Diego, pp. 83-92.
- Roper, C.F.E. & G.L. Voss. 1983. Guidelines for taxonomic descriptions of cephalopod species. Mem. Natl. Mus. Victoria, 44: 49-63.
- Sánchez-Velasco, L., E.D. Ruvalcaba-Aroche, E. Beier, V.M. Godínez, E.D. Barton, N. Díaz-Viloria, M.R. Pacheco. 2016. Paralarvas of the complex *Sthenoteuthis oualaniensis-Dosidicus gigas* in the northern limit of the shallow oxygen minimum zone of the Eastern Tropical Pacific Ocean (April 2012). J. Geophys. Res., 121: 1998-2015.
- Shimura, T., J. Yamamoto, Y. Kamei & Y. Sakurai. 2005. Possible spawning by the Japanese common squid, *Todarodes pacificus* at Yamato Rise, Sea of Japan. Phuket Mar. Biol. Center Res. Bull., 66: 267-273.
- Smith, P.E. & S.L. Richardson. 1979. Técnicas modelo para prospecciones de huevos y larvas de peces pelágicos. FAO Doc. Téc. Pesca, Rome, 107 pp.
- Staaf, D.J., J.V. Redfern, W.F. Gilly, W. Watson & L.T. Balance. 2013. Distribution of ommastrephid paralarvae in the eastern tropical Pacific. Fish. Bull., 111: 78-89.
- Sweeney, M.J., C.F.E. Roper, K.M. Mangold, M.R. Clarke & S.V. Boletzky. 1992. Larval and juvenile cephalopods: a manual for their identification Smithsonian Institution Press, Washington DC, 282 pp.
- Ter Braak, C.J.F. & I.C. Prentice. 2004. A theory of gradient analysis. Adv. Ecol. Res., 34: 235-282.
- Trasviña, A., E.D. Barton, H.S. Velez & J. Brown. 2003. Frontal subduction of a cool surface water mass in the Gulf of Tehuantepec. Geofis. Int., 42(1): 101-114.
- Trasviña, A. & E.D. Barton. 2008. Summer circulation in the Mexican tropical Pacific. Deep-Sea Res., 55: 587-607.
- Vecchione, M. 1999. Extraordinary abundance of squid paralarvae in the tropical eastern Pacific Ocean during El Niño of 1987. Fish. Bull., 94(4): 1025-1030.
- Vega, M.A., F.J. Rocha, A. Guerra & C. Osorio. 2002. Morphological differences between the Patagonian squid *Loligo gahi* populations from the Pacific and Atlantic oceans. Bull. Mar. Sci., 71(2): 903-913.
- Velázquez-Muñoz, F.A., J.A. Martínez & R. Durazo. 2014. Numerical simulation of ocean response by offshore wind stress events. In: J. Klapp & A. Medina (eds.). Experimental and computational fluid mechanics. Springer-Verlag, New York, pp. 93-110.
- Wakabayashi, T., K. Saito, K. Tsuchiya & S. Segawa. 2002. Description of *Eucleoteuthis luminosa* (Sasaki, 1915) and *Ornithoteuthis volatilis* (Sasaki, 1915) paralarvae in the Northwestern Pacific. Venus, 60(4): 237-260.
- Young, J.W. 1972. The systematics and areal distribution of pelagic cephalopods from the seas off Southern California. Smith. Contr. Zool., 97: 1-159.
- Zamudio, L., H.E. Hurlburt, E.J. Mertzger, S.L. Morey, J. O'Brien, C. Tilburg & J. Zavala-Hidalgo. 2006. Interannual variability of Tehuantepec eddies. J. Geophys. Res., 111: C05001.