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Distribución tridimensional de paralarvas de cefalópodos en el Sistema Arrecifal Mesoamericano

TESIS

Presentada como requisito parcial para optar al grado de Maestría en Ciencias en Recursos
Naturales y Desarrollo Rural

por:

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Dedicatorias

A las mujeres que han compartido su camino conmigo

A mi mamá

A mi padre y hermanos

> Y cantaba una canción maravillosa porque cantaba de los moradores del mar…; Cantaba de las sirenas que cuentan cosas tan prodigiosas; de las guerras hundidas con sus altos mástiles y de cadáveres helados de marinos, aferrados todavía a las jarcias; ... y de las jibias que viven en las laderas de los riscos y extienden sus largos brazos negros y hacen venir la noche cuando quieren. Cantaba del Nautilo que tiene barco propio tallado en ópalo y gobernado con vela de seda………
>
> (El pescador y su alma, Oscar Wilde)

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Resumen

El conocimiento sobre la abundancia y distribución de las paralarvas (PL) de muchas especies de cefalópodos es escaso, especialmente en áreas tropicales. El presente estudio examina por primera vez la fauna de cefalópodos en las aguas superficiales del Sistema Arrecifal Mesoamericano (SAM), a partir de una campaña oceanográfica a mesoescala realizada a bordo del B/O Gordon Gunter (NOAA) del 14 al 30 de enero de 2007 desde el canal de Yucatán, México, hasta el Golfo de Honduras. Se colectaron un total de 108 muestras en cuatro estratos de profundidad (0-25, 25-50, 50-75 y 75-100 m) utilizando una red MOCNESS-1 de 333 µm. Se registraron 451 PL pertenecientes a 10 familias, 16 especies, 7 formas y un complejo de especies. Las familias Enoploteuthidae (60%), Onychoteuthidae (22%) y Ommastrephidae (8%) representadas por *Abralia* sp.1, *Onychoteuthis banksi* y *Ornithoteuthis antillarum* respectivamente, fueron las más abundantes. La mayor abundancia de PL se encontró en los primeros 25 m de la columna de agua en toda el área de estudio. En cuanto a la distribución horizontal, se observó mayor abundancia en el Golfo de Honduras. La distribución vertical y horizontal de las PL se relacionó con la migración ontogénica y con el transporte de agua por los regímenes de circulación dominados por la Corriente de Yucatán, zonas de retención tales como el Giro de Honduras, el remolino al sur de Cozumel y la zona de afloramiento del norte del SAM. El SAM es un importante sistema de dispersión para las paralarvas, que conecta el Caribe con el Golfo de México.

Palabras clave: Paralarvas, distribución tridimensional, arrecife Mesoamericano, Corriente de Yucatán.

CAPÍTULO I

I. Introducción

Los cefalópodos habitan exclusivamente ambientes marinos, desde aguas someras hasta aproximadamente 7,000 m de profundidad (Díaz *et al.*, 2000; Brusca y Brusca, 2003). En su estadio adulto, la mayoría son nectónicos ocupando tanto la zona nerítica como la oceánica a diferentes niveles de profundidad (epi, meso o batipelágicos), aunque algunas especies pueden ser demersales. Son de gran importancia en la transferencia de energía dentro de la trama trófica ya que constituyen un importante recurso alimenticio para una gran variedad de depredadores como son los peces, aves y mamíferos marinos (Piatkowski *et al*, 2001; Boyle y Rodhouse, 2008); son a su vez, depredadores oportunistas voraces de peces y crustáceos (Boyle y Rodhouse, 2005). Aunque actualmente se reconocen entre 800 y 1000 especies, solamente algunas son reconocidas mundialmente por ser importantes recursos pesqueros.

Los cefalópodos, presentan dimorfismo sexual, con diversas estrategias reproductivas que van desde el desove simultáneo a múltiples desoves intermitentes, donde prácticamente todas las estrategias terminan en la muerte después del período de desove (Jereb y Roper, 2005). El tiempo de desarrollo embrionario en los cefalópodos varía desde pocos días hasta varios meses dependiendo de la especie y de las condiciones ambientales (Roper *et al*., 1984; Boletsky, 2003). El desarrollo es directo, distinguiéndose tres modos de vida temprana: 1) en calamares (nectónicos y demersales) y algunos octópodos (nectónicos y merobentónicos) las crías o paralarvas son planctónicas, 2) las crías de algunos octópodos bentónicos antes de asentarse exhiben un comportamiento nectónico-bentónico, no presentan paralarva, son adultos miniatura (i.e. *Octopus ocellatus, Octopus maya*) y 3) las crías de todos los sepiólidos y algunos octópodos (holobentónicos) adoptan inmediatamente un modo de vida bentónico (Bolestsky, 2003; Robin *et al*., 2014).

El término *paralarva* fue propuesto y definido por Young y Harman (1988) como el primer estadio del crecimiento post-desove de cefalópodos, que es pelágico en aguas superficiales durante el día y que tiene un modo de vida distinto respecto a sus conespecíficos adultos, bajo el argumento de que paralarva está basado en criterios ecológicos y morfológicos, y no en el desarrollo del organismo en el cual se basan los términos larva o juvenil. Recientemente, Shea y Vecchione (2010) propusieron una redefinición: cefalópodos recién eclosionados que tienen un modo de vida diferente a la de los adultos, con un punto final identificado por cambios ecológicos y alométricos significativos.

Las paralarvas son depredadoras activas de zooplancton,). Aunque en general tienen una morfología similar a la de los adultos, los cambios que hay entre estos dos estadios son sutiles y se refieren a la variación en las tasas y tipos de crecimiento (alométrico, isométrico), los cambios en la forma y/o función de estructuras específicas, i.e. la separación de los tentáculos fusionados o proboscis en las de la familia Ommastrephidae (Robin *et. al*., 2014).

A pesar de su importancia económica y ecológica, el número de estudios sobre estos moluscos a nivel mundial es reducido en comparación con otros grupos taxonómicos (Piatkowski *et al*., 2001). La falta de conocimiento es mayor en el caso de sus paralarvas, debido a las dificultades en la toma de muestras (baja abundancia y falta de sistematización), la incertidumbre en la identificación de las especies y a los problemas relacionados con su mantenimiento en cautiverio que son importantes limitaciones para su estudio (Vecchione, 1987; Boyle y Rodhouse, 2005). La taxonomía es probablemente el mayor obstáculo a superar, ya que la identificación de prácticamente todos los estadios larvarios y juveniles de cefalópodos ha sido, en muchos casos, confuso y problemático (Sweeney *et al*., 1992).

En relación a la colecta de paralarvas, esta ha sido realizada con diferentes artes alrededor del mundo: con redes Bongo en el Atlántico Norte (Shea, 2005), con redes exploratorias de media agua en el mar de los sargazos (Diekmann y Piatkowski, 2002), con red Manta (Vecchione, 2001), redes múltiples de apertura y cierre MOCNESS en el Pacífico Nororiental (Wakabayashi *et al*., 2002) con redes cónicas simples (Yatsu, 1999) en aguas de Perú y con redes CalCOFI y neuston (en superficie) y Bongo (en arrastres oblicuos) (De Silva-Dávila *et al*., 2015). En este sentido, Saito (1994) comparó las capturas de paralarvas obtenidas utilizando diferentes tipos de redes y concluyó que el uso de redes Bongo resultaba ser el arte de recolecta más eficiente para éstos organismos, tanto por la mayor abundancia de paralarvas como por la diversidad encontradas.

En cuanto a su distribución vertical, se reconoce que la mayoría se distribuye en los primeros 200 m de profundidad y su abundancia es baja (Vecchione, 2001), y al igual que los adultos, pueden efectuar desplazamientos nictimerales relativamente cortos en la columna de agua, aunque han sido poco estudiados. Los estudios sobre su distribución vertical indican que auque se distribuyen con mayor abundancia en los primeros 50 m de la columna de agua, existen diferencias significativas en las profundidades ocupadas por las diferentes especies, así como variaciones día-noche (Okutani, 1966; Kubodera, 1982; Bower y Takagi, 2004).

II. Antecedentes

Los estudios más completos acerca del ciclo de vida de los cefalópodos, incluyendo el estadio de paralarva se han realizado en aguas japonesas (Sakurai *et al*., 2000).

Se ha observado que la abundancia y distribución de las paralarvas responde a los cambios ambientales y a la dinámica oceánica. La temperatura, la salinidad así como la termo- y haloclina, la disponibilidad de alimento también juegan un papel preponderante en la tasa de crecimiento y la sobrevivencia de las paralarvas de cefalópodos, determinando el desove de muchas especies y limitando la distribución de sus paralarvas (Ichii *et al*., 2004). Las corrientes son importantes en el transporte de los productos del desove desde las zonas de puesta hasta las de alimentación (Díaz *et al*., 2000; Iglesias *et al.*, 2006), influyen en la dispersión de paralarvas con diferentes afinidades biogeográficas (Anderson y Rodhouse, 2001; Diekmann y Piatkowski, 2002; Haimovici *et al*., 2002), y las mantienen generalmente dentro de sistemas de macroescala que son parte estratégica esencial en su ciclo de vida (Roberts y van den Berg, 2002). En paralarvas de lolíginidos se sabe que las surgencias modulan la distribución y abundancia a lo largo del año (González *et al*., 2005), mientras que los frentes termohalinos y de masas de agua determinan límites de distribución entre comunidades de diferente afinidad biogeográfica (Roper *et al*., 1999; Diekmann y Piatkowski, 2002; De Silva-Dávila *et al*., 2015).

La fauna de cefalópodos del Caribe ha sido poco estudiada en comparación con el Golfo de México y Florida, y se ha centrado en el reconocimiento de individuos adultos con listados taxonómicos y su distribución (Díaz *et al*., 2000; Gracia, 2002; Judkins *et al*., 2010), con excepción de algunos trabajos enfocados al desarrollo post-embrional de *Octopus maya* (Moguel *et al*., 2010). La revisión más actualizada de la distribución y abundancia en el Caribe fue realizada por Judkins (2009), quien en su listado taxonómico reportó un total de noventa y tres especies. Entre estas, las de importancia comercial son: *Octopus maya, O. vulgaris, Illex coindetii, Sthenoteuthis pteropus, Lolliguncula brevis, Doryteuthis (Loligo) pealei, y Doryteuthis (Loligo) plei*.

En el Sistema Arrecifal Mesoamericano (SAM), el estudio de paralarvas es escaso, con el único registró realizado por Nesis (1975) al describir algunos ejemplares.

III. Justificación

La identificación específica de los estadios tempranos de cefalópodos a nivel mundial tiene un carácter relevante dado la creciente importancia comercial y ecológica que registra este grupo de organismos.

El establecimiento de áreas de distribución y abundancia de las paralarvas sobre la base de una certidumbre taxonómica y su relación con el ambiente, permitiría eventualmente la detección de zonas de concentración de adultos reproductores, inferencias de desove, complementando el conocimiento sobe la biología reproductiva de estos moluscos.

Dada la importancia y el escaso conocimiento de la fase planctónica de cefalópodos, este trabajo pretende identificar por primera vez las paralarvas presentes en el Sistema Arrecifal Mesoamericano (SAM) y su relación con algunas variables ambientales.

IV. Hipótesis

La estructura hidrográfica y la circulación generada por los giros y remolinos de mesoscala y submesoescala (el giro de Honduras, del sur de Cozumel, y los de Banco Chinchorro) en el Sistema Arrecifal Mesoamericano, determinarán una mayor retención de paralarvas y por lo tanto una mayor abundancia en estas zonas.

V. Objetivos

Objetivo general

- Analizar los patrones de distribución tridimensional de paralarvas de cefalópodos en el Sistema Arrecifal Mesoamericano durante enero de 2007.

Objetivos particulares

- Identificar las paralarvas de cefalópodos al nivel taxonómico mínimo posible.
- Caracterizar los patrones de distribución vertical y horizontal en relación con procesos oceanográficos.

CAPITULO II

Three-dimensional distribution of cephalopod paralarvae in the surface waters of the Mesoamerican Barrier Reef System

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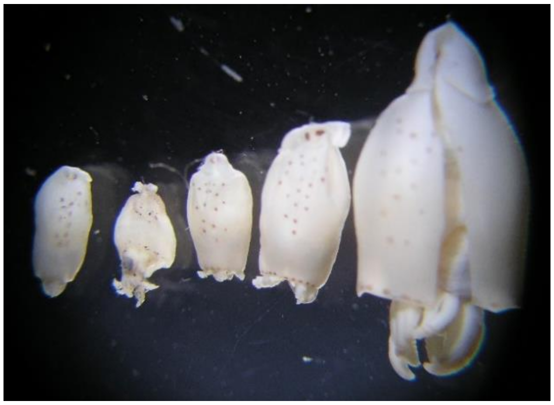
Abralia sp 1.



Onychoteuthis banksii

Three-dimensional distribution of cephalopod paralarvae in the surface waters of the Mesoamerican Barrier Reef System

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ABSTRACT

Tridimensional distribution of cephalopod paralarvae (PL) from the Mesoamerican Barrier Reef System (MBRS) was studied. A total of 451 PL belonging to 10 families, 16 species, 7 morphotypes, and a species complex were identified. Abralia sp.1, Onychoteuthis banksii, and Ornithoteuthis antillarum were the most abundant taxa. Most PL that occupied the homogenous Caribbean Surface Water mass were observed in the 0-25 m strata throughout the area. Largest paralarval abundances were related with the Honduras Gyre and Cozumel eddy. No day-night differences were found in PL abundance, although Abralia sp.1 showed evidence of diel vertical migration. Exploratory canonical correspondence analysis showed significant but low correlations of the PL abundance with zooplankton volume (0.56) and current velocity (0.29). However, dominant species correlated well to different environmental variables such as zooplankton volume and salinity. Tridimensional distribution of PL in surface waters of the MBRS was probably related to ontogenetic migration, hydrographic features of meso and subscale, and to circulation regimes dominated by the Yucatan Current. The MBRS represent an important dispersion area for PL, potentially connecting a species rich Caribbean community with the Gulf of Mexico.

KEYWORDS: Cephalopod, paralarvae, tridimensional distribution, Mesoamerican Barrier Reef System, Yucatan Current.

INTRODUCTION

Cephalopods are mainly nektonic mollusks ecologically and commercially important in the world ocean (Boyle and Rodhouse, 2005). Hatchings of squid and several octopods are represented by planktonic stages known as paralarva (PL). They are relatively rare in plankton communities because their ephemeral existence due to fast growth (Roura et al., 2016). Knowledge on cephalopod paralarvae is still limited, especially in their horizontal and vertical distribution and abundance in tropical waters.

PL abundance in the water column is influenced by environmental changes caused by ocean dynamics. Frontal areas at the edges of water masses segregate different PL assemblages (De Silva-Dávila et al., 2015). Thermocline, halocline and food availability related to mesoscale eddies and upwelling fronts, also play an important role in distribution, growth and survival of PL (Ichii et al., 2004; Aceves-Medina et al., 2017). Current systems are also a key factor transporting eggs or egg masses and PL from the spawning areas to the hatching, nursery or feeding grounds (Díaz et al., 2000; Iglesias et al., 2006), influence the dispersion of PL of different biogeographic affinities (Diekmann & Piatkowski, 2002; Haimovici et al., 2002), and usually keep the PL inside a macroscale circulation cell that results an essential strategy to complete their life cycles (Roberts and van den Berg, 2002).

Cephalopod fauna from the Caribbean has been studied much less comparing with the Florida oceanic area, resulting in an apparently smaller cephalopod diversity (Díaz et al., 2000; Gracia, 2002; Judkins et al., 2010). The few studies about cephalopod paralarvae in this sea corresponds to specimens descriptions by Nesis

(1975). The western Caribbean has been paid even less attention, even when the Mesoamerican Barrier Reef System (MBRS) is one of the largest marine biodiversity hotspots worldwide. This area shows a highly dynamic oceanography with physical processes driving the dispersion of planktonic larval stages (Carrillo et al., 2017). Oceanographic background and the distribution of larval fish, lobster phylosomas and pteropods of this cruise have been published elsewhere (Parra-Flores and Gasca, 2009; Muhling et al., 2013; Carrillo et al., 2015, 2016, 2017; Canto-García et al., 2016). However, there is still a lack of studies of cephalopod paralarvae in the western Caribbean.

The aim of this study is to show for the first time the abundance, diversity and horizontal and vertical distribution patterns of cephalopod paralarvae from the surface waters of the western Caribbean, in particular, the MBRS, and discuss the influence of oceanographic features on these patterns.

METHOD

Study area

The Mesoamerican Barrier Reef System (MBRS) runs along nearly 1,000 km from the northern tip of Yucatan Peninsula to the Gulf of Honduras (Fig. 1). The oceanography of the region is defined by the latitude of impingement of the Cayman Current (CC, pass of the Caribbean Current throughout the Cayman basin) on the MBRS that separates three main dynamical environments: a northern region with a well-defined Yucatan Current (YC), a southern region with weak southward and/or variable flow, and a central, transitional region where the CC impinges upon the coast (Carrillo et al. 2015). The north of the MBRS shows a generally strong northwesterly current with a uniform speed (~1.10 m/s) until it approaches the Yucatan Channel where maximum speeds of 2 m/s are reached. In the transitional region most of the CC turns west with onshore flow at the Belize-Mexico border, and the bifurcation of this current with a divergence zone results in a southerly flow along the coast of Belize and a northward flow along the coast of Mexico (Carrillo et al., 2015). The southern MBRS region is characterized by a large cyclonic gyre located north of Honduras (the Honduras Gyre) (Carrillo et al., 2015).

The MBRS receives water masses that are imported by the Cayman Current and the Caribbean currents entering from the Atlantic Ocean through the multiple passages between the northern and eastern Caribbean islands (Carrillo et al., 2016). The Caribbean Surface Water (CSW) represents the surface mixed layer with a mean thickness of 85 m and a mean temperature of 27 °C, and low salinity (<36 at surface) occupied almost all the stations. Below 100 m, the high-salinity (>36.75) North Atlantic Subtropical Underwater (SUW), centered at about 150 m depth, lies beneath the CSW.

Dissolved oxygen in the surface mixed layer is >4 mL/L (Carrillo et al., 2016). The northernmost area of the MBRS was characterized by an upward displacement of water close to the shelf due to the upwelling associated with the YC forming a marked thermal front. At the shelf edge the 25 °C isotherm was displaced 100 m and the mixed layer was ~50 m thick (Carrillo et al., 2016).

Sampling

An oceanographic campaign during January 14–30, 2007 aboard the NOAA ship Gordon Gunter surveyed the MBRS, a total of 27 stations were sampled along six transects (Fig. 1). Line A, the northernmost transect offshore Contoy Island to ~115 km offshore; Line C, located 60 km north of Ascension Bay and south of Cozumel Island; Lines G and I, north and south of Chinchorro Bank respectively, and in the Cayman Current impingement zone; and Lines N and P, which are representative cross-transects in Belizean coastal waters, with Line P just south of Glovers Reef and in the Gulf of Honduras (HG). In each station temperature, salinity, and dissolved oxygen were recorded with calibrated CTD casts and published elsewhere (Carrillo et al., 2016). Current velocity measurements were obtained from a hull-mounted Acoustic Doppler Current Profiler (ADCP), except for line (Carrillo et al., 2015). Transects A, C, I and P were selected to plot vertical oceanographic features that could be related with PL abundance.

Depth-stratified plankton sampling was performed using a multiple opening and closing net environmental sensing system (MOCNESS) with 1 m^2 mouth. This net was fitted with 333 µm mesh nets, and sampled four depth strata: 0–25 m, 25–50 m, 50–75 m and 75–100 m (Muhling et al., 2013; Canto-García et al., 2016). Flowmeters were fitted to the center of the mouth of each net to estimate the water volume filtered in each tow. Plankton samples were preserved in 95% ethanol, which was replaced after 24 h to ensure proper preservation.

Sampling time was classified as during the day (06:00–18:00 hrs) or at night (18:01–05:59 hrs) (Canto-García et al., 2016).

Data analysis

Zooplankton volume (ZV) was measured (Beers, 1976) and standardized for each tow. All cephalopod paralarvae were sorted from the samples and identified to the lowest possible taxonomic level according to Sweeney et al. (1992), Vecchione et al. (2001), Bolstad (2010), De Silva-Dávila (2013), and Roper et al. (2015). Abundance of paralarvae was standardized for each tow to number of paralarvae (PL) in 1000 m^3 of filtered water (PL/1000 $m^{3)}$ (Postel et al., 2000). Horizontal and vertical distribution of the paralarval abundance and the environmental variables in the MBRS were plotted using Surfer 14 from Golden Software. Differences of abundance among the four depth strata where assessed through a Kruskal-Wallis ANOVA test. The Mann-Whitney test was used to assess the statistical significance of differences in total paralarval abundance between daytime and nighttime. The abundance-weighted mean depth for both day and night samples for the most common taxa were calculated (Muhling et al., 2013).

A canonical correspondence analysis (CCA) was applied to explore the relation between PL abundance and environmental variables using Canonical Community Ordination (CANOCO) software 4.56. The paralarval abundance main matrix of the CCA was screened, excluding all taxa with only one species and log transformed [log10 (x ij+1)], where x is the abundance of species i in station j. The environmental (second matrix) contained five variables: zooplankton volume (ZV), temperature (T 25), salinity (S 25), and dissolved oxygen (O 25) at 25 m depth where the highest numbers of paralarvae were observed and as indicators of average conditions of the water column, and current velocity (CV). Procedures were made according the criteria of Ter Braak and Prentice (2004) and Legendre and Legendre (2012).

RESULTS

A total of 451 paralarvae were collected in all the transects. They belonged to 10 families, 16 species, seven morphotypes and a species complex (Table I). Three families accounted for 90% of the total abundance: Enoploteuthidae (60%) represented by *Abralia* sp. 1, Onychoteuthidae (22%) represented by *Onychoteuthis banksii*, and Ommastrephidae (8%) by *Ornithoteuthis antillarum*. The remaining 10% was represented by seven families: Octopodidae, Thysanoteuthidae, Loliginidae, Ancistrocheiridae, Lycoteuthidae, Pyroteuthidae, and Cranchiidae.

Cephalopod paralarvae were found almost exclusively in the CSW, defined over the 25 °C isoline and low salinities <36.6 (Fig. 2). Larger abundances were found in shallow waters of transects C and P. At the northernmost transect A, upwelling associated with the Yucatan Current favored the inshore shallowing of the SUW. There 53 PL/1000 m^3 were found at 100 m depth (Fig. 2).

Horizontal, depth-aggregated distribution of total PL abundance showed a clear tendency. In the northern region, transect A yielded a low mean abundance (30 PL/1000 m^3) while at transect C abundance reached 44 PL/1000 m^3. The transitional central transects (G, I, and N) showed minimum means (31-32 PL/1000 m ^{3}). The southernmost transect P, in the Honduras Gulf, recorded a mean of 97 PL/1000 m ^{3} (Fig. 3).

The most abundant and frequent morphotype distributed along the MBRS was Abralia sp. 1. It was very abundant in transect P where two stations yielded a mean of 504 PL/1000 m^{3} . Moderate abundances were documented in central and northern regions (Fig. 4B). Onychoteuthis banksii, the second most abundant taxa, ranged 15-80 PL/1000 m^{3} at stations south of Cozumel and at central transects, although it was almost absent from southern transects (Fig. 4C). The third most abundant species, Ornithoteuthis antillarum of the family Ommastrephidae, showed a similar horizontal distribution as O. banksii (Fig. 4D).

No significant differences were found in PL total abundances between daytime and nighttime for all stations and depth-aggregated (Mann-Whitney U test, $p>0.05$). PL total abundances among strata (for all stations-aggregated) showed significant differences (Kruskal-Wallis, $H = 8.63$, $df = 2$, $P<0.05$). Largest PL abundances were encountered in the upper 25 m (Fig. 5). Abralia sp. 1 was distributed until 100 m depth at day with maximum values of 145 PL/1000 m 3 in the uppermost stratum. At night occupied the shallowest waters to 50 m depth (Fig. 5A). Onychoteuthis banksii occupied all the strata except for the deepest of 75-100 at both day and night with maximum abundances at the surface (10-12 PL/1000 m^{3}) (Fig. 5B). Ornithoteuthis antillarum occupied all the strata with abundances decreasing with depth. Night abundances doubled those by the day (Fig. 5C).

Abundance-weighted mean depths did not show either much dial differences for these three species. *Abralia* sp. 1 showed the shallowest mean depths at 30-40 m, while *O. banksii* and *O. antillarum* distributed in the 70-90 m depth range in average (Fig. 5D).

There was no correlation between total PL abundance and CV, even when zero abundances were extracted from the analysis (r = -0.1; P>0.05). Most positive trawls were widely dispersed between CVs from 0.2 to 0.8 m/s (not shown).

The CCA showed that environmental variables explained 67% of the variance in the relationship of PL abundance-environment. Axis 1 explained 42% of the variance and showed a significant positive correlation with zooplankton volume (0.56). Axis 2 explained 25% of the variance with significant, positive, but low correlations with current velocity (0.29) and negatively with temperature (-0.26). The distribution diagram showed a clear relationship between Abralia sp.1, the dominant species, with CV (Fig. 6). Its abundance was higher at surface CV >0.5 m/s, as occurred in Southern Cozumel. Onychoteuthis banksii which had high abundance in the 0–25 m stratum was associated with low salinity values, and *Ornithoteuthis antillarum* that concentrated around Chinchorro Bank showed a clear association with zooplankton volume. Other less abundant and frequent species *(Sthenoteuthis-Illex complex*, *Enoploteuthis* sp. 1) showed no relation with environmental variables.

DISCUSSION

We report, for the first time, the abundace, diversity and tridimensional distribution of the cephalopod paralarval community registered in surface waters of the Mesoamerican Barrier Reef System during January 2007, showing differences in the distribution patterns of the three dominant taxa.

The sampled were collected basically in the CSW well-mixed warm surface layer of the MBRS that showed the presence of a rich cephalopod paralarval assemblage comprised by 23 taxa at species level, identified from 451 specimens in only one cruise. This number represented about 52.3% of the 44 taxa identified in one of the most comprehensive studies on cephalopod paralarvae performed in the western Atlantic Ocean that included 21 oceanographic cruises covering from north of Greater Antilles to the Scotian Shelf, collecting 3731 PL (Vecchione et al., 2001). Besides, only five taxa were registered both in the western Atlantic Ocean and in the MBRS. These results indicates that the MBRS supports a paralarval community with high species richness and diversity. It is important to consider that probably more temporal regional observations of PL could increase species richness.

Absence of a wide continental shelf on the MBRS accounted for the dominance of families Enoploteuthidae, Onychoteuthidae, and Ommastrephidae, also dominant in the paralarval asemblages of other Atlantic oceanic waters

(Goldman, 1993; Haimovici et al., 2002; Diekmann et al., 2006). Nesis (1975) described Abralia redfieldi PL and stated that it was the most numerous species in the eastern Caribbean. PL of *A. cf. veranyi* have been described by Vecchione et al. (2001), which considered the most common species of the genus in the Northwestern Atlantic. *Onychoteuthis banksii* PL were described in Vecchione et al. (2001). They are numerous in the Caribbean (Nesis, 1975) and adjacent Atlantic (Vecchione et al., 2001). The absence of reliable descriptions of smaller paralarval stages (<2 -3 mm ML, mantle length) precluded more specific identification of several morphotypes collected in the MBRS.

Commercially potential squid species of the Ommastrephidae were particularly scarce in this study. Rynchoteuthion from the Caribbean described by Nesis (1975) as *Sthenoteuthis pteropus* were in fact *Ornithoteuthis antillarum* (Nesis, 1979). Spawning peak takes place in February and March (Nesis, 1975), although our sampling limited to one month could not confirm this point. Roper and Lu (1979) considered that their Rynchoteuthion Type "B" belongs to *O. antillarum.* Thus, *O. antillarum* probably is not so rare in the western North Atlantic (Vecchione et al., 2001).

The first two depth strata (0-25 m and 25-50 m) registered the highest PL abundance, as observed in other studies and they were also higher in areas such as 1) within the effect of coastal upwelling in the northern transect A, 2) Cozumel eddy area located at south Cozumel Island (transect C), and 3) within the Honduras Gyre at the southern transect P*. Abralia sp* 1. occupied the entire 100 m of the water column by day, but seems to be confined to the upper 50 m by night which evidences some diel vertical migration. However, there is no much evidence of diel vertical migration for *O. banksii* and *O. antillarum*. Similarly, paralarval enoploteuthids did show vertical migrations while onychoteuthids did not (Diekmann et al., 2006). Vecchione et al. (2001) did not found consistent diel patterns in paralarval vertical distribution. They proposed that diel variability in abundance observed in surface samples probably was a result of changes in the ability of young squids to visually avoid the sampler in different light conditions. This explanation however is not consistent with the occurrence of larger catches in our day tows. Furthermore, minimum moonlight indexes (< 1) during all the nights of the cruise (see Fig. 7 in Canto-García et al., 2016) should impede visual net avoidance and yield larger catches at night. Bower and Takagi (2004) found no evidence of diel vertical migration in any of the three major taxa (gonatid species) of the northeastern Pacific Ocean, indicating that this behavior appears to develop in post-paralarval stages. On the contrary, Young and Harman (1987) found significant differences between day-night catches of PL of two Onychoteuthis species in Hawaii, ranging mainly 3.0-5.9 mm ML. These authors recognized that a sudden increase in chromatophores and hooks in the manus of tentacles may indicate the change to the juvenile stage. Juveniles then reach their final habitat through ontogenetic migration (Boyle and Rodhouse, 2005). In the MBRS a high proportion of PL ranged between 1.0-3.0 mm ML, sizes at which morphology, swimming, and feeding abilities are probably not fully developed in all taxa. Diel vertical migration in small PL is therefore absent or very limited, preventing significant differences in general day-night abundance distributions.

The PL abundance horizontal pattern registered in the MBRS showed a similar pattern than the distribution for ichthyoplankton (particularly myctophids) and phylosomas studied in the same campaign (Muhling et al., 2013; Canto-García et al., 2016). Their distribution were explained by the oceanographic processes of different scale. The largest PL abundance were found in the mesoscale Honduras Gyre at transect P. This gyre is not always present nor having the same strength or size, but it has been also associated with larval retention, particularly for pelagic phylosomas (Muhling et al., 2013; Canto-García et al., 2016; Carrillo et al., 2017). The area northeast of Chinchorro Bank (transect G) with an average abundance of PL has been pointed as another possible area of larval retention because the wake island effect may produce small eddies (Canto-García et al., 2016; Carrillo et al., 2017). Other area with large abundance of PL was located at south of Cozumel Island. It might be associated with the presence of the sub-mesoscale cyclonic eddy in that area, “Cozumel eddy”, which presumably is generated by the separation of the YC from the coast (Carrillo et al., 2015, 2017). Sub-mesoscale cyclonic eddies like this one tend to retain and concentrate larvae at their edges. In this area, more grouper fish larvae have been recorded (Carrillo et al., 2017). It has been suggested also that it represents a zone of local fish larval and phylosoma retention (Muhling et al., 2013; Canto-García et al., 2016). Other areas however may act as dispersal zones where little abundances of pelagic larvae and even an homogeneous horizontal distribution might be expected. Here we observed a relatively little heterogeneity on the horizontal distributuion of PL within the MBRS, except from the northernmost and the Honduras gyre transects, and the submesoscale Cozumel eddy. This is true for the northernmost area of the MBRS where the strong YC reaches up to 2 m/s (Carrillo et al., 2015, 2017). However, the role that retention oceanographic structure play in PL distribution and abundance requieres futher detailed observations. We found also average PL abundance in the Yucatan Channel, it is clear that dispersal of PL by the currents in the MBRS. Strong currents could potentially transport paralarvae from MBRS to distant areas such as off Florida Keys in a few days, although there is little evidence of connectivity between both regions, at least for reef fishes (Muhling et al., 2013), genetic and growth of PL studies together with regional oceanographic numerical models could lead to a better understanding of the role of the MBRS in exporting marine resources such as cephalops to other systems.

CONCLUSION

The three-dimensional distribution of the PL in the MBRS surface water can be summarized as follows: major abundances occurred mainly in the first 25 m depth with no significant differences between day-night collections and in moderate velocity currents ranging 0.2–0.8 m/s. PL were observed at temperatures of 25–27 °C, oxygen values of 4.2-4.5 mL/L, and salinities <36.0.

The planktonic environment along much of the MBRS is characterized by low retention conditions with northward transport of PL, largely influenced by the Yucatán Current and coastal upwelling in the northernmost MBRS. Cayman Current impingement area, around Chinchorro Bank (transects G, I, and N), showed low PL abundances. High paralarval abundance were concentrated in stations where current velocity was <0.6 m/s as observed in the 25–50 m depth stratum, and in transects C and P, related with the sub-mesoscale cyclonic eddy south of Cozumel and the mesoscale Honduras Gyre, respectively (Carrillo et al., 2015). The slow, cyclonic Honduras Gyre could act as an important retention area for PL that were registered at the nearshore edge of the gyre.

Dominant *Abralia sp.* 1 showed some evidence of diel vertical migration, in contrast with *Onychoteuthis banksii* and *Ornithoteuthis antillarum*. The MBRS represent an important dispersion area for PL, connecting a species rich Caribbean community with the Gulf of Mexico.

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Figures and tables

Table I. Cephalopod paralarvae species composition in the Mesoamerican Barrier Reef System during January 2007. Code is for species shown in Fig. 6. N = total numbers. Ab = Abundance (PL/1000 m^3).

Taxa	**CCA**	**N**	**Ab**
Order Oegopsida			
Family Enoploteuthidae Pfeffer 1900			**146**
Abralia sp. 1 Gray, 1849	1	269	129
Abralia sp. 2		11	5
Abraliopsis sp. 1 Joubin, 1896		3	1
Enoploteuthis sp.1 D'Orbigny in Rüppell, 1844	2	18	9
Enoploteuthis sp. 2		2	1
Family Onychoteuthidae Gray, 1847			**36**
Onychoteuthis banksii (Leach, 1817)	3	39	19
Onychoteuthis compacta (Berry, 1913)		2	1
Onychoteuthis prolata Bolstad, Vecchione & Young, in Bolsdtad, 2008	4	3	1
Onychoteuthis sp.		32	15
Family Ommastrephidae Steenstrup 1857			**23**
Ornithoteuthis antillarum (Adam, 1957)	5	40	19
Sthenoteuthis pteropus (Steenstrup, 1855)	6	2	1
Complejo *Sthenoteuthis-Illex*	7	5	2
Family Cranchiidae Prosch, 1847			**18**
Bathothauma lyromma Chun, 1906	8	2	3
Heliocranchia papillata (Voss, 1960)		1	2
Liguriella podophtalma Issel, 1908	9	3	7
Liocranchia reinhardti (Steenstrup 1856)	10	1	2
Megalocranchia sp. Pfeffer, 1884	11	2	4
Family Pyroteuthidae Pfeffer, 1912			**10**
Pterygioteuthis giardi Fischer, 1896	12	2	7
Pterygioteuthis sp.	13	3	3
Family Ancistrocheiridae Pfeffer, 1912			**5**
Ancistrocheirus cf lesueuri (d'Orbigny, 1842)	14	1	5
Family Thysanoteuthidae Keferstein, 1866			**2**
Thysanoteuthis rhombus Troschel, 1857	15	1	2
Family Lycoteuthidae Pfeffer, 1908			**9**
Lycoteuthis lorigera (Steenstrup, 1875)		1	9
Order Myopsida			
Family Octopodidae (D' Orbigny 1939-1842)			**10**
Macrotritopus defilippi Vérany, 1851	16	1	0.5
Octopus vulgaris Cuvier, 1791	17	3	1.4
Octopus sp. 1 Cuvier, 1797	18	1	0.5
Octopus sp. 2	19	2	7.4
Octopus sp. 1 Cuvier, 1797	20	1	0.5
Family Loliginidae Lesueur, 1821	21	1	**2**
TOTAL		**451**	

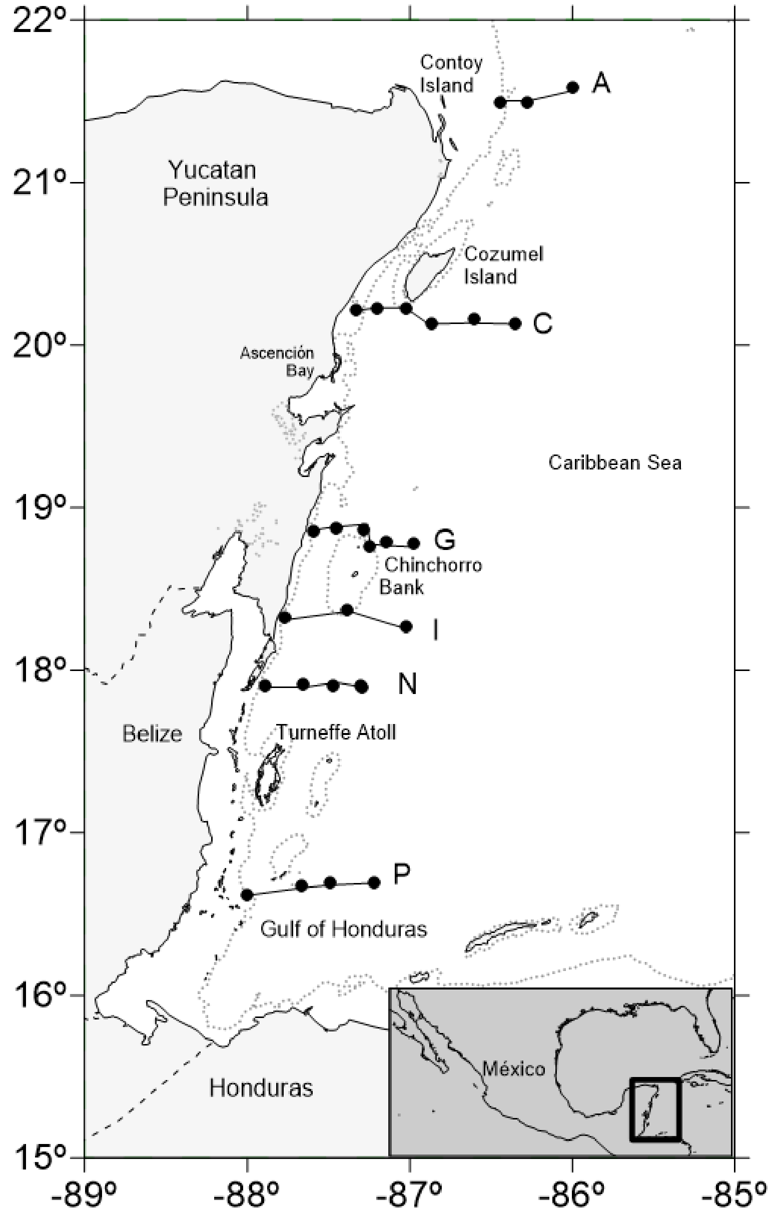

Figure 1. The Mesoamerican Barrier Reef System showing oceanographic transects (A, C, G, I, N, P) where sampling stations were conducted during July 2007. Dashed line: 200 m depth isobath.

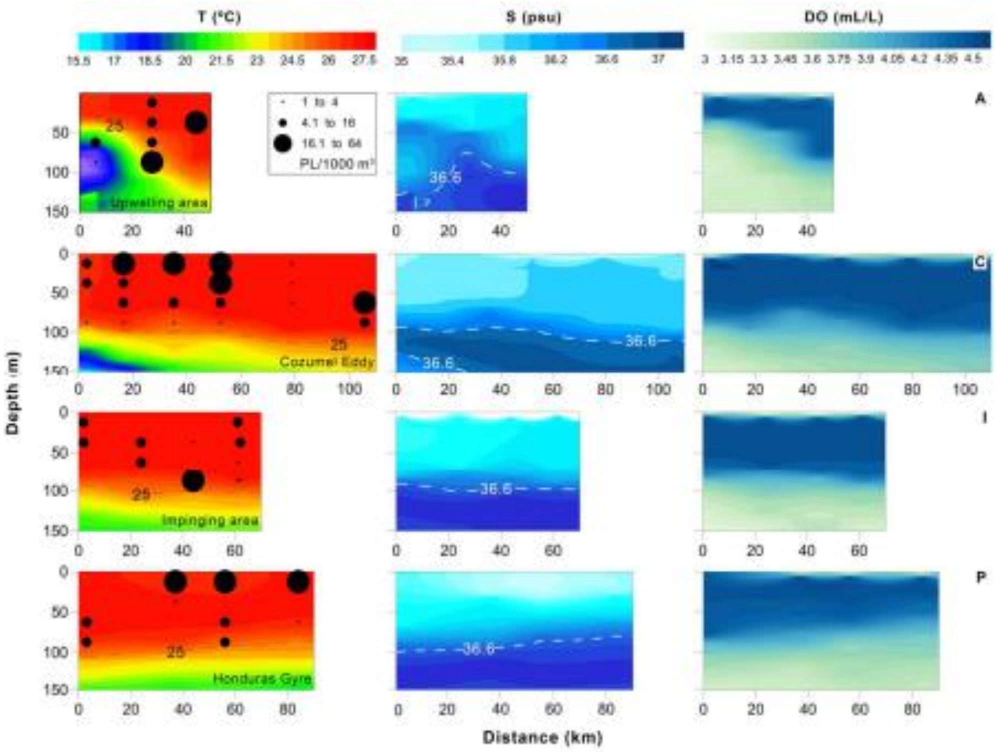

Figure 2. Vertical structure of temperature, along transects A, C, I and P from the Mesoamerican Barrier Reef System during January 2007. Black isolines indicate the 25.5 ºC isotherm close to the limit of the Caribbean Surface Water (≥25 °C,) according to Carrillo et al. (2016). Main oceanographic features for each section are indicated. Standardized PL abundances are shown only in temperature panels.

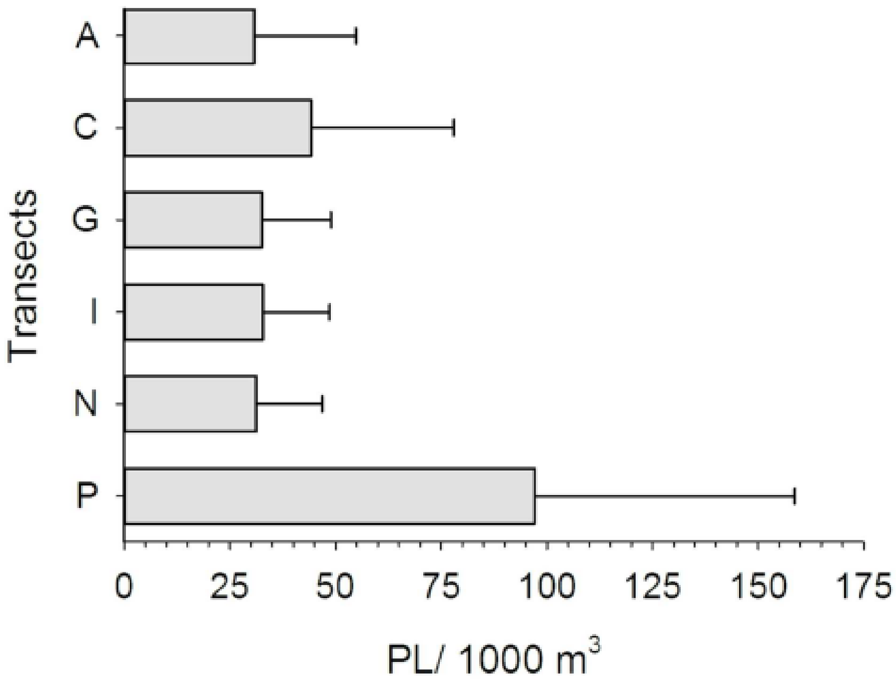

Figure 3. Mean and standard deviation standardized paralarval abundance by transect calculated from depth-aggregated stations.

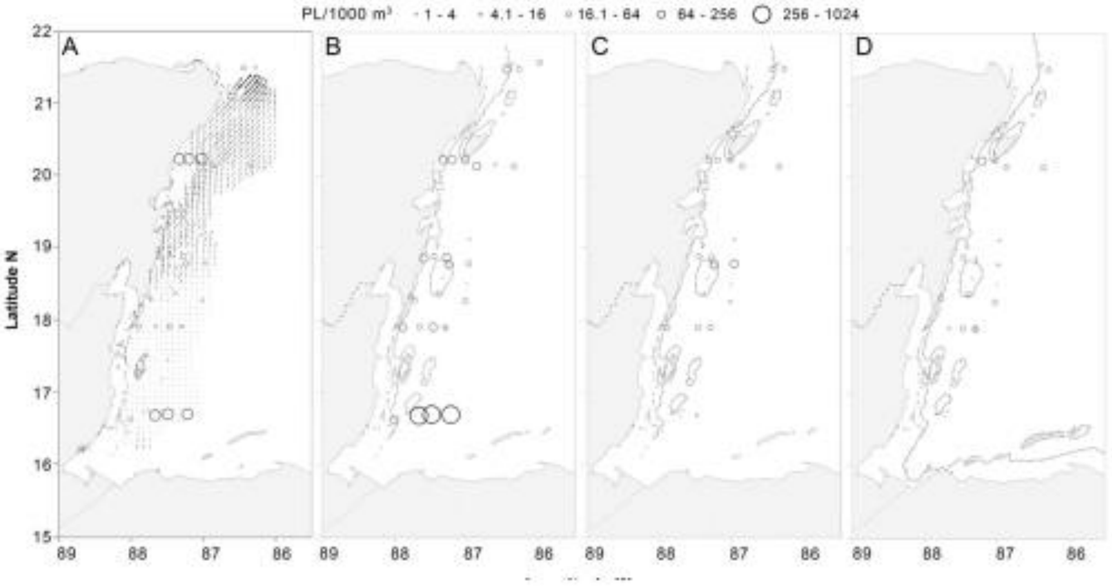

Figure 4. Horizontal distribution of depth-aggregated standardized paralarval abundances in the Mesoamerican Barrier Reef System (open circles) (A) All paralarvae coupled to surface geostrophic velocities (vectors, m/s) during January 2007 (Modified from Carrillo et al., 2016). Velocity vectors. Grey, <0.5 m/s; black, 0.5-1 m/s (B) *Abralia* sp. 1, (C) *Onychoteuthis banksii* and (D) *Ornithoteuthis antillarum*.

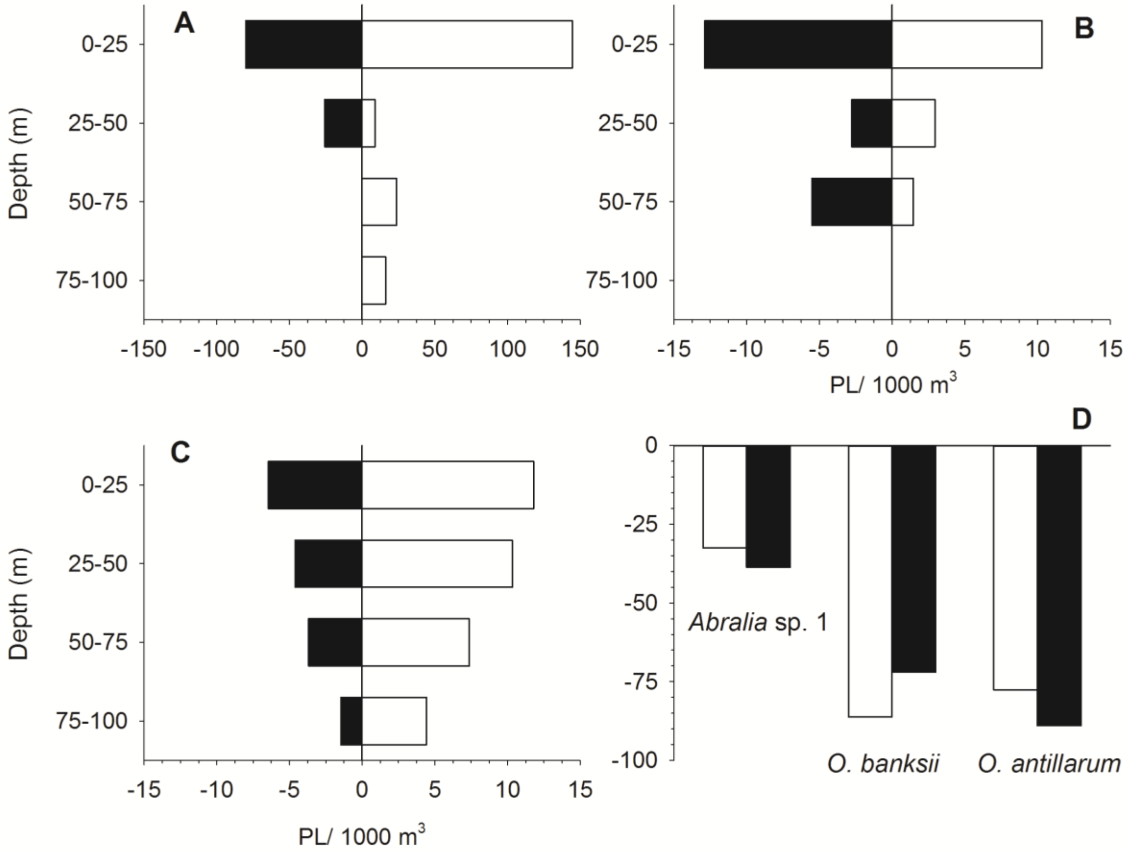

Figure 5. Day (white) and night (black) vertical distribution of most abundant paralarval species in the Mesoamerican Barrier Reef System, station-aggregated: (A) Abralia sp. 1, (B) Onychoteuthis banksii and (C) Ornithoteuthis antillarum. (D) Abundance-weighted mean depths of these species, for both day and night samples.

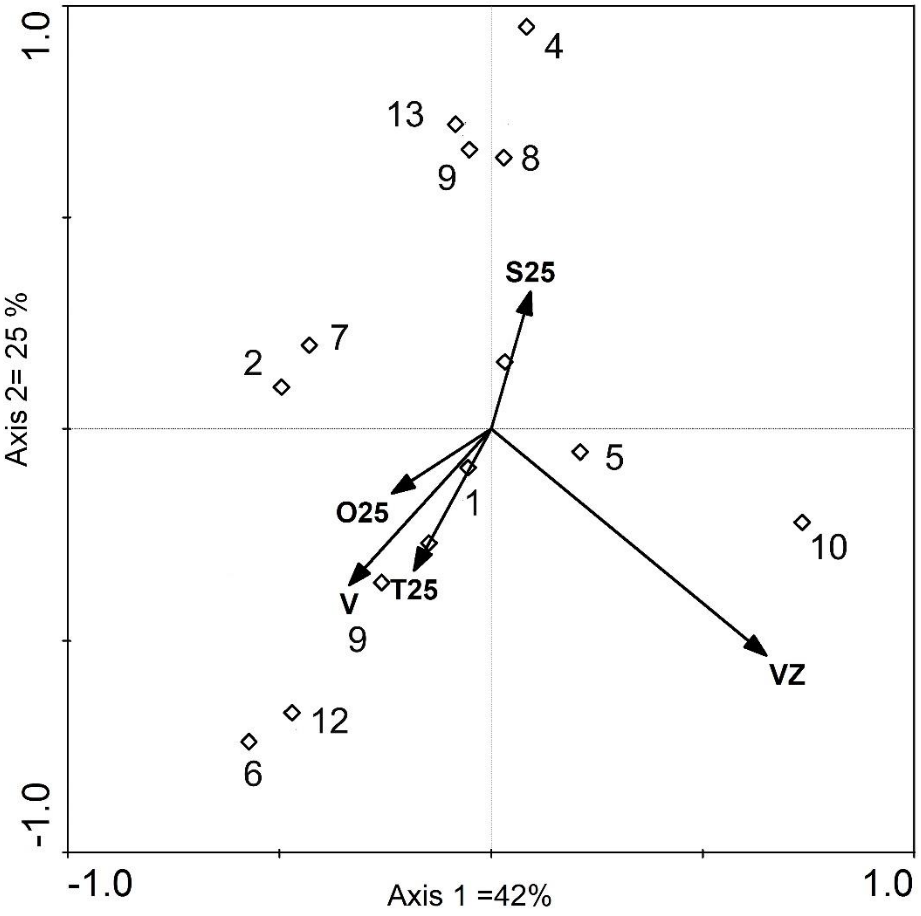

Figure 6. Dispersion diagram of the canonical correspondence analysis between cephalopod paralarval abundance and oceanographic variables: T 25 , S 25 , and O 25 , temperature, salinity, and dissolved oxygen at 25 m depth, respectively; ZV= zooplankton volume. Code for species as given in Table I.

CAPITULO III

Conclusiones

- Este trabajo muestra por primera vez los patrones de distribución horizontal y vertical de paralarvas (PL) de cefalópodos de las aguas superficiales del Caribe occidental, en particular en el SAM y discute la influencia de las características oceanográficas en los patrones observados.
- Se registraron 451 PL pertenecientes a 10 familias, 16 especies, 7 formas y un complejo de especies. Las familias Enoploteuthidae (60%), Onychoteuthidae (22%) y Ommastrephidae (8%) representadas por *Abralia* sp.1, *Onychoteuthis banksi* y *Ornithoteuthis antillarum* respectivamente, fueron las más abundantes.
- La distribución tridimensional de PL se puede resumir como sigue: las PL se encontraron en la masa agua superficial del Caribe (CSW) con temperaturas de 25-27 ° C, valores de oxígeno de 4.2-4.5 ml / L y salinidades <36.0. Las principales abundancias se produjeron principalmente en los primeros 25 m de profundidad, sin diferencias significativas entre las colecciones de día y noche, donde las corrientes de velocidad fueron de 0,2-0,8 m / s.
- La especie más dominante *Abralia* sp.1 se presentó en los primeros 25 m de profundidad mostrando evidencia de migración vertical en contraste con *Onychoteuthis banksii y Ornithoteuthis antillarum,* quienes se distribuyeron de manera homogénea en los 75 m de profundidad.
- La abundancia de PL estuvo asociada a la estructura hidrográfica y a la circulación presente en el área de estudio. El giro de de Honduras localizado en la zona más austral es una zona de retención de paralarvas, mientras que la

Corriente de Yucatán juega un rol importante en la dispersión de PL, conectando a especies del Caribe con el Golfo de México.

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