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Cephalopod paralarvae (Cephalopoda: Mollusca) in the neritic environment of the northern Colombian Pacific

Manuela Davila-Arce[1], Arminda Mejía-Rebollo[2], Alan Giraldo[1]*

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Corresponding author
* E-mail: alan.giraldo@correounivalle.edu.co

1 Grupo de Investigación en Ecología Animal, Departamento de Biología, Universidad del Valle, 760042 Valle del Cauca, Colombia.
2 Laboratorio de Invertebrados Marinos, Centro de Investigaciones Biológicas del Noroeste, 23096 La Paz, Baja California Sur, Mexico.

Abstract. Knowledge of the ecological aspects of cephalopod paralarvae is essential to understand the composition and dynamics of their populations, as well as to identify spawning seasons and areas. In the northern Colombian Pacific (NCP), studies on this early life stage are scarce. The purpose of this study was to establish the taxonomic composition of paralarvae in the neritic environment of the NCP, quantify their abundance, and describe their spatio-temporal variation. A total of 315 zooplankton samples were collected through surface tows between January and November 2022 in 3 sectors. One hundred and two paralarvae were found in 16.5% of the samples and were classified into 4 families: Loliginidae, Octopodidae, Ommastrephidae, and Ancistrocheiridae. The presence of loliginid squid paralarvae and the Chango Octopus (*Octopus* cf. *mimus*) is reported for the first time in this region. The highest abundance values were recorded in March (>6 Pl·1,000 m^{-3}) and coincided with the upwelling period, which suggests synchrony between reproductive events and the increase in biological productivity that favored paralarval survival. The distribution of the most representative groups was influenced by the ecological behavior of each family and the geomorphological characteristics of each sector. Octopodidae predominated in the northern and central NCP, where rocky bottoms and a narrow continental shelf are present, whereas Loliginidae were found in the southern sector, where the shelf is wider and sandy beaches predominate. The presence of early stages of commercially important groups suggests the importance of the NCP as a reproductive area for these cephalopods and highlights the need to deepen research on their reproductive biology and ecology. These findings provide the basis for understanding patterns of temporal variation in paralarval abundance in neritic environments of the Eastern Tropical Pacific.

Key words: squids, octopuses, morphological identification, paralarvae, Eastern Tropical Pacific, zooplankton.

Introduction

Cephalopods are key species in marine ecosystems and an essential fishery resource worldwide (Boyle and Rodhouse 2005, FAO 2024). Although they exhibit direct development and a consistent body plan throughout their life cycle, most species undergo a planktonic phase after hatching. This stage, known as the paralarva, differs from the adult mainly in its ecology, since as part of the zooplankton it occupies a habitat different from that of its neritic, pelagic, or benthic adult congeners. In contrast, some species hatch as juveniles and develop in the same habitat as the adults (Vidal and Shea 2023).

Knowledge of the ecological aspects of paralarvae allows us to understand the composition and dynamics of cephalopod populations, as well as the factors that affect their abundance and distribution, and the establishment of spawning seasons and areas. This is essential to determine recruitment and fishery stock of commercially important species (Vidal et al. 2010, Zaragoza et al. 2015). In addition, paralarvae can serve as indicators of species richness in a given area, since they are often easier and more accessible to sample than adults (Aceves-Medina et al. 2017, De Silva-Dávila et al. 2018).

Despite their importance, paralarvae have been little studied compared with other zooplankton groups (Boletzky 2003). Sweeney et al. (1992) mentioned that there is a high

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degree of taxonomic uncertainty, which persists to the present due to morphological similarity among species and the lack of detailed descriptions for most of them (Zaragoza et al. 2015).

In the eastern Pacific, most research on this taxonomic group has been conducted in the Mexican Pacific, where the most representative families are Ommastrephidae, Pyroteuthidae, Argonautidae, Enoploteuthidae, and Loliginidae (De Silva-Dávila et al. 2018). The relationship of paralarval communities with oceanographic conditions has also been explored, as well as the effects of mesoscale phenomena and the El Niño–Southern Oscillation on their abundance and spatio-temporal variation (Granados-Amores et al. 2010; Aceves-Medina et al. 2017; García-Guillén et al. 2018; Ruvalcaba-Aroche et al. 2018, 2020). However, in the southern sector of the eastern Pacific, studies are scarce. In Peru, Yatsu et al. (1999) described for the first time the paralarvae of the Jumbo Squid (*Dosidicus gigas*) through artificial fertilization, providing relevant information on hatching time, as well as on the size and morphological characteristics of the early stage of the species. More recently, the families Ommastrephidae and Octopodidae, the genus *Argonauta*, and the species *Abraliopsis* sp. were identified as the most abundant groups in that region (Orosco and Ayón 2022), while in southern Chile, the genera with the highest incidence were *Octopus* and *Gonatus* (Vega et al. 2000). In the Colombian Pacific, knowledge of paralarvae is restricted to the work of Vargas and López (2020), in which 8 families were identified, among which Ommastrephidae was dominant. In addition, Vargas and López (2020) reported that the high temperatures of the area favor early hatching of paralarvae and highlighted the importance of the neritic zone as a spawning ground.

The northern Colombian Pacific (NCP), located in the northwestern region of Colombia, is situated in the low atmospheric pressure zone of the Eastern Tropical Pacific (ETP), where the migration of the Intertropical Convergence Zone (ITCZ) modulates seasonal changes in climate, hydrography, and circulation. Between January and April, the season of lower precipitation occurs, during which the northerly trade winds intensify, causing the displacement of the ITCZ to its southernmost position. This leads to the strengthening of upwelling processes in the Panama Bight, causing the influx of colder and saltier waters into the surface layer, which results in the development of a shallow thermocline (around 15 m). Conversely, during the rainy season (May–November), the influence of the southerly trade winds intensifies, causing the displacement of the ITCZ to its northernmost position. This generates an increase in precipitation and, with it, a reduction in surface salinity and the dominance of warm surface waters (26–28 °C), which leads to the interruption of the upwelling process and deepening of the thermocline (around 90 m) (Valencia and Giraldo 2009; Jerez-Guerrero et al. 2017; Velandia et al. 2019; Valencia et al. 2019, 2024).

Along the NCP coastline, the continental shelf is narrow (1–6 km; >80 m depth) and dominated by cliffs, bays, and enclosed beaches along the shoreline (Díaz et al. 2016). In contrast, in the southern zone, the continental shelf is wider and shallower (16–20 km; <50 m depth), with extensive sandy beaches and intertidal flats with mangrove areas inland, as well as large river mouths (Velandia et al. 2019). This heterogeneity of the zone allows for a diversity of biological groups, including paralarvae.

This study aimed to describe the taxonomic composition of cephalopod paralarvae in the neritic environment of the NCP and to evaluate spatial and temporal changes in their abundance. Considering the temporal variation in oceanographic conditions and the effect of processes that enhance local productivity in the study area, such as upwelling, the central hypothesis of this work was that the highest abundance of paralarvae would occur during the dry season, when the presence of upwelling waters in the Panama Bight increases productivity and food availability in the neritic environment. Additionally, it was hypothesized that, taking into account the geomorphological characteristics of the NCP, a higher abundance of taxonomic groups with coastal habitats, particularly octopuses and loliginid squids, would be recorded.

Materials and methods

Study Area

Three sampling sectors were established in the NCP: the first between Cabo Marzo and the Gulf of Cupica (6.2–6.8°N; 18 stations), the second in the Gulf of Tribugá (5.5–5.9°N; 18 stations), and the third to the south, encompassing the coastal zone of Bajo Baudó (4.7–5.2°N; 17 stations) (Fig. 1). The study region has a warm climate throughout the year (between 27 and 30 °C) and is characterized as one of the rainiest in the world, with high precipitation ranging from 5,030 to 7,700 mm·y^{-1} (Velandia and Díaz 2016).

Sampling and environmental data

Six bimonthly oceanographic campaigns were conducted between January and November 2022, following a sampling grid of 53 stations systematically located across the 3 study sectors (Fig. 1). At each station, surface zooplankton tows were performed and environmental variables were recorded at 1 m depth from a small boat with an outboard motor, such as sea surface temperature (SST [°C]), salinity (PSU), dissolved oxygen (DO [mg·L^{-1}]), and chlorophyll-*a* concentration (μg·L^{-1}), which was calculated according to the protocol of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) (CalCOFI 2011). Due to adverse weather conditions, sampling was not completed at all established stations during September (52 stations) and November (51 stations).

Zooplankton samples were collected with 2 conical nets (diameter: 71 cm; mesh opening: 200 μm and 500 μm) equipped with flowmeters (model 438 110, Hydro-Bios, Altenholz, Germany) to quantify the volume of filtered water.

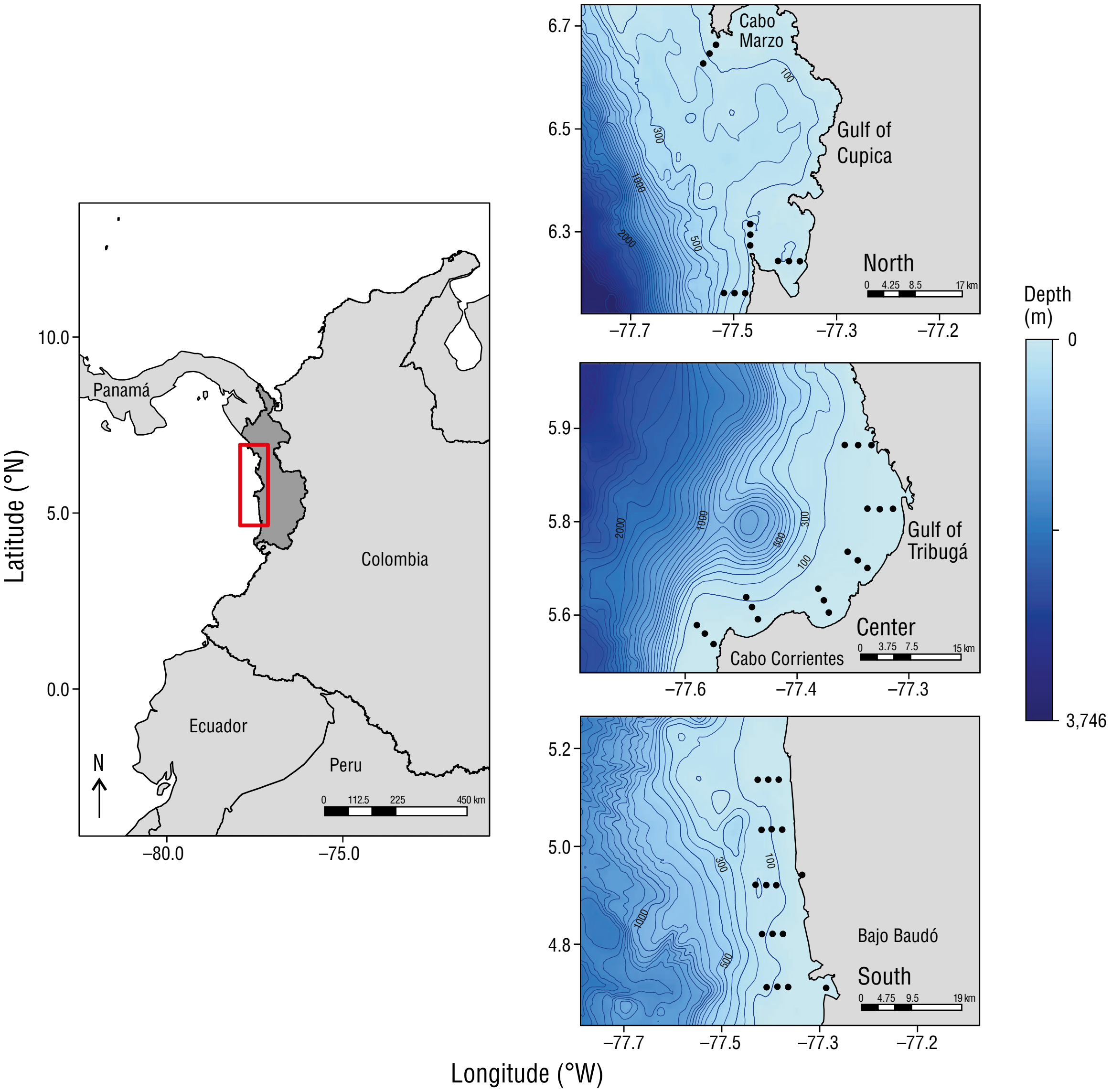

Figure 1. Geographic location of the northern Colombian Pacific (NCP) and sampling grid used for obtaining samples in each sector. Each station is located at a distance of 2 km..

The average tow duration was 4 min and 25 s. Samples were fixed onboard with 4% formalin neutralized with sodium borate. In the laboratory, all samples were examined to separate paralarvae using a stereomicroscope SMZ745T (Nikon, Tokyo, Japan), which were then preserved in 70% ethanol. Zooplankton biomass (mg·m^{-3}) was estimated as ash-free dry weight following the protocol of Giraldo et al. (2022) and considered as an indicator of biological productivity.

Taxonomic identification

The paralarvae found were classified to the most precise taxonomic level possible with the identification guides of Sweeney et al. (1992), Vecchione et al. (2001), Diekmann et al. (2002), Haimovici et al. (2002), and Zaragoza et al. (2015), and the criteria used by Granados-Amores (2008) and De Silva-Dávila (2013). Each specimen was measured for dorsal mantle length (ML, mm) using a stereomicroscope STEMI 2000-C (Carl Zeiss, Oberkochen, Germany) with a precision scale of 0.01 mm, coupled to an AxioCam ERc 5s camera (Carl Zeiss) and Zen Blue 3.7 software (Carl Zeiss). It should be noted that all characteristics were related to the size of each organism. The taxonomic identification characteristics reviewed included mantle shape (e.g., globose, oval, or bell-shaped), arm formula (Sweeney et al. 1992), eye type (pedunculated or fixed), number and arrangement of suckers on arms and tentacles, tentacular club differentiated or not differentiated, proboscis present or absent, photophores present or absent, shape of the cartilaginous funnel locking apparatus, chromatophore pattern, and siphon size. The chromatophore pattern and siphon size were determinant characteristics for identification and are described in detail in Table S1 (Supplementary Material).

In particular, for specimens of the family Octopodidae, a dissection was performed in the anterior region of the dorsal mantle surface in order to expose the surface of the digestive gland and describe the arrangement of chromatophores, referred to in this study as the chromatophore pattern of the digestive gland (DGCP). Taxonomic classification was carried out considering recent systematic revisions and the Integrated Taxonomic Information System (ITIS 2024). Individuals that were in poor condition or lacked sufficient morphological characteristics for identification were classified as "unidentified."

Data analysis

For the calculation of abundance, individuals recorded in both mouths of the bongo net (200 μm and 500 μm) were integrated so that each station was represented by a single sample. Subsequently, the samples were regrouped into units corresponding to all stations sampled within the same sector and month. Paralarval abundance in each unit was standardized to 1,000 m^3 considering the total volume of filtered water, obtaining comparable values among sectors and study periods.

Relative abundance of each taxonomic group identified and its frequency of occurrence (*FO*) were calculated in the sampling units grouped by sector and month. The *FO* was calculated as the percentage of stations with presence of a taxonomic group relative to the total number of stations sampled in each unit.

Additionally, a species accumulation curve was constructed as a function of the samples examined to estimate sampling effort, considering species richness as the number of taxonomic groups found and the ecological richness indicators Jackknife1, Chao2, and Bootstrap in the program EstimateS v. 9.1.0.

To evaluate significant differences in paralarval abundance among sectors and sampling months, data were transformed to natural logarithm [$\log(x + 1)$] in order to reduce variability and correct distribution bias of the dataset. Although the Shapiro–Wilk normality test indicated non-compliance with the assumption of normality of the transformed data ($W = 0.84$; $P = 0.007$), Levene's test detected homogeneity of variances in the abundance among months ($F = 0.6192$; $P = 0.6881$) and sectors ($F = 0.3369$; $P = 0.7193$). Since the analysis of variance (ANOVA) is robust to deviations from normality (Meier 2022) and considering the homoscedasticity of the data, a two-factor ANOVA without interaction was applied. In this model, residuals showed a normal distribution ($W = 0.95119$; $P = 0.444$), so a Tukey post hoc test was performed for multiple comparisons ($\alpha = 0.05$). These analyses were carried out in RStudio v. 4.5.1.

RESULTS

Environmental conditions in the study area

During the study period, SST remained warm across the 3 sectors of the NCP without a defined spatial variation pattern, with mean values ranging from 26.33 ± 0.22 °C in the southern sector (November) to 28.63 ± 0.33 °C in the northern sector (March) (Fig. 2a, Table S2). Salinity showed the highest values in the northern and central sectors, ranging between 24.10 ± 0.46 PSU and 31.06 ± 0.28 PSU.

In contrast, the southern sector exhibited greater variability and the lowest values, fluctuating between 17.27 ± 3.10 PSU (September) and 25.11 ± 6.04 PSU (January) (Fig. 2b, Table S2). DO varied between 2.82 ± 0.62 $\mu g \cdot L^{-1}$ and 4.78 ± 0.40 $\mu g \cdot L^{-1}$, with the lowest concentrations recorded in the southern sector during September and November (Fig. 2c, Table S2). Meanwhile, chlorophyll-*a* concentration was higher in the southern sector, ranging from 1.27 ± 0.75 $\mu g \cdot L^{-1}$ (May and July) to 2.90 ± 1.05 $\mu g \cdot L^{-1}$ (November), whereas lower concentrations were recorded in the central and northern sectors, ranging from 0.24 ± 0.08 $\mu g \cdot L^{-1}$ to 0.94 ± 0.33 $\mu g \cdot L^{-1}$, with minimum values in July and maximum in March (Fig. 2d, Table S2). Finally, zooplankton biomass ranged from 2.16 ± 1.22 $mg \cdot m^{-3}$ to 42.79 ± 22.82 $mg \cdot m^{-3}$, reaching the highest values in March across all 3 sectors (Fig. 2e, Table S2).

Taxonomic composition

A total of 102 cephalopod paralarvae were found in 52 of the 315 zooplankton samples examined (16.5%), with the sampling effort carried out being representative of the taxonomic groups recorded (Fig. S1). The paralarvae were classified into 2 orders, Teuthida and Octopoda, comprising 4 families (Table 1). In the family Loliginidae, 3 distinct morphotypes were identified; in Ommastrephidae, a species complex composed of *Sthenoteuthis oualaniensis* and *D. gigas* (S–D complex) was recognized; and in the families Ancistrocheiridae and Octopodidae, *Ancistrocheirus* cf. *lesueurii* and *Octopus* cf. *mimus* were identified, respectively. Thirteen percent of the paralarvae corresponded to unidentified individuals. Table S3 shows the detailed description of each taxonomic group.

Individuals of the family Loliginidae Lesueur, 1821 (Fig. 3) exhibited an ocular membrane or cornea covering both eyes (Fig. 3a–b) and a straight cartilaginous funnel locking apparatus. Important differences were distinguished in the morphology of the tentacular club (arrangement and number of suckers), clearly differentiating 3 morphotypes (I, II, and III; Fig. 3c–h). Morphotype I ($n = 18$; $ML = 1.2–2.0$ mm) was characterized by an undifferentiated tentacular club, equal in width to the stalk, with 2 rows of suckers (Fig. 3c–d). Morphotype II ($n = 8$; $ML = 1.9–2.9$ mm) was characterized by a differentiated tentacular club wider than the stalk; stalk without suckers; a proximal region with 2 rows of suckers, and a medial and distal region with suckers arranged in 3 to 4 rows (Fig. 3e–f). Morphotype III (*n* = 4; *ML* = 1.8–2.8 mm) exhibited a differentiated tentacular club, stalk without suckers, and club suckers arranged in 4 rows (Fig. 3g–h).

Individuals of the family Ancistrocheiridae Pfeffer, 1912 (*n* = 6; *ML* = 0.8–1.1 mm) (Fig. 4) were characterized by a bell-shaped mantle, straight cartilaginous funnel locking apparatus, presence of gelatinous tissue covering the head, eyes, and proximal portion of the arm crown (Fig. 4a–b), and pedunculated tentacular suckers arranged in 2 rows (Fig. 4c–d). No photophores were observed on the mantle, head, arms, or tentacles at the sizes examined. Considering that the family Ancistrocheiridae is monotypic, individuals that met these characteristics were identified as a form

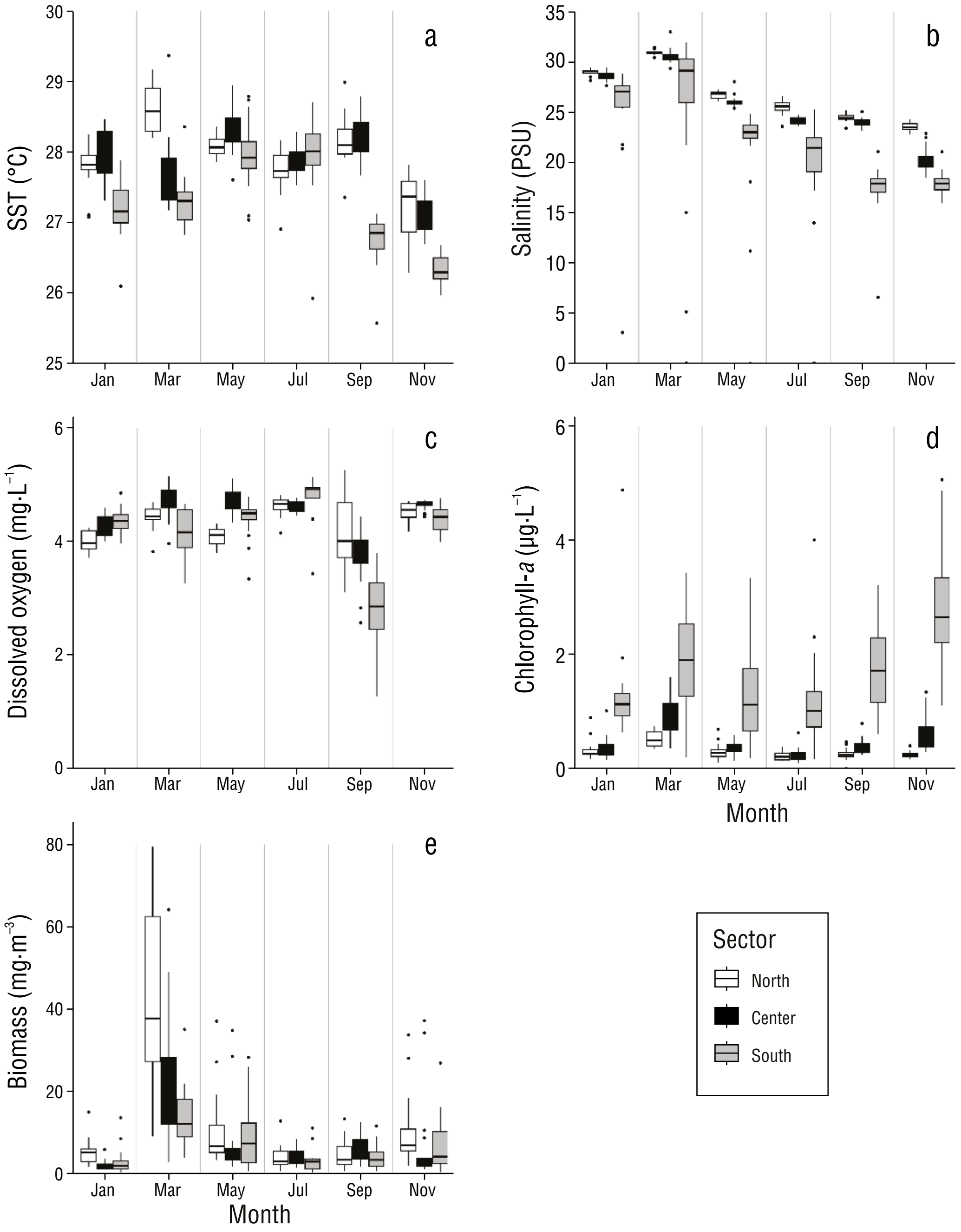

Figure 2. Spatio-temporal variation of environmental conditions in the neritic environment of the northern Colombian Pacific (NCP) between January and November 2022. Sea surface temperature (SST) (**a**), salinity (**b**), dissolved oxygen (**c**), chlorophyll-*a* (**d**), and zooplankton biomass (**e**).

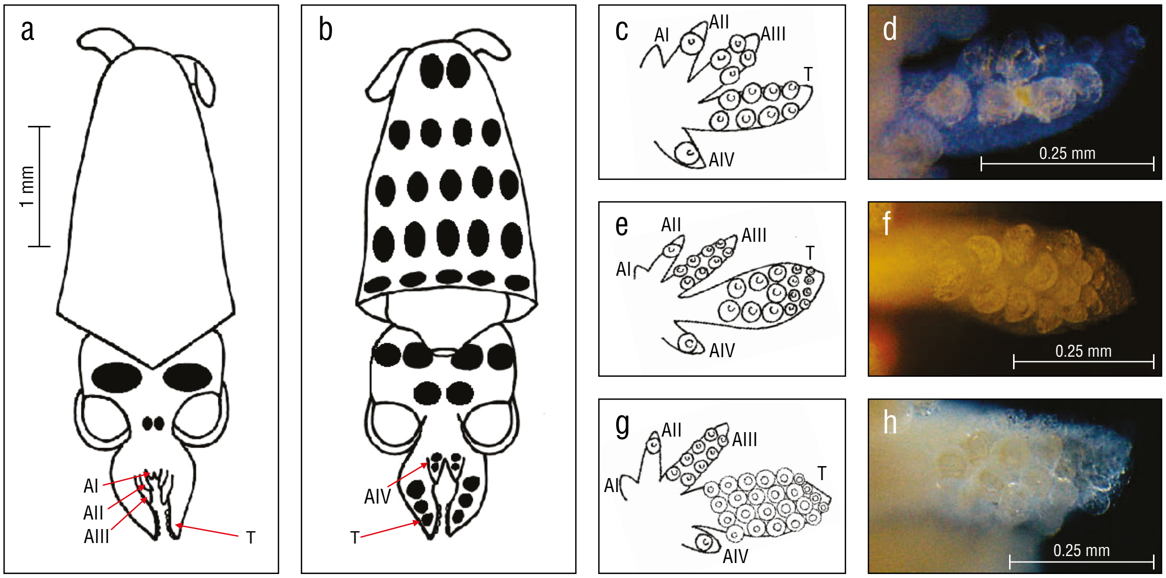

Figure 3. Generalized scheme of a paralarva of the family Loliginidae found in the neritic environment of the northern Colombian Pacific (NCP) between January and November 2022 (ML = 2.8 mm). Dorsal view (**a**); ventral view (**b**); arm crown in oral view of Morphotypes I (**c**), II (**e**), and III (**g**); and details of the tentacular club of Morphotypes I (**d**), II (**f**), and III (**h**) (AI: arm I; AII: arm II; AIII: arm III; AIV: arm IV; T: tentacle).

of the species *Ancistrocheirus lesueurii* D'Orbigny, 1842 (*Ancistrocheirus* cf. *lesueurii*).

Individuals of the family Ommastrephidae Steenstrup, 1857 ($n = 28$; ML = 0.8–1.93 mm) (Fig. 5) were characterized by a pair of posterior paddle-shaped fins (Fig. 5a–b), a funnel locking apparatus shaped like an inverted "T," and a proboscis with 8 equal-sized distal suckers (Fig. 5c–d), without intestinal or ocular photophores. Individuals presenting these characteristics were identified as the species complex *S. oualaniensis* and *D. gigas* (S–D complex).

Paralarvae of the family Octopodidae D'Orbigny, 1842 ($n = 25$; ML = 0.73–1.45 mm) (Fig. 6) were characterized by a muscular, oval mantle without fins (Fig. 6a–b) and subequal arms with suckers arranged in a single row (Fig. 6c–d), characteristic of the genus *Octopus* Cuvier, 1797 (Sweeney et al. 1992, De Silva-Dávila 2013). The number and arrangement of suckers, as well as the DGCP (6 to 8 chromatophores, Fig. 6e–f), coincided with the observations of Castro-Fuentes et al. (2002) for the species *O. mimus* Gould, 1852 (Table 2); therefore, the individuals were identified as a form of the species (*Octopus* cf. *mimus*).

Abundance, distribution, and temporal variation

Paralarval abundance in the neritic environment of the NCP between January and November 2022 ranged from 0.6 to 9.2 Pl·1,000 m^{-3}, with a median of 0.7 Pl·1,000 m^{-3}. In most sampling events, low abundance values were obtained (<2.45 Pl·1,000 m^{-3}), although punctual peaks were observed in certain months and sectors (Fig. 7a). The highest abundance values were observed in March across the 3 sectors of the study area (north: 8.5 Pl·1,000 m^{-3}; center: 6.1 Pl·1,000 m^{-3}; south: 9.2 Pl·1,000 m^{-3}), mainly due to the contribution of the family Loliginidae in the south (7.9 Pl·1,000 m^{-3}) and center (3.0 Pl·1,000 m^{-3}) and of Octopodidae in the north (4.0 Pl·1,000 m^{-3}). In contrast, January, September, and November showed considerably lower abundances in the 3 sectors (<1.5 Pl·1,000 m^{-3}) (Fig. 7, Table 3). The analysis of variance detected significant differences in abundance among sampling months ($F = 10.097$; $P = 0.001$), but not among sectors ($F = 1.549$; $P = 0.259$), with March being the source of variation in abundance, showing significantly higher values than the others (Tukey post hoc, $P < 0.05$) (Table S4).

The composition of paralarval families identified showed variations among sampling months and sectors in the NCP (Fig. 7b, Table 3). In January, Ommastrephidae dominated in the northern sector, while Loliginidae and Octopodidae predominated in the center. In March, all families were recorded, with greater representativeness of Octopodidae in the north and Loliginidae in the central and southern sectors. In May, Ommastrephidae was dominant in the north, while Octopodidae and Ancistrocheiridae were evenly distributed in the center. In July, Ommastrephidae showed the highest representativeness in both the north and south, while Octopodidae and Loliginidae dominated in the center. In September, only

Table 1. Systematic list of cephalopod paralarval taxa identified in the neritic environment of the northern Colombian Pacific (NCP) between January and November 2022.

Phylum Mollusca Linaeus, 1758
Class Cephalopoda Cuvier, 1797
Subclass Coleoidea Bather, 1888
Superorder Decabrachia Boettger, 1952
Order Teuthida Naef, 1916
Suborder Myopsina D'Orbigny, 1841
Family Loliginidae Lesueur, 1821
Morphotype I
Morphotype II
Morphotype III
Suborder Oegopsina D'Orbigny, 1845
Family Ancistrocheiridae Pfeffer, 1912
Ancistrocheirus cf. *lesueurii* D'Orbigny, 1842
Family Ommastrephidae Steenstrup, 1857
S-D complex (*Sthenoteuthis oualaniensis–Dosidicus gigas*)
Superorder Octobrachia Fioroni, 1981
Order Octopoda Leach, 1818
Suborder Incirrina Grimpe, 1916
Family Octopodidae D'Orbigny, 1842
Octopus cf. *mimus* Gould, 1852

Octopodidae was recorded in the north, and in November Ommastrephidae was recorded in the south.

Complementarily, the frequency of occurrence of families showed marked spatial and temporal variations (Fig. 8, Table 3). Loliginidae exhibited the highest frequencies in the central and southern sectors, particularly in March (Fig. 8a), while Octopodidae showed high occurrence in both the north and center, especially during March and July (Fig. 8b). Ommastrephidae also showed marked occurrence in the north, reaching the highest frequencies in May and July (Fig. 8c). For its part, Ancistrocheiridae was the least frequent family in all sectors and sampling months (Fig. 8d).

DISCUSSION

The surface oceanographic conditions of the neritic environment of the NCP showed spatial and temporal variability, probably associated both with the dynamics of local precipitation and with the oceanographic processes characteristic of Panama Bight. According to Velásquez-Restrepo and Poveda (2019) and Valencia et al. (2024), the frequency of sunny days increases and precipitation levels decrease (350 to 400 mm·month^{-1}) in the NCP during the months of January and April, and therefore river discharges also decrease, which causes an increase in temperature and low variability in sea surface salinity. In contrast, maximum precipitation (650 to 750 mm·month^{-1}) occurs between June and November, increasing continental input and leading to the decrease of both variables. It is worth highlighting the spatial variability observed among sectors; the southern sector showed the greatest variability in salinity, along with the highest concentrations of chlorophyll-*a*. This behavior could be associated with the constant input of nutrients of continental origin from the discharge of the Baudó River, the third largest river in the region, with an estimated mean annual flow of 1,021.5 m^3·s^{-1} (Velásquez-Restrepo and Poveda 2019). In addition, this sector receives the highest annual precipitation, with 6,544 mm·year^{-1}, compared to the central and northern sectors, which receive 5,086 mm·year^{-1} (Lobo-Guerrero 1993, Restrepo 2006, Valencia et al. 2024), which intensifies river runoff during the rainy season and would explain the higher chlorophyll-*a* values recorded in November for this sector.

Among the families identified, Ommastrephidae, Ancistrocheiridae, and Octopodidae had already been previously reported in the Colombian Pacific (Vargas and López 2020). This study expands the knowledge of cephalopod paralarvae in the region by recording, for the first time, groups typical of coastal waters, such as *Octopus* cf. *mimus* (Octopodidae) and the family Loliginidae (morphotypes I, II, and III).

Regarding the family Loliginidae, records exist in the area of adults of the species *Lolliguncula argus*, *L. diomedeae*, and *L. panamensis*, which are considered of fishery and ecological importance (Gómez et al. 2003, Jereb and Roper 2010, Díaz et

Table 2. Chromatophore patterns in paralarvae of *Octopus mimus* (Octopodidae). Mean and standard deviation of mantle length of individuals (ML), chromatophore pattern of the mantle on the dorsal surface (DMCP), chromatophore pattern of the mantle on the ventral surface (VMCP), chromatophore pattern of the head on the dorsal surface (DHCP), chromatophore pattern of the digestive gland (DGCP), and chromatophore pattern of the siphon (SCP).

	Octopus mimus Castro-Fuentes et al. (2002)	*Octopus* cf. *mimus* (This study)
ML	1.53 ± 0.08	1.14 ± 0.21
DMCP	3 to 7	7 to 10
VMCP	24 to 31	20 to 33
DHCP	10 (2 + 4 + 4)	10 (2 + 4 + 4)
DGCP	6 to 8	6 to 8
SCP	6 (4 + 2)	5 (3 + 2) and 6 (4 + 2)

al. 2014). Nevertheless, no official fishery records exist (De la Hoz et al. 2017). Of these 3 species, only the paralarvae of *L. diomedeae* (1.20–1.39 mm ML) have been described, which present 2 rows of suckers on the tentacles and arm III and a single sucker on arms II and IV (Fernández-Álvarez et al. 2017). This arrangement of suckers is compatible with Morphotype I described in this study (arm III and tentacle with 2 rows of suckers and a single sucker on arms II and IV), so it could presumably correspond to the same species. It should be clarified that to confirm or discard such a situation, the corresponding molecular analyses are necessary, which, due to the fixation of the samples in formalin, could not be carried out in the present study. On the other hand, due to the absence of morphological descriptions of the paralarvae of *L. argus* and *L. panamensis*, it was not possible to associate them with morphotypes (II or III) described. The detailed description of the tentacular club of Morphotypes I, II, and III described in this family (Loliginidae) provides valuable morphological information that will facilitate future comparisons and taxonomic studies, thus contributing to the advancement of knowledge of the paralarvae of this family in the region.

In the family Ancistrocheiridae, the presence of photophores on the mantle, head, arms, and tentacles is a diagnostic character from 5–7 mm ML, as well as hooks on the arms and tentacles from 9 mm ML (Sweeney et al. 1992, Granados-Amores 2008). Given the size of the paralarvae examined belonging to this family (<2 mm ML), it was not possible to observe these characteristics. De Silva-Dávila (2013) described paralarvae of this family at sizes similar to those observed in the present study (2 mm LM), and we confirmed the correspondence in the peduculated arm crown covered with gelatinous tissue, as well as in the formula of the arms at 1.1 mm LM (Table S3), which suggests its identification as *Ancistrocheirus* cf. *lesueurii*. Currently, this family is considered monospecific; however, the variation in the arrangement of photophores in paralarvae from different oceans and the lack of critical comparisons with adult specimens suggest the possible existence of more than one species (Sweeney et al. 1992, Arnold et al. 2025). To contribute to this point, it would be valuable to have larger specimens from different regions to carry out morphological and genetic comparisons and, thus, provide more solid taxonomic conclusions.

Regarding the family Ommastrephidae, in the Colombian Pacific, *D. gigas* and *S. oualaniensis* coexist spatially and their paralarvae are morphologically similar at sizes <4 mm ML, showing proboscis suckers of equal size; in both cases, the intestinal or ocular photophores that allow for species differentiation are not yet present, so they are grouped as a species complex (S-D Complex) (Ramos-Castillejos et al. 2010, De Silva-Dávila et al. 2015, Sánchez-Velasco et al. 2016). The paralarvae examined from this family measured between 0.8 and 1.93 mm ML and had these characteristics, which confirms their identification as S-D Complex. It is worth noting that the chromatophore pattern of the mantle and head in dorsal view in the S-D Complex paralarvae identified in this study is similar to that reported by Ramos-Castillejos et al. (2010) for *D. gigas* at 3.2 mm ML (Table S3). However, in their description, Ramos-Castillejos et al. (2010) include a morphometric analysis corroborated molecularly. In the present work, such analyses were not contemplated, which prevents making a

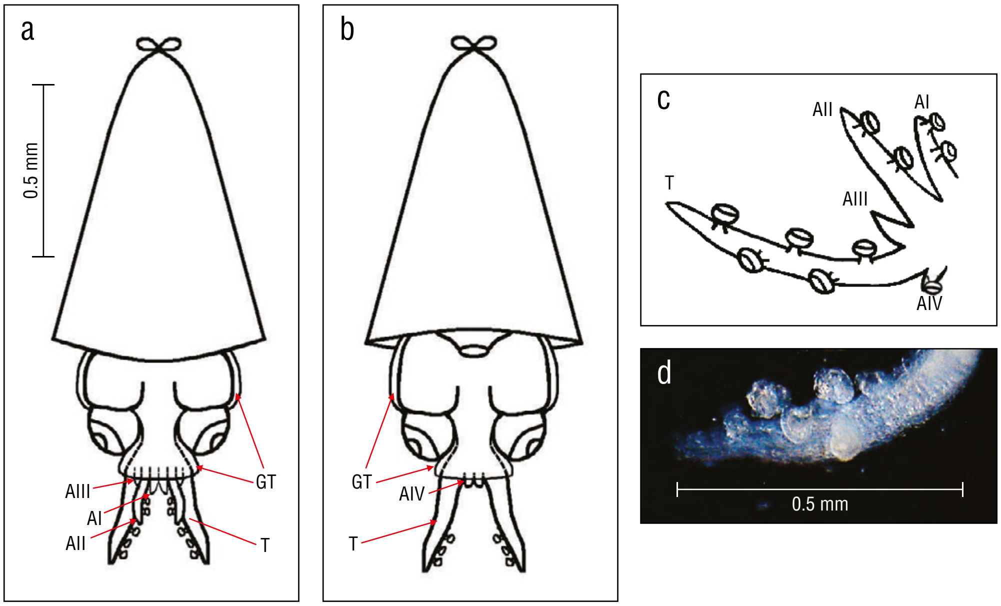

Figure 4. Scheme of a paralarva of the family Ancistrocheiridae: *Ancistrocheirus* cf. *lesueurii* found in the neritic environment of the northern Colombian Pacific (NCP) between January and November 2022 (*ML* = 1 mm). Dorsal view (**a**), ventral view (**b**), arm crown in oral view (**c**), and detail of the tentacular club (**d**) (AI: arm I; AII: arm II; AIII: arm III; AIV: arm IV; T: tentacle; GT: gelatinous tissue).

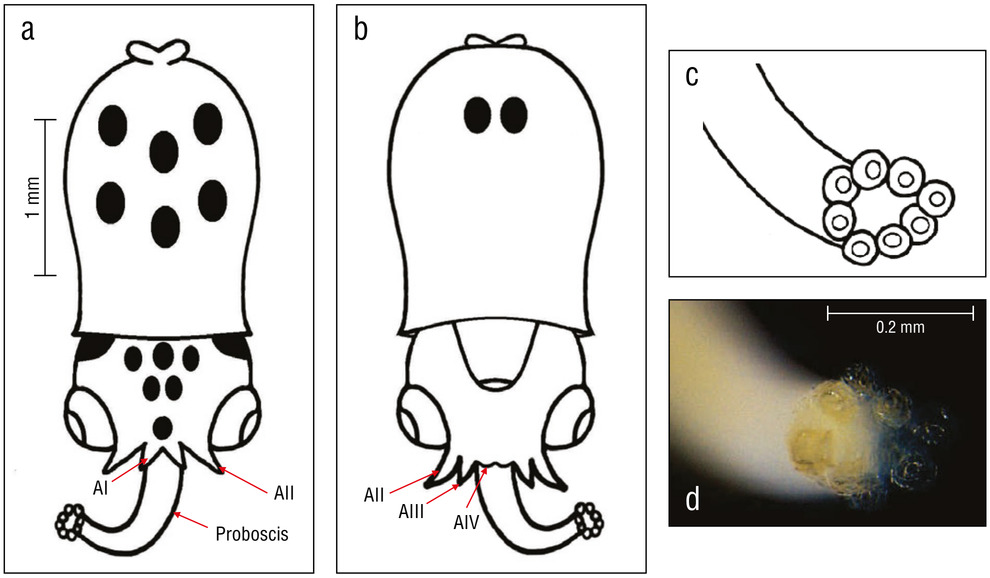

Figure 5. Scheme of a paralarva of the family Ommastrephidae (S–D complex: *Sthenoteuthis oualaniensis–Dosidicus gigas*) found in the neritic environment of the northern Colombian Pacific (NCP) between January and November 2022 (ML = 1.69 mm). Dorsal view (**a**), ventral view (**b**), and detail of the proboscis (**c** and **d**).

direct comparison between both studies. The molecular and morphometric approach could be a future line of research that contributes more specifically to the separation of the S–D complex and supports morphological observations, providing greater certainty in taxonomic identification.

The DGCP observed in the specimens of the family Octopodidae in this study corresponds to that described for *O. mimus* (Castro-Fuentes et al. 2002) and *O. hubbsorum* (Montero-Ruíz et al. 2023), which suggests a case of synonymy, as affirmed by Pliego-Cárdenas et al. (2014) based on mitochondrial molecular data. To take a position in this regard with the paralarvae of the Colombian Pacific, further studies are required that include morphological and molecular identification, as well as the description of habitat and distribution of both adults and paralarvae.

During the study period, the highest abundance of paralarvae coincided with the dry season of the NCP, in which the upwelling of subsurface waters from the Panama Bight promotes an increase in productivity and zooplankton biomass in the region (Valencia et al. 2019). In this period, high abundance values have already been reported for other zooplankton organisms in neritic environments of the Colombian Pacific due to the increase in food availability (Valencia and Giraldo 2009; Giraldo et al. 2014; Jerez-Guerrero et al. 2017; Valencia et al. 2019, 2024). This trend of temporal variation in paralarval abundance associated with upwelling episodes has already been documented in several regions of the eastern Pacific (Vega et al. 2000, De Silva-Dávila et al. 2015, Aceves-Medina et al. 2017, García-Guillén et al. 2018, Ruvalcaba-Aroche et al. 2018) and the Atlantic Ocean (González et al. 2005, Moreno et al. 2009, Vidal et al. 2010, Otero et al. 2016), and has been related to increased survival, growth, and recruitment of cephalopod populations (Araujo and Gasalla 2018).

In this study, the family Loliginidae was the most abundant and frequent in the central and southern sectors of the NCP, where the continental shelf is wider and shallower and presents an important freshwater influx. Loliginids are characterized by inhabiting shallow coastal zones of low salinity and by preferring soft or sandy bottoms for spawning (Rodrigues and Gasalla 2008, Zeidberg et al. 2012, Fernández-Álvarez et al. 2018). Therefore, their presence in these sectors reflects the ecological habits of the group. On the other hand, the absence of paralarvae of this family in the northern sector may be related to the geomorphological characteristics of this area, which presents a narrow and relatively deep continental shelf with rocky bottoms. In this regard, Martínez-Soler et al. (2021) justified the absence of this family in zones that do not offer a suitable habitat for the benthic reproduction characteristic of the group.

In addition to the above, members of this family are known to migrate for feeding or reproductive purposes, which appears to be part of their life strategy to ensure the development and growth of their paralarvae. This has been reported for several species in different regions; for example, *L. panamensis* migrates to areas with greater enrichment and food availability (Arizmendi-Rodríguez et al. 2012), and *L. diomedeae* and *L. argus* exhibit opportunistic reproductive migrations in response to variations in environmental conditions (León-Guzmán et al. 2020, Olvera et al. 2023). This trend could explain the greater abundance of Loliginidae paralarvae in March, a period that corresponds to the dry season and the highest zooplankton biomass values in the study area. This suggests a synchronicity between the reproductive events of this family and periods of high secondary productivity associated with upwelling conditions, which increase food availability and favor paralarvae survival. On the other hand, although the highest chlorophyll-*a* concentrations were recorded in the southern sector during the rainy season, indicating high primary productivity, the characteristic increase in precipitation and river inflow of this season generates low salinity and greater turbidity in the water (Valencia et al. 2024). This could reduce secondary productivity and, therefore, the availability of food for paralarvae, which would explain the absence of the Loliginidae family in September and November.

On their part, the family Octopodidae is characterized by having different lifestyles. Most species are benthic and inhabit rocky and shallow areas. Within this group, some exhibit a planktonic free-swimming phase after hatching, such as paralarvae, while others hatch as more developed benthic juveniles (Jereb et al. 2016). These ecological preferences coincide with the geomorphological characteristics of the northern and central sectors of the study area, which present a narrow continental shelf with coral and rocky ecosystems dominating the subtidal and coastal landscape (Díaz et al. 2016). In this investigation, paralarvae of this family were present in almost all sampling months, except November, which coincides with the reproductive biology of the group. It has been documented that populations of *O. mimus* and *Octopus hubbsorum* spawn throughout the year, with defined peaks that vary among regions. For example, in the Gulf of California, these peaks occur in September and December (Pliego-Cárdenas et al. 2011); in the central Mexican Pacific, in June (López-Uriarte and Ríos-Jara 2009); and in the southern Mexican Pacific, between March–June and October–November (Alejo-Plata et al. 2009, Alejo-Plata and Gómez 2015). In addition, it has been documented that variation in the reproductive biology of *O. hubbsorum* depends on the environmental conditions of each region, with temperature being the most important factor (Alejo-Plata and Gómez 2015, Montero-Ruíz et al. 2023). Therefore, the high occurrence of this family could be related to the warm waters characteristic of the NCP and the low variability of SST throughout the study period (26–28 °C). In this sense, the higher abundance observed in March could be associated with the increase in food availability characteristic of this period, which would favor optimal conditions for paralarval development.

Paralarvae of the family Ommastrephidae (S–D complex) are considered the most abundant in surface-type tows (Staaf et al. 2013). Nevertheless, in this study their abundance and frequency of occurrence were lower than those recorded for Loliginidae and Octopodidae in most sectors and months of sampling. This finding contrasts with what has been previously reported in the Colombian Pacific (Vargas and López 2020) and the Mexican Pacific (Granados-Amores et al. 2010, García-Guillén et al. 2018), where this family has been the most representative group. This difference could be attributed to the presence of taxa with greater affinity to coastal environments, such as loliginid squids and octopuses, which were mainly highlighted in the southern and northern sectors, respectively. Ommastrephidae may have a lower probability of being captured in coastal waters due to their pelagic behavior. The recurrent presence of paralarvae of the S–D

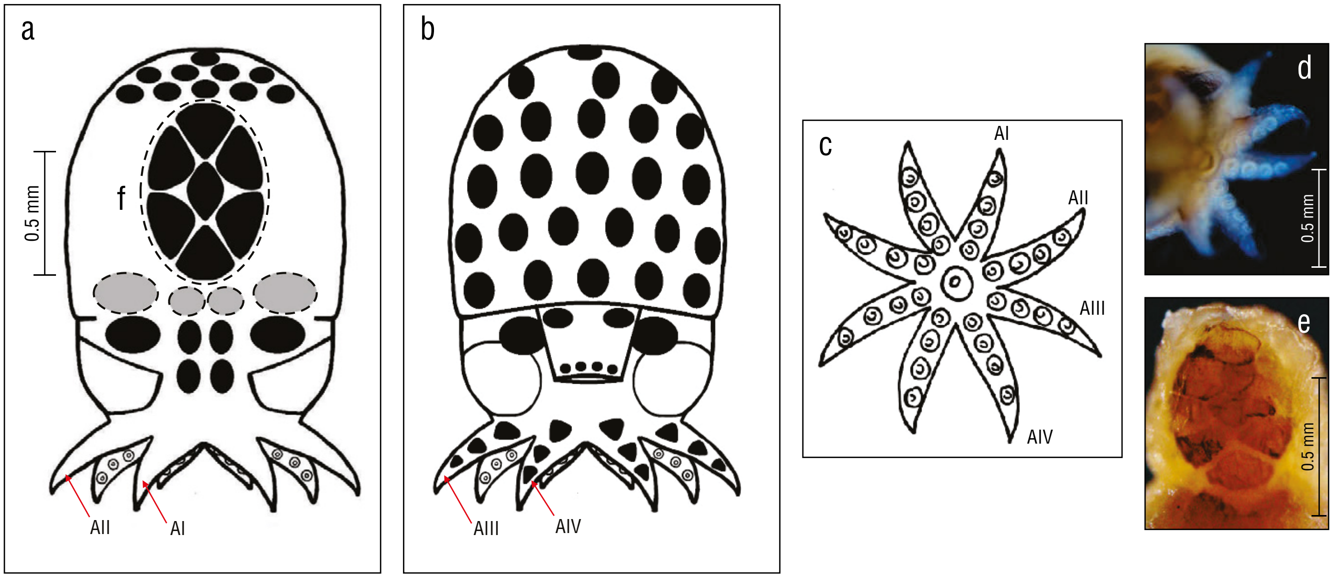

Figure 6. Scheme of a paralarva of the family Octopodidae (*Octopus* cf. *mimus*) found in the neritic environment of the northern Colombian Pacific (NCP) between January and November 2022 (*ML* = 1.3 mm). Dorsal view (**a**), ventral view (**b**), arm crown in oral view (**c** and **d**), and digestive gland with chromatophore pattern (**e** and **f**).

Table 3. Abundance and frequency of occurrence (*FO*) of cephalopod paralarval families (Pl) identified between January and November 2022 in the neritic environment of the northern Colombian Pacific (NCP) (N: north; C: center; S: south).

		Abundance (Pl·1,000 m^{-3}) | *FO* (%)			
Month	Sector	Loliginidae	Ommastrephidae	Ancistrocheiridae	Octopodidae
January	N	0.0	0.5 | 5.6	0.0	0.0
	C	0.5 | 11.1	0.3 | 5.6	0.0	0.5 | 11.1
	S	0.0	0.0	0.0	0.0
March	N	0.4 | 5.6	1.8 | 5.6	0.4 | 5.6	4.0 | 22.2
	C	3.0 | 27.8	0.0	0.4 | 5.6	1.1 | 16.7
	S	7.9 | 41.2	0.0	1.3 | 11.8	0.0
May	N	0.0	1.4 | 16.7	0.0	0.7 | 11.1
	C	0.0	0.0	0.3 | 5.6	0.3 | 5.6
	S	0.0	0.0	0.0	0.0
July	N	0.0	3.1 | 22.2	0.0	1.1 | 22.2
	C	0.4 | 5.6	0.0	0.0	0.4 | 5.6
	S	0.0	1.1 | 11.8	0.0	0.0
September	N	0.6 | 5.6	0.0	0.0	0.0
	C	0.0	0.0	0.0	0.0
	S	0.0	0.0	0.0	0.0
November	N	0.0	0.0	0.0	0.0
	C	0.0	0.0	0.0	0.0
	S	0.0	0.5 | 6.7	0.0	0.0

complex in most sampling months coincides with what has been reported for adults of *D. gigas* in the Colombian Pacific, which exhibit continuous reproductive activity throughout the year (Córdoba-Rojas et al. 2024). Furthermore, the increase in paralarval abundance observed in March could be related to the period of greater gonadal maturity recorded in the first months of the year by the same authors. Although in this study the direct effect of environmental variables was not evaluated nor mesoscale structures analyzed in relation to their abundance or distribution, previous studies have shown that paralarvae of the S–D complex are associated with the presence of anticyclonic eddies and convergence zones (Sánchez-Velasco et al. 2016, Ruvalcaba-Aroche et al. 2020). These structures appear to influence the distribution and aggregation of paralarvae, as they provide a favorable habitat for their retention, survival, and initial development (Ruvalcaba-Aroche et al. 2020). Considering that *D. gigas* is the main squid species captured globally (FAO 2024) and that in the Colombian Pacific it has gained relevance as a potential fishery resource for artisanal fishing (Díaz et al. 2014, Villanueva and Flores-Nava 2019, Córdoba et al. 2024), it is fundamental to continue studies that allow monitoring spatial and temporal variation of paralarvae in the study area in order to deepen knowledge of the ecology and reproductive biology of adults. Considering its greater abundance in surface tows, this sampling method could represent a low-cost and high-efficiency tool for monitoring its early stages in the Colombian Pacific, as suggested by García-Guillén et al. (2018) in their study of the Mexican Pacific.

The low representativeness and frequency of the family Ancistrocheiridae (*Ancistrocheirus* cf. *lesueurii*) could be related to its oceanic habitat, which reduces the probability of finding it in neritic environments. This coincides with what has been reported in the Colombian Pacific (Vargas and López 2020) and the Mexican Pacific (De Silva-Dávila et al. 2015), where Ancistrocheiridae represented less than 1% of the total taxa. Being a group of low abundance worldwide, its biology and ecology are poorly known, highlighting the importance of its paralarvae as a way to increase knowledge of its reproductive biology in the study regions.

Most paralarvae in this study had sizes smaller than 2 mm ML, which indicates recent spawning (Sweeney et al. 1992). These sizes coincide with what was found by Vargas and López (2020) in the Colombian Pacific, who mention that spawning and hatching are more frequent in the neritic zone. These sizes could also be due to the type of tow used for zooplankton collection, since as paralarvae grow they may occupy adult habitats. Therefore, an alternative for future research could be to complement surface tows with oblique tows, since the latter are usually more effective in providing a more complete view

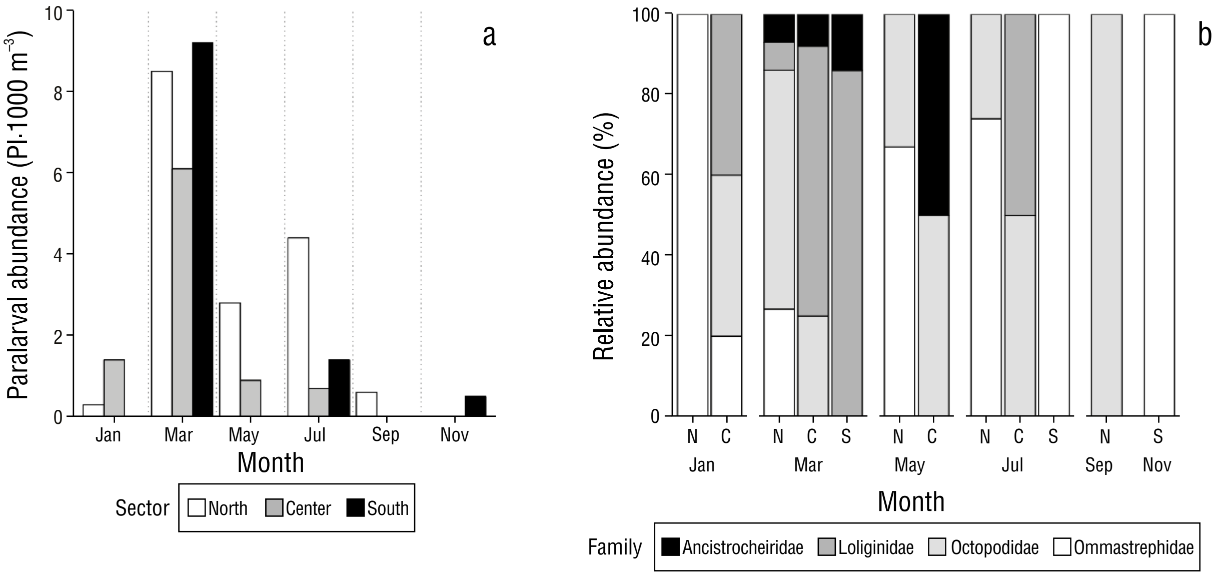

Figure 7. Spatio-temporal variation of cephalopod paralarval abundance found between January and November 2022 in the neritic environment of the northern Colombian Pacific (NCP). Paralarval abundance (Pl·1,000 m^{-3}); dotted lines represent separation of sampling months (**a**). Relative abundance of families recorded (N: north; C: center; S: south) (**b**).

of the paralarval community, as they capture more developed individuals, as well as greater diversity and species richness (De Silva-Dávila et al. 2015, García-Guillén et al. 2018). On the other hand, it is important to mention that the small sizes of the individuals found made paralarval identification difficult, since key taxonomic structures are not developed until larger sizes in many taxa (Camarillo-Coop 2006, Zaragoza et al. 2015). In addition, the lack of information on the reproductive biology and ecology of cephalopods in the Colombian Pacific, the high plasticity of the group, and the lack of morphological descriptions of paralarvae aggravate this situation, as they increase uncertainty in identification (Guarneros-Narváez et al. 2022). Therefore, to complement biological information on this important taxonomic group, it is necessary to implement molecular and genetic tools to better understand community structure, as has been done in the Gulf of Mexico (Guarneros-Narváez et al. 2022).

CONCLUSIONS

The taxonomic composition and the spatio-temporal variation patterns of paralarvae in the neritic environment of the NCP during 2022 were consistent with expectations based on adults reported in the region and in other areas of the Eastern Pacific. In this study, paralarval species richness in the NCP increased with the first record of the family Loliginidae, represented by 3 clearly differentiated morphotypes (Morphotype I, Morphotype II, and Morphotype III), and the first record of *Octopus* cf. *mimus*. It was demonstrated that the ecological behavior of each group, the hydrology, and the geomorphological characteristics of the study area influenced the taxonomic composition and distribution of the groups. In addition, it was confirmed that the highest abundance of paralarvae occurred during the upwelling season, evidencing synchrony between adult reproductive events and the conditions that favor paralarval development. It was also shown that the presence of Octopodidae and Loliginidae may be related to the availability of suitable habitats for their reproduction and the development of early stages. Therefore, the variety of ecosystems in the NCP constitutes a crucial and relevant factor for the conservation of these groups, for which biological and ecological knowledge is still limited.

The presence of paralarvae from groups considered of commercial interest, such as Loliginidae, Ommastrephidae, and Octopodidae, suggests the existence of active populations in the NCP that could become relevant for artisanal fishing activities. These findings highlight the importance of increasing knowledge of their reproductive biology and ecology in order to have the technical information necessary to propose conservation strategies and appropriate management of these resources. The limitations in the morphological identification of paralarvae reflect the need to complement it with genetic studies to achieve greater certainty in taxonomic identification. This work lays the foundation for understanding patterns of variation in paralarval abundance both in the neritic environment of the NCP and in the ETP and serves as a tool for future research aimed at increasing knowledge of cephalopods in the region.

English translation by the authors.

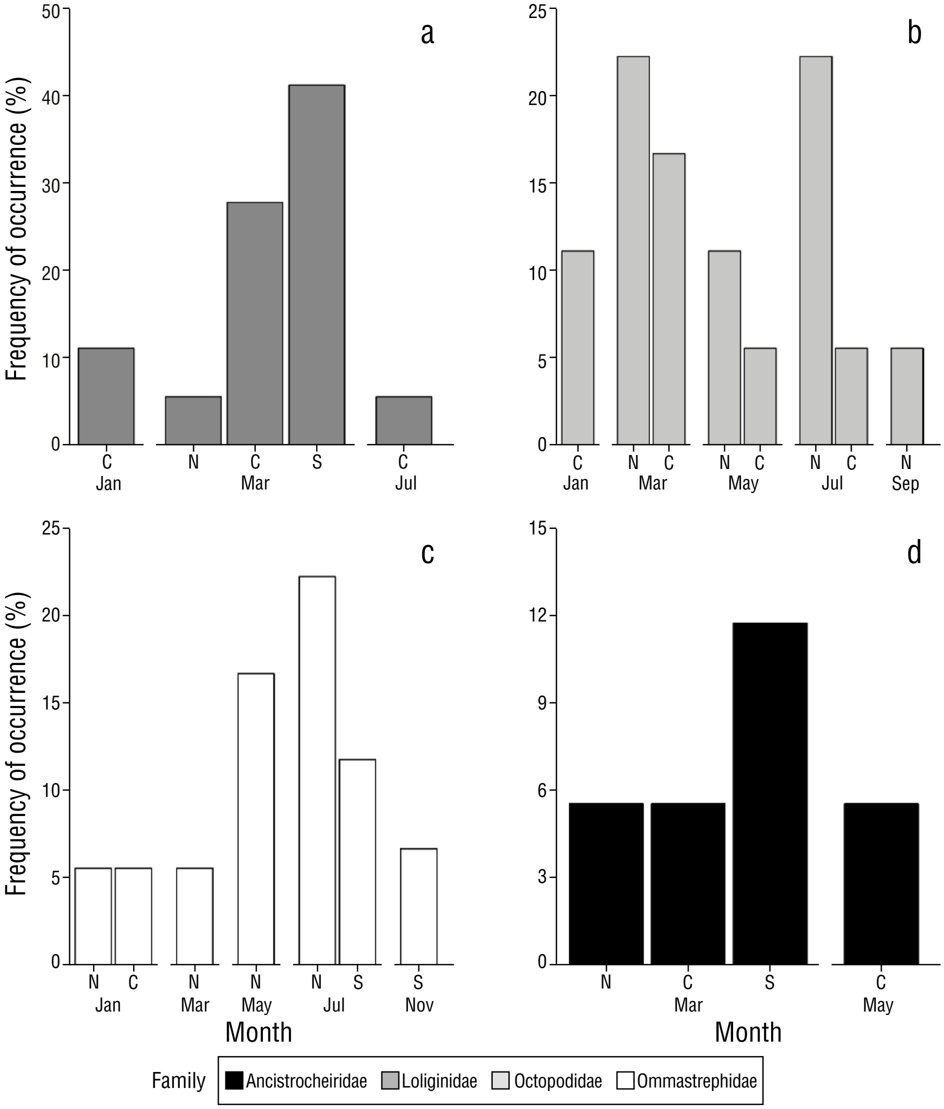

Figure 8. Spatio-temporal variation of frequency of occurrence (*FO*) of cephalopod paralarval families found between January and November 2022 in the neritic environment of the northern Colombian Pacific (NCP) (N: north; C: center; S: south). Loliginidae (**a**), Octopodidae (**b**), Ommastrephidae (**c**), and Ancistrocheiridae (**d**).

DECLARATIONS

Supplementary Material

Supplementary material for this study can be downloaded from: https://cienciasmarinas.com.mx/index.php/cmarinas/article/view/3538/420421262.

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Conflict of interest

The authors of this manuscript declare that we have no conflicts of interest.

Author contributions

Conceptualization: MD, AG; Data curation: MD; Formal analysis: MD; Funding acquisition: AG; Investigation: MD, AG; Methodology: MD, AG, AMR; Resources: AG, MD; Supervision: AMR, AG; Validation: AMR, AG; Visualization: MD; Writing—original draft: MD; Writing—review & editing: MD, AMR, AG.

Data availability

The data for this study are available from the corresponding author upon prior request.

Ethical approvals and permits for studies involving animals

The collection of zooplankton samples conducted for this work falls within the permit granted for the Biology academic program of Universidad del Valle, described in Resolution 1070 of August 28, 2015, issued by the National Authority of Environmental Licenses, which authorizes the collection and mobilization of specimens of wild biodiversity species within national territory, exclusively for the execution of non-commercial scientific research projects.

Use of AI tools

The authors did not use any AI tools in this work.

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