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research paper

Cephalopod paralarvae in a tropical Brazilian basin: distribution throughout oceanographic features and water masses

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ABSTRACT.—The composition and distribution of cephalopod paralarvae were investigated in the Campos Basin, a tropical area on the southeastern Brazilian continental margin with extensive oil exploration. Zooplankton hauls with a multimesh net system were conducted during two seasonal oceanographic cruises in 2009 along eight isobaths (25–3000 m) and vertical sampling in five water mass cores (1–2300 m depth). A total of 825 paralarvae belonging to 11 families and at least 16 genera were captured. The majority had a dorsal mantle length of less than 2.60 mm, with a mean of 1.50 mm. The rainy summer showed higher total densities and number of families compared to the drier winter. Most paralarvae were collected at Surface Water (1 m depth), only four at South Atlantic Central Water (250 m), and two at Antarctic Intermediate Water (800 m). Enoploteuthidae and Ommastrephidae were the most abundant families and were positively associated with temperature, with higher densities during the rainy summer. Loliginidae were collected exclusively in the neritic zone. In the oceanic zone, Cranchiidae, Onychoteuthidae, Octopoteuthidae, and Tremoctopodidae were collected at 1 m depth, and Ancistrocheiridae and Thysanoteuthidae at 250 m depth. Density peaks of paralarvae occurred during the summer along the continental shelf break and slope, an area known for frequent upwelling driven by cyclonic meanders of the Brazil Current.

Cephalopods are important components of all marine ecosystems and both young and adults connect many marine trophic webs (Boyle and Rodhouse 2005). In addition, these mollusks are of great importance to fisheries worldwide (Arkhipkin et al. 2015, Sauer et al. 2021). Squids and octopuses have life cycles with direct development (i.e., absence of both metamorphosis and true larva) and many species produce planktonic hatchlings that are referred to as “paralarva” to distinguish them from adults in ecological and morphological terms (Young and Harman 1988, Vidal and Shea 2023).

Understanding how the cephalopod paralarvae are related to plankton production and oceanographic processes is important for better knowledge about cephalopod biodiversity and zooplanktonic community dynamics. The taxonomic composition, abundance, and distribution of cephalopod paralarvae are associated with different oceanographic features, such as the pycnocline (Röpke et al. 1993), upwellings (González et al. 2005, Otero et al. 2009, 2016, Vidal et al. 2010, Roura et al. 2016, 2019, García-Cordova et al. 2023), marine currents (Rodhouse et al. 1992, Vecchione et al. 2001), river discharge (Sluis et al. 2021), cyclonic and anticyclonic eddies (Sánchez-Velasco et al. 2016, Aceves-Medina et al. 2017, Taite et al. 2020), and seamounts and oceanic islands (Haimovici et al. 2002, Diekmann and Piatkowski 2004).

In Brazil, the cephalopod fauna is relatively well known (Haimovici and Andriguetto 1986, Haimovici and Perez 1991, Haimovici et al. 2007, 2009, Vaske and Costa 2011, Alvarenga et al. 2024) and several oceanographic surveys have reported the taxonomic composition and distribution of paralarvae (Haimovici et al. 1995, 2002, Santos and Haimovici 2007, Vidal et al. 2010, Araújo and Gasalla 2019, Ortiz et al. 2024). However, few studies have formally associated cephalopod paralarvae with oceanographic features and measured environmental variables in Brazilian waters (Vidal et al. 2010, Araújo and Gasalla 2018, Araújo and Gasalla 2022, Ortiz et al. 2024).

The Campos Marine Sedimentary Basin (CMSB), located in the southeastern Brazilian continental margin, is a tropical and oligotrophic environment (Suzuki et al. 2017). The higher primary productivity is associated with river discharge points and upwelling induced by wind or cyclonic meanders/eddies of the Brazil Current (Castelão et al. 2004, Pedrosa et al. 2006, Rezende et al. 2006, Aguiar et al. 2014). The Campos Basin has been extensively explored for oil (Falcão et al. 2017). The risk of oil spills represents potential toxicity to marine biota (Brussaard et al. 2016) and therefore to the planktonic community (Hook et al. 2022). For cephalopods, the toxicity levels of crude oil have been quantified for paralarvae (Long and Holdway 2002) and bioaccumulation of polycyclic aromatic hydrocarbons has been reported in adults even years after oil spills (Romero et al. 2020). Therefore, a multidisciplinary characterization of the pelagic environment and a biodiversity framework is desirable to monitor possible changes during oil exploration (Falcão et al. 2017).

At the request of the Brazilian Institute of Environment and Renewable Natural Resources (IBAMA), a series of baseline studies on the hydrography and biodiversity in the Campos Basin were carried out (Falcão et al. 2017). Among them, zooplankton sampling during two seasonal cruises provided the opportunity to collect cephalopod paralarvae at different depths and water masses (Bonecker et al. 2014, Moreira et al. 2017). The aim of this study was to describe the cephalopod paralarvae assemblage and relate its distribution pattern to oceanographic features and water masses in the Campos Basin.

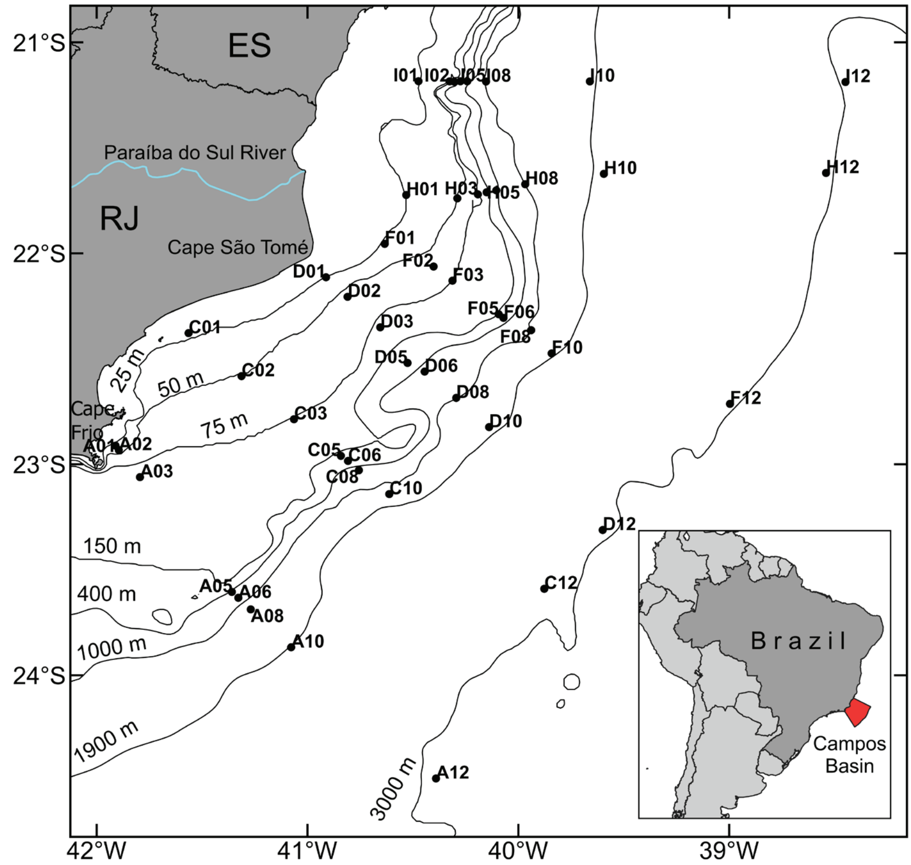

Figure 1. Map of Campos Basin, Brazil. Zooplankton sample design by Habitats Project, with 48 oceanographic stations. Eight sampling isobaths were selected: 25, 50, 75, and 150 m in the neritic zone/continental shelf (numbered as 01, 02, 03, and 05, respectively), and 400, 1000, 1900, and 3000 m in the oceanic zone/continental slope and São Paulo Plateau (numbered as 06, 08, 10, and 12, respectively). Each isobath crosses six transects perpendicular to the coast in the South–North direction (A, C, D, F, H, and I). ES = Espírito Santo state, RJ = Rio de Janeiro state.

Materials and Methods

Study Area.—The CMSB corresponds to an area of 115,800 km^2 along the Brazilian continental margin, from the southern coast of Espírito Santo state (20.5°S) to the northern coast of Rio de Janeiro state (23°S; Fig. 1). The neritic zone covers the continental shelf and the oceanic zone covers the continental slope and the São Paulo Plateau. The shelf break is located 100 km from the coast and at a depth of 110 m, on average. CMSB extends to a maximum depth of 3600 m in the oceanic zone (Viana et al. 1998, Castro Filho et al. 2015).

In the neritic zone, the Coastal Water (CW) occupies the inner continental shelf and has low salinities due to fluvial discharge, mainly the Paraíba do Sul River (20.5°S; Castro-Filho et al. 2015). The warm salty Tropical Water (TW) and the colder nutrient-rich South Atlantic Central Water (SACW) occupy the outer continental shelf and the oceanic zone, both forming the Brazil Current, which flows southward

Table 1. Number and distribution of zooplankton hauls according to the isobaths and water mass cores. Isobaths: 25, 50, 75, 150 m on the neritic zone/continental shelf; and 400, 1000, 1900, 3000 m on the oceanic zone/continental slope and São Paulo Plateau. Water masses cores and their depth: SW = Surface Water, SACW = South Atlantic Central Water, AIW = Antarctic Intermediate Water, UCDW = Upper Circumpolar Deep Water, and NADW = North Atlantic Deep Water. SW can correspond to Tropical Water or Coastal Water. Modified from Bonecker et al. (2014) and Moreira et al. (2017).

Water mass cores and depth	Zones and isobaths depth							
	Neretic zone					Oceanic zone		
	25 m	50 m	75 m	150 m	400 m	1,000 m	1,900 m	3,000 m
SW (1 m)	12	12	12	12	12	12	12	10
SACW (250 m)	- - -	- - -	- - -	- - -	12	12	12	10
AIW (800 m)	- - -	- - -	- - -	- - -	- - -	12	12	9
UCDW (1200 m)	- - -	- - -	- - -	- - -	- - -	- - -	12	9
NADW (2300 m)	- - -	- - -	- - -	- - -	- - -	- - -	- - -	8

as a part of the South Atlantic Subtropical Gyre (Silveira et al. 2015). Beneath them, the Antarctic Intermediate Water (AIW) and Upper Circumpolar Deep Water (UCDW) run northward; at the bottom, the North Atlantic Deep Water (NADW) runs southward (Table 1; Foloni Neto 2010, Silveira et al. 2015). In Campos Basin, the summer is rainy with northeast dominant winds that promote coastal upwelling of SACW in Cape Frio (23°S) and Cape São Tomé (22°S). The winter is dry and colder due to the influence of the South Atlantic Subtropical Anticyclone in the atmosphere and more frequent frontal systems of polar air masses that move northward (Dereczynski and Menezes 2015). Cyclonic meanders and eddies of the Brazil Current occur during all seasons in the continental slope of Campos Basin. These rotating features promote upwelling in its leading edge, advecting upwelled water to the continental shelf break as well as downwelling in its trailing edge (Campos et al. 2000, Castelão et al. 2004, Aguiar et al. 2014).

Sampling.—The Habitats Project - Campos Basin Environmental Heterogeneity (CENPES/PETROBRAS) performed two oceanographic cruises in the Campos Basin, between latitudes 21°10′S and 24°26′S: the first in the rainy season, from February to April 2009 (austral summer–autumn), aboard RV Gyre, and the second in the dry season, from August to September 2009 (austral winter), aboard RV Luke Tomas (Moreira et al. 2017). The sampling design in both cruises included eight isobaths: 25, 50, 75, and 150 m in the neritic zone and 400, 1000, 1900, and 3000 m in the oceanic zone. Vertically, the water mass cores were previously identified through Optimal Multiparametric Analysis by Foloni Neto (2010) and were collected according to the isobaths (Table 1). Samples at 1 m depth were considered Surface Water (SW), corresponding to the Coastal or Tropical Water (Table 1).

Water and environmental samples were collected in nine transects perpendicular to the coast throughout the eight isobaths, totaling 72 oceanographic stations. A rosette was used, equipped with a CTD profiler (Sea-Bird Electronics Inc.) and a set of 12 bottles each with 10 liters of capacity (Niskin or GO-FLO, General Oceanics; Moreira et al. 2017). Zooplankton hauls were performed in six transects, throughout the eight isobaths, totaling 48 oceanographic stations (Fig. 1). A Multinet type midi (Hydro-Bios) was used, equipped with 64, 120, 200, and 500 μm mesh nets white in color with a frame opening of 50 × 50 cm (Bonecker et al. 2014, Moreira et al. 2017). A remote system for opening and closing the nets and a depth sensor allowed individual sampling of each water mass core. The volume of water filtered was determined using digital flow meters attached to the inner net mouth, while the filtration efficiency was assessed using an external meter (Bonecker et al. 2014). Zooplankton collections were performed at night, from 6 pm to 6 am, to standardize the sampling due to the diel vertical migration and to maximize the capture in superficial layers (Moreira et al. 2017). Hauls were conducted at a speed of 2 knots and varied according to the water mass: horizontal hauls in SW, SACW, AIW, and UCDW with a duration of 5, 10, 15, and 15 minutes respectively, and vertical hauls in NADW with a duration of 15 minutes (Moreira et al. 2017). Some samples were unavailable for stations A12, H12, and I12. Zooplankton samples were fixed and preserved in 4% buffered formalin (Bonecker et al. 2014). Cephalopod paralarvae were screened from 120, 200, and 500 µm mesh net samples.

Morphological Identification.—Paralarvae were identified to the most precise taxonomic level according to the literature—Sweeney et al. (1992), Vecchione et al. (2001), Haimovici et al. (2002), Santos and Haimovici (2007) for all groups, and Roper and Lu (1978), Haimovici et al. (1995), and Fernández-Álvarez et al. (2017) for ommastrephid rhynchoteuthion paralarvae. Higher taxa classification followed Young et al. (2019).

Dorsal mantle length (ML in mm) was measured from the anterior to the posterior margin of the mantle in squids (orders Oegopsida and Myopsida), and from the midline between the eyes to the posterior margin of the mantle in octopuses (order Octopoda). Ommastrephid paralarvae proboscis length was measured and its sucker pattern was recorded. Arm proportions were recorded for all specimens and chromatophore and photophore patterns were documented if present. Few paralarvae were identified at the species taxonomic level because most of them lost the chromatophore pattern due to preservation in formalin or were too small to show specific diagnostic characters; most paralarvae of Octopoda Incirrata (n = 78) could not be differentiated into families for these reasons.

Data Analysis.—Paralarvae densities were standardized as the number of individuals per 100 m^3 (ind 100 m^{-3}) of filtered water. The scarce and patchy distribution of cephalopod paralarvae in the samples resulted in a data set that was zero-inflated (absence in 45.7% among hauls), nonnormal (Shapiro–Wilk test: $W = 0.62$, $P < 0.001$), and overdispersed (standard deviation greater than the mean). Therefore, we assumed the negative binomial distribution for density data (Zuur et al. 2012), since it provided the best fit (Kolmogorov–Smirnov test: $D = 0.096$, $P = 0.584$) and showed suitable results for cephalopod paralarvae data (Roura et al. 2016).

Generalized Linear Models (GLMs) with negative binomial distribution were built to assess the effect of fixed factors and environmental variables on the paralarvae counts, using the log-transformed volume of filtered water as an offset to standardize the data as densities. A preliminary GLM was built only with the fixed factor mesh net (120, 200, and 500 µm) and the mean number of paralarvae per haul did not show significant differences among the mesh nets: 2.76 in 120 µm, 3.41 in 200 µm, and 2.53 in 500 µm (Online Table S1). For this reason, we assumed that all nets had the same efficiency and the number of paralarvae per haul was pooled, in each station, according to the equation:

$$(\sum \text{paralarvae of the three nets} / \sum \text{volume of water filtered in } m^3 \text{ of the three nets}) * 100.$$

This pooling allowed to reduce the number of hauls without paralarvae (i.e., zeros) from 45.7% to 16.1%.

Subsequent GLMs with pooled data evaluated the fixed factors season (rainy/dry) and zone (neritic/oceanic), as well as quantitative environmental variables: seawater temperature (19.6–28.5 °C), salinity (35.4–37.3), and dissolved oxygen (4.7–7.7 ml L^{-1}). Suspended particulate matter (SPM; 0.1–6.5 mg L^{-1}) was obtained by 0.45 and 0.7 μm filtration (Moreira et al. 2017) and included both organic and inorganic matter. Chlorophyll-*a* concentration (0.03–5.93 μg L^{-1}) was considered a proxy for primary production. The total zooplankton density ranged from 409.6 to 166,955.5 individuals per m^3, considering the pooled data from all mesh nets (64, 120, 200, and 500 μm), and was considered a proxy for secondary production. The zooplankton community was dominated by copepods, with important representation of gastropods and cladocerans (Bonecker et al. 2017c). All environmental variables were previously scaled for GLMs (i.e., normalized using the mean value and standard deviation). Potential collinearity among environmental variables was assessed using pair plots and calculating variance inflation factors (VIF). The residual plots indicated heteroscedasticity in the dispersion of model residues.

The continuous data of dorsal mantle length were also nonnormal (Shapiro–Wilk test: $W = 0.81$, $P < 0.001$). GLMs with gamma distribution were independently built to assess the effect of the fixed factors mesh net, season, and zone on the paralarvae sizes. All GLMs in this study used the logarithmic link function and were considered satisfactory by diagnostics: residuals plots, half-normal plots, and deviance on degrees of freedom.

Multivariate analyses were performed on a matrix of the paralarvae densities (individuals per 100 m^3) per station and per main taxa, using the pooled data among the mesh nets. For this, the data were previously square root–transformed and converted in a Bray–Curtis dissimilarity matrix. A Multivariate Permutational Analysis of Variance (PERMANOVA; Anderson et al. 2008) with 9999 permutations and sum of squares Type III was used to evaluate the significance of the fixed factors season (rainy/dry) and zone (neritic/oceanic) on the paralarvae assemblage. A priori, a Permutational Dispersion Analysis (PERMDISP) was conducted to verify the multivariate homogeneity between the levels of each factor. A two-way Similarity Percentage (SIMPER) was used to assess the contribution of the different taxa to the observed difference in assemblages between factors season and zone, with a cut-off for low contributions of 99%.

The exploratory analyses, graphics, and GLMs were performed in R 4.2.1 (R Core Team 2023) using MASS (Venables and Ripley 2002), car (Fox and Weisberg 2019), nortest (Gross and Ligges 2015), ggplot2 (Wickham 2016), sciplot (Morales 2020), and faraway (Faraway 2022) packages. Multivariate analyses were performed in Primer 6 (Clarke and Gorley 2006) with the PERMANOVA+ add-on (Anderson et al. 2008). The map and spatial plots were built in QGIS 3.28.12 (QGIS Development Team 2023).

Results

A total of 825 cephalopod paralarvae were collected belonging to three orders, 11 families, and 16 genera (Table 2). Detailed taxonomic descriptions and paralarvae images can be found in the Online Supplementary Material (Online Table S2, Online

Figs. S1 and S2). During the rainy season, 611 paralarvae of 10 families were collected at 40 of 48 stations. During the dry season, 214 paralarvae of 7 families were collected at 39 of 46 stations sampled (Table 2). The families Enoploteuthidae and Ommastrephidae were more abundant during the rainy season, while Loliginidae (present only in the neritic zone) and Octopoda Incirrata showed the opposite pattern and were more abundant during the dry season (Fig. 2). The dorsal mantle length of the paralarvae ranged from 0.4 to 8.5 mm, with an overall mean of 1.50 mm (SD 0.67 mm). Only specimens from the families Cranchiidae and Tremoctopodidae had a mantle length longer than 4 mm, while 95% of the data set was less than 2.6 mm (Fig. 3A). The gamma GLM revealed a significant difference in the ML mean among the nets: paralarvae caught by the 500 µm mesh were larger than those caught by the 200 µm mesh, which in turn were larger than those caught by the 120 µm mesh (Fig. 3B, Online Table S3). However, no significant differences were observed between periods or zones (Online Table S3).

Most paralarvae (*n* = 819) and nine families were collected in the Surface Water (Online Table S4). In this layer, the total paralarvae density ranged from 0 to 16.8 ind 100 m^{-3} [mean 1.95 (SD 3.22); Fig. 4]. The families Enoploteuthidae and Ommastrephidae were the most abundant in Surface Water (Fig. 4) and their densities ranged from 0 to 9.7 ind 100 m^{-3} [mean 0.79 (SD 1.83)] and from 0 to 7.3 ind 100 m^{-3} [mean 0.70 (SD 1.42)], respectively. The higher densities were along the isobath 150 m, followed by the 75, 400, and 1900 m isobaths (Fig. 5). In the South Atlantic Central Water, the total paralarvae density ranged from 0 to 0.42 ind 100 m^{-3} and four specimens

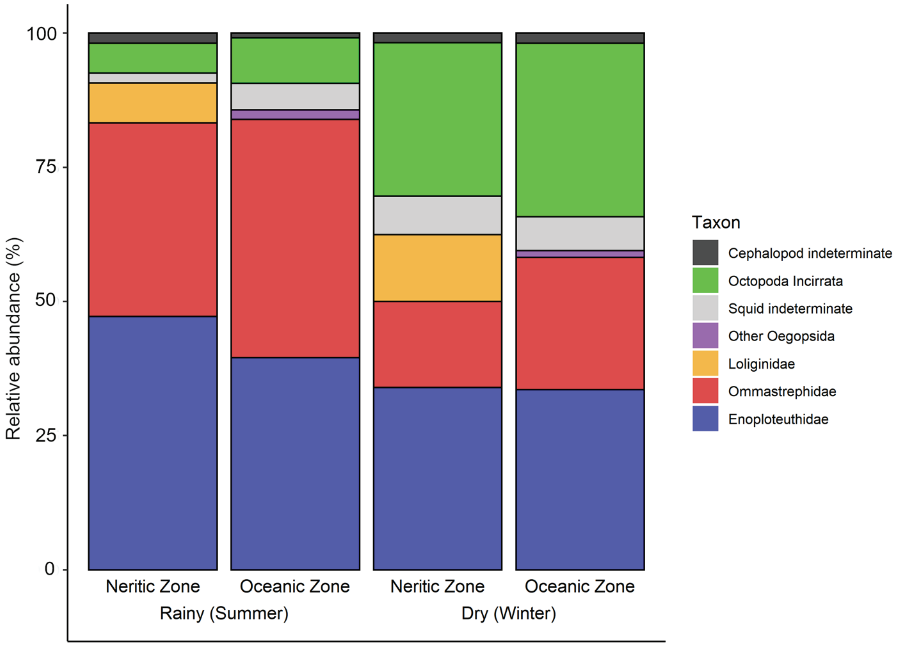

Figure 2. Relative abundance (%) of cephalopod paralarvae taxa in Campos Basin, during the rainy and dry seasons, in the neritic zone and oceanic zone. Other Oegopsida include the families Cranchiidae, Octopoteuthidae, Onychoteuthidae, Ancistrocheiridae, and Thysanoteuthidae. Squid indeterminate includes any Oegopsida or Myopsida. Octopoda Incirrata includes the families Argonautidae, Octopodidae, and Tremoctopodidae.

Table 2. Taxonomic list of cephalopod paralarvae collected by Multinet in Campos Basin, Brazil. Sampling: rainy season from February to April 2009; dry season from August to September 2009. Mantle length in mm; ind = indeterminate.

Taxon: superorder, order, family, genus (or type), and species	Abundance			Mantle length	
	Rainy (Summer)	Dry (Winter)	Total number	Min	Max
DECAPODIFORMES	559	143	702	0.4	8.5
Oegopsida	517	122	639	0.4	8.5
Enoploteuthidae	262	72	334	0.5	3.8
Abralia spp.	41	7	48	1.5	3.8
Abraliopsis spp.	5	- - -	5	2.0	3.0
Enoploteuthidae ind.	216	65	281	0.5	2.8
Ommastrephidae	249	48	297	0.4	4.0
Hyaloteuthis pelagica	1	- - -	1	4.0	4.0
Sthenoteuthis pteropus	7	2	9	0.8	2.6
Rhynchoteuthion Type A (*Ommastrephes cylindraceus*)	111	30	141	0.5	3.3
Rhynchoteuthion Type B (*Ornithoteuthis antillarum, Hyaloteuthis pelagica*)	109	11	120	0.5	3.2
Rhynchoteuthion Type C (*Illex argentinus, Illex coindettii*)	7	- - -	7	1.0	2.8
Rhynchoteuthion ind.	14	5	19	0.4	3.0
Ancistrocheiridae	1	- - -	1	1.9	1.9
Ancistrocheirus cf. *lesueurii*	1	- - -	1	1.9	1.9
Cranchiidae	1	2	3	4.0	8.5
Liocranchia sp.	1	- - -	1	4.0	4.0
Megalocranchia spp.	- - -	2	2	7.2	8.5
Octopoteuthidae	1	- - -	1	2.4	2.4
Octopoteuthis sp.	1	- - -	1	2.4	2.4
Onychoteuthidae	2	- - -	2	1.3	1.7
Onychoteuthis spp.	2	- - -	2	1.3	1.7
Thysanoteuthidae	1	- - -	1	2.0	2.0
Thysanoteuthis sp.	1	- - -	1	2.0	2.0
Myopsida	20	7	27	1.1	3.5
Loliginidae	20	7	27	1.1	3.5
Decapodiformes ind.	22	14	36	0.5	2.0
OCTOPODIFORMES	44	67	111	0.7	4.3
Octopoda Incirrata	44	67	111	0.7	4.3
Argonautidae	9	1	10	0.7	1.4
Argonauta spp.	9	1	10	0.7	1.4
Octopodidae	15	5	20	1.2	3.7
Macrotritopus spp.	11	5	16	1.2	3.7
Octopodidae ind.	4	- - -	4	1.3	2.5
Tremoctopodidae	- - -	3	3	4.0	4.3
Tremoctopus spp.	- - -	3	3	4.0	4.3
Octopoda Incirrata ind.	20	58	78	1.0	2.5
Cephalopoda ind.	8	4	12	0.6	1.5
All Cephalopod Paralarvae	611	214	825	0.4	8.5

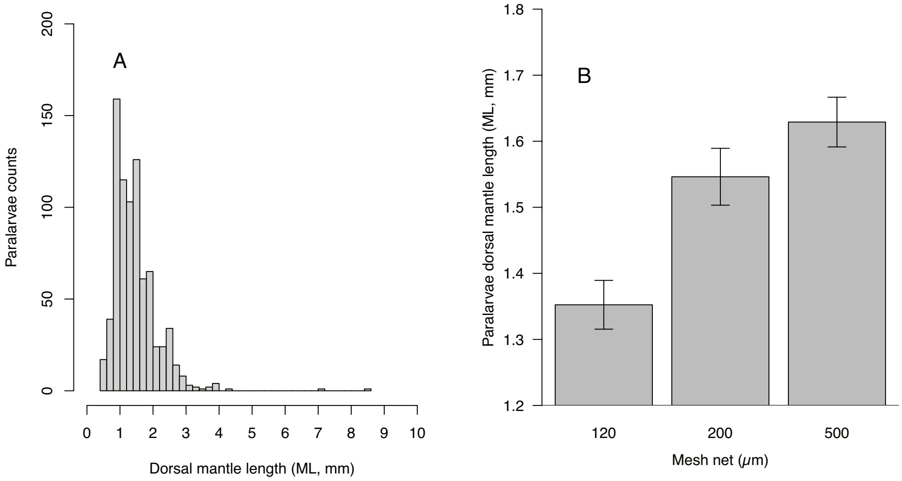

Figure 3. Dorsal mantle length (ML) of cephalopod paralarvae: (A) ML distribution and (B) ML mean in each mesh net (120, 200, and 500 µm).

were collected: one indeterminate enoploteuthid, one *Ancistrocheirus* cf. *lesueurii*, and one *Thysanoteuthis* sp. during the rainy season, and one rhynchoteuthion Type A during the dry season (Fig. 4). In the Antarctic Intermediate Water, the total paralarvae density ranged from 0 to 0.0039 ind 100 m^{-3} and two specimens were collected during the rainy season: one *Abralia* spp. and one rhynchoteuthion Type B (Fig. 4). No paralarvae were caught in the Upper Circumpolar Deep Water or in the North Atlantic Deep Water (Online Table S4).

Negative binomial GLMs were built with densities of total paralarvae and the most abundant families, Enoploteuthidae and Ommastrephidae, only for Surface Water. Data for the other taxa were insufficient for meaningful results. Model I considered only the season and zone as factors, Model II added the interaction between the two factors. Model III considered only the environmental variables (quantitative), Model IV included both factors and environmental variables (full model), and Model V was an optimization of Model IV using the backward stepwise method, selecting the best model based on the Akaike Information Criterion (AIC). The models for total paralarvae and Ommastrephidae retained the variables season and temperature; however, given the high correlation between these predictors (VIF from 6.2 to 29.4), Model VI excluded the factor season (Table 3). The mean density of total paralarvae was significantly higher during the rainy season (2.84 ind 100 m^{-3}) compared to the dry season (1.08 ind 100 m^{-3}) and showed a significant positive relationship with temperature in most models, a pattern that was also observed for Enoploteuthidae and Ommastrephidae (Tables 3 and 4, Fig. 6, Online Fig. S3). Suspended particulate matter showed a negative relationship, significant for Ommastrephidae and retained for Enoploteuthidae by AIC, despite no significance ($P = 0.52$), where higher density of these paralarvae was associated with SPM < 2 mg L^{-1} (Tables 3 and 4, Fig. 6, Online Fig. S3). In some models, dissolved oxygen had a significant and positive relationship with total paralarvae and Ommastrephidae, where higher paralarvae density was related to dissolved oxygen >6 ml L^{-1} (Tables 3 and 4, Fig. 6, Online Fig. S3). There

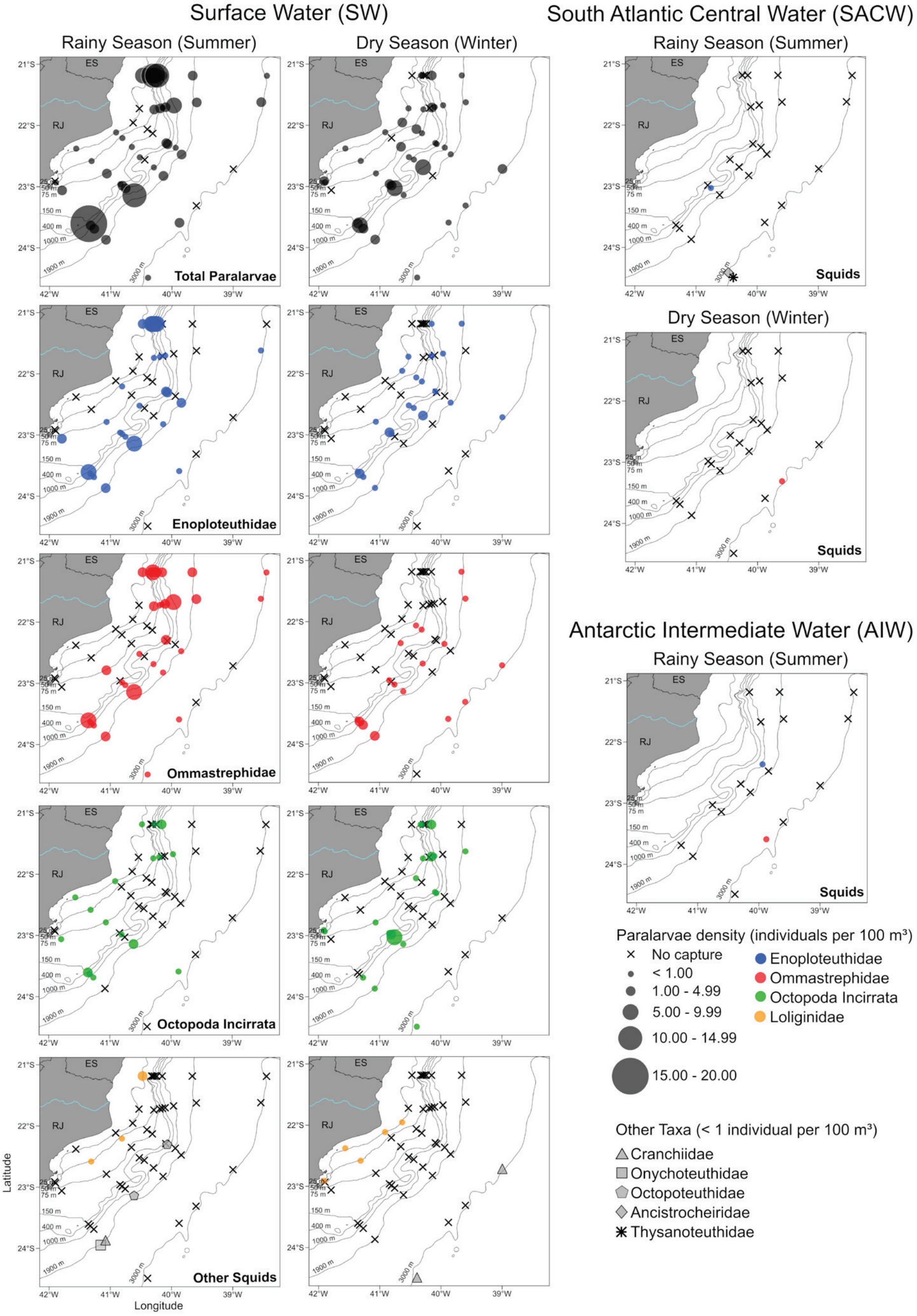

Figure 4. Spatial distributions of cephalopod paralarvae in Campos Basin, during the rainy and dry seasons, for Surface Water (SW), South Atlantic Central Water (SACW), and Antarctic Intermediate Water (AIW). ES = Espírito Santo state, RJ = Rio de Janeiro state.

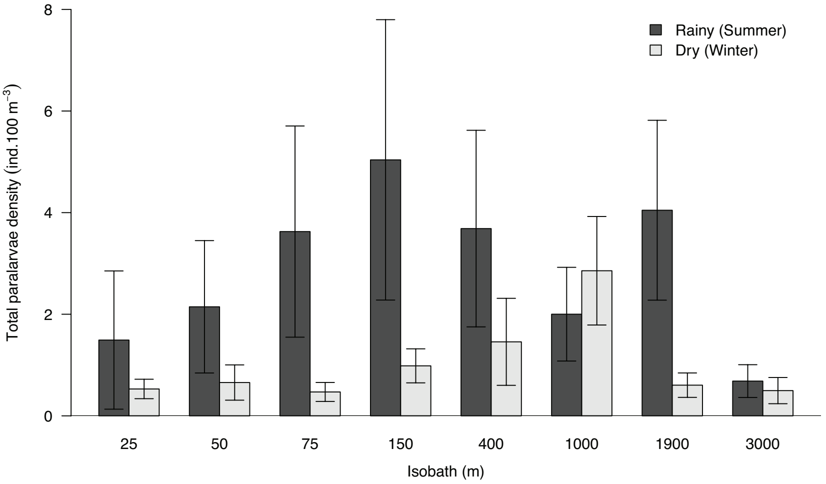

Figure 5. Total paralarvae density (individuals per 100 m^3) throughout the isobaths (m) in each season (rainy/dry).

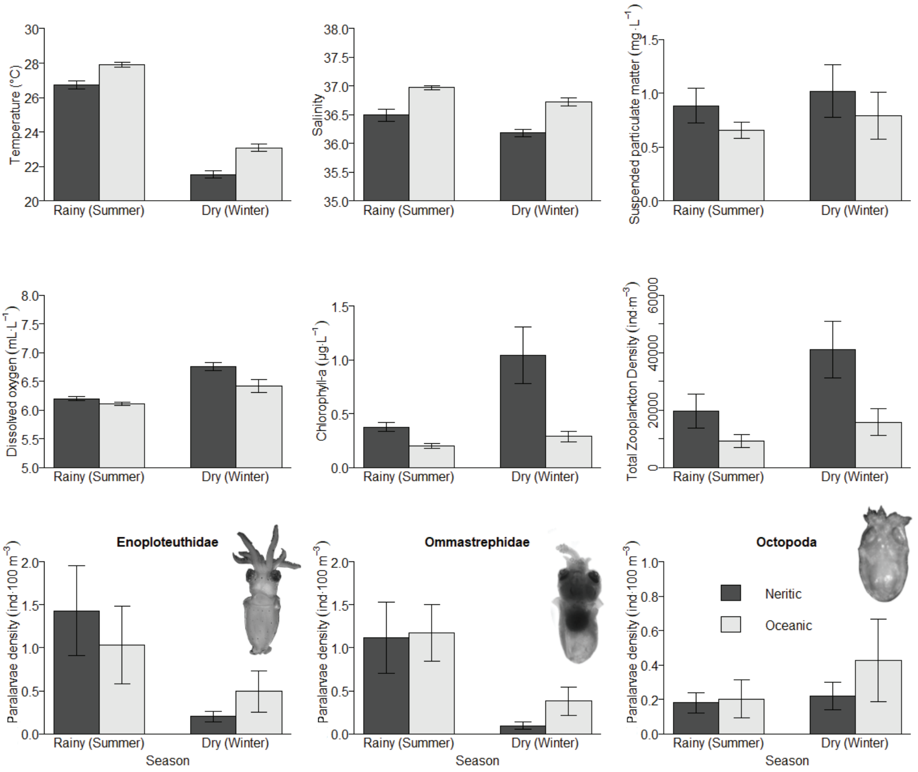

Figure 6. Bar graphs with standard error bars of environmental variables analyzed and paralarvae densities of the main taxa (individuals per 100 m^3), during the rainy and dry seasons, in the neritic zone and oceanic zone. Octopoda includes the families Argonautidae, Octopodidae, and Tremoctopodidae.

Table 3. Generalized Linear Models (GLMs), built with negative binomial distribution, relating the densities of total paralarvae, Enoploteuthidae, and Ommastrephidae to fixed factors and environmental variables. The models were evaluated by Akaike Information Criterion (AIC). Bold variables are significant in each model: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. SPM = suspended particulate matter.

Paralarvae density	Model	Description	AIC
Total	I	**season***** + zone	535.79
	II	**season***** + zone + season × zone	534.01
	III	**temperature**** + salinity + SPM + oxygen + chlorophyll-*a* + total zooplankton	531.77
	IV	**season*** + zone + **temperature**** + salinity + SPM + **oxygen*** + chlorophyll + total zooplankton	530.51
	V	**season**** + **temperature*****	525.74
	VI	**temperature*****	528.71
Enoploteuthidae	I	**season**** + zone	353.76
	II	**season**** + zone + season × zone	353.16
	III	**temperature*** + salinity + SPM + oxygen + chlorophyll-*a* + total zooplankton	352.48
	IV	season + zone + temperature + salinity + SPM + oxygen + chlorophyll + total zooplankton	355.53
	V	**temperature**** + SPM	346.88
Ommastrephidae	I	**season***** + zone	346.56
	II	**season***** + zone + season × zone	345.25
	III	**temperature**** + salinity + **SPM***** + oxygen + chlorophyll-*a* + total zooplankton	324.79
	IV	**season*** + zone + **temperature**** + salinity + **SPM***** + **oxygen*** + chlorophyll + total zooplankton	323.45
	V	**season**** + **temperature***** + **SPM***** + **oxygen***	317.93
	VI	**temperature***** + **SPM*****	321.10

Table 4. Statistical parameters of the selected Generalized Linear Models (GLMs) from Table 3 for densities of total paralarvae, Enoploteuthidae, and Ommastrephidae in the Campos Basin.

Paralarvae density	Coefficients	Estimate	Standard error	Z	P (>|z|)
Total (Model VI)	Intercept	−4.07	0.14	−28.85	<0.001
	Temperature	0.62	0.14	4.31	<0.001
Enoploteuthidae (Model V)	Intercept	−5.19	0.23	−22.37	<0.001
	Temperature	0.73	0.22	3.27	0.001
	SPM	−0.95	0.49	−1.94	0.052
Ommastrephidae (Model VI)	Intercept	−6.05	0.25	−24.09	<0.001
	Temperature	1.00	0.20	5.00	<0.001
	SPM	−2.56	0.62	−4.10	<0.001

were no significant effects for the factor zone, the interaction between zone and season, salinity, chlorophyll-*a*, and total zooplankton (Table 3).

Among the less abundant families, Loliginidae was exclusively present in the neritic zone at the 25 and 50 m isobaths (Figs. 2 and 4). Taxa exclusive from the oceanic zone in Surface Water were *Liocranchia* sp., *Onychoteuthis* spp., and *Octopoteuthis* sp. only during the rainy season and *Megalocranchia* spp. and *Tremoctopus* spp. only during the dry season. *Ancistrocheirus* cf. *lesueurii* and *Thysanoteuthis* sp. were collected only in SACW during the rainy season (Figs. 2 and 4). Octopoda Incirrata were slightly more abundant during the dry season in both neritic and oceanic zones (Figs. 4 and 6). We could not establish a distributional pattern for the families Argonautidae and Octopodidae.

The assemblage multivariate analyses in the Surface Water were performed with a matrix of 94 objects (lines) and seven taxa (columns): Enoploteuthidae, Ommastrephidae, Cranchiidae, Onychoteuthidae, Octopoteuthidae, Loliginidae, Octopoda Incirrata. PERMANOVA applied to the paralarvae assemblage indicated a significant difference between the rainy and dry seasons (pseudo-F = 5.30, P < 0.01) and between the neritic and oceanic zones (pseudo-F = 3.88, P < 0.05), with no interaction between the factors season and zone (pseudo-F = 0.11, P = 0.91; Table 5). PERMDISP identified multivariate dispersion only to the season (F = 5.77, P < 0.05) and not to the zone (F = 0.32, P = 0.62; Table 5). SIMPER showed the family Enoploteuthidae as the main contributor to the neritic zone assemblage (40.9%) and the family Ommastrephidae to the oceanic zone (57.7%) and the rainy season (56.3%) assemblages. Octopoda Incirrata and Enoploteuthidae had similar contributions to the dry season (35.0% and 34.4%, respectively). The other taxa had less expressive contributions (Fig. 2, Online Table S5).

Table 5. Multivariate Permutational Analysis of Variance (PERMANOVA) results for total paralarvae assemblage in Campos Basin. Fixed factors: season (rainy/dry) and zone (neritic/oceanic). Previously, Permutational Dispersion Analysis (PERMDISP) verified the multivariate homogeneity between the levels of each factor.

Source	PERMANOVA					PERMDISP	
	Degrees of freedom	Sum of squares	Mean square	Pseudo-F	P	F	P
Season	1	4,271.60	4271.60	5.30	0.004	5.77	0.03
Zone	1	3,124.30	3124.30	3.88	0.017	0.32	0.62
Season × Zone	1	90.87	90.87	0.11	0.907	- - -	- - -
Residual	90	72,472.00	805.25	- - -	- - -	- - -	- - -
Total	93	80,086.00	- - -	- - -	- - -	- - -	- - -

Discussion

Paralarvae Distribution Patterns.—This is the first study in the Brazilian continental margin investigating the presence of cephalopod paralarvae in deep water masses and one of the few describing the paralarvae distribution on the continental slope. Eleven families and 16 genera of cephalopod paralarvae have been identified, the majority in small sizes, indicating reproductive activity in or around this area. Previous studies in Brazil using Bongo net reported 11 to 15 families of cephalopod paralarvae from northeastern to southern Brazil (Haimovici et al. 2002, Santos and Haimovici 2007, Araújo and Gasalla 2019, Ortiz et al. 2024), while a study using rectangular midwater trawl reported six families for a restricted area around coastal upwelling in southern Brazil (Vidal et al. 2010; Table 6).

The efficiency of the open/close systems of the Multinet allows to determine the vertical distribution of plankton in each depth layer separately. The Surface Water (1 m depth) showed a higher number of taxa and density of cephalopod paralarvae, as well as a higher density and biomass of zoo- and ichthyoplankton (Bonecker et al. 2017b,c). This pattern was already expected due to the horizontal hauls conducted at night, which maximize the zooplankton capture in the surface layers (Moreira et al. 2017). In posterior samplings, Bonecker et al. (2017a) investigated the vertical and nictemeral variations in Campos Basin and reported the different zoo- and ichthyoplankton communities in Surface Water through the daytime, with higher densities at night. The distribution of zooplankton in the water column changes throughout the day due to diel vertical migrations (Cohen and Forward 2016) and this behavior is also known for early cephalopod stages (Diekmann and Piatkowski 2004, Roura et al. 2016, 2019, Castillo-Estrada et al. 2020, Sluis et al. 2021). Paralarvae preferentially ascend in the water column during the night, so the probability of capturing them in the surface layer is higher during the nocturnal period (Diekmann and Piatkowski 2004, Zaragoza et al. 2015, Otero et al. 2016, Roura et al. 2019). On the other hand, along the water column, Röpke et al. (1993) indicated the pycnocline (20–50 m) as the center of mass for paralarvae; moreover, Diekmann and Piatkowski (2004) indicated that paralarvae of Enoploteuthidae, Ommastrephidae, and Ancistrocheiridae were generally more numerous between 50 and 70 m depth at night and twilight. For this reason, other studies carried out in Brazilian waters using oblique hauls of Bongo net were more efficient in capturing rare families and larger paralarvae or juveniles (Haimovici et al. 2002, Santos and Haimovici 2007, Ortiz et al. 2024; Table 6), as they collected through the water column and integrated different layers where paralarvae are more abundant.

The presence of six oegopsid squids in the SACW (250 m depth) and AIW (800 m depth), ranging from 1.5 to 2.8 mm ML, can be explained by passive movement induced by currents and/or by active vertical migration. Cyclonic meanders and eddies of the Brazil Current are present in the continental slope of the Campos Basin during all seasons and can transport paralarvae from the surface to deeper layers through downwelling (Campos et al. 2000, Castelão et al. 2004, Aguiar et al. 2014). For example, cephalopod paralarvae have been observed at 200–290 m depth (Diekmann and Piatkowski 2004) and 500 m, the so-called deep scattering layer (Roura et al. 2019). However, the occurrence of paralarvae is not expected in layers deeper than 1000 m, where there is a predominance of juvenile and adult cephalopods

Table 6. Studies on cephalopod paralarvae in the Brazilian coast: study area, sampling method, number of families and genera identified and size range.

Area, latitude, and isobath	Plankton sampler	Hauls method	Families and genera	Mantle length range	Reference
Northeast Brazil, oceanic island and seamounts 2°N – 4°S	Bongo net 300 and 500 µm meshes	Oblique; diurnal; from 50, 100 and 150 m depth to the surface	15 families, 21 genera	0.8 – 25.0 mm	Haimovici et al. (2002)
Southeast-South Brazil 22°S – 34°S 80 – 2,400 m	Bongo net 300 µm mesh	Oblique; diurnal; from the bottom or 200 m depth to the surface	15 families, 19 genera	0.7 – 18.5 mm	Santos and Haimovici (2007)
South Brazil 28°09´S – 29°56´S 30 – 146 m	Rectangular midwater trawl 1 mm mesh	Oblique; from the bottom to the surface	6 families, 5 genera	2.0 – 40.0 mm	Vidal et al. (2010)
Southeast Brazil 22°S – 25°S Shelf up to approx. 200 m	Bongo net 333 and 505 µm meshes	Oblique; from the bottom or 10 m depth to the surface	11 families, 13 genera	Not measured	Araújo and Gasalla (2019)
Southeast-South Brazil 22°S – 34°S 150 – 3,000 m	Bongo net 300 and 500 µm meshes	Oblique; from 5 m depth to the surface on the shelf; from 250 m depth to the surface on the slope	14 families, 22 genera	0.9 – 11.5 mm	Ortiz et al. (2024)
Southeast Brazil 21°10´S – 24°26´S 25 – 3,000 m	Multinet 120, 200, and 500 µm meshes	At five water mass cores: 1, 250, 800, 1,200 (horizontal hauls) and 2,300 m depth (vertical hauls)	11 families, 16 genera	0.4 – 8.5 mm	This study

(Judkins and Vecchione 2020), which may explain the absence of paralarvae in our samples at UCDW and NADW.

Enoploteuthidae and Ommastrephidae were present in the three upper water masses and were the main contributors to the cephalopod paralarvae assemblage of Surface Water. These are among the most abundant squid families in planktonic surveys throughout tropical and subtropical waters (Haimovici et al. 1995, 2002, Santos and Haimovici 2007, Zaragoza et al. 2015, Aceves-Medina et al. 2017, Castillo-Estrada et al. 2020, Sluis et al. 2021, Ortiz et al. 2024). Both families have a broad dispersion of eggs and hatchlings: enoploteuthids release planktonic eggs freely in the water column (Boyle and Rodhouse 2005), while ommastrephids produce egg masses neutrally buoyant that tend to float above the pycnocline (Boyle and Rodhouse 2005, Vijai 2016). In addition, midwater and bottom trawl surveys for adult cephalopods from the northeastern to southern Brazilian coast reported high abundances of the enoploteuthids *Abralia veranyi* and *Abralia redfieldi*, and the ommastrephids *Illex argentinus*, *Illex coindettii*, and *Ornithoteuthis antillarum* (Haimovici et al. 2007, 2008). In lesser abundance was also reported the enoploteuthids *Abraliopsis atlantica*, *Abraliopsis morisii*, *Enoploteuthis anapsis*, and *Enoploteuthis leptura*, and the omastrephids *Ommastrephes cylindraceus* (from *Ommastrephes bartramii* complex; Fernández-Álvarez et al. 2020), *Sthenoteuthis pteropus*, and *Eucleoteuthis luminosa*, all predominantly living in the oceanic zone (Haimovici et al. 2007, 2008). These squid species can potentially breed and spawn throughout the study area.

Loliginidae paralarvae occurred exclusively in shallow waters, consistent with the neritic habits described for both adults and paralarvae of the family (Rosa et al. 2013, Roura et al. 2019), where breeding and spawning occur close to the coast and the egg capsules are attached to the substrate (Rodrigues and Gasalla 2008, Rosa et al. 2013). Lagrangian models indicate that the southeastern Brazilian continental shelf is a retention zone for loliginids, where oceanographic conditions are favorable for squid recruitment (Martins et al. 2014). Autumn surveys for adult nekton in the Campos Basin found concentrations of *Doryteuthis sanpaulensis* around Cape Frio and *Doryteuthis pleii* around Cape São Tomé (Haimovici et al. 2017). Paralarvae of *Doryteuthis* were also found around these capes and coastal islands during periods with enriched water column by SACW upwelling, while *Lolliguncula brevis* was found in bays and estuaries (Araújo and Gasalla 2018).

The families found exclusively in the oceanic zone were Cranchiidae, Onychoteuthidae, Octopoteuthidae, and Tremoctopodidae in Surface Water, and Ancistrocheiridae and Thysanoteuthidae in SACW. All these families occur in a wide depth range (Jereb and Roper 2010). Octopoda Incirrata occurred in both neritic and oceanic zones in Surface Water, had higher densities during the dry season, and was one of the main contributors to the cephalopod assemblage of this season. However, a clear distinction between Octopodidae and Argonautidae was not possible for our samples. Octopodidae spawn eggs attached to the bottom in neritic zone and the adults occupy different habitats (Boyle and Rodhouse 2005). *Octopus americanus* (*Octopus vulgaris* type II) inhabits tropical and temperate waters and a high concentration of adults has been reported around Cape Frio associated with SACW (Haimovici et al. 2017), while the genus *Macrotritopus* inhabits sand and mud bottoms in tropical waters (Haimovici et al. 2009, Alvarenga et al. 2024). Argonautidae spawn continuously in the water column and high abundances of paralarvae were reported in southeastern and southern Brazil, mainly during the summer and autumn (Araújo and Gasalla 2022, Ortiz et al. 2024). Genetic analysis and alternative fixatives that preserve chromatophore patterns are recommended in further studies for better differentiation among cephalopod paralarvae species in the Brazilian continental margin.

Paralarvae Related to Environmental Variables, Plankton Production, and Oceanographic Features.—Temperature was the main environmental variable associated with the densities of total paralarvae, Enoploteuthidae, and Ommastrephidae. Densities were up to three times higher in warmer waters of the rainy season. A positive relationship between temperature and paralarvae abundance was also found for *Abralia* (García-Cordova et al. 2023, Ortiz et al. 2024), Ommastrephidae (Staaf et al. 2013, Zaragoza et al. 2015, Sánchez-Velasco et al. 2016), Loliginidae, and *Octopus vulgaris* (Otero et al. 2016) using different statistical methods. In general, temperature directly affects the reproductive success of cephalopods and accelerates the eggs development (Boyle and Rodhouse 2005). Dissolved oxygen and SPM showed some relationship with the paralarvae densities, especially Ommastrephidae. Paralarvae were associated with well-oxygenated waters, consistent with previous studies (Sánchez-Velasco et al. 2016, Castillo-Estrada et al. 2020), and with low levels of SPM. The negative relationship between SPM and rhynchoteuthions was unexpected, given that these paralarvae can use particles retained in the skin as a substrate for microbial development and take this mucus as a food source (Vidal and Haimovici 1998).

Cephalopod paralarvae depend on primary and secondary productivity, since most prey on zooplankton (Boyle and Rodhouse 2005, Roura et al. 2012) and rhynchoteuthions even feed on bacteria, flagellates, and ciliates (Vidal and Haimovici 1998). However, chlorophyll-*a* and total zooplankton were not significant in any of the models and there was low or no synchronicity between paralarvae and other plankton groups. Paralarvae density and zooplankton biomass (caught by the 120 and 200 μm meshes) were higher during the rainy season, whereas orthophosphate and chlorophyll-*a* concentrations and zoo- and ichthyoplankton densities were higher during the dry season (Bonecker et al. 2017b,c, Gonzalez-Rodriguez et al. 2017, Suzuki et al. 2017). This mismatch is probably due to a lag time for the nutrient incorporation by primary and secondary productivity and finally by the paralarvae assemblage (Otero et al. 2009, Zaragoza et al. 2015).

Although the SACW intrusion in the surface was not reported at any point in Campos Basin during the sampling period (Castro Filho et al. 2015), several authors suggested that upwelling occurred previously, since peaks of nutrients, chlorophyll-*a*, and all plankton groups were found in the vicinity of Cape Frio and Cape São Tomé (Cabral et al. 2017, Bonecker et al. 2017b,c, Gonzalez-Rodriguez et al. 2017, Rodrigues et al. 2017, Suzuki et al. 2017, Tenenbaum et al. 2017). Peaks of paralarvae density were observed during the rainy season along the continental shelf break and slope (Fig. 4), which could be related to upwelling and water column enrichment promoted by the cyclonic meandering of the Brazil Current (Campos et al. 2000, Castelão et al. 2004, Aguiar et al. 2014). Unexpectedly, stations near Cape Frio, Cape São Tomé, and the Paraíba do Sul River showed low paralarvae densities. For a better investigation of coastal upwelling or fluvial influence, a finer sample design and a larger temporal sampling would be necessary, since these regions are described as reproductive zones for cephalopods and consequently contain a higher concentration of paralarvae (González et al. 2005, Vidal et al. 2010, Roura et al. 2016, Sluis et al. 2021, García-Cordova et al. 2023).

Conclusions

This study showed the composition and distribution of cephalopod paralarvae for a tropical area with extensive oil exploration in the southeastern Brazilian continental margin, through seasonal variations, eight isobaths from 25 m to 3000 m, and in five water mass cores from 1 to 2300 m depth. Higher paralarvae density was associated with warmer temperatures of Surface Water during the rainy season (summer), especially along the upwelling region of the continental shelf break and slope. The squid families Enoploteuthidae and Ommastrephidae were the most abundant and the small paralarvae indicate reproductive activity and recent spawning in or around this area. Further studies are needed to better understand how paralarvae density relates to plankton production and suspended particulate matter, as well as their sensibility to potential oil spills.

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Literature Cited

Aceves Medina G, De Silva-Dávila R, Cruz-Estudillo I, Durazo R, Avendaño-Ibarra R. 2017. Influence of the oceanographic dynamic in size distribution of cephalopod paralarvae in the southern Mexican Pacific Ocean (rainy seasons 2007 and 2008). Lat Am J Aquat Res. 45(2):356–369. https://doi.org/10.3856/vol45-issue2-fulltext-11

Aguiar AL, Cirano M, Pereira J, Marta-Almeida M. 2014. Upwelling processes along a western boundary current in the Abrolhos-Campos region of Brazil. Cont Shelf Res. 85:42–59. https://doi.org/10.1016/j.csr.2014.04.013

Alvarenga MET, Bertoncini AT, Leite TS. 2024. Guia de identificação de polvos de águas rasas do território brasileiro. Florianópolis SC: Projeto Cephalopoda, Universidade Federal de Santa Catarina (UFSC). [In Portuguese]

Anderson MJ, Gorley RN, Clarke KR. 2008. PERMANOVA for PRIMER: guide to software and statistical methods. Plymouth, PRIMER-E.

Araújo CC, Gasalla MA. 2018. Distribution patterns of loliginid squid paralarvae in relation to the oceanographic features off the South Brazil Bight (22°–25°S). Fish Oceanogr. 27:63–75. https://doi.org/10.1111/fog.12238

Araújo CC, Gasalla MA. 2019. Biodiversity of cephalopod early-life stages across the Southeastern Brazilian Bight: spatio-temporal patterns in taxonomic richness. Mar Biodivers. 49(5):2429–2443. https://doi.org/10.1007/s12526-019-00980-w

Araújo CC, Gasalla MA. 2022. Influence of ocean dynamics on the route of argonauts in the Southeastern Brazil Bight. Prog Oceanogr. 209:102906. https://doi.org/10.1016/j.pocean.2022.102906

Arkhipkin AI, Rodhouse PGK, Pierce GJ, Sauer W, Sakai M, Allcock L, Arguelles J, Bower JR, Castillo G, Ceriola L, et al. 2015. World squid fisheries. Rev Fish Sci Aquacult. 23(2):92–252. https://doi.org/10.1080/23308249.2015.1026226

Bonecker ACT, Araújo AV, Oliveira DC, Castro MS, Carvalho PF, Lopes RM, Bonecker SLC. 2017a. Comunidades zooplanctônicas e ictioplanctônicas: variações verticais e nictemerais ao longo de oito dias. *In:* Falcão APC, Moreira DL, editors. Ambiente pelágico: caracterização ambiental regional da Bacia de Campos, Atlântico Sudoeste. Rio de Janeiro: Elsevier. Habitats. 5:247–281. [In Portuguese]

Bonecker ACT, Katsuragawa M, Castro MS, Gomes EAP, Namiki CAP, Zani-Teixeira ML. 2017b. Estrutura espacial e temporal da comunidade ictioplanctônica. *In:* Falcão APC, Moreira DL, editors. Ambiente pelágico: caracterização ambiental regional da Bacia de Campos, Atlântico Sudoeste. Rio de Janeiro: Elsevier. Habitats. 5:207–245. [In Portuguese]

Bonecker SLC, Araújo AV, Carvalho PF, Dias CO, Fernandes LFL, Aguilar TIM, Lopes RM. 2017c. Estrutura espacial e temporal da comunidade zooplanctônica. *In:* Falcão APC, Moreira DL, editors. Ambiente pelágico: caracterização ambiental regional da Bacia de Campos, Atlântico Sudoeste. Rio de Janeiro: Elsevier. Habitats. 5:171–206. [In Portuguese]

Bonecker SLC, Araújo AV, Carvalho PF, Dias CO, Fernandes LFL, Migotto AE, Oliveira OMP. 2014. Horizontal and vertical distribution of mesozooplankton species richness and composition down to 2,300 m in the Southwest Atlantic Ocean. Zoologia. 31:445–462. https://doi.org/10.1590/S1984-46702014000500005

Boyle P, Rodhouse P. 2005. Cephalopods: ecology and fisheries. Oxford: Blackwell Science Ltd. https://doi.org/10.1002/9780470995310

Brussaard CPD, Peperzak L, Beggah S, Wick LY, Wuerz B, Weber J, Arey JS, van der Burg B, Jonas A, Huisman J, et al. 2016. Immediate ecotoxicological effects of short-lived oil spills on marine biota. Nat Commun. 7(1):11206. https://doi.org/10.1038/ncomms11206

Cabral AS, Andrade L, Paranhos R. 2017. Virioplâncton e bacterioplâncton: descritores espaciais e temporais. *In:* Falcão APC, Moreira DL, editors. Ambiente pelágico: caracterização ambiental regional da Bacia de Campos, Atlântico Sudoeste. Rio de Janeiro: Elsevier. Habitats. 5:29–42. [In Portuguese]

Campos EJ, Velhote D, Silveira ICA. 2000. Shelf break upwelling driven by Brazil Current cyclonic meanders. Geophys Res Lett. 27(6):751–754. https://doi.org/10.1029/1999GL010502

Castelão RM, Campos EJ, Miller JL. 2004. A modelling study of coastal upwelling driven by wind and meanders of the Brazil Current. J Coast Res. 20(3):662–671. https://doi.org/10.2112/1551-5036(2004)20[662:AMSOCU]2.0.CO;2

Castillo-Estrada G, De Silva-Dávila R, Carrillo L, Vásquez-Yeomans L, Silva-Segundo CA, Avilés-Díaz L, Markaida U. 2020. Horizontal and vertical distribution of cephalopod paralarvae in the Mesoamerican Barrier Reef System. J Mar Biol Assoc U K. 100(6):927–937. https://doi.org/10.1017/S0025315420000648

Castro-Filho BM, Pereira AF, Caroli A, Neto HF, Paschoal GCA, Silveira ICA, Amor CC. 2015. Correntes e massas de água na plataforma continental. *In:* Martins RP, Grossmann-Matheson GS, editors. Meteorologia e oceanografia. Rio de Janeiro: Elsevier. Habitats. 2:191–254. [In Portuguese]

Clarke RK, Gorley RN. 2006. PRIMER v6: User manual/tutorial (Plymouth Routines in Multivariate Ecological Research). Plymouth: PRIMER-E.

Cohen JH, Forward RB. 2016. Zooplankton diel vertical migration – a review of proximate control. Oceanogr Mar Biol. 47:77–110.

Dereczynski CP, Menezes WF. 2015. Meteorologia da Bacia de Campos. *In:* Martins RP, Grossmann-Matheson GS, editors. Meteorologia e oceanografia. Rio de Janeiro: Elsevier. Habitats. 2:1–54. [In Portuguese]

Diekmann R, Piatkowski U. 2004. Species composition and distribution patterns of early life stages of cephalopods at Great Meteor Seamount (subtropical North-east Atlantic). Arch Fisch Meeresforsch. 51:115–131.

Falcão APC, Curbelo-Fernandez MP, Borges ALN, Filgueiras VL, Kowsmann RO, Martins RP. 2017. Importância ecológica e econômica da Bacia de Campos: ambiente transicional na margem continental do Oceano Atlântico Sudoeste. *In:* Curbelo-Fernandez MP, Braga AC, editors. Ambiente Pelágico: caracterização ambiental regional da Bacia de Campos, Atlântico Sudoeste. Rio de Janeiro: Elsevier. Habitats. 5:1–13. Publicado também nos volumes 3, 4, 6 e 7 desta série. [In Portuguese]

Faraway J. 2022. faraway: functions and datasets for books by Julian Faraway. R package v1.0.8. Available from: https://CRAN.R-project.org/package=faraway

Fernández-Álvarez FÁ, Braid HE, Nigmatullin CM, Bolstad KS, Haimovici M, Sánchez P, Sajikumar KK, Ragesh N, Villanueva R. 2020. Global biodiversity of the genus *Ommastrephes* (Ommastrephidae: Cephalopoda): an allopatric cryptic species complex. Zool J Linn Soc. 190(2):460–482. https://doi.org/10.1093/zoolinnean/zlaa014

Fernández-Álvarez FÁ, Martins CP, Vidal EA, Villanueva R. 2017. Towards the identification of the ommastrephid squid paralarvae (Mollusca: Cephalopoda): morphological description of three species and a key to the north-east Atlantic species. Zool J Linn Soc. 180(2):268–287. https://dx.doi.org/10.1111/zoj.12496

Foloni Neto H. 2010. As massas de água na Bacia de Campos, RJ. M.Sc. Dissertation. University of São Paulo. [In Portuguese]

Fox J, Weisberg S. 2019. An R companion to applied regression. 3rd ed. Thousand Oaks, California: Sage. Available from: https://socialsciences.mcmaster.ca/jfox/Books/Companion/

García-Cordova EA, De Silva-Dávila R, Velázquez-Abunader I, García-Maldonado JQ, Ardisson PL. 2023. Distribution of squid paralarvae and related oceanographic features in the eastern Campeche Bank, Mexico. J Plankton Res. 45:278–290. https://doi.org/10.1093/plankt/fbac073

González AF, Otero J, Guerra A, Prego R, Rocha FJ, Dale AW. 2005. Distribution of common octopus and common squid paralarvae in a wind-driven upwelling area (Ria of Vigo, Northwestern Spain). J Plankton Res. 27:271–277. https://doi.org/10.1093/plankt/fbi001

Gonzalez-Rodriguez E, Rodrigues SV, Marinho MM, de Carvalho WF, Pinto FN, Paranhos R. 2017. Biomassa fitoplanctônica e produção primária. *In:* Falcão APC, Moreira DL, editors. Ambiente pelágico: caracterização ambiental regional da Bacia de Campos, Atlântico Sudoeste. Rio de Janeiro: Elsevier. Habitats. 5:69–87. [In Portuguese]

Gross J, Ligges U. 2015. Nortest: tests for normality. R package v1.0-4. Available from: https://CRAN.R-project.org/package=nortest

Haimovici M, Andriguetto JM. 1986. Cefalópodes costeiros na pesca de arrasto do litoral sul do Brasil. Arq Biol Tecnol. 29(3):473–495. [In Portuguese]

Haimovici M, Costa PAS, Santos RA, Martins AS, Olavo G. 2007. Composição de espécies, distribuição e abundância de cefalópodes do talude da região central do Brasil. *In:* Costa PAS, Olavo G, Martins AS, editors. Biodiversidade da fauna marinha profunda na costa central brasileira. Rio de Janeiro: Museu Nacional. Série Livros. 24:109–132. [In Portuguese]

Haimovici M, Martins AS, Costa PAS, Braga AC, Mincarone MM. 2017. Distribuição e abundância do nécton demersal da plataforma e talude continental da Bacia de Campos. *In:* Curbelo-Fernandez MP, Braga AC, editors. Comunidades demersais e bioconstrutores: caracterização ambiental regional da Bacia de Campos, Atlântico Sudoeste. Rio de Janeiro: Elsevier. Habitats. 4:111–138. [In Portuguese]

Haimovici M, Perez JAA. 1991. Coastal cephalopod fauna of Southern Brazil. Bull Mar Sci. 49:221–230.

Haimovici M, Perez JAA, Vidal EAG. 1995. Larvae of *Illex argentinus* from five surveys on the continental shelf of southern Brazil. ICES Mar Sci Symp. 199:414–424. https://dx.doi.org/10.17895/ices.pub.19271489

Haimovici M, Piatkowski U, Santos RA. 2002. Cephalopod paralarvae around tropical seamounts and oceanic islands off the north-eastern coast of Brazil. Bull Mar Sci. 71(1):313–330.

Haimovici M, Santos RA, Fischer LG. 2009. Class Cephalopoda. *In:* Rios EC, editor. Compendium of Brazilian sea shells. Rio Grande RS: Evangraf. 610–649.

Haimovici M, Wongtschowski CLDBR, Bernardes RA, Fischer LG, Vooren CM, Santos RA, Rodrigues AR, Santos S. 2008. Prospecção pesqueira de espécies demersais com rede de arrasto-de-fundo na região Sudeste-Sul do Brasil. Série Documentos REVIZEE - Score Sul, IO-USP. [In Portuguese]

Hook SE, Strzelecki J, Adams MS, Binet MT, McKnight K, Golding LA, Elsdon TS. 2022. The influence of oil-in-water preparations on the toxicity of crude oil to marine invertebrates and fish following short-term pulse and continuous exposures. Environ Toxicol Chem. 41:2580–2594. https://doi.org/10.1002/etc.5437

Jereb P, Roper CFE. 2010. Cephalopods of the world. An annotated and illustrated catalogue of cephalopod species known to date. Myopsid and Oegopsid squids. FAO Species Cat Fish Purp. 2(4):1–605.

Judkins H, Vecchione M. 2020. Vertical distribution patterns of cephalopods in the Northern Gulf of Mexico. Front Mar Sci. 7:47. https://doi.org/10.3389/fmars.2020.00047

Long SM, Holdway DA. 2002. Acute toxicity of crude and dispersed oil to *Octopus pallidus* (Hoyle, 1885) hatchlings. Water Res. 36(11):2769–2776. https://doi.org/10.1016/S0043-1354(01)00520-6

Martins RS, de Camargo R, Gasalla MA. 2014. The São Paulo shelf (SE Brazil) as a nursery ground for *Doryteuthis plei* (Blainville, 1823) (Cephalopoda, Loliginidae) paralarvae: a Lagrangian particle-tracking Individual-Based Model approach. Hydrobiologia. 725:57–68. https://doi.org/10.1007/s10750-013-1519-4

Morales M. 2020. sciplot: scientific graphing functions for factorial designs. R Package v1.2-0. Available from: https://CRAN.R-project.org/package=sciplot

Moreira DL, Falcão APC, Curbelo-Fernandez MP, Filgueiras V, Paranhos R, Gonzalez-Rodriguez E, Rodrigues SV, Tenenbaum DR, Nascimento SM, Bonecker ACT, et al. 2017. Desenho amostral e metodologias de coleta no sistema pelágico. *In:* Falcão APC, Moreira DL, editors. Ambiente pelágico: caracterização ambiental regional da Bacia de Campos, Atlântico Sudoeste. Rio de Janeiro: Elsevier. Habitats. 5:15–28. [In Portuguese]

Ortiz DO, Baldoni LC, Muxagata E, Vidal EAG. 2024. Cephalopod paralarvae from the southeast–south Brazilian outer shelf and slope. Mar Biol. 171(4):84. https://doi.org/10.1007/s00227-024-04401-w

Otero J, Álvarez-Salgado XA, González ÁF, Gilcoto M, Guerra Á. 2009. High-frequency coastal upwelling events influence *Octopus vulgaris* larval dynamics on the NW Iberian shelf. Mar Ecol Prog Ser. 386:123–132. https://doi.org/10.3354/meps08041

Otero J, Álvarez-Salgado XA, González ÁF, Souto C, Gilcoto M, Guerra Á. 2016. Wind-driven upwelling effects on cephalopod paralarvae: *Octopus vulgaris* and Loliginidae off the Galician coast (NE Atlantic). Prog Oceanogr. 141:130–143. https://doi.org/10.1016/j.pocean.2015.12.008

Pedrosa P, Paranhos R, Suzuki MS, Andrade L, Silveira ICA, Schmidt ACK, Falcão AP, Lavrado HP, Rezende CE. 2006. Hidroquímica de Massas d'Água Oceânicas em Regiões da Margem Continental Brasileira, Bacia de Campos, Estado do Rio de Janeiro, Brasil. Geochemica Brasiliensis. 20:101–119. [In Portuguese]

QGIS Development Team. 2023. QGIS Geographic Information System. Open Source Geospatial Foundation Project. Available from: http://qgis.osgeo.org

R Core Team. 2023. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Available from: https://www.R-project.org/

Rezende CE, Andrade L, Suzuki MS, Faro BCMT, Gonzalez ASM, Paranhos R. 2006. Hidroquímica. *In:* Valentin JL, editor. Características hidrobiológicas da região central da Zona Econômica Exclusiva brasileira (Salvador, BA, ao Cabo de São Tomé, RJ). Brasília: Ideal Gráfica e Editora. Série Documentos REVIZEE/SCORE Central. 31–60. [In Portuguese]

Rodhouse PG, Symon C, Hatfield EMC. 1992. Early life cycle of cephalopods in relation to the major oceanographic features of the southwest Atlantic Ocean. Mar Ecol Prog Ser. 89:183–195. https://doi.org/10.3354/meps089183

Rodrigues AR, Gasalla MA. 2008. Spatial and temporal patterns in size and maturation of *Loligo plei* and *Loligo sanpaulensis* (Cephalopoda: Loliginidae) in southeastern Brazilian waters, between 23°S and 27°S. Sci Mar. 72:631–643. https://doi.org/10.3989/scimar.2008.72n4631

Rodrigues SV, Marinho MM, Jonck CCAC, Correa RM, Oliveira ACL, Gonçalves ES, Santos MC, Brant VF, Brandão FP. 2017. Composição do fitoplâncton a partir da avaliação de pigmentos marcadores (carotenoides e clorofilas). *In:* Falcão APC, Moreira DL, editors. Ambiente pelágico: caracterização ambiental regional da Bacia de Campos, Atlântico Sudoeste. Rio de Janeiro: Elsevier. Habitats. 5:89–125. [In Portuguese]

Romero IC, Judkins H, Vecchione M. 2020. Temporal variability of polycyclic aromatic hydrocarbons in deep-sea cephalopods of the northern Gulf of Mexico. Front Mar Sci. 7:54. https://doi.org/10.3389/fmars.2020.00054

Roper CFE, Lu C. 1978. Rhynchoteuthion larvae of ommastrephid squids of the western North Atlantic, with the first description of larvae and juveniles of *Illex illecebrosus.* Proc Biol Soc Wash. 91:1039–1059.

Röpke A, Nellent W, Piatkowski U. 1993. A comparative study on the influence of the pycnocline on the vertical distribution of fish larvae and cephalopod paralarvae in three ecoligically different areas of the Arabian Sea. Deep Sea Res Part II Top Stud Oceanogr. 40(3):801–819. https://doi.org/10.1016/0967-0645(93)90059-V

Rosa R, O'dor R, Pierce G, editors. 2013. Advances in squid biology, ecology and fisheries. Part I – Myopsid Squids. New York: Nova Biomedical.

Roura Á, Álvarez-Salgado XA, González ÁF, Gregori M, Rosón G, Otero J, Guerra Á. 2016. Life strategies of cephalopod paralarvae in a coastal upwelling system (NW Iberian Peninsula): insights from zooplankton community and spatio-temporal analyses. Fish Oceanogr. 25:241–258. https://doi.org/10.1111/fog.12151

Roura Á, Amor M, González ÁF, Guerra Á, Barton ED, Strugnell JM. 2019. Oceanographic processes shape genetic signatures of planktonic cephalopod paralarvae in two upwelling regions. Prog Oceanogr. 170:11–27. https://doi.org/10.1016/j.pocean.2018.10.005

Roura A, González AF, Redd K, Guerra A. 2012. Molecular prey identification in wild *Octopus vulgaris* paralarvae. Mar Biol. 159:1335–1345. https://doi.org/10.1007/s00227-012-1914-9

Sánchez-Velasco L, Ruvalcaba-Aroche ED, Beier E, Godínez VM, Barton ED, Díaz-Viloria N, Pacheco MR. 2016. Paralarvae of the complex *Sthenoteuthis oualaniensis-Dosidicus gigas* (Cephalopoda: Ommastrephidae) in the northern limit of the shallow oxygen minimum zone of the Eastern Tropical Pacific Ocean (April 2012). J Geophys Res Oceans. 121(3):1998–2015. https://doi.org/10.1002/2015JC011534

Santos RA, Haimovici M. 2007. Composição de espécies, distribuição e abundância relativa de cefalópodes do ambiente pelágico da plataforma externa e talude superior da região Sudeste e Sul do Brasil. *In:* Bernardes RA, Wongtschowski CLDBR, Madureira LSP. Prospecção pesqueira de espécies pelágicas de pequeno porte na Zona Econômica Exclusiva da região Sudeste-Sul do Brasil. 101–136. [In Portuguese]

Sauer WHH, Gleadall IG, Downey-Breedt N, Doubleday Z, Gillespie G, Haimovici M, Ibáñez CM, Katugin ON, Leporati S, Lipinski MR, et al. 2021. World octopus fisheries. Rev Fish Sci Aquacult. 29(3):279–429. https://doi.org/10.1080/23308249.2019.1680603

Silveira ICA, Foloni Neto H, Costa TP, Schmidt ACK, Pereira AF, Castro Filho BM, Soutelino RG, Grossmann-Matheson GS. 2015. Caracterização da Oceanografia Física do Talude Continental e Região Oceânica da Bacia de Campos *In:* Martins RP, Grossmann-Matheson

GS, editors. Meteorologia e oceanografia. Rio de Janeiro: Elsevier. Habitats. 2:135–189. [In Portuguese]

Sluis MZ, Judkins H, Dance MA, Vecchione M, Cornic M, Sutton T, Rooker JR. 2021. Taxonomic composition, abundance and habitat associations of squid paralarvae in the northern Gulf of Mexico. Deep Sea Res Part I Oceanogr Res Pap. 174:103572. https://doi.org/10.1016/j.dsr.2021.103572

Staaf DJ, Redfern JV, Gilly WF, Watson W, Ballance LT. 2013. Distribution of ommastrephid paralarvae in the eastern tropical Pacific. Fish Bull. 111(1):78–89. https://doi.org/10.7755/FB.111.1.7

Suzuki MS, Paranhos R, Rezende CE, Pinto FN, Gobo AAR, Pedrosa P. 2017. Hidroquímica, carbono orgânico e nutrientes dissolvidos e particulados na Bacia de Campos. *In:* Falcão APC, Wagener ALR, Carreira RS, editors. Química ambiental: caracterização ambiental regional da Bacia de Campos, Atlântico Sudoeste. Rio de Janeiro: Elsevier. 6:65–94. [In Portuguese]

Sweeney MJ, Roper CFE, Mangold KM, Clarke MR, Boletzky SV. 1992. "Larval" and juvenile cephalopods: a manual for their identification (Smithsonian Contributions to Zoology Number 513). Smithson Contrib Zool. 513:1–182. https://doi.org/10.5479/si.00810282.513

Taite M, Vecchione M, Fennell S, Allcock LA. 2020. Paralarval and juvenile cephalopods within warm-core eddies in the North Atlantic. Bull Mar Sci. 96(2):235–262. https://doi.org/10.5343/bms.2019.0042

Tenenbaum DR, Nascimento SM, Vianna S, Fragoso G, Hatherly M, de Moraes R. 2017. Estrutura espacial e temporal da comunidade microplanctônica. *In:* Falcão APC, Moreira DL, editors. Ambiente pelágico: caracterização ambiental regional da Bacia de Campos, Atlântico Sudoeste. Rio de Janeiro: Elsevier. Habitats. 5:127–170. [In Portuguese]

Vaske T Jr, Costa FAP. 2011. Lulas e polvos da Costa Brasileira. 1st ed. Fortaleza: NAVE-LABOMAR. [In Portuguese]

Vecchione M, Roper CFE, Sweeney MJ, Lu CC. 2001. Distribution, relative abundance and developmental morphology of paralarval cephalopods in the Western North Atlantic Ocean. NOAA Tech Rep NMFS. 152:1–54.

Venables WN, Ripley BD. 2002. Modern applied statistics with S. 4th ed. New York: Springer.

Viana AR, Faugères JC, Kowsmann RO, Lima JAM, Caddah LFG, Rizzo JG. 1998. Hydrology, morphology and sedimentology of the Campos continental margin, offshore Brazil. Sediment Geol. 115:133–157. https://doi.org/10.1016/S0037-0738(97)00090-0

Vidal EAG, Haimovici M. 1998. Feeding and the possible role of the prosboscis and mucus cover in the ingestion of microorganisms by rhynchoteuthion paralarvae (Cephalopoda; Ommastrephidae). Bull Mar Sci. 63(2):305–316.

Vidal EAG, Haimovici M, Hackbart VCS. 2010. Distribution of paralarvae and small juvenile cephalopods in relation to primary production in an upwelling area off southern Brazil. ICES J Mar Sci. 67(7):1346–1352. https://doi.org/10.1093/icesjms/fsq080

Vidal EAG, Shea EK. 2023. Cephalopod ontogeny and life cycles patterns. Front Mar Sci. 10:1162735. https://doi.org/10.3389/fmars.2023.1162735

Vijai D. 2016. Egg masses of flying squids (Cephalopoda: Ommastrephidae). J Shellfish Res. 35(4):1007–1012. https://doi.org/10.2983/035.035.0423

Wickham H. 2016. ggplot2: elegant graphics for data analysis. New York: Springer-Verlag.

Young RE, Harman RF. 1988. "Larva," "Paralarva" and "Subadult" in cephalopod terminology. Malacologia. 29:201–207.

Young RE, Vecchione M, Mangold KM. 2019. Cephalopoda Cuvier 1797. Octopods, squids, nautiluses, etc. The Tree of Life Web Project. Version 26 March, 2019 (under construction). Available from: http://tolweb.org/Cephalopoda/19386/2019.03.26

Zaragoza N, Quetglas A, Hidalgo M, Álvarez-Berastegui D, Balbín R, Alemany F. 2015. Effects of contrasting oceanographic conditions on the spatiotemporal distribution of Mediterranean cephalopod paralarvae. Hydrobiologia. 749:1–14. https://doi.org/10.1007/s10750-014-2132-x

Zuur AF, Saveliev AA, Ieno EM. 2012. Zero inflated models and generalized linear mixed models with R. Highland Statistics Ltd.

SUPPLEMENTAL MATERIAL

Cephalopod paralarvae in a tropical Brazilian basin: distribution throughout oceanographic features and water masses

Davi M. Vasconcellos, Mara C.R.S. Bainy, Maurício G. Camargo, Ana Cristina Teixeira Bonecker, Sérgio Luiz Costa Bonecker, Manuel Haimovici

Supplemental Tables:

Table S1: Statistical parameters of the preliminary Generalized Linear Model (GLM), built with negative binomial distribution, relating the total paralarvae density to the factor mesh net: 120 µm (incorporated into the intercept), 200 µm and 500 µm.

Coefficients	Estimate	Std. Error	Z value	P-value
Intercept	-3.85	0.18	-21.30	<0.001
200 µm mesh	0.21	0.25	0.84	0.403
500 µm mesh	-0.41	0.25	-1.60	0.110

Table S2: General morphological characteristics used to identify the cephalopod paralarvae in Campos Basin, Brazil.

Taxa	Description and remarks on cephalopod paralarvae
DECAPODIFORMES	-
Oegopsida	-
Enoploteuthidae	Cone-shaped mantle, prominent eyes, arm formula II>I>III>IV, rounded fins in the posterior extremity of the mantle.
Abralia spp.	Three rounded photophores forming a single row on the ventral surface of the eyeball, arms shorter than the mantle.
Abraliopsis spp.	One photophore at the end of the arms IV, absence of photophores on the eyeballs, robust tentacles, arms equal or longer than the mantle.
Ommastrephidae	Tentacles fused into a proboscis with eight suckers at the distal tip.
Hyaloteuthis pelagica	One photophore on the ventral surface of each eyeball and one central photophore on the intestine.
Sthenoteuthis pteropus	Proboscis length longer the mantle length. All suckers in the proboscis with similar diameter.
Rhynchoteuthion Type A (*Ommastrephes cylindraceus*)	The two lateral suckers of the proboscis are 2 to 3 times the diameter of the remaining six suckers. *Ommastrephes cylindraceus* from *Ommastrephes bartramii* complex (Fernández-Álvarez et al. 2020).
Rhynchoteuthion Type B (*Ornithoteuthis antillarum, Hyaloteuthis pelagica*)	The two lateral suckers of the proboscis are slightly larger than the remaining six suckers, but below 2 times the diameter.

Rhynchoteuthion Type C (*Illex argentinus*, *Illex coindetti*)	All suckers in the proboscis with similar diameter.
Ancistrocheiridae, *Ancistrocheirus* cf. *lesueurii*	Rounded and cup-shaped mantle, gelatinous tissue layer on the head, relatively small eyes broadly separated by the arm bases, stout and long tentacles, arm formula II>I=III>>IV. More morphological studies with adults and paralarvae are necessary for taxonomic confirmation, once barcode genes recently suggested the cryptic species *Ancistrocheirus alessandrinii* (Roura et al. 2019).
Cranchiidae	Semitransparent body and a thin-walled mantle, which is fused to the head at the nuchal region and to funnel at posterolateral corners.
Liocranchia sp.	Spindle-shaped broad mantle, sessile eyes, relatively short tentacles. We could not observe the hyaline strips in the ventral mantle.
Megalocranchia spp.	Spindle-shaped mantle with diamond-shaped lanceola and without ventral hyaline lines, stalked eyes, long stout tentacles, short arms in a stalked arm-crown.
Octopoteuthidae, *Octopoteuthis* sp.	Short and rounded mantle, gelatinous tissue layer on the anterior head, stout tentacles with up to eight large suckers, stalked eyes, stalked arm-crown.
Onychoteuthidae, *Onychoteuthis* spp.	Elongate mantle, thinned posteriorly, short tentacles, arm formula I=II>>III=IV
Thysanoteuthidae, *Thysanoteuthis* sp.	Short and rounded mantle, protruded eyes, stout tentacles, short and equal arms.
Myopsida	-
Loliginidae	Elongated and bullet-shaped mantle, head squarish, eyes covered by a corneal membrane, well-developed ventral arms longer than the dorsal ones (arms IV>I).
OCTOPODIFORMES	-
Octopoda Incirrata	-
Argonautidae, *Argonauta* spp.	Short mantle, short head wider than the mantle, wide eyes laterally protrude, equal-sized arms and conspicuous cuff-shape brachial membrane surrounding arms. One specimen of 1.3 mm ML had slightly longer arms I and probably was a female. We could not detect the mantle-locking apparatus in our specimens.
Octopodidae *Macrotritopus* spp.	Longer arms III, already recognizable in specimens of 1.2 - 1.5 mm ML and becoming conspicuously longer in those over 2.0 mm ML.
Octopodidae indeterminate	Equal-sized arms, remaining preserved chromatophores pattern that excludes the argonautids.
Tremoctopodidae, *Tremoctopus* spp.	Much longer arms I bearing large suckers, with arm formula I>>II>IV>>III.

References: Sweeney et al. (1992), Vecchione et al. (2001), Haimovici et al. (2002), Santos and Haimovici (2007) for all groups; Roper and Lu (1978), Haimovici et al. (1995) and Fernández-Álvarez et al. (2017) for ommastrephid rhynchoteuthion paralarvae. Higher taxa classification followed Young et al. (2019).

Table S3: Statistical parameters of the Generalized Linear Model (GLM), built with gamma distribution, relating the dorsal mantle length to the factors season (rainy and dry), zone (neritic and oceanic) and mesh net (120, 200 and 500 µm). The first level of each factor was incorporated into the intercept.

Coefficients	Estimate	Std. Error	Z value	P-value
Intercept	0.34	0.03	9.48	<0.001
Dry Season	0.01	0.04	0.17	0.867
Oceanic Zone	-0.07	0.03	-2.04	0.041
200 µm mesh net	0.14	0.04	3.66	<0.001
500 µm mesh net	0.18	0.04	4.40	<0.001

Table S4: Number of cephalopod paralarvae collected per water mass core and season in Campos Basin, Brazil. Sampling: rainy season from February to April 2009; dry season from August to September 2009. Water mass cores and their depth: Surface Water (SW), South Atlantic Central Water (SACW), Antarctic Intermediate Water (AIW), Upper Circumpolar Deep Water (UCDW) and North Atlantic Deep Water (NADW). SW can correspond to Tropical Water or Coastal Water.

Water mass cores and depth	Rainy Season (Summer)	Dry Season (Winter)	Total
SW (1 m)	606	213	819
SACW (250 m)	3	1	4
AIW (800 m)	2	0	2
UCDW (1200 m)	0	0	0
NADW (2300 m)	0	0	0
Total	611	214	825

Table S5: Two-way Similarity Percentage (SIMPER) results show the taxa contribution to assemblages in each season (rainy/dry) and zone (neritic/oceanic). Average abundance, average similarity, similarity standard deviation, percentage of contribution, percentage of cumulative contribution.

Rainy Season (Average similarity: 27.87)					
Taxon	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Ommastrephidae	0.74	15.7	0.77	56.35	56.35
Enoploteuthidae	0.69	9.12	0.6	32.72	89.07
Octopoda	0.24	2.86	0.31	10.28	99.35
Dry Season (Average similarity: 23.05)					
Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Octopoda	0.32	8.06	0.42	34.98	34.98
Enoploteuthidae	0.34	7.93	0.46	34.42	69.4
Ommastrephidae	0.26	5.65	0.38	24.49	93.9
Loliginidae	0.07	1.34	0.14	5.81	99.71
Neritic Zone (Average similarity: 20.12)					
Taxon	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Enoploteuthidae	0.51	8.22	0.51	40.86	40.86
Octopoda	0.27	6.52	0.38	32.42	73.28
Ommastrephidae	0.39	3.94	0.35	19.57	92.85
Loliginidae	0.14	1.44	0.15	7.15	100.00
Oceanic Zone (Average similarity: 31.16)					
Taxon	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Ommastrephidae	0.63	17.99	0.82	57.72	57.72
Enoploteuthidae	0.52	8.88	0.54	28.49	86.22

Supplemental Figures:

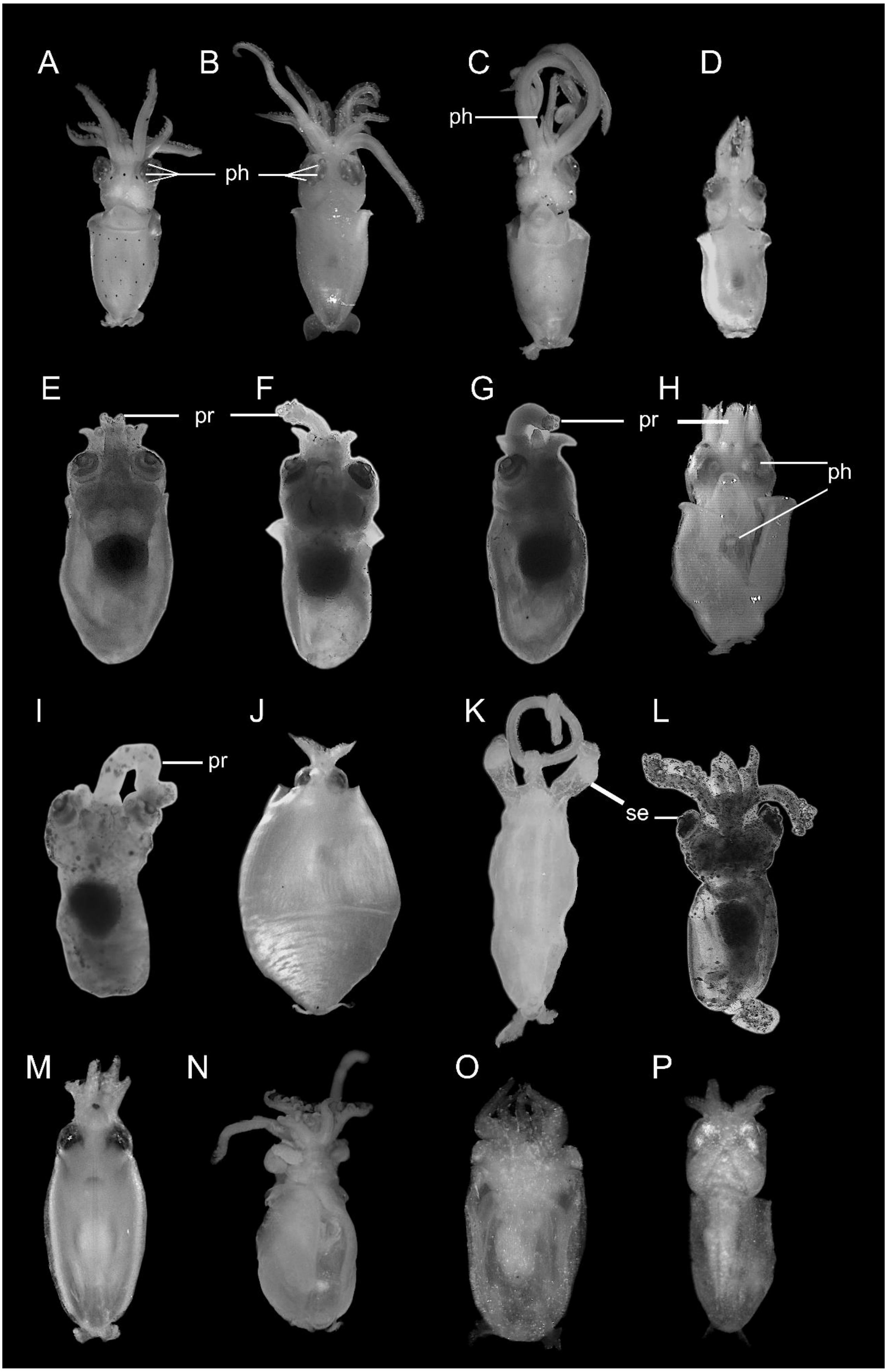

Figure S1: Cephalopod paralarvae of Campos Basin, orders Oegopsida and Myopsida (squids): (A) *Abralia* spp., ML 2.5 mm, ventral view. (B) *Abralia* spp., ML 3.8 mm, ventral view. (C) *Abraliopsis* spp., ML 3.0 mm, ventral view. (D) Enoploteuthidae indeterminate, ML 1.2 mm, ventral view. (E) Rhynchoteuthion Type A, ML 1.3 mm, ventral view. (F) Rhynchoteuthion Type B, ML 1.0 ML, ventral view. (G) Rhynchoteuthion Type C, ML 1.8 ML, dorsal view. (H) *Hyaloteuthis pelagica*, ML 4.0 mm, ventral view. (I) *Sthenoteuthis pteropus*, ML 0.8 mm, dorsal view. (J) *Liocranchia* sp., ML 4.0 mm, ventral view. (K) *Megalocranchia* spp., ML 8.5 mm, ventral view. (L) *Octopoteuthis* sp., ML 2.4 mm, dorsal view. (M) *Onychoteuthis* spp., 1.7 mm ML, dorsal view. (N) *Ancistrocheirus* cf. *lesueurii*, ML 1.9 mm, dorsal view. (O) *Thysanoteuthis* sp., ML 2.0 mm, dorsal view. (P) Loliginidae indeterminate, ML 3.2 mm, dorsal view. ph = photophore; pr = proboscis; se = stalked eyes.

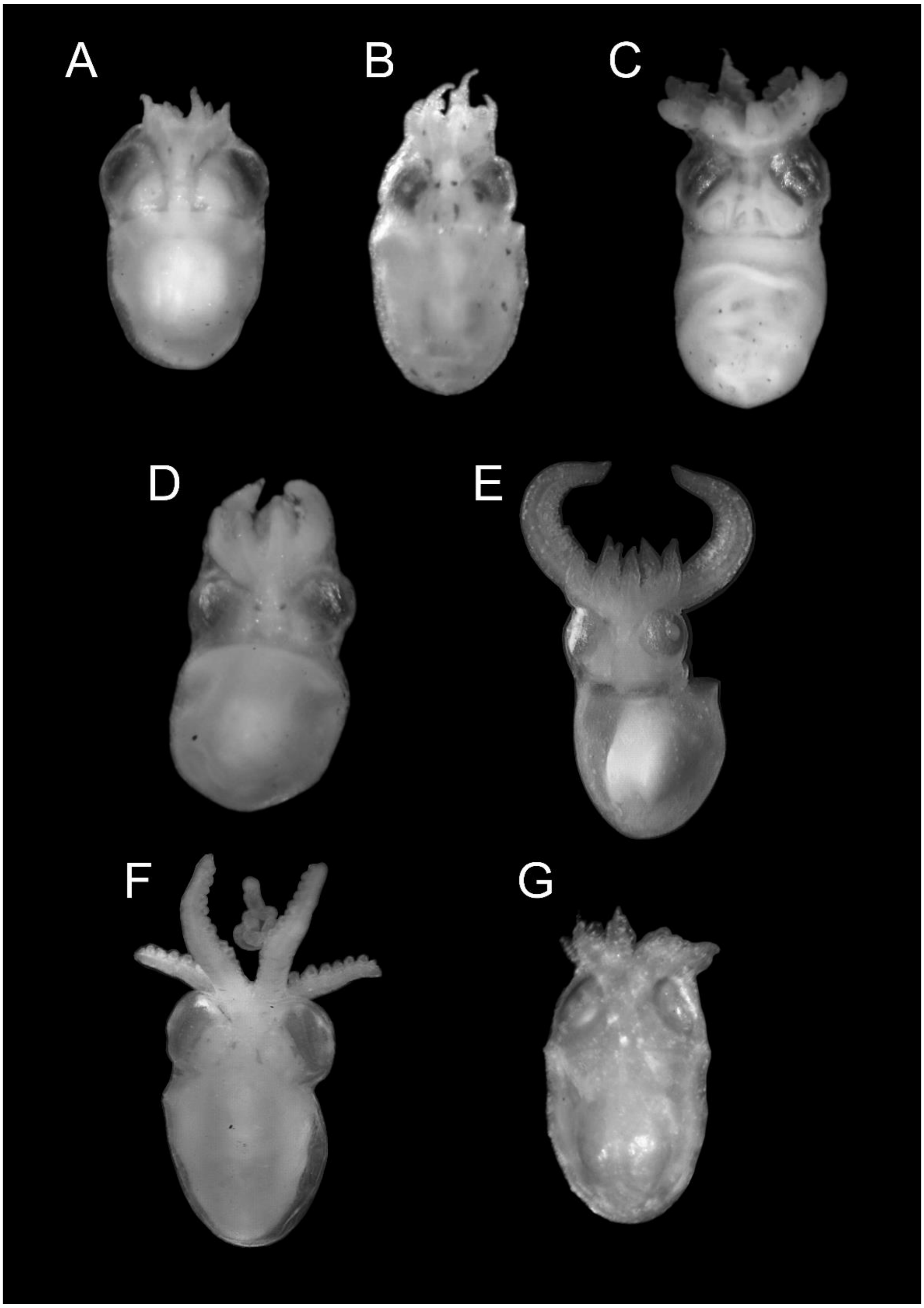

Figure S2: Cephalopod paralarvae of Campos Basin, order Octopoda (octopus): (A) *Argonauta* spp., ML 1.3 mm. (B) Octopodidae indeterminate, ML 1.3 mm. (C) Octopodidae indeterminate, ML 2.5 mm. (D) *Macrotritopus* spp., ML 1.8 mm. (E) *Macrotritopus* spp., ML 3.7 mm. (F) *Tremoctopus* spp., ML 4.3 mm. (G) Octopoda Incirrata indeterminate, ML 1.6 mm. All with dorsal view.

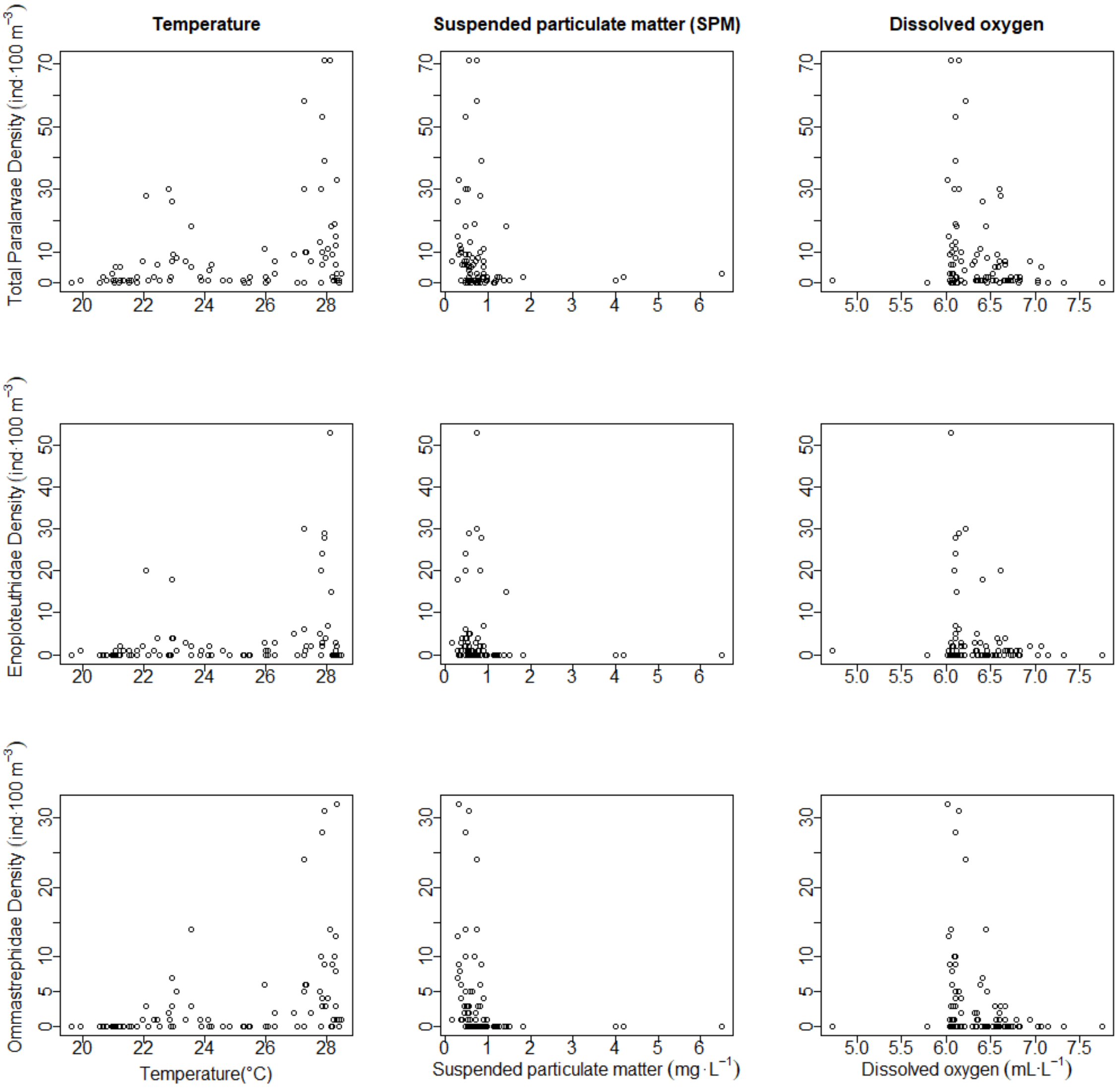

Figure S3: Total paralarvae, Enoploteuthidae and Ommastrephidae densities (individuals per 100 m^3) related to temperature, suspended particulate matter (SPM) and dissolved oxygen.