Horizontal and vertical distribution of cephalopod paralarvae in the Mesoamerican Barrier Reef System

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Abstract

Horizontal and vertical distribution of cephalopod paralarvae (PL) from the Mesoamerican Barrier Reef System (MBRS) in the Western Caribbean was studied during two oceanographic cruises in 2006 and 2007. A total of 1034 PL belonging to 12 families, 22 genera, 24 species, 5 morphotypes and a species complex were identified. *Abralia redfieldi*, *Onychoteuthis banksii* and *Ornithoteuthis antillarum* were the most abundant taxa. The taxonomic identification from these three species was corroborated with DNA barcoding (99.8–100% of similarity). Paralarvae of *Octopus insularis* were reported for the first time in the wild. Most PL occupied the Caribbean Surface Water mass in the 0–25 m depth stratum. Largest paralarval abundances were related to local oceanographic features favouring retention such as the Honduras Gyre and Cozumel eddy. No day-night differences were found in PL abundance, although *Abralia redfieldi* showed evidence of diel vertical migration. Distribution of PL in epipelagic waters of the MBRS was probably related to ontogenetic migration, hydrographic features of meso and subscale, and to the circulation regimes dominated by the Yucatan Current. The MBRS represents an important dispersion area for PL, potentially connecting a species-rich Caribbean community with the Gulf of Mexico and Florida waters.

Introduction

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

Paralarval 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 play important roles in distribution, growth and survival of PL (Ichii *et al.*, 2004; Aceves-Medina *et al.*, 2017). Ocean currents are also a key factor in transporting eggs or egg masses and PL from the spawning areas to the hatching, nursery or feeding grounds (Díaz *et al.*, 2000; Downey-Breedt *et al.*, 2016). They influence the dispersion of PL of different biogeographic affinities (Diekmann & Piatkowski, 2002; Haimovici *et al.*, 2002), and may keep the PL inside a macroscale circulation cell that results in an essential strategy to complete their life cycles (Roberts & van den Berg, 2002). Thus cephalopods are likely to be affected by fluctuations in oceanic circulation due to global change with unknown effects (Xavier *et al.*, 2015).

Cephalopod fauna from the Caribbean has only been considered in one study (Nesis, 1975), resulting in an apparently smaller cephalopod diversity than adjacent Florida waters (Díaz *et al.*, 2000; Gracia *et al.*, 2002; Judkins *et al.*, 2010). Nesis (1975) did not consider the Mesoamerican Barrier Reef System (MBRS) of the western Caribbean, which represents one of the largest marine biodiversity hotspots worldwide (Roberts *et al.*, 2002). This area shows a highly dynamic oceanography with physical processes driving the dispersion of planktonic larval stages. During 2006 and 2007 the oceanographic background and the distribution of larval fish, lobster phylosomas and pteropods were studied in the MBRS (Parra-Flores & Gasca, 2009; Muhling *et al.*, 2013; Carrillo *et al.*, 2015, 2016, 2017; Canto-García *et al.*, 2016). The aim of this study is to show for the first time the abundance, diversity and
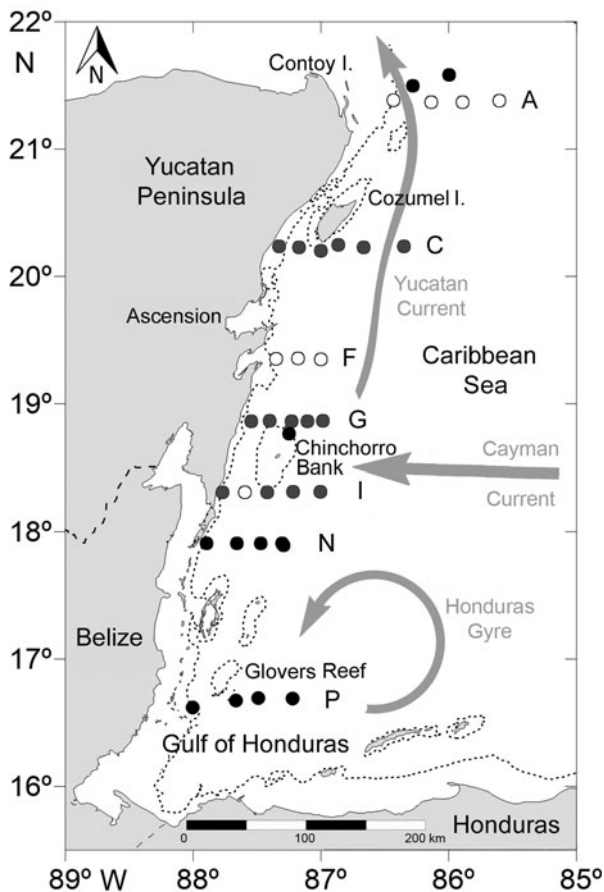
Fig. 1. The Mesoamerican Barrier Reef System in the western Caribbean, Mexico, showing oceanographic lines A, C, F, G, I, N and P where sampling was conducted. White dots represent stations occupied during March 2006, black dots during January 2007, and grey dots during both years. Dashed line represents the 200 m depth isobaths. Main currents are in grey.

horizontal and vertical distribution patterns of cephalopod paralarvae from the surface waters of the MBRS and to discuss the influence of oceanographic features on these organisms.

Materials and methods

Study area

The Mesoamerican Barrier Reef System (MBRS) runs along nearly 1000 km from the north-eastern tip of the Yucatan Peninsula to the Gulf of Honduras (Figure 1). Physical parameters are defined by the latitude of impingement of the Cayman Current (CC) on the MBRS separating into three main dynamic 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). A strong north-westerly current with a uniform speed ($\sim$1.1 m s^{-1}) in the north of the MBRS approaches the Yucatan Channel where YC reaches maximum speeds of 2.0 m s^{-1}. 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. The southern MBRS region is characterized by the large cyclonic Honduras gyre (Carrillo et al., 2015).

The MBRS receives water masses that are imported by the CC and the Caribbean currents entering from the Atlantic Ocean through the multiple passages between the northern and eastern

Caribbean islands. The Caribbean Surface Water (CSW) represents the surface mixed layer with a mean thickness of 85 m depth, a mean temperature of 27°C and a low salinity (<36 at surface). CSW occupied almost all the sampling stations. Below 100 m depth, the high-salinity (>36.75) North Atlantic Subtropical Underwater (SUW), centred at about 150 m depth, lies beneath the CSW. Dissolved oxygen in the surface mixed layer is >4 ml l^{-1}. The northernmost region 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 by 100 m and the mixed layer was $\sim$50 m thick (Carrillo et al., 2016).

Sampling

Two oceanographic campaigns during 18 March–1 April 2006 and 14–30 January 2007 aboard the NOAA ship 'Gordon Gunter' surveyed the MBRS, with 23 and 27 sampling stations visited respectively, along seven lines (Figure 1): Line A, the north-ernmost line offshore Contoy Island to $\sim$115 km offshore; Line C, located 60 km north of Ascension Bay and south of Cozumel Island; Line F south of Ascension Bay; Lines G and I, north and south of Chinchorro Bank respectively, in the Cayman Current impingement zone (Carrillo et al., 2015); and Lines N and P, which are representative in Belizean coastal waters, with Line P just south of Glovers Reef in the Gulf of Honduras. Lines A, C, G and I were occupied both years. Line F was occupied in 2006 while southernmost lines N and P were visited only during 2007.

At each station temperature, salinity and dissolved oxygen were recorded with calibrated CTD casts and published elsewhere (Carrillo et al., 2016). Current velocity measurements at 35 m depth were obtained from a hull-mounted Acoustic Doppler Current Profiler (Carrillo et al., 2015). Vertical oceanographic features that could be related to PL abundance were plotted at lines A, C, F, G and I for 2006 and at lines A, C, G, I, N and P for 2007.

Depth-stratified plankton sampling was performed using a multiple opening and closing net environmental sensing system (MOCNESS) with 1 m^2 mouth and 333 μm mesh. It 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 centre 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. All stations were sampled once. Sampling local time was classified as during the day (0600–1800 h) or at night (1801–0559 h) (Canto-García et al., 2016).

Data analysis

All cephalopod paralarvae were sorted from the samples and identified to the most precise taxonomic level possible according to Nesis (1979), Young & Harman (1987), Sweeney et al. (1992), Vecchione et al. (2001), Bolstad (2010), De Silva-Dávila (2013), Lenz et al. (2015) and Roper et al. (2015). Abundance of PL was standardized for each tow to number of paralarvae (PL) in 1000 m^3 of filtered water (PL 1000 m^{-3}) (Diekmann et al., 2006). Paralarvae were measured for mantle length (ML) to the nearest 0.1 mm. Those smaller than 2.0–3.0 mm ML are seldom described in oceanic squids (Sweeney et al., 1992). Therefore, paralarvae at these sizes not matching published descriptions, but with similar chromatophore patterns, were classified as mor-photypes of a given genus, e.g. *Enoploteuthis* sp. 1, *Octopus* sp. 1. Unpigmented paralarvae without chromatophores within these sizes were identified only to genus or family level, e.g. *Onychoteuthis* spp., Onychoteuthidae. Unidentified paralarvae
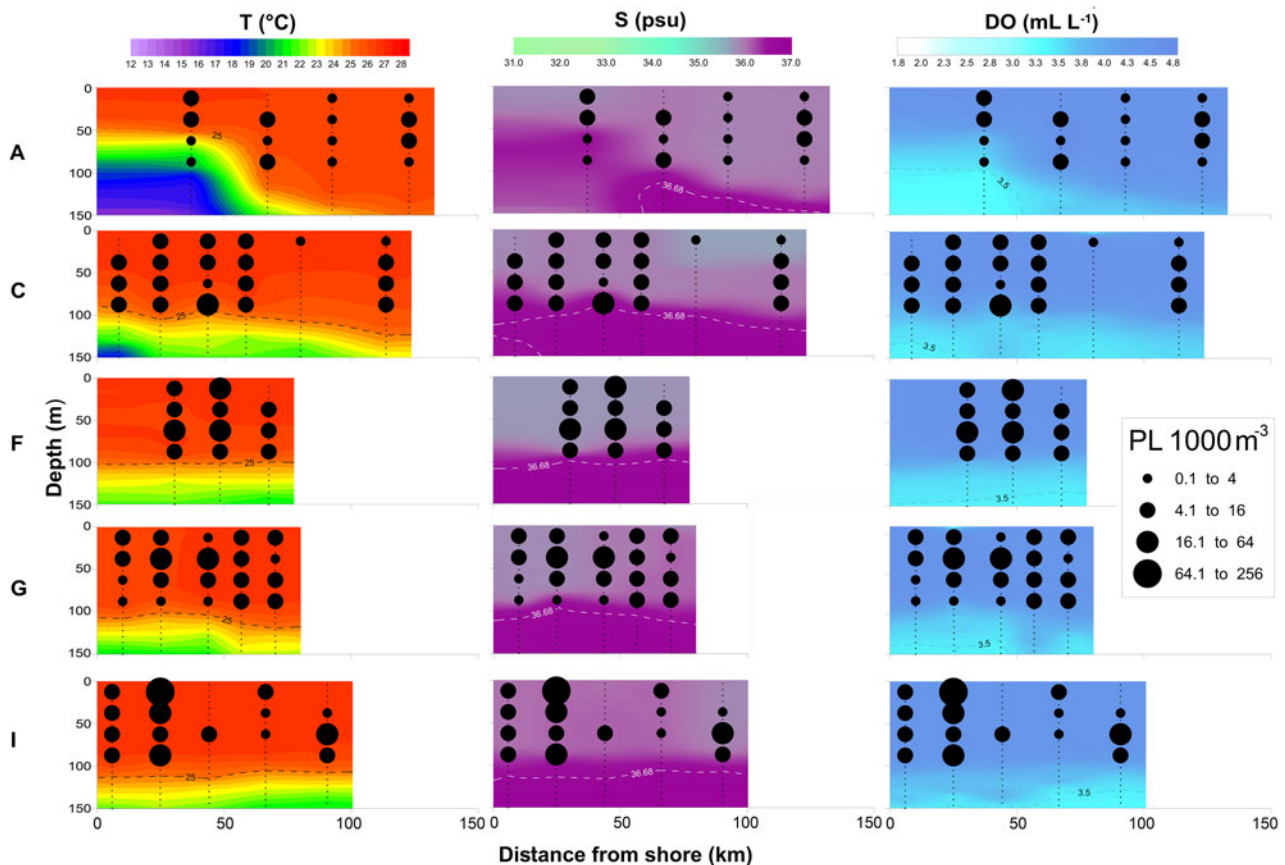
Fig. 2. Environmental variable profiles of temperature (T, °C), salinity (S, psu) and dissolved oxygen (DO, ml l^{-1}) along lines A, C, F, G and I from the Mesoamerican Barrier Reef System during March 2006. Isolines indicate the limits of the Caribbean Surface Water ($\geq$25°C, 34.5–36.6 psu) according to Carrillo et al. (2016). Paralarval abundances (PL 1000 m^{-3}) are shown in black circles.

included deteriorated, strongly twisted specimens lacking arms, eyes, heads and/or chromatophores.

DNA barcoding was performed for the taxonomic identification of the three dominant taxa, for the smallest paralarvae of the Ommastrephidae family ($\leq$2.0–3.0 mm ML), and for paralarvae of species of commercial importance such as *Octopus insularis* Leite & Haimovici, 2008. Representatives of these taxa were photographed and DNA extraction, amplification and sequencing followed Elías-Gutiérrez *et al.* (2018). DNA strands were sequenced in both directions and were assembled and edited manually, using the Geneious premium 2019.2.1. software (Kearse *et al.*, 2012). A total of 22 sequences (654 bp) of the mitochondrial partial gene COI from individuals with different sizes were analysed. The basic local alignment search tool (BLAST) was applied to each sequence to corroborate the specific identification using the NCBI-BLAST also performed in Geneious software. These sequences were aligned with Clustal W (Thompson *et al.*, 1994), with default values included in the MEGAX v10.0.5 software (Kumar *et al.*, 2016). Observed alignment was clean, without gaps, and was translated into amino acid sequences as an additional check of alignment.

These sequences were deposited at BOLD system (available in the dataset Mexican Caribbean molluscs; DS-MOCAR) and at NCBI with the registration GenBank accession numbers. The voucher specimens were deposited in the reference collection at El Colegio de la Frontera Sur, Campus Chetumal.

Horizontal and vertical distribution of total PL abundance of the three dominant taxa, and the environmental variables in the MBRS were plotted using Surfer 14 from Golden Software. Total PL numbers were summed for each station and divided by summed total volumes of seawater filtered for the four sampled

strata. This resulted in one depth-aggregated assemblage per station (Muhling *et al.*, 2013). PL abundances were standardized to 1000 m^3, then square-root-transformed prior to further analyses as follows. Differences of PL abundance among lines were assessed through an ANOVA or through a Kruskal–Wallis test when normality assumptions were not satisfied. The paired t test or the Mann–Whitney U test were used to assess the statistical significance of differences in PL abundances between daytime and night-time stations.

Abundances of PL for each depth stratum were calculated in each station, standardized to 1000 m^3 and square-root-transformed. Differences among strata were tested using either ANOVA or a Kruskal–Wallis test when normality assumptions were not satisfied. Abundances for the most common taxa were calculated also by depth strata for day and night. Their abundance-weighted mean depths were calculated according to Muhling *et al.* (2013).

Results

In March 2006, 603 cephalopod paralarvae (PL) (8.6 PL 1000 m^{-3}) were collected and 431 PL (6.7 PL 1000 m^{-3}) were collected in January 2007. All were found in the Caribbean Surface Water, defined as being >25°C, oxygen values of 4.2–4.5 ml l^{-1}, and low salinities <36.6 (Figures 2 & 3).

In 2006, larger mean PL abundances were found in the central lines F, G and I (Figure 4A) where relatively weak flows ($\leq$0.25 m s^{-1}, Carrillo *et al.*, 2015) of the Caiman Current were present. A maximum abundance of 76 PL 1000 m^{-3} occurred in a surface tow of line I (Figure 2). In 2007 larger PL abundances occurred in surface waters (<25 m depth) of southern Cozumel (line C,
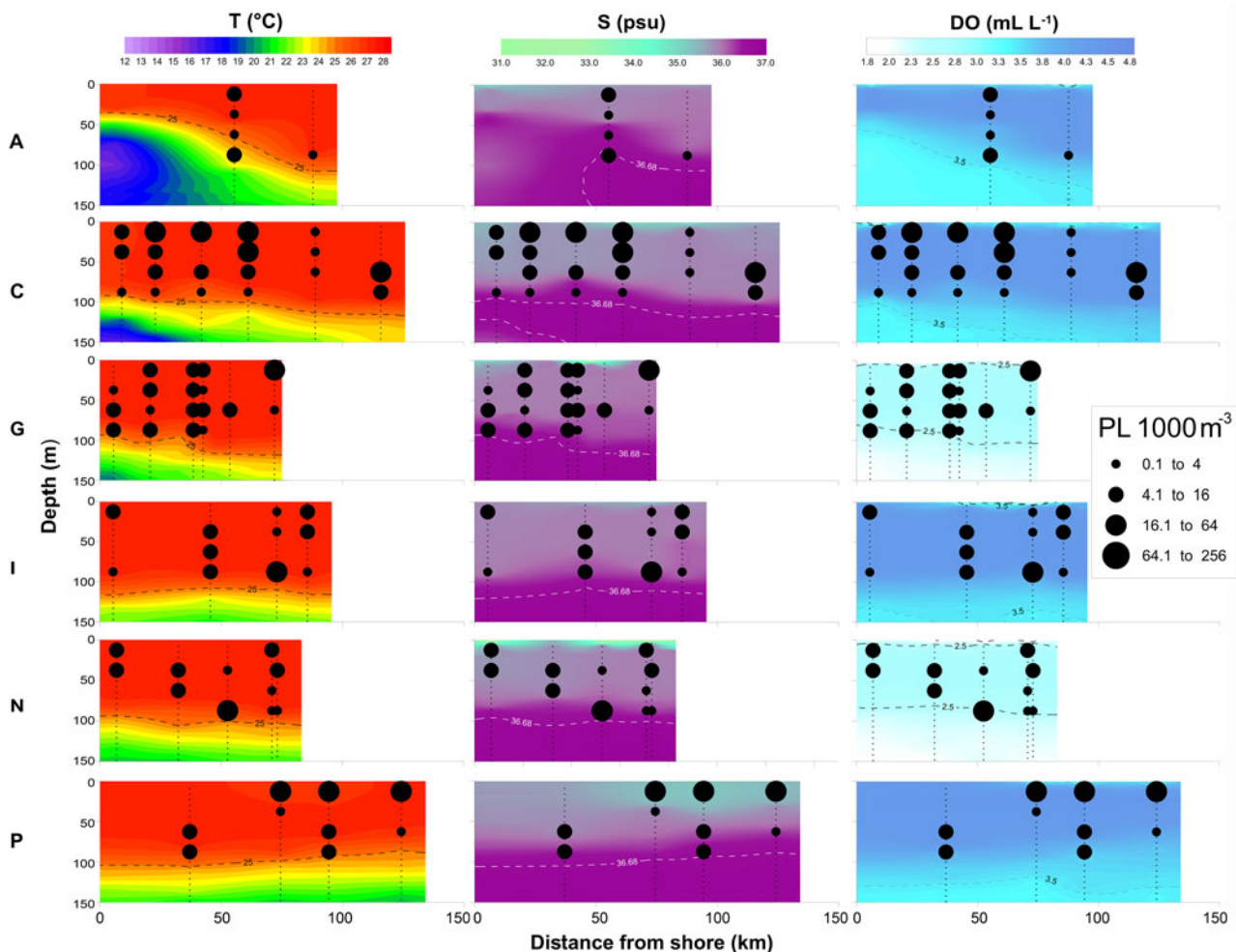
Fig. 3. Environmental variable profiles of temperature (T, °C), salinity (S, psu) and dissolved oxygen (DO, ml l^{-1}) along lines A, C, G, I, N and P from the Mesoamerican Barrier Reef System during January 2007. Isolines indicate the limits of the Caribbean Surface Water (≥25°C, 34.5–36.6 psu) according to Carrillo *et al.* (2016). Paralarval abundances (PL 1000 m^{-3}) are shown in black circles.

characterized by moderate velocity currents ranging 0.2–0.8 m s^{-1}; Carrillo *et al.*, 2015) and the Gulf of Honduras (Line P, with southward flow and speeds ≤0.25 m s^{-1}). Central lines G and I yielded lower PL abundances than in 2006, as the Yucatan Current (YC) formed south of Chinchorro and a stronger flow exceeding 1.0 m s^{-1} builds north of that bank (Carrillo *et al.*, 2015). Lower mean abundances were consistently found in the northernmost line A in both years (Figure 4A), where YC attains the highest speeds >1.25 m s^{-1} (Figure 5A, E). In this region, coastal upwelling associated with the YC favoured the inshore shallowing of the SUW (Figures 2A & 3A). In this line, the maximum (11 PL 1000 m^{-3}) and the minimum (1 PL 1000 m^{-3}) abundances were found at surface and at 100 m depth (Figure 2).

Horizontal mean PL abundances (considering stations depth-aggregated) did not show significant differences among lines for 2006 (Kruskal–Wallis test, $H = 9.34$, df = 4.23, $P > 0.05$), nor for 2007 (ANOVA, $F(4,15) = 1.2$, $P > 0.05$) (Figure 4A). Regarding vertical distribution, PL largest mean abundances (stations-aggregated) were found in the upper 25 m (Figure 4B). Nevertheless, differences in abundances among strata were not statistically significant, for 2006 (ANOVA, $F(3,85) = 0.16$, $P > 0.05$) or for 2007 (Kruskal–Wallis test, $H = 6.13$, df = 3107, $P > 0.05$), probably because of large variances. PL mean abundance for stations (depth-aggregated) visited during daytime were larger than those occupied during night-time (Figure 4C). However, these differences were not significant for 2006 (Mann–Whitney

U test, $Z = 1.67$, N = 11, $P > 0.05$) or 2007 (Paired t test, $t25 = 0.21$, $P > 0.05$).

Morphological identification of paralarvae found in the MBRS indicated the presence of 12 families, 22 genera, 24 species, 5 morphotypes and a species complex (Table 1). The number of species plus morphotypes was very similar between years, with 24 species in 2006 and 19 in 2007. However, 10 species (*Onykia carriboea, Ommastrephes bartrammii, Helicocranchia pfefferi, Lycoteuthis lorigera, Selenoteuthis scintillans, Chiroteuthis veranii, Amphioctopus burryi, Octopus insularis, Argonauta argo* and *A. hians*) occurred only in 2006, while five taxa at species level (*Bathothauma lyromma, Helicocranchia papillata, Liocranchia reinhardti, Lycoteuthis springeri* and *Octopus* sp. 2), and a paralarva of the Loliginidae family, were collected only in 2007.

Three squid families accounted for 85–91% of the total cephalopod abundance by year: Enoploteuthidae (49–61%) represented mainly by *Abralia redfieldi*, Onychoteuthidae (20–24%) represented by *Onychoteuthis banksii*, and Ommastrephidae (10–12%) by *Ornithoteuthis antillarum*. The remaining 9–15% was represented by nine families: Lycoteuthidae, Cranchiidae, Ancistrocheiridae, Thysanoteuthidae, Pyroteuthidae, Chiroteuthidae, Loliginidae, Argonautidae and Octopodidae. Small PL (≤3.0 mm ML) dominated the samples (81% of all). They ranged from 90–93% in Enoploteuthidae, 73–76% in Onychoteuthidae, and 62–80% in Ommastrephidae. *Octopus insularis* PL were found for the first time in the wild. They were represented by three specimens 1.4, 1.4 and 3.6 mm ML.
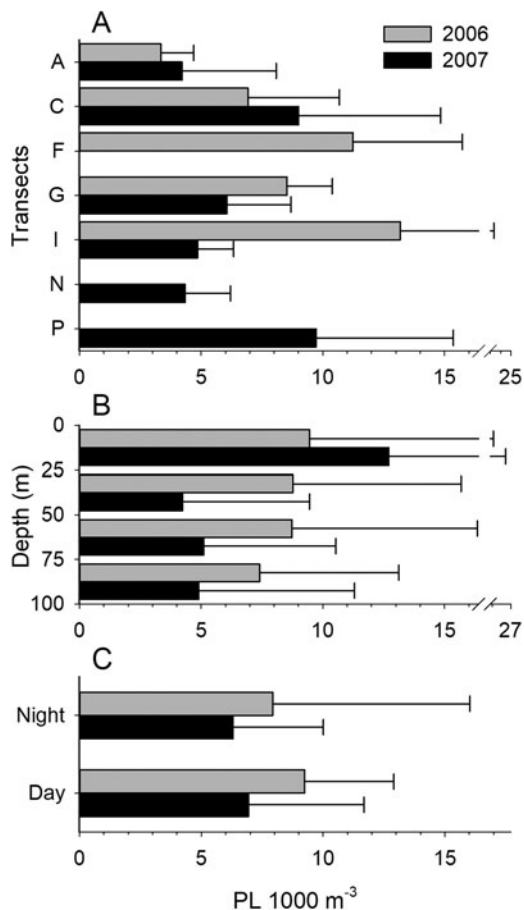
Fig. 4. Mean and standard deviation of paralarval abundance (PL 1000 m^{-3}) at the Mesoamerican Barrier Reef System for 2006 and 2007 by (A) lines from depth-aggregated stations; (B) depth strata from stations; and (C) daytime vs night-time depth-aggregated stations.

DNA barcoding of dominant species corroborated the taxonomic identification for *A. redfieldi*, *O. banksii* and *O. antillarum*, as well as the octopus *O. insularis* (Table 2). In the BLAST analysis, three out of 22 sequences (654 bp) revealed high similarity with *A. redfieldi* (99.5–99.8% and E Value 0.0), three sequences with *O. banksii* (98.7–100% and E Value 0.0), six sequences with *O. antillarum* (98.2–100% and E Value 0.0) and three with *O. insularis* (99.8% and E Value 0.0). This analysis (seven sequences) also allowed us to identify smaller ommastrephid PL (≤2.0–3.0 mm ML), which could not have been identified using morphological features, as *O. antillarum* (Table 2).

The most abundant and frequent species distributed along the MBRS was *Abralia redfieldi*. In 2006 larger abundance occurred in nearshore tows of lines C to I. In 2007 it was very abundant in line P where two surface tows yielded 33 and 41 PL 1000 m^{-3}. Moderate abundances were found south of Cozumel Island and north of Chinchorro Bank (Figure 5B, F). *Onychoteuthis banksii*, the second most abundant taxon, occurred in all lines with a maximum of 25 PL 1000 m^{-3} in a shallow tow south of Cozumel during 2006 (Figure 5C, G). The third most abundant species, *Ornithoteuthis antillarum*, showed a similar horizontal distribution as *Onychoteuthis banksii*. A maximum of 9 PL 1000 m^{-3} occurred in a shallow tow of line G in 2006 (Figure 5D, H). *Octopus insularis* PL were found in the shallower layers of shoreward stations of lines C, F and G during 2006 (Figure 5A).

Abralia redfieldi showed evidence of vertical migration with highest abundance of 4 PL 1000 m^{-3} at the surface at night, while maximum values during daytime occurred below 50 m depth in 2006 (Figure 6A). *Onychoteuthis banksii* was almost absent from the deepest strata >75 m depth, with higher abundances at the surface at night (3 PL 1000 m^{-3}) than during the day (Figure 6B). *Ornithoteuthis antillarum* occupied all the strata with abundances decreasing with depth at night and increasing during daytime (Figure 6C). Abundance-weighted mean depths showed slight diel differences of 12 m depth for these three species. *Abralia redfieldi* and *Ornithoteuthis antillarum* distributed around 50 m depth day and night, while *Onychoteuthis banksii* showed the shallowest mean depths at 25 m depth (Figure 6D).

Depth distributions for 2007 were contrasting with those from the previous year. Maximum day abundances occurred at the surface for the three species (Figure 6E–G). Mean depths during daylight were shallower than during night for *Abralia redfieldi* and *Onychoteuthis banksii* (Figure 6H).

Discussion

We report, for the first time, a systematic cephalopod paralarvae study based on physical parameters in the Caribbean Sea, while identifying and corroborating genetically the identity of the three dominant taxa and of *Octopus insularis*. Abundance and horizontal and vertical distribution of PL from the epipelagic waters of the Mesoamerican Barrier Reef System (MBRS) during March 2006 and January 2007 showed differences in the distribution patterns of the three dominant taxa.

Paralarvae were collected in the Caribbean Surface Water, the relatively well-mixed warm surface layer of the MBRS. 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^{-1}. The PL were encountered at relatively high temperatures of 25–27°C, high oxygen concentrations (4.2–4.5 ml l^{-1}) and salinities (<36.0). In these conditions, the horizontal pattern in PL abundance showed a similar pattern of horizontal distribution to ichthyoplankton (particularly myctophids) and lobster phyllosoma larvae studied in the same campaigns (Muhling *et al.*, 2013; Canto-García *et al.*, 2016). Oceanographic processes can therefore explain their similar distributions.

In March 2006 the central lines (F, G, I) around Chinchorro Bank accounted for larger abundances. The region north-east of this bank (line G) with an average abundance of PL has been identified as another possible area of larval retention because the island-wake effect may produce small eddies probably responsible for accumulation of the plankton (Canto-García *et al.*, 2016; Carrillo *et al.*, 2017).

In January 2007 the largest PL abundance was found in the mesoscale Honduras Gyre at line P. This gyre has also been associated with larval retention, particularly for myctophid larvae and pelagic phyllosomas (Muhling *et al.*, 2013; Canto-García *et al.*, 2016; Carrillo *et al.*, 2017). Moreover, virtual fish larvae tracking from numerical models in the MBRS showed that the Honduras Gyre potentially could retain particles for over 40 days (Martínez *et al.*, 2019, 2020). Another region with large abundance of PL was located south of Cozumel Island (line C). It might be associated with the presence of the sub-mesoscale cyclonic eddy, the '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, higher abundances of tuna, myctophid and phyllosoma larvae and pteropods were also observed in the same cruise (Parra-Flores & Gasca, 2009; Muhling *et al.*, 2013; Canto-García *et al.*, 2016; Carrillo *et al.*, 2017). The planktonic environment along much of the MBRS is characterized by low retention conditions (Martínez *et al.*, 2019, 2020) and with northward transport of
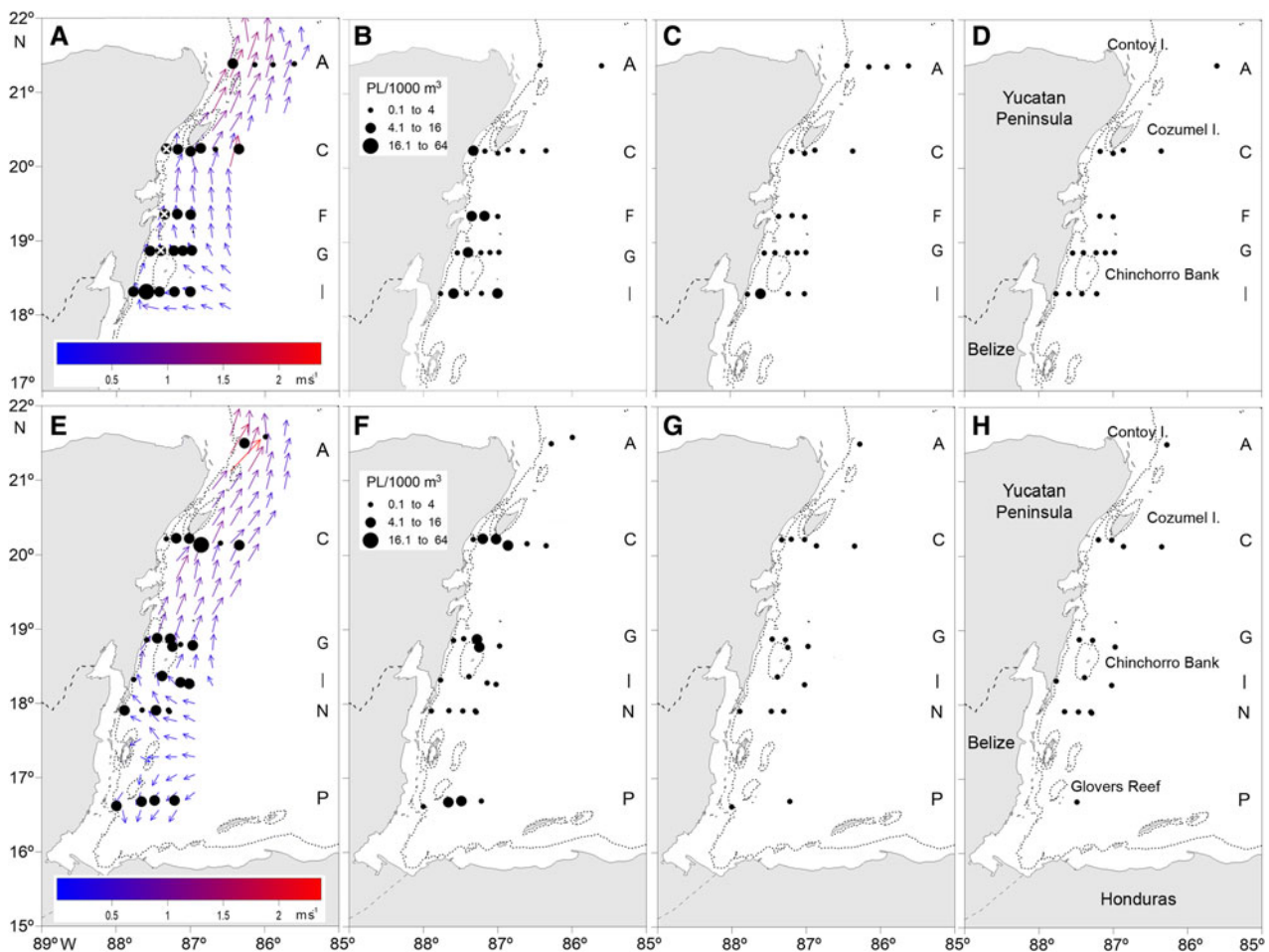
Fig. 5. Horizontal distribution of depth-aggregated paralarval abundances (PL 1000 m^{-3}) by station in the Mesoamerican Barrier Reef System (black circles) for 2006 (A–D) and 2007 (E–H). (A, E) all paralarvae coupled to surface geostrophic velocities (vectors, m s^{-1}) (modified from Carrillo et al., 2015); (B, F) *Abralia redfieldi*; (C, G) *Onychoteuthis banksii*; and (D, H) *Ornithoteuthis antillarum*. *Octopus insularis* single occurrences are denoted with a white × in (A).

PL, largely influenced by the YC and coastal upwelling in the northernmost MBRS.

In sharp contrast with a tendency for larval retention and local recruitment in the southern and impingement regions of the MBRS, the northern region shows northward advection and connectivity (Martínez et al., 2019, 2020), which yielded the lowest paralarval abundances. In this northernmost region of the MBRS strong YC reaches up to 2.0 m s^{-1} (Carrillo et al., 2015, 2017) and could potentially transport paralarvae from there to the Gulf of Mexico and as far as distant areas such as off Florida Keys in a few days (Martínez et al., 2019). The most abundant paralarvae *Abralia redfieldi*, *Onychoteuthis banksii* and *Ornithoteuthis antillarum* were also among the most common adult and juvenile squid collected in the north-eastern Gulf of Mexico (Passarella, 1990; Judkins et al., 2016) as well as in the Straits of Florida (Cairns, 1976). They could most likely come from an upstream source such as the MBRS. However some marine taxa such as reef fishes showed little genetic evidence of connectivity between MBRS and the Florida Keys (Muhling et al., 2013). Morphological, genetic and growth studies on PL together with regional oceanographic numerical models could lead to a better understanding of the role of the MBRS in exporting marine resources such as cephalopods to other systems.

A rich cephalopod paralarval assemblage comprising at least 24 species, was identified from 1034 specimens collected in only two cruises. The same number of species was identified from 3731 PL in one of the most comprehensive studies on cephalopod paralarvae performed in the western Atlantic Ocean that included

21 oceanographic cruises covering a vast area from north of the Greater Antilles to the Scotian Shelf (Vecchione et al., 2001). However, only seven species coincided in both the western Atlantic and the MBRS. These results indicate that the MBRS supports a paralarval community with a high species richness. A wider spatial and temporal monitoring of PL in this region could have revealed additional species. Our study suggests a greater species richness for the Caribbean than the maximum of 20 species of adult cephalopods from selected regions in this sea (Judkins et al., 2010).

Absence of a wide continental shelf on the MBRS accounted for the dominance of the oceanic families Enoploteuthidae, Onychoteuthidae and Ommastrephidae, also dominant in the paralarval assemblages of other Atlantic oceanic waters (Goldman, 1993; Haimovici et al., 2002; Diekmann et al., 2006).

Three species, *Abralia grimpei* (Voss, 1959), *Abralia redfieldi* and *Abralia veranyi* (Rüppell, 1844) in adult stage are known to occur in the tropical western Atlantic (Jereb & Roper, 2010). Adults of the last two species are found in the Florida Straits and in the north-eastern Gulf of Mexico, where *A. redfieldi* is the most common (Cairns, 1976; Passarella, 1990; Judkins et al., 2016). Paralarvae of these three species currently are not morphologically distinguishable. Nesis (1975) described *A. redfieldi* PL from the eastern Caribbean, where it is one of the most numerous species although it avoids the continental coasts. Unfortunately, his description lacks information on the chromatophore patterns that are important for the identification of this species. Otherwise, *Abralia veranyi* is the most abundant paralarvae found in east

Table 1. Cephalopod paralarvae (PL) collected in the Mesoamerican Barrier Reef System during March 2006 and January 2007

Taxa	2006			2007		
	N	Ab	%	N	Ab	%
Family Enoploteuthidae Pfeffer 1900	**296**	**4.2**	**49.1**	**263**	**4.1**	**61.0**
Abralia redfieldi Voss, 1955	189	2.7	31.3	231	3.6	53.6
Abraliopsis spp.	3	<0.1	0.5	3	<0.1	0.7
Enoploteuthis sp. 1	1	<0.1	0.2	19	0.3	4.4
Enoploteuthis sp. 2	25	0.4	4.1	6	<0.1	1.4
Enoploteuthis sp. 3	14	0.2	2.3	2	<0.1	0.5
Enoploteuthis spp.	64	0.9	10.6	2	<0.1	0.5
Family Onychoteuthidae Gray, 1847	**142**	**2.0**	**23.5**	**86**	**1.3**	**20.0**
Onychoteuthis banksii (Leach, 1817)	77	1.1	12.8	40	0.6	9.3
Onychoteuthis prolata Bolstad, 2008	9	0.1	1.5	2	<0.1	0.5
Onychoteuthis spp.	55	0.8	9.1	44	0.7	10.2
Onykia carriboea Lesueur, 1821	1	<0.1	0.2	0	0	0
Family Ommastrephidae Steenstrup 1857	**72**	**1.0**	**11.9**	**43**	**0.7**	**10.0**
Ornithoteuthis antillarum (Adam, 1957)	58	0.8	9.6	36	0.6	8.4
Ommastrephes bartramii (Lesueur 1821)	1	<0.1	0.2	0	0	0
Sthenoteuthis pteropus (Steenstrup, 1855)	1	<0.1	0.2	2	<0.1	0.5
Sthenoteuthis-Illex complex	12	0.2	2.0	5	<0.1	1.2
Family Cranchiidae Prosch, 1847	**10**	**0.1**	**1.7**	**10**	**0.2**	**2.3**
Bathothauma lyromma Chun, 1906	0	0	0	2	<0.1	0.5
Helicocranchia papillata (Voss, 1960)	0	0	0	1	<0.1	0.2
Helicocranchia pfefferi Massy 1907	1	<0.1	0.2	0	0	0
Helicocranchia spp.	1	<0.1	0.2	0	0	0
Liguriella podophthalma Issel, 1908	8	0.1	1.3	5	<0.1	1.2
Liocranchia reinhardti (Steenstrup 1856)	0	0	0	1	<0.1	0.2
Cranchiidae spp.	0	0	0	1	<0.1	0.2
Family Pyroteuthidae Pfeffer, 1912	**2**	**<0.1**	**0.3**	**6**	**<0.1**	**1.4**
Pterygioteuthis giardi Fischer, 1896	2	<0.1	0.3	2	<0.1	0.5
Pterygioteuthis spp.	0	0	0	4	<0.1	0.9
Family Ancistrocheiridae Pfeffer, 1912	**6**	**0.1**	**1.0**	**1**	**<0.1**	**0.2**
Ancistrocheirus lesueurii (d'Orbigny, 1842)	6	<0.1	1.0	1	<0.1	0.2
Family Thysanoteuthidae Keferstein, 1866	**3**	**<0.1**	**0.5**	**1**	**<0.1**	**0.2**
Thysanoteuthis rhombus Troschel, 1857	3	<0.1	0.5	1	<0.1	0.2
Family Lycoteuthidae Pfeffer, 1908	**32**	**0.5**	**5.3**	**1**	**<0.1**	**0.2**
Lycoteuthis lorigera (Steenstrup, 1875)	5	<0.1	0.8	0	0	0
Lycoteuthis springeri (Voss, 1956)	0	0	0	1	<0.1	0.2
Lycoteuthis spp.	26	0.4	4.3	0	0	0
Selenoteuthis scintillans Voss, 1959	1	<0.1	0.2	0	0	0
Family Chiroteuthidae Gray, 1849	**2**	**<0.1**	**0.3**	**0**	**0**	**0**
Chiroteuthis veranii (Ferussac, 1835)	2	<0.1	0.3	0	0	0
Family Loliginidae Lesueur, 1821	**0**	**0**	**0**	**1**	**<0.1**	**0.2**
Family Octopodidae (D' Orbigny 1939-1842)	**11**	**0.2**	**1.8**	**5**	**<0.1**	**1.2**
Amphioctopus burryi (Voss, 1950)	3	<0.1	0.5	0	0	0
Macrotritopus defilippi Vérany, 1851	3	<0.1	0.5	1	<0.1	0.2
Octopus insularis Leite & Haimovici, 2008	3	<0.1	0.5	0	0	0

Table 1. (*Continued.*)

	2006			2007		
Taxa	N	Ab	%	N	Ab	%
Octopus sp. 1	2	<0.1	0.3	3	<0.1	0.7
Octopus sp. 2	0	0	0	1	<0.1	0.2
Family Argonautidae Tryon, 1879	**19**	**0.3**	**3.2**	**0.0**	**0.0**	**0.0**
Argonauta argo Linnaeus, 1758	13	0.2	2.2	0	0	0
Argonauta hians Lightfoot, 1786	6	<0.1	1.0	0	0	0
Unidentified	8	0.1	1.3	14	0.2	3.2
Total	**603**	**8.6**	**100**	**431**	**6.7**	**100**

N, Total catch by numbers; Ab, total abundance expressed as PL 1000 m^{-3}; %, percentage of abundance. Bold numbers indicate total abundance by family.

Table 2. Partial COI-gene sequences of the three dominant taxa of cephalopod paralarvae from the Mesoamerican Barrier Reef System

Taxonomy ID	ML	Sample ID	BIN	GenBank accession number	Similarity %
Abralia redfieldi	2.7	MOCAR700-E02	AAJ4262	MT048494	99.5–99.8
A. redfieldi	3.3	MOCAR700-E03	AAJ4262	MT048490	
A. redfieldi	3.4	MOCAR700-C09	AAJ4262	MT048492	
Onychoteuthis banksii	5.7	MOCAR700-D09	ADC7276	MT048480	98.7–100
O. banksii	3.3	MOCAR700-D11	ADC7276	MT048489	
O. banksii	4.5	MOCAR700-F11	ADC7276	MT048481	
Ornithoteuthis antillarum	5.6	MOCAR700-A11	ACG7636	MT048485	98.2–100
O. antillarum	3.6	MOCAR700-A12	ACG7636	MT048495	
O. antillarum	4.0	MOCAR700-B01	ACG7636	MT048493	
O. antillarum	3.0	MOCAR700-D12	ACG7636	MT048488	
O. antillarum	2.9	MOCAR700-E01	ACG7636	MT048479	
O. antillarum	2.1	MOCAR700-E06	ACG7636	MT048491	
O. antillarum	3.5	MOCAR700-H02	ACG7636	MT048484	
O. antillarum	6.2	MOCAR700-H03	ACG7636	MT048483	
O. antillarum	2.7	MOCAR700-H04	ACG7636	MY048482	
O. antillarum	1.0	MOCAR700-H05	ACG7636	MT048498	
O. antillarum	1.1	MOCAR700-H06	ACG7636	MT048496	
O. antillarum	2.4	MOCAR700-H07	ACG7636	MT048486	
O. antillarum	2.3	MOCAR700-H08	ACG7636	MT048497	
Octopus insularis	3.6	MOCAR700-B08	ADI2098	MT048487	99.8
O. insularis	1.4	MOCAR700-B12	ADI2098	MT048499	
O. insularis	1.4	MOCAR700-C01	ADI2098	MT103932	

ID, identification; ML, mantle length (mm).

Florida (Adams, 1997; Erickson *et al.*, 2017). Paralarvae of *A.* cf. *veranyi* have been described by Vecchione *et al.* (2001) who considered it the most common species of the genus north of the Caribbean, associated with continental shelf and slope waters. However, these same authors mention that some of the specimens they refer to as *A.* cf. *veranyi* might include other *Abralia* species in the region. Information on the distribution of *A. grimpei* is scarce, being only reported for the West Indies, North Atlantic and from the northern Sargasso Sea (Tsuchiya, 2009). The COI analysis concluded that *A. redfieldi* is the only species in the genus found in the MBRS.

At least three species of the *Onychoteuthis* genus, *Onychoteuthis banksii*, *O. compacta* and *O. prolata* occur in the tropical western Atlantic (Bolstad, 2010). Descriptions of paralarvae of the latter two (Young & Harman, 1987; Sweeney *et al.*, 1992) allowed the identification of some of our specimens. A very abundant morphotype different from *O. compacta* and *O. prolata* lead us to identify them as *O. banksii*, even when the chromatophore pattern in this species is still undescribed. *Onychoteuthis banksii* was corroborated with the DNA barcoding with a similarity of 98.7–100%. Paralarvae of this species have been collected from February through August in the western
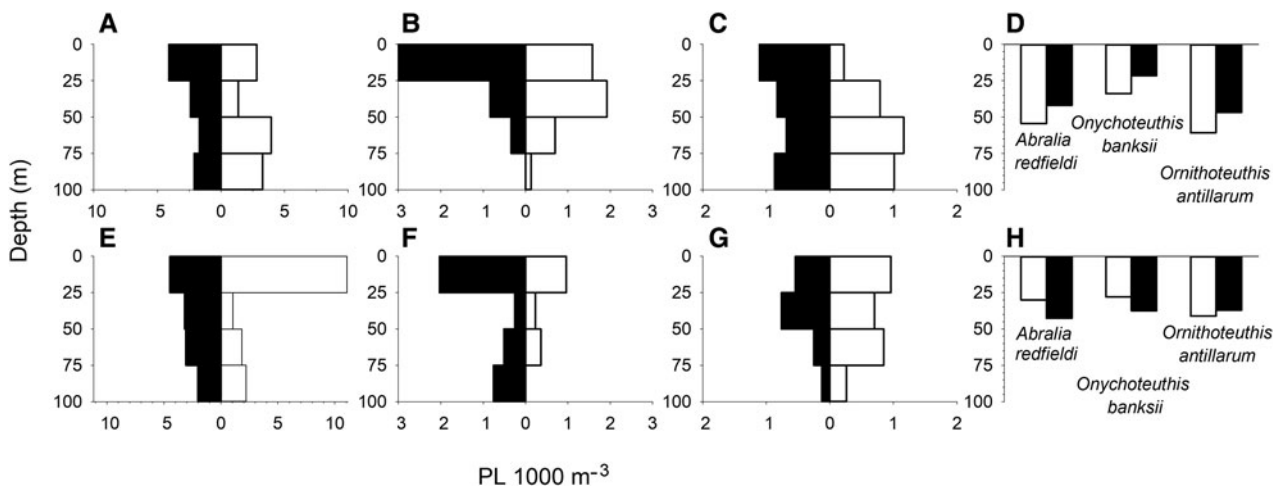
Fig. 6. Day (white) and night (black) paralarval abundance vertical distribution of dominant species in the Mesoamerican Barrier Reef System, station-aggregated for 2006 (A–D) and 2007 (E–H). (A, E) *Abralia redfieldi*; (B, F) *Onychoteuthis banksii*; and (C, G) *Ornithoteuthis antillarum*. (D, H) Abundance-weighted mean depths of these species, for both day and night samples.

North Atlantic (Vecchione *et al.*, 2001). In the MBRS higher abundance of this species in March 2006 compared with January 2007 may be related to the beginning of the reproductive season of the species as these are abundant paralarvae in the Caribbean (Nesis, 1975) and the adjacent Atlantic (Vecchione *et al.*, 2001). The absence of reliable descriptions of small paralarvae (≤3.0 mm ML) precluded a more detailed identification of *Onychoteuthis* species and 44% of them were left at genus level.

Two forms of ommastrephid PL, rynchoteuthion types 'A' and 'B', have been described from the North-west Atlantic, and *Ornithoteuthis antillarum* have been assigned to both in the literature (Roper & Lu, 1979; Goldman, 1993; Vecchione *et al.*, 2001). Rynchoteuthions from the Caribbean described by Nesis (1975) as *Sthenoteuthis pteropus* were in fact *O. antillarum* (Nesis, 1979). We identified *O. antillarum* by the presence of both ocular and visceral photophores and enlarged lateral proboscis suckers (Nesis, 1979; Sweeney *et al.*, 1992). Spawning peak in the Caribbean takes place in February and March (Nesis, 1975), and our PL abundances for this species were slightly higher in March than in January. Roper & Lu (1979) considered that their Rynchoteuthion Type 'B' belongs to *O. antillarum*. Thus, this species probably is not so rare in the western North Atlantic (Vecchione *et al.*, 2001). Other authors found that Type 'A' are the most abundant paralarvae off southern and eastern Florida, identifying this type solely as *O. antillarum* (Goldman, 1993) or together with *Ommastrephes bartramii* (Adams, 1997; Erickson *et al.*, 2017). The DNA barcoding revealed that the smallest paralarvae ≤2.0–3.0 mm ML of this family collected in the MBRS were also *O. antillarum*, suggesting that this species is the most abundant ommastrephid in the Caribbean. Paralarvae of other ommastrephid species, some with commercial potential in the wider Caribbean such as *Sthenoteuthis pteropus*, were particularly scarce in this study.

Our study reports the first three paralarvae of *Octopus insularis* found in the wild as they have only been described in captivity (Lenz *et al.*, 2015). Recent studies have increased its known distribution in the western tropical Atlantic, with a single adult reported in the MBRS at Isla Mujeres (Lima *et al.*, 2017). This octopus supports commercial fisheries in distant waters such as Veracruz reefs and central and northern Brazil (Sauer *et al.*, 2019), so pelagic paralarvae may interconnect different populations along this geographic range. Remarkably, no PL of *Octopus vulgaris* which supports a fishery downstream in the neighbouring Campeche Bank (Sauer *et al.*, 2019) was found.

In 2006 only *Abralia redfieldi* PL showed clear evidence of performing a diel vertical migration (DVM), while there was no evidence of DVM for *Onychoteuthis banksii* and *Ornithoteuthis antillarum*. For 2007 no clear evidence of DVM was shown for any species at all. In the eastern Atlantic, paralarval enoploteuthids did show vertical migrations while onychoteuthids did not (Diekmann *et al.*, 2006). On the contrary, Young & Harman (1987) reported significant differences between day–night catches of PL of two *Onychoteuthis* species in Hawaii, ranging mainly 3.0–5.9 mm ML. Juveniles of *Abralia* and *Onychoteuthis* are known to perform diel migrations in the Straits of Florida (Cairns, 1976; Roper & Young, 1975). In contrast *O. antillarum* PL occur mainly in the thermocline water layer, avoiding uppermost waters, and do not perform vertical migrations (Nesis, 1979; Arkhipkin *et al.*, 1998), as we found in the MBRS. Vertical distribution of *O. antillarum* recorded here in the MBRS, however, closely resembles that of ommastrephid Type 'A' off the Florida Keys (Goldman & McGowan, 1991) by night in 2007, but by day in 2006.

Vecchione *et al.* (2001) did not find 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. Vertical distribution patterns of squid paralarvae differ among squid taxa and at least in some cases DVM behaviour appears to develop in post-paralarval stages (Vecchione, 1987; Bower & Takagi, 2004; Shea & Vecchione, 2010). In the MBRS dominance of small PL sizes at which morphology, swimming and feeding abilities may not be fully developed could account for an absent or very limited DVM. Prevalence of small PL also could indicate reproductive activity during the winter.

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