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# Amazon river plume influence on planktonic decapods in the tropical Atlantic

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Abstract:

The western tropical Atlantic is strongly influenced by the Amazon, receiving the full discharge from the largest river basin of the world. In order to ascertain the coastal-oceanic gradient in abundance and composition of planktonic decapod communities along the Amazon River Plume (ARP) and its retroflection, 33 plankton samples were obtained along three sampling transects: Coastal and oceanic area influenced by the ARP (**Coastal IARP** and **Ocean IARP**, respectively), and oceanic waters without ARP influence (**Ocean**). A total of 13,117 specimens, belonging to 33 taxa, were analyzed. The distribution of planktonic decapod communities was strongly influenced by the Amazon discharge, showing the following patterns: (1) The coastal-oceanic gradients in decapod abundance are similar to other shelf areas of eastern South America, with higher abundance in the area under ARP influence, (2) meroplanktonic decapods dominate in coastal and some oceanic areas due to the offshore transport of coastal organisms along the ARP retroflection, and (3) the ARP is clearly responsible for the observed differences in community structure between the three transects. Furthermore, this study highlights the importance of coastal and shelf environments as main sources of planktonic decapods for pelagic ecosystems in the tropical Atlantic during the period of strong North Brazil Current retroflection.

**Keywords:** Decapod crustacean larvae    Amazon River-Ocean Continuum    North Brazilian Current retroflection    Western tropical Atlantic    Mesoscale distribution

## 1. Introduction

The discharges of large tropical rivers have a huge influence on adjacent coastal waters, mainly due to the transfer of sediments from the continent, changes in nutrient dynamics and the input of organic matter. All these mechanisms together can change the physical-chemical properties of coastal marine environments and consequently affect their biological communities (Nixon et al., 1986; Meade, 1996; Dagg et al., 2004; Wu et al., 2017).

The Amazon river basin, the world's largest hydrographic basin, enriches not only the coastal area, but also the adjacent oceanic region of the retroflection of the North Brazilian Current (NBC) through complex hydrological processes that transport the Amazon buoyant plume offshore (Araujo et al., 2017; Varona et al., 2019). The NBC retroflection is associated with changes in trade wind patterns (south-easterly trades), migration of the Intertropical Convergence Zone (ITCZ) and geostrophic gyres, jointly with the period of major discharge at the Amazon river mouth and more intense flow of the strong NBC

(Csanady, 1985; Lentz, 1995a; Lentz, 1995b). As the wind stress increases, it creates an eastward water counter flow that feeds the North Equatorial Countercurrent (NECC) along the tropical Atlantic (Busalacchi and Picaut, 1983; Philander and Pacanowski, 1986). This complex current dynamics also generates a series of anticyclonic eddies ranging from 400 to 500 km diameter, which are displaced north-westwards and are responsible for part of the water mass transport between the South and North Atlantic Ocean (Johns et al., 1990; Hu et al., 2004). Upwelling events associated with anticyclonic eddies (Muller-Karger et al., 1988; Woods, 1988), can increase the nutrient supply in the ARP, favoring the occurrence of phytoplankton blooms and consequently an increase in the productivity of zooplankton communities (Muller-Karger et al., 1995; Carpenter et al., 1999; Subramaniam et al., 2008; Goes et al., 2014; Conroy et al., 2016, 2017).

One of the key features of zooplankton in tropical coastal waters under estuarine influence is the high abundance of decapod larvae (Schwamborn et al., 1999; Brandão et al., 2015). This group of organisms is an important component of zooplankton communities in

many tropical marine environments, such as coastal areas lined by extensive mangrove forests, such as on the north Brazilian shelf. In these environments, the exportation of meroplanktonic decapod larvae from mangroves to the open shelf is significant, since these habitats act as nurseries for several brachyuran and anomuran crabs species, penaeidean and caridean shrimps, and axiidean and gebiidean mud shrimps (Schwamborn et al., 1999; Kathiresan and Bingham, 2001). However, previous studies on the north Brazilian shelf influenced by the ARP and NBC retroflection indicated a low abundance of decapod larvae and a dominance of holoplanktonic decapods, mainly represented by holoplanktonic shrimps of the families Luciferidae and Sergestidae (Melo et al., 2014; Conroy et al., 2016; Neumann-Leitão et al., 2018). A dominance of holoplanktonic decapod shrimps is usually reported from oceanic areas without any estuarine influence (Judkins, 2014). Thus, the abundance ratio of meroplanktonic/holoplanktonic decapods may be useful as an indicator of estuarine influence.

Hydrological processes on micro- and mesoscale, such as eddies and fronts, are described by many studies as important for the enhanced abundance, dispersion and retention of decapod larvae (McConaughy, 1992; Epifanio and Garvine, 2001; Queiroga and Blanton, 2005; Landeira et al., 2017; Brandao et al., 2020). These hydrological processes act directly on the abundance and distribution of planktonic communities and are potential factors that can cause disturbances on the coastal-oceanic gradient of plankton distributions. Usually, there is a gradient with higher abundance in coastal mesotrophic waters, as opposed to oligotrophic oceanic areas (Boltovskoy et al., 1999; Lopes et al., 2006).

Accordingly, a previous study on holoplanktonic luciferid shrimps (Melo et al., 2014) showed that their abundance decreased substantially along a gradient from the coast towards offshore waters, on the North Brazilian Shelf. Other studies of decapods in the study area were conducted by Cavalcante et al. (2012), de Oliveira et al. (2012), Carvalho et al. (2013) and Nóbrega et al. (2014). Nevertheless, most of these studies were carried out on the continental shelf close to the Amazon River mouth, and there are few published studies in oceanic areas near the shelf break and slope (Melo et al., 2014) or following the ARP (Calef and Grice, 1967; Conroy et al., 2016, 2017). Therefore, a possible influence of small estuaries and spatial fluctuations on abundance of planktonic decapods in the Amazonian shelf influenced by ARP remain undescribed. Furthermore, there is no published information available on a possible large-scale transport of ARP decapods across the NBC retroflection into the oceanic waters of the Tropical Atlantic.

The present study provides, for the first time, a detailed description of the composition and spatial variability of planktonic decapods at coastal and oceanic areas influenced by the ARP and the NBC retroflection. The main objective was to test the hypothesis that the ARP has a significant influence on the abundance and community structure of planktonic decapods in these areas.

## 2. Material and methods

### 2.1. Study area

This study was conducted in the North (Pará and Amapá states) and Northeastern (Ceará state) coastal and oceanic regions of Brazil. The Northern Brazilian continental shelf and adjacent oceanic waters are under the influence of the large Amazon and Tocantins river basins, corresponding to the discharge of the Amazon and Pará rivers in to the western tropical Atlantic.

The Amazon river basin is the largest of the world, with an input of  $206,000 \text{ m}^3 \text{ s}^{-1}$ , equivalent to 17% of all freshwater discharge into the world's oceans (Callède et al., 2010). The dominant climates are equatorial rainforest, fully humid (Af) and equatorial monsoon (Am) (Köppen-Geiger classification system) with rainfall during all months of

the year and the absence of a well-defined dry season (Kottek et al., 2006; Peel et al., 2007).

Due to the difference in density between freshwater and marine waters, a large-scale surface plume is formed when the Amazon reaches the ocean. This huge plume carries a large amount of sediments, nutrients and organic matter that are transported by complex currents, thousands of kilometers offshore, exceeding distances of 3000 km into the open ocean (Hu et al., 2004). These plume waters are characterized, in the oceanic province, by salinities lower than 35. Tides are an important factor acting in the mixing between plume and oceanic waters (Muller-Karger et al., 1988; Varona et al., 2019). The Amazon river discharge shows a characteristic seasonal pattern in consequence of changes in rainfall across the basin, with a maximum in discharge between late May to early June and a minimum in mid-November, at the river mouth (Lentz, 1995b).

The NBC flows along the shelf in northwestward direction and intercepts the Amazon and Pará waters, transporting the ARP along the north Brazilian continental shelf. However, due to the NBC retroflection (July to November) and consequent NECC intensification, the ARP is dragged out from the shelf into the oligotrophic tropical Atlantic. There, the ARP waters boost planktonic production due to the transported nutrients (Carpenter et al., 1999; Del Vecchio and Subramaniam, 2004; Subramaniam et al., 2008; Chong et al., 2014) (Figs. 1 and 2a).

### 2.2. Sampling strategy

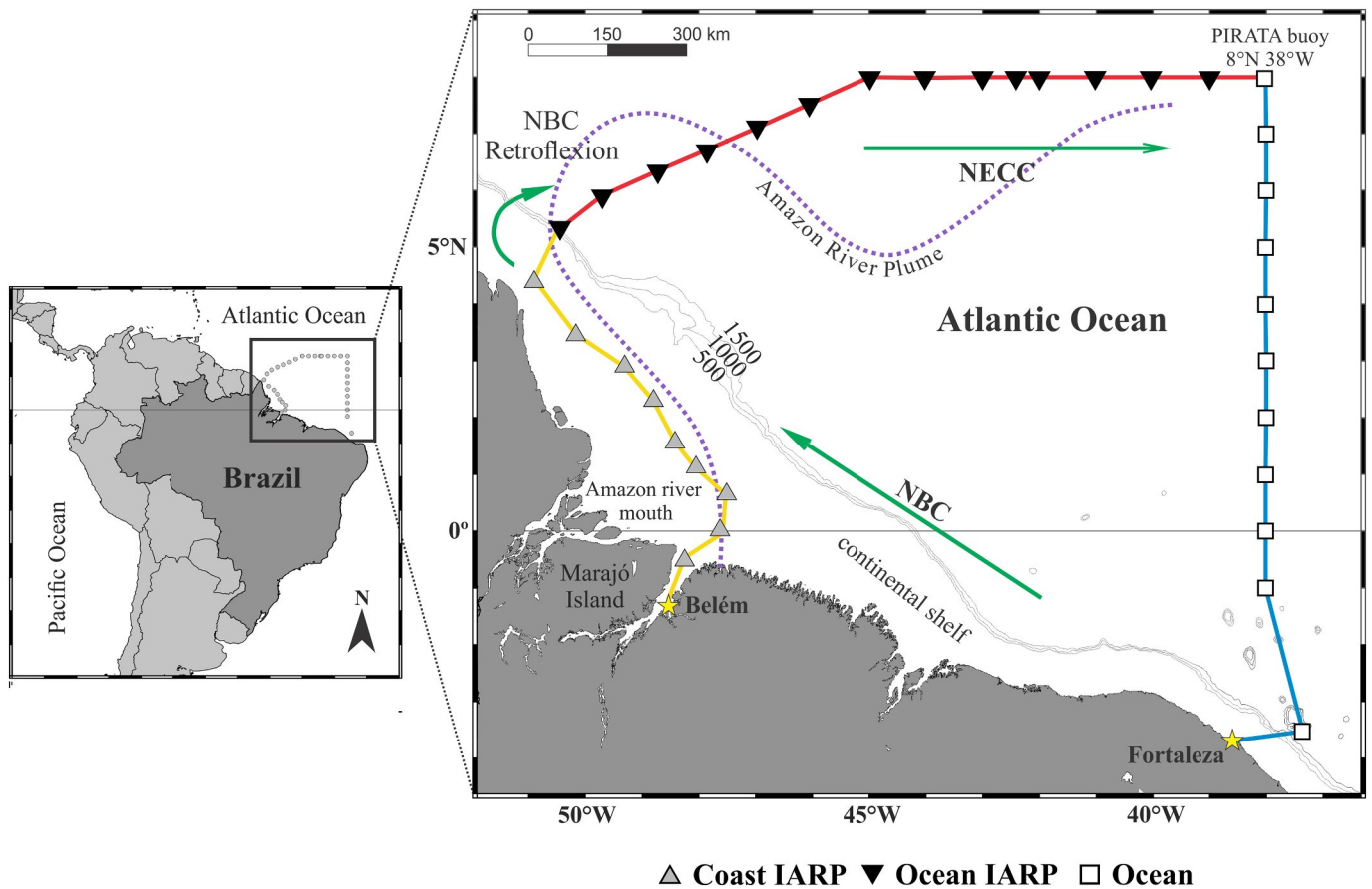
Zooplankton sampling was carried out in the context of the "Camadas Finas III" cruise, from Belém to Fortaleza, from October 13th to November 1st, 2012, on board NHO. Cruzeiro do Sul (H-38, Brazilian Navy). Sampling stations were previously defined based on a satellite image showing the chlorophyll-a distribution along the Amazon River Plume. The cruise track followed the NBC along the northern border of the North Brazilian shelf, then leading offshore towards northeast until reaching 8°N latitude. From this latitude, the cruise followed the NECC along 8°N until reaching the PIRATA buoy station at 8°N38°W (Bourlès et al., 2019). From there, the cruise followed straight southwards (Fig. 1), towards the city of Fortaleza (Ceará State, Brazil).

Samples were collected along three transects: Coastal transect influenced by the Amazon River Plume (**Coastal IARP**), with 9 stations; Oceanic transect influenced by the Amazon River Plume (**Ocean IARP**) with 14 stations; and Oceanic transect without an influence of the Amazon River Plume (**Ocean**), with a total of 11 stations. Samples were taken at different times of the day ( $n = 18$ ) and night ( $n = 16$ ), following a continuous trajectory (Coastal IARP: 6 daytime and 3 nighttime stations; Ocean IARP: 6 daytime and 8 nighttime stations; Ocean transect: 6 daytime and 5 nighttime stations). Local depth ranged from 9.2 to 65 m on the shelf and 1830 to 4816 m in the oceanic area.

At each station, oblique tows were carried out from the surface to 200 m (or 90% of local depth at shallow stations), using Bongo nets with 60 cm diameter and 300  $\mu\text{m}$  mesh size, equipped with a Hydro-Bios (Kiel, Germany) flowmeter. The duration of the tows varied from 6 to 9 min at coastal stations and from 20 to 30 min at oceanic stations. At the most shallow station, a subsurface horizontal tow was conducted with a standard plankton net of the same mesh size, during 6 min, because of the extremely shallow depth in Marajó Bay. All samples were fixed with 4% formaldehyde buffered with sodium tetraborate ( $0.5 \text{ g L}^{-1}$ ).

### 2.3. Environmental data

During fieldwork, in situ temperature and salinity profiles were obtained at each station with a CTD (Seabird 25). Discrete values were used at two different water layers: surface and depth of the chlorophyll a maximum (DCM). Results of extensive hydrodynamic simulations using the Regional Ocean Modeling System model (ROMS)



**Fig. 1.** Map of the study area and cruise route showing the sampling stations located along three transects: Coastal area influenced by the Amazon River Plume (yellow line); Oceanic area influenced by the Amazon River Plume (red line); and Oceanic area without influence of the Amazon River Plume (blue line). Green arrows indicate the current flow direction: North Brazil Current (NBC); NBC retroflexion and North Equatorial Countercurrent (NECC). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(Shchepetkin and McWilliams, 2005) were used to analyze plankton abundance in relation to the behavior of abiotic factors, taken from Varona et al. (2019). Monthly and seasonal climatological patterns of currents, temperature and salinity were simulated. The region was spatially discretized with a spatial resolution of  $0.25^\circ$  and 32 vertical levels from a bathymetry of 2 min resolution and concentrating the 20 higher levels in the first 500 m. Surface forcings were taken from a weekly climatology of the Comprehensive Ocean Atmosphere Dataset 2005 (COADS), initial conditions and lateral boundaries were obtained from the World Ocean Atlas 2009 (WOA).

#### 2.4. Laboratory work

Most samples were analyzed in toto. Some coastal samples with very large decapod abundances were analyzed in fractions containing ~300 decapods using a Motoda Splitter (Omori and Ikeda, 1984). Planktonic decapods were identified to the lowest taxonomic level possible (except for the infraorder Brachyura), using standard literature and larval descriptions, such as Kurata (1970); Calazans (1993); Dos Santos et al. (2004); Fernandes et al. (2006) and Martin et al. (2014).

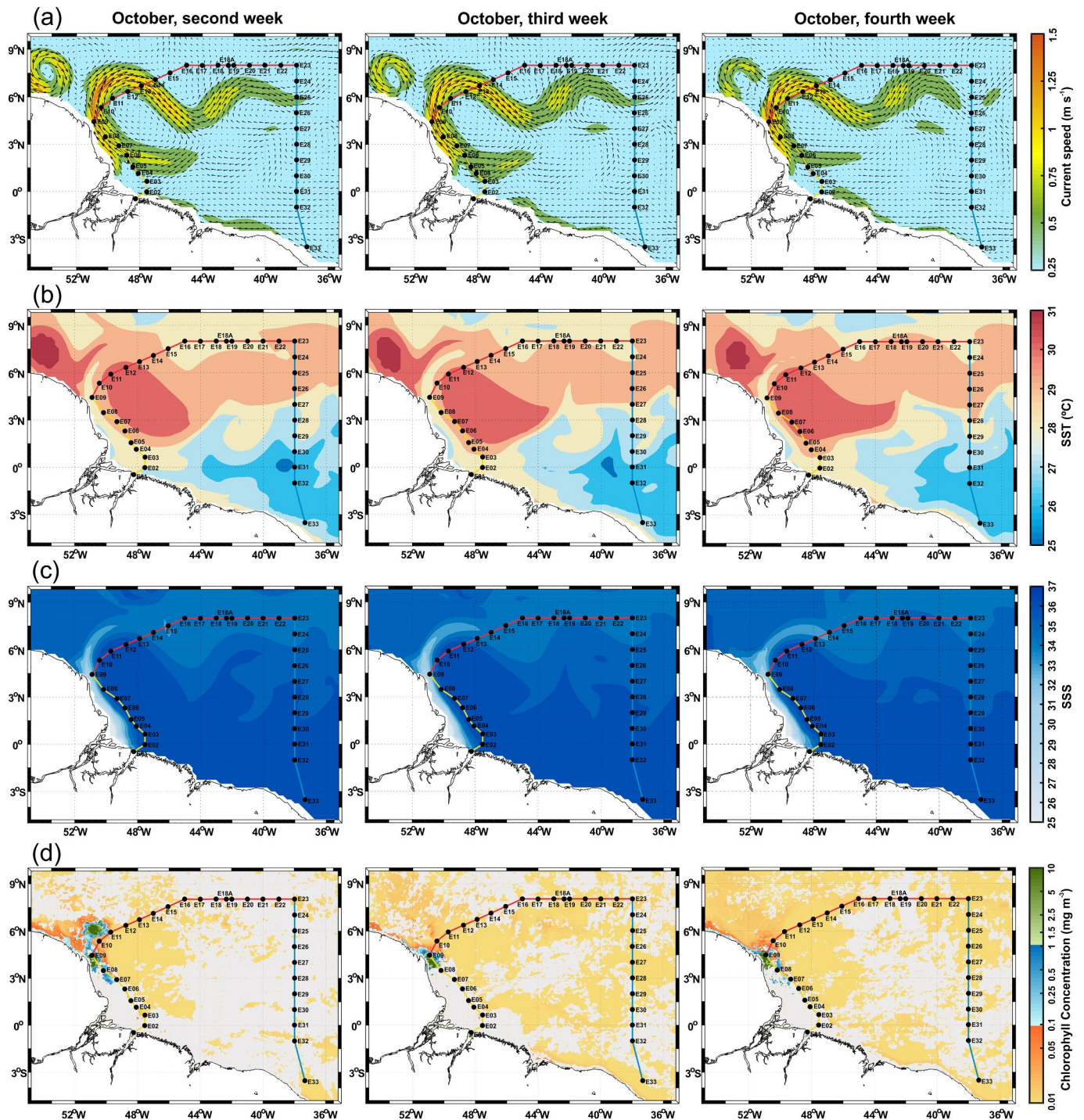
#### 2.5. Data analyses

Decapod abundance was expressed in individuals per  $100 \text{ m}^3$  (ind.  $100 \text{ m}^{-3}$ ) of filtered water. The abundance data of all taxa were used to calculate the relative abundance (RA) and frequency of occurrence (FO) of each taxon. Abundance data were used to calculate the meroplankton/holoplankton ratio.

All data were classified according to transect (Coastal IARP vs Ocean IARP vs Ocean) and period of the day (day vs night). Total abundances were  $\log_{10}(x + 1)$ -transformed to improve the normality and homoscedasticity of the data. Normality was tested by means of a Kolmogorov-Smirnov test and homoscedasticity was tested with Levene's test (Zar, 1999).

ANOVA one-way or Kruskal-Wallis ANOVA were used with post-hoc comparisons (Tukey or Mann-Whitney tests, respectively), to test possible differences between factors (spatial and day/night) in total abundance, for main taxa (with > 2% of relative abundance) and for meroplankton/holoplankton ratios. A similarity matrix (between samples) was created using the Bray-Curtis index (Bray and Curtis, 1957), based on square-root transformed abundances. This similarity matrix was used for non-metric multidimensional scaling (nMDS) ordination plots (Clarke and Warwick, 2001), and for a multivariate PERMANOVA, to test differences in community structure between factors (Anderson, 2001). SIMPER (Clarke and Warwick, 2001) was carried out to identify the taxa responsible for differences between groups. To verify the existence of characteristic species (i.e., bioindicators) for each sampling transect and the ARP influence area, the Indicator Value (IndVal) analysis (Dufrene and Legendre, 1997) was conducted, based on specificity and fidelity of each taxon in relation to the spatial factor.

All analyses mentioned above were performed using the R (v. 3.2.5) statistical environment (available at <https://cran.r-project.org/>) through the RStudio (v. 0.99) user interface (available at <http://www.rstudio.com/>). Redundancy Analysis (RDA) was used to evaluate how spatial and environmental factors may influence the planktonic decapod community structure, using the CANOCO software (Legendre and



**Fig. 2.** Weekly variability of environmental conditions during October in the Western Tropical Atlantic. (a) variability of surface current dynamics; (b) variability of sea surface temperature (SST) °C; (c) variability of sea surface salinity (SSS); (d) variability of chlorophyll a concentration ( $\text{mg}^3\text{m}^{-3}$ ) obtained from MODIS (Moderate-Resolution Imaging Spectroradiometer) in October 2012 (available from <http://oceancolor.gsfc.nasa.gov/>). Sampling transects indicated by colored lines: Coastal IARP (yellow); Oceanic IARP (red); and Oceanic area without ARP influence (blue). Climatology data source (a, b and c): Varona et al. (2019). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Gallagher, 2001). Abundance data of the main taxa were Hellinger-transformed previous to RDA.

### 3. Results

#### 3.1. Environmental conditions

Surface currents during boreal mid-autumn showed a well-defined

anticyclonic meandering ring in the NBC retroflexion region, that deflects the Amazon River Plume towards the open ocean (Fig. 2a). The retroflexion water flow presented higher values in the second week during the early October (Fig. 2a). Anticyclonic eddies originated from the retroflexion were dislocated northwestwards towards the Caribbean Sea. The Amazon mouth area was mainly under the influence of high-speed coastal waters from Brazilian Current and oceanic currents flowing westward contributing to the maintenance of Amazon waters

**Table 1**

Variation (mean  $\pm$  standard deviation) of environmental parameters (temperature and salinity) in the superficial layer (surface) and deep chlorophyll maximum layer (DCM), during the sampling period.

	Temperature ( $^{\circ}$ C)			Salinity (psu)		
	Coastal IARP	Ocean IARP	Ocean	Coastal IARP	Ocean IARP	Ocean
Surface	28 $\pm$ 0.2	28.9 $\pm$ 0.8	27.5 $\pm$ 0.7	33.4 $\pm$ 6.1	34.7 $\pm$ 1.4	35.8 $\pm$ 0.6
DCM	27.1 $\pm$ 1.3	25.5 $\pm$ 2.7	25.8 $\pm$ 1	36.4 $\pm$ 0.3	36.2 $\pm$ 0.2	36.3 $\pm$ 0.1

close along the coast until the retroflection latitude. In oceanic areas, the surface water flow is more intense in NECC meandering transport and cyclonic and anticyclonic eddies of smaller size are present along all NECC pathway stream (Fig. 2a).

The western tropical Atlantic showed great variability in surface temperature and salinity within this short time period, due to the complex distribution of ARP influence and current dynamics. Sea Surface temperature (SST) varied from a minimum of 26.5  $^{\circ}$ C at station E33 to maximum of 29.7  $^{\circ}$ C at station E22 (Table 1). In the deep chlorophyll maximum layer (DCM) the mean temperature varied from a minimum of 17.5  $^{\circ}$ C at station E20 to maximum of 28.2 $^{\circ}$  at station E02. Since the DCM deepens at most oceanic stations, its temperature decreases towards the oceanic transects influenced and without influence of the ARP (Table 1). A warm pool of SST was observed, concentrated in the region of the NBC retroflection and inside of retroflection-originated eddies (Fig. 2b).

Sea Surface Salinity (SSS) varied from estuarine plume conditions with a minimum of 18.1 at the mouth of the Par River (station E01) to typically oceanic salinities, generally found at most oceanic stations (maximum of 37 at station E02). At the DCM, salinity varied from a minimum of 35.8 at station E17 to maximum of 37 at station E02. Generally, the variation of salinity was greater in the Coastal IARP and Ocean IARP area due to the strong ARP influence (Table 1; Fig. 2c).

The distribution of surface chlorophyll-a (Chl-a) concentrations from MODIS (Moderate-Resolution Imaging Spectroradiometer) data, observed in October 2012, showed that highest values were recorded in the coastal region, mainly in the NBC retroflection ring area, close to stations E07, E08, E09 and E11. Chl-a values tend to decrease along the NECC stream, being considerably lower in the oceanic transect without influence, than in those directly influenced by the ARP (Fig. 2d).

### 3.2. Taxonomic composition and abundance

In this study 13,117 specimens of planktonic decapods were analyzed, belonging to 33 taxa (Supplementary Table 1). Seventeen taxa were present in all transects, three taxa were only found at coastal stations (Penaeoidea nauplii; Upogebiidae and Porcellanidae zoeae) and 11 taxa only at oceanic stations (Aristeidae; Sergestidae protozoeae; Caridea morphotype I; Spongicolidae; Stenopodidae; *Amphionides reynaudii* larvae; Oplophoroidea; Lysmatidae; Axiidae; Enoplometopidae and Galatheidae). The coastal and oceanic area influenced by the ARP showed four exclusive taxa (Solenoceridae protozoeae; *Acetes* protozoeae; Anomura and Paguridae). Only one taxon (Bresiliidae) was exclusive for the oceanic area without ARP influence. Total abundance of planktonic decapods in the present study showed a mean of 4445  $\pm$  12,444 ind. 100 m<sup>-3</sup>, varying between 765 ind. 100 m<sup>-3</sup>, at station E28, to 66,527 ind. 100 m<sup>-3</sup> at station E10.

At the **Coastal IARP** transect, total abundance of decapods presented a mean of 9137  $\pm$  8691 ind. 100 m<sup>-3</sup>, ranging from 765 ind. 100 m<sup>-3</sup> (station E04) to a maximum of 28,986 ind. 100 m<sup>-3</sup> (station E09). The most abundant taxa at the **Coastal IARP** were Brachyura (zoeae): 2307  $\pm$  2292 ind. 100 m<sup>-3</sup> (25.3%), Luciferidae (protozoeae): 1825  $\pm$  3490 ind. 100 m<sup>-3</sup> (19.9%); Luciferidae: 1534  $\pm$  2084 ind. 100 m<sup>-3</sup> (16.8%); Palaemonidae: 869  $\pm$  1579 ind. 100 m<sup>-3</sup> (9.5%); and Callianassidae: 625  $\pm$  1279 ind. 100 m<sup>-3</sup> (6.8%).

At the **Ocean IARP** transect, total abundance of decapods presented a mean of 4889  $\pm$  17,741 ind. 100 m<sup>-3</sup>, ranging from 16.8 ind. 100 m<sup>-3</sup>

(station E18) to 66,527 ind. 100 m<sup>-3</sup> (station E10) (Fig. 3). There, the most abundant taxa were: Luciferidae: 1141  $\pm$  4194 ind. 100 m<sup>-3</sup> (23%); Brachyura (zoeae): 1107  $\pm$  4113 ind. 100 m<sup>-3</sup> (22%); Callianassidae: 533  $\pm$  1972 ind. 100 m<sup>-3</sup> (10.9%); Luciferidae (protozoeae): 406  $\pm$  1492 ind. 100 m<sup>-3</sup> (8.3%), and Palaemonidae: 364  $\pm$  1324 ind. 100 m<sup>-3</sup> (7.5%).

At the **Ocean** transect, total abundance of decapods presented a mean of 74.3  $\pm$  22.8 ind. 100 m<sup>-3</sup>, range from 14.4 ind. 100 m<sup>-3</sup> (station E28) to 100.7 ind. 100 m<sup>-3</sup> (station E31) (Fig. 3). There, the most abundant taxa were: Sergestidae (protozoeae): 7.2  $\pm$  8.2 ind. 100 m<sup>-3</sup> (17.8%); Callianassidae: 6.8  $\pm$  8.1 ind. 100 m<sup>-3</sup> (16.8% RA); Penaeoidea (protozoeae): 3.2  $\pm$  4.2 ind. 100 m<sup>-3</sup> (8.0%); Luciferidae: 3.1  $\pm$  1.5 ind. 100 m<sup>-3</sup> (7.6%), and Luciferidae (protozoeae): 2.7  $\pm$  6.5 ind. 100 m<sup>-3</sup> (6.7%).

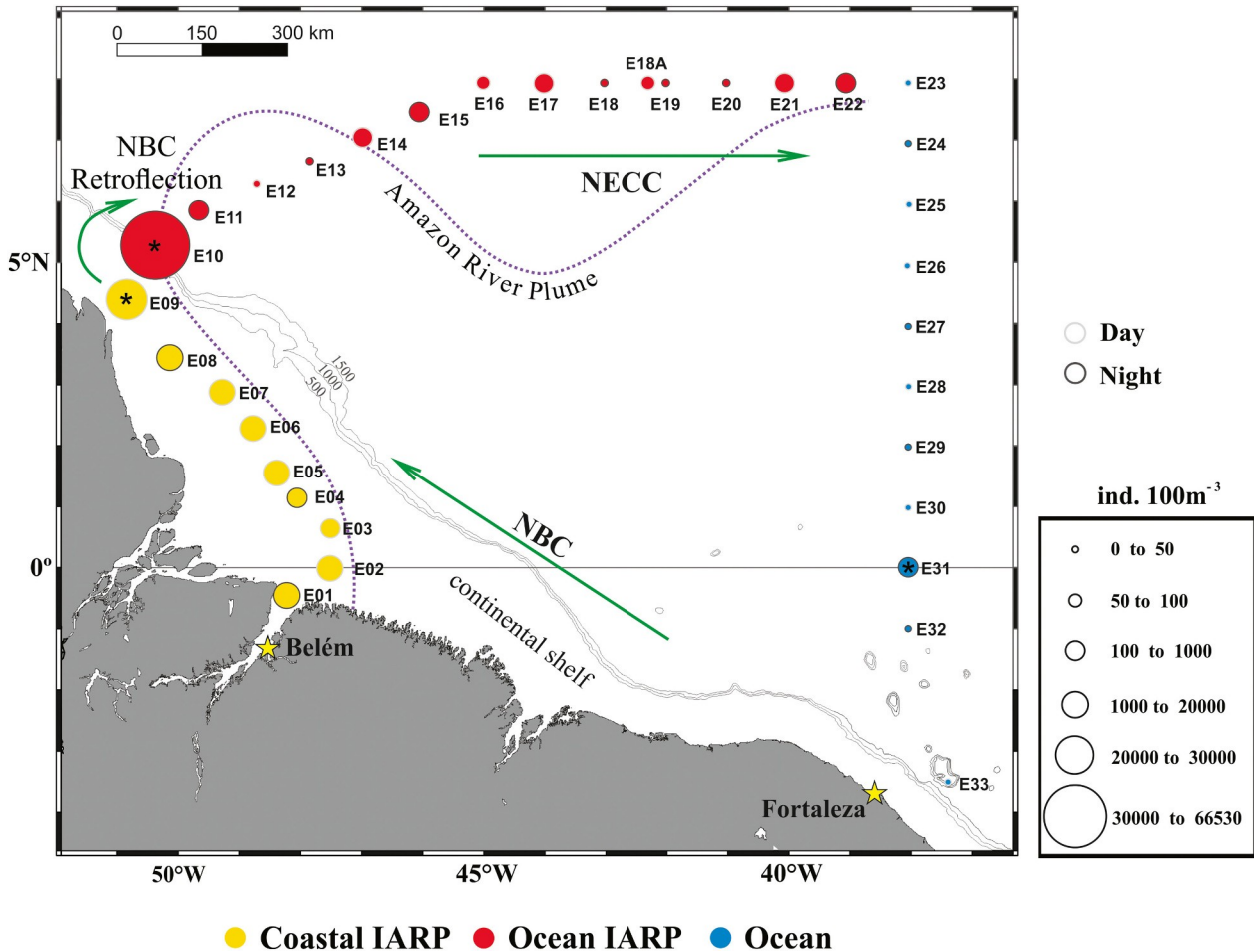
One striking feature of the distribution of decapods was the abundance peak recorded at station E10 of the Ocean IARP transect, located at the shelf break of the northern Brazilian shelf. Decapod abundance was twice as large as observed at station E09 and 28 times higher than at station E31, the stations with the greatest abundance at the Coastal IARP and Ocean transects, respectively (Fig. 3).

Overall, luciferid shrimps were the most abundant decapods (adults and larvae: 1528  $\pm$  4619 ind. 100 m<sup>-3</sup>, all stations), contributing with 34.4% of decapod abundance. Considering life history stages separately, the most abundant groups were brachyuran zoeae, with an average abundance of 1067  $\pm$  2956 ind. 100 m<sup>-3</sup> (24%), luciferid adults with 876  $\pm$  2895 ind. 100 m<sup>-3</sup> (19%) and luciferid protozoeae with 651  $\pm$  2091 ind. 100 m<sup>-3</sup> (14%), Callianassidae 387  $\pm$  1415 ind. 100 m<sup>-3</sup> (8.7%) and Palaemonidae with 380  $\pm$  1187 ind. 100 m<sup>-3</sup> (8.6%). All values of abundance, relative abundance and frequency of occurrence of decapods specimens per transect are summarized in Supplementary Table 1.

### 3.3. Variability in abundance

Total abundance of planktonic decapods showed significant differences between transects ( $p < 0.001$ , one-way ANOVA, Fig. 4). Higher abundances of planktonic decapods were found in the coastal area under ARP influence (Coastal IARP) when compared to oceanic stations influenced (Ocean IARP) and not influenced (Ocean) by the ARP (Tukey tests,  $p = 0.001$ ). Nevertheless, station E10 in the Ocean IARP showed the highest abundance among all samples (Fig. 3, \*red circle). No differences in total abundance were observed between oceanic areas influenced and not influenced by the ARP. No differences in total abundance of decapods were observed in relation to the periods of day, whether pooling all data together or testing each transect separately ( $p > 0.05$  ANOVA one-way, Fig. 4). No significant interactions between spatial and day/night factors were observed.

Several taxa (with total RA  $> 2\%$ ) showed significant differences in abundance between transects: *Acetes* sp. (protozoeae) ( $p = 0.02$ ), Luciferidae ( $p = 0.0001$ ), Palaemonidae ( $p = 0.006$ ) and Brachyura (zoeae) ( $p = 0.0001$ ) showed higher abundances at the Coastal transect when compared to both offshore areas. Luciferidae (protozoeae) ( $p = 0.01$ ) and Caridea (others) ( $p = 0.02$ ) presented higher abundances at Oceanic stations influenced by ARP when compared to the Ocean transect without ARP influence. Diogenidae showed differences in abundance between all the transects ( $p = 0.002$ ), presenting higher



**Fig. 3.** Spatial distribution of total planktonic decapods abundance at the sampling stations located along transects influenced and not influenced by the Amazon River Plume. Yellow circles: Coastal area influenced by the Amazon River Plume (Coastal IARP); red circles: Oceanic area influenced by the Amazon River Plume (Ocean IARP); and blue circles: Oceanic area without Amazon River Plume influence (Ocean). Diameters of circles are proportional to the value of each respective abundance interval. Outlines of circles indicate sampling during the day (light gray) or night (dark gray). Surface currents are indicated by green arrows. \*: station of each transect with the highest abundance. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

abundance at Coastal stations and lower values at Ocean stations, particularly at the Ocean transect without ARP influence (Fig. 5, Supplementary data Table 1). No significant differences in abundance between day and night were found for any of the analyzed taxa (RA > 2%).

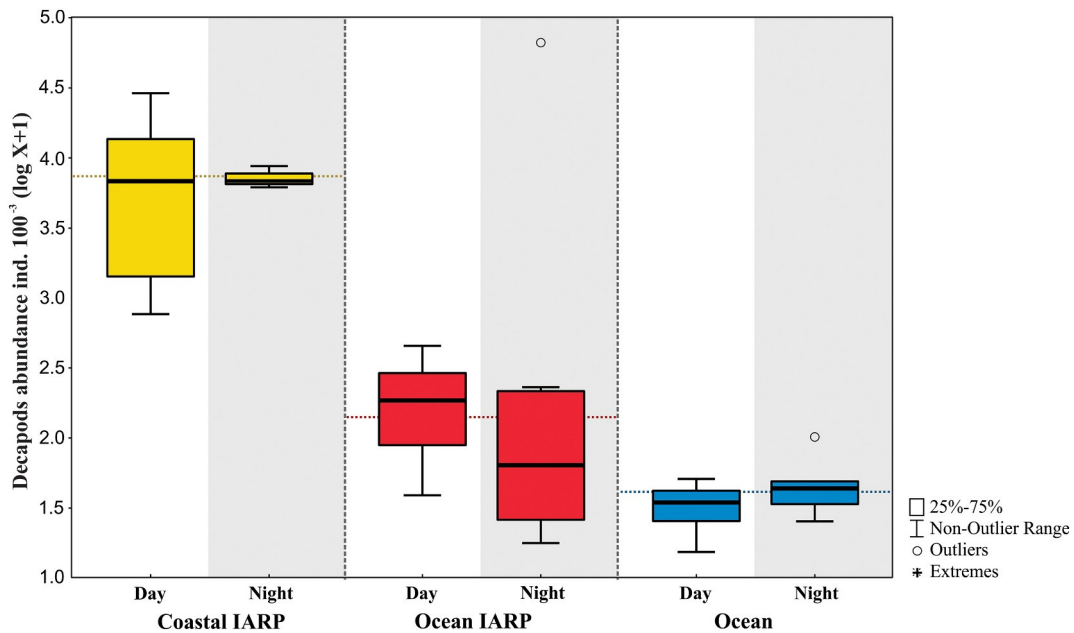
In both transects influenced by the ARP, the meroplankton / holoplankton ratio presented values > 1 (1.11 and 1.07 for the Coastal IARP and Ocean IARP respectively), indicating a major contribution of meroplanktonic decapods (e.g., larvae of brachyuran and anomuran crabs). Conversely, the oceanic area without ARP influence showed ratios lower than 1 (mean: 0.81 for the Ocean transect), indicating major contributions of holoplanktonic decapods (e.g., sergestid and penaeid shrimps) (Fig. 6). The meroplankton/holoplankton ratio did not display significant differences in relation to the spatial and day/night factors.

### 3.4. Community structure

The nMDS ordination revealed considerable differences in community structure between transects (Fig. 7). Samples taken at the coastal region influenced by the ARP showed a clear distinction from those collected at the oceanic transects, mainly in the oceanic region without ARP influence. The three first stations of the Ocean transect are clearly grouped with the Ocean IARP transect, indicating an influence of the ARP on these sampling stations. These differences in community

structure of planktonic decapods in relation to the spatial factor (transects) were confirmed by PERMANOVA. All pairwise PERMANOVA tests revealed differences between all sampling transects (Tables 2, 3). None of the tests performed regarding community structure indicated any differences between day and night (Table 2).

The SIMPER test showed average similarities of 37.1, 33.8 and 44.3 for transects Coastal IARP, Ocean IARP and Ocean, respectively. The main taxa responsible for the similarity were brachyuran zoeae (31.5%), Luciferidae (20.2%) and Palaemonidae (9.9%) for the Coastal IARP; Sergestidae (protozoae) (22.7%), Penaeoidea (protozoae) (16.6%), Luciferidae (15.3%) for the Ocean IARP; and Sergestidae (protozoae) (20.0%), Luciferidae (15.7%) and Callianassidae (11.5%) for the Ocean transect. Dissimilarities between sampling transects were very high (above 60%). The main taxa responsible for the dissimilarity between areas are summarized in Table 4. The IndVal analysis showed that some groups were indicative of a specific transect: Anomura (IndVal = 0.812,  $p = 0.005$ ), Pasiphaeidae (IndVal = 0.796,  $p = 0.005$ ), Solenoceridae (protozoae) (IndVal = 0.654,  $p = 0.045$ ) and Upogebiidae (IndVal = 0.577,  $p = 0.020$ ) were indicator taxa for the coastal transect influenced by the ARP. Spongicolidae (IndVal = 0.505,  $p = 0.05$ ) was the only taxon detected as indicator of the Ocean transect without ARP influence. Despite the Ocean IARP transect not showing any singular indicator taxa, the group consisting of transects under the ARP influence together (Coastal IARP and Ocean IARP) included Luciferidae (protozoae) (IndVal = 0.908,  $p < 0.01$ ),



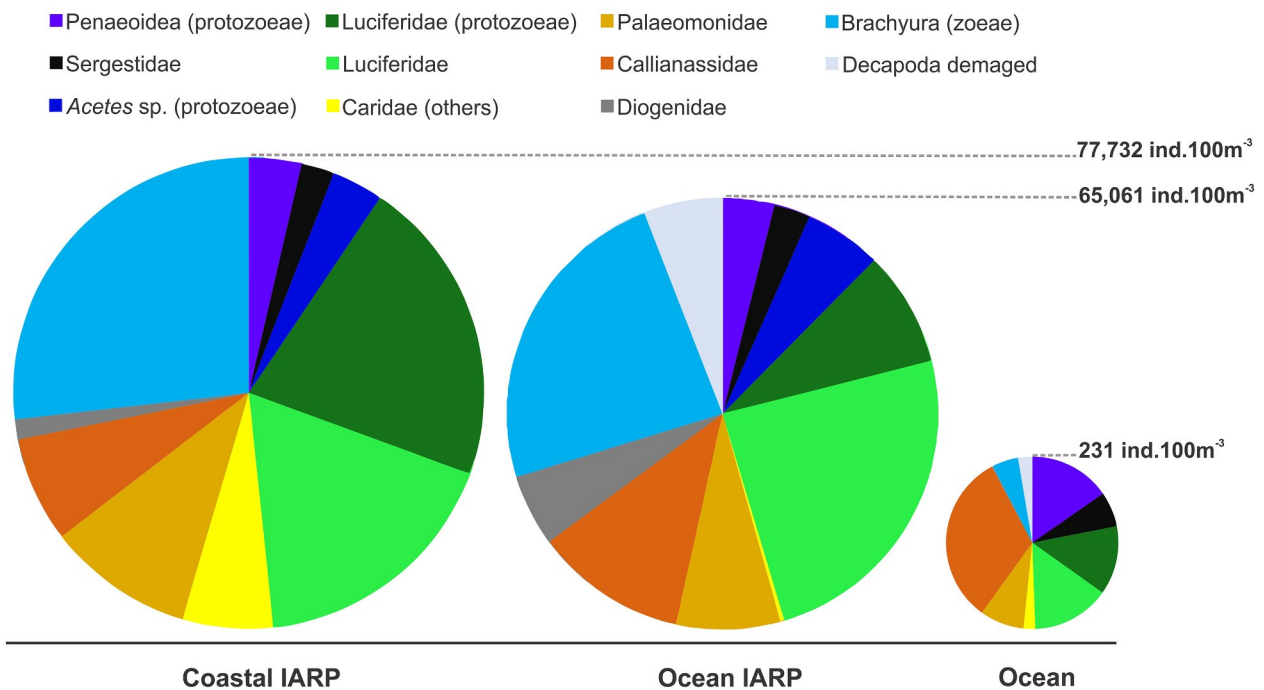
**Fig. 4.** Box-Plot (median and quartiles) of day/night spatial distribution of planktonic decapods total abundance (ind. 100 m<sup>-3</sup>) (log X + 1) in the sampling transects: Coastal area influenced by Amazon River Plume (Coastal IARP); Oceanic area influenced by Amazon River Plume (Ocean IARP); and Oceanic area without the Amazon River Plume influence (Ocean). The median of total abundance (day and night samples pooled together) per transect are indicated by horizontal dashed lines.

Brachyura (zoeae) (IndVal = 0.885, p < 0.01) and Diogenidae (IndVal = 0.725, p < 0.05) as indicator species. The indicator taxa for the group of ocean transects (Ocean IARP and Ocean, pooled together) were Sergestidae (protozoae) (IndVal = 1.000, p < 0.005) and Oplophoroidea zoeae (IndVal = 0.693, p < 0.020).

Redundancy Analysis (RDA) showed that 15% of the variance of the main taxa was explained by the spatial factor (transects) (RDA, p < 0.05) (Fig. 8). The Coastal IARP transect explained 10% of the variance (p < 0.05). Axis 1 was represented by ARP influenced areas,

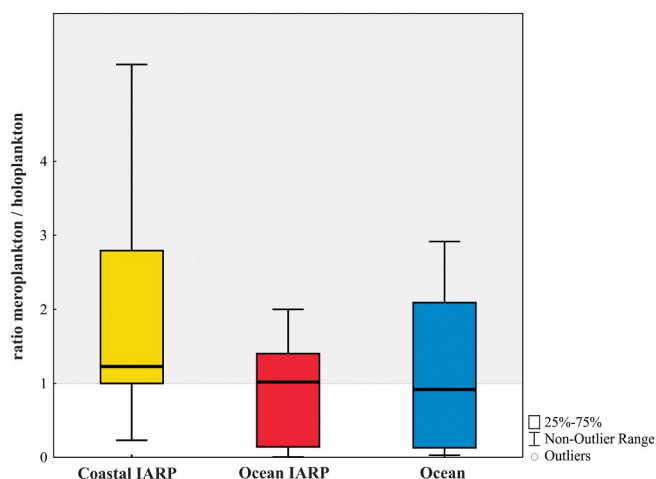
hence describing the relation between decapod assemblages with hyposaline and mesohaline waters with the high primary production of ARP, while Axis 2 was more related to the distance from the coast.

Two main groups were detected: one group mostly related to the transects influenced by ARP, composed mostly by coastal meroplanktonic decapods (Luciferidae protozoae; Diogenidae; Palaemonidae; brachyuran zoeae and other Carideans) and another group mostly related to the ocean area under ARP influence, composed mostly by oceanic holopelagic decapods (Penaetidae protozoae;



**Fig. 5.** Relative abundance of main decapod taxa (total RA > 2%) at three sampling transects: Coastal area influenced by Amazon River Plume (Coastal IARP); Oceanic area influenced by Amazon River Plume (Ocean IARP); Oceanic area without the Amazon River Plume influence (Ocean). The total abundance of main taxa is indicated by dashed lines.





**Fig. 6.** Boxplot (median and quartiles) representing the ratio of meroplankton: holoplankton abundance of planktonic decapods ( $\log X + 1$ ) at the sampling transects. The gray area (ratio  $\geq 1$ ) indicates samples with higher contribution of meroplankton. Coastal IARP: Coastal transect influenced by the Amazon River Plume; Ocean IARP: Ocean transect influenced by the Amazon River Plume; Ocean: Ocean transect without plume influence.

Sergestidae and Callianassidae). *Acetes* sp. protozoa larvae were more related to the Coastal IARP transect, while Luciferidae (post-larvae and adults) were more related to the Ocean IARP transect. Although callianassid zoeae showed greater abundances at the Coastal IARP and Ocean IARP transects, they were more related to the Ocean transect, due to the dominance in abundance, when compared to the other taxa in the area without ARP influence (Fig. 8).

#### 4. Discussion

This study brought new insights into the community structure of planktonic decapods and their spatial variation in coastal and oceanic waters influenced by the Amazon River Plume (ARP). A huge abundance of planktonic decapods was recorded in coastal and oceanic regions influenced by the ARP when compared to the oceanic region without the direct influence of the ARP. These results corroborate

**Table 2**

PERMANOVA results of the planktonic decapod community structure in relation to the spatial factor (sampling transects) and periods of day (day/night) along the Amazon River Plume.

Factor	df	MS	Pseudo-F	p
Spatial	2	13,048	6.9347	0.001
Day/night	1	1825.4	0.97014	0.468

**Table 3**

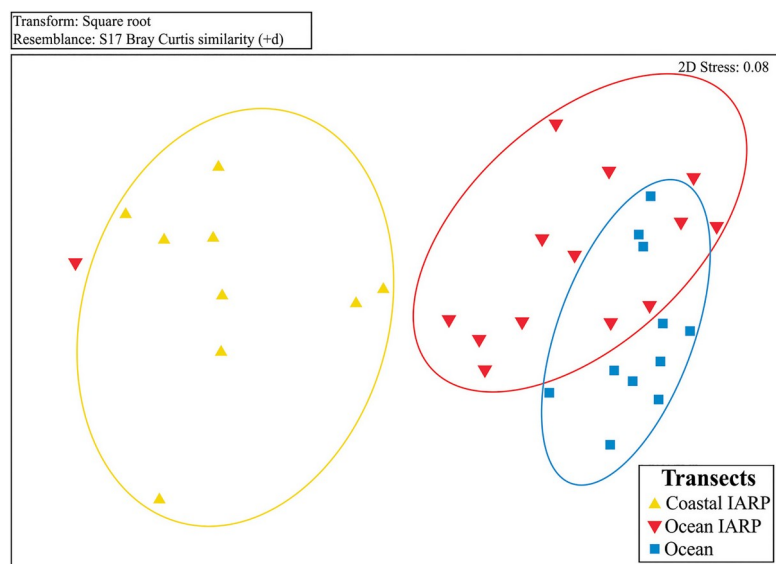
Pairwise PERMANOVA of planktonic decapod community structure between sampling transects along the Amazon River Plume. Coastal IARP: Coastal transect influenced by the Amazon River Plume; Ocean IARP: Ocean transect influenced by Amazon River Plume; and Ocean: Ocean Transect without the plume influence.

Groups	t	p
Coastal IARP, Ocean IARP	2.7001	0.001
Coastal IARP, Ocean	3.64	0.001
Ocean IARP, Ocean	1.5541	0.013

previous studies in the region that inferred this enormous plume as a true fertilizer for the oligotrophic waters of the western tropical north Atlantic, thus increasing planktonic productivity in this environment. Previous studies on planktonic decapods of the Amazon river mouth did not consider the oceanic waters of the NBC retroflection. Thus, this is the first study to investigate the distribution of planktonic decapods throughout the retroflection and oceanic region influenced by the ARP.

#### 4.1. Planktonic decapods as indicators of river plume influence

Generally, the influence of river plumes is studied by the analysis of physicochemical parameters (Chong et al., 2014; Gouveia et al., 2019). However, the extent of this influence on the pelagic ecosystems can be underestimated based only on such parameters. This can be observed by the much wider spatial reach of the ARP effect on the biological community, than its physicochemical signature. In the present study, many oceanic stations with fully marine salinities ( $> 35$ ) displayed large amounts of typical coastal planktonic decapods (e.g., adults of *Belzebub faxoni* and larvae of *Brachyura*, *Upogebiidae*, *Anomura*, and *Thalassinidea*), showing that



**Fig. 7.** Non-metric multidimensional scaling (nMDS) plot, based on the similarity between samples, based on the abundance of 33 planktonic decapod taxa. Samples were taken at the coastal transect influenced by the Amazon River Plume (Coastal IARP); ocean transect influenced by the Amazon River Plume (Ocean IARP) and ocean transect without Amazon River Plume influence (Ocean).

**Table 4**

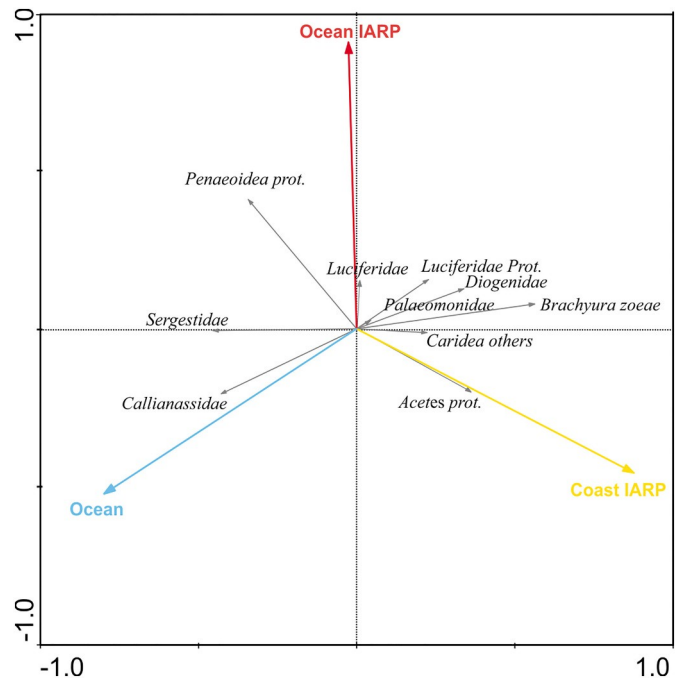
Contributions (< 70%) of planktonic decapod taxa to the mean dissimilarity between the sampling transects: Coast area influenced by the ARP (Coastal IARP), Ocean area influenced by the ARP (Ocean IARP) and Ocean area without influence of ARP (Ocean).

Group/taxa	Mean dissimilarity	Contribution (%)	Cumulative value (%)
<b>Coastal IARP and Ocean IARP</b>			
4.17			
Brachyura (zoeae)	17.13	17.13	
Luciferidae	11.85	28.98	
Luciferidae (protozoeae)	9.69	38.67	
Palaemonidae	8.68	47.35	
Callianassidae	6.07	53.43	
Caridea (others)	5.27	58.7	
Penaeoidea (protozoeae)	4.50	63.20	
Acetes sp. (protozoeae)	3.35	66.55	
Sergestidae	3.13	69.68	
<b>Coastal IARP and Ocean</b>			
60.72			
Brachyura (zoeae)	18.32	18.32	
Luciferidae	12.91	31.22	
Luciferidae (protozoeae)	10.12	41.34	
Palaemonidae	9	50.34	
Callianassidae	5.74	56.08	
Caridea (others)	5.57	61.65	
Penaeoidea (protozoeae)	4.39	66.04	
Acetes sp. (protozoeae)	3.10	69.14	
<b>Ocean IARP and Ocean</b>			
64.72			
Luciferidae	7.83	7.83	
Callianassidae	6.54	14.37	
Luciferidae (protozoeae)	6.48	20.85	
Sergestidae (protozoeae)	5.99	26.84	
Brachyura (zoeae)	5.94	32.78	
Penaeoidea (protozoeae)	5.58	38.35	
Palaemonidae	5.14	43.5	
Penaeidae	3.95	47.45	
Brachyura (megalopae)	3.85	51.3	
Sergestidae	3.62	54.92	
Alpheidae	3.31	58.23	
Caridea morphotype I.	3.22	61.45	
Solenoceridae (mysis)	2.99	64.44	
Decapoda damaged	2.98	67.42	

planktonic decapods may be relevant indicators of river plume influence, additionally to physicochemical parameters.

In the hyposaline and mesohaline zones of the NBC retroflexion, phytoplankton productivity and mesozooplankton grazing are high, and consequently also plankton abundance, biomass and productivity (Conroy et al., 2016, 2017; Gouveia et al., 2019). However, the Ocean IARP area shows great variability in current dynamics and hydrographical parameters (such as salinity and temperature) in a short time period, mainly along the NECC flow (Araujo et al., 2017; Varona et al., 2019). This complex hydrodynamics can act on the transport of the decapods away from areas of low salinity lenses and high primary production.

The lack of a quick response between food availability (mainly phytoplankton) and mesozooplankton is not new and the plankton response can be expressed in a variable time scale with a delay of days to weeks (Yebrá and Hernández-León, 2004; Decima et al., 2015). Once the mesozooplankton shows a variable vertical migration behavior, this group may be advected to regions which do not overlap with high primary productivity areas, as already observed by Landry et al. (2011) and Décima et al. (2011) in Equatorial Pacific upwelling zones. This rationale may explain the high abundance found in stations erroneously considered not influenced by ARP, based only on salinity. This approach can open new insights and help to find new ways to investigate the patterns of productivity and plankton biomass in waters influenced by the ARP and other large-scale river plumes.



**Fig. 8.** Redundancy Analysis (RDA) plot, showing the distribution of the taxa with relative abundance > 2%. Samples were taken at three sampling transects: area influenced (Coastal IARP; Ocean IARP) and without the influence (Ocean) of the Amazon River Plume in October–November 2012.

#### 4.2. Taxonomic composition and spatial variability in abundance

Decapod abundance at coastal and oceanic areas influenced by the ARP were considerably different from other coastal and oceanic regions of the Atlantic, that present plankton enrichment processes (such as continental runoff, upwelling events, island mass effect and the presence of eddies). Coastal abundance was lower than those recorded at the shelf areas in northeastern Brazil (Schwamborn et al., 1999), and greater than recorded in the Abrolhos Bank, eastern Brazilian shelf (Koettker and Lopes, 2013), at the south Brazilian shelf (Brandão et al., 2015) and in the Balearic Sea, during autumn (Torres et al., 2014). Oceanic abundances were greater than those recorded for oceanic regions in northeastern Brazil (Schwamborn et al., 1999) and southern Brazil (Brandão et al., 2015). When compared to oceanic islands, the abundance was greater than those observed in a coastal area off the Fernando de Noronha archipelago, open waters off Saint Peter and Saint Paul Rock's (SPSP) and off the Canary Islands, being lower than the decapod abundance recorded in the inshore inlet area of SPSP (Brandão et al., 2013; Landeira et al., 2013; Santana et al., 2018).

The planktonic decapod community was dominated by meroplanktonic larvae, especially in transects directly influenced by the ARP. The Amazonian coastal region concentrates the largest and most biomass-rich mangrove forests of the world (Herz, 1991; Giri et al., 2011), as well as the largest muddy coast (stretching from the Amazon River mouth to Orinoco River mouth in Venezuela), due to the sediments transported by the Amazon River dispersal system (Kjerfve et al., 2002). In addition to other complex habitats linked to the continental shelf, such as the extensive reef area recently recorded by Cordeiro et al. (2015) and Moura et al. (2016). These environments are potential habitats for different decapod taxa that produce meroplanktonic larvae, such as brachyuran and anomuran crabs, mud and reef shrimps. Mangrove areas may provide food and shelter for both adults and larvae (Robertson and Duke, 1987; Sasekumar et al., 1992; Loneragan et al., 1997; Giraldez et al., 2015; de Carvalho et al., 2016). These huge adult decapod stocks explain the dominance of meroplanktonic larvae in the coastal region influenced by the ARP.

Despite the greater dominance of meroplanktonic larvae, luciferid shrimps (larvae and adults) had the highest contribution in abundance, in the coastal and oceanic region influenced by the ARP. Low salinity coastal waters are preferred for the reproduction of many of these organisms, in particular for the luciferid *Belzebub faxoni* (Borradaile, 1915) (Harper, 1968; Lee et al., 1992; Teodoro et al., 2012), as well as other sergestid shrimps, such as *Acetes* sp. (Robertson and Duke, 1987; D'Incao and Martins, 2000). Thus, the low salinity and high productivity observed at the coastal and oceanic regions influenced by the ARP, associated with their holoplanktonic life history, may be an explanation for the huge abundance of these planktonic shrimps.

In the present study, the strong discharge of the huge Amazon and Pará rivers played an important role in the export of planktonic larvae from the coast towards the continental shelf. Migrations of decapod larvae from more coastal regions to the shelf may reduce the mortality by planktivorous predators (mainly planktivorous fish and gelatinous plankton), but expose larvae to a greater risk of transport to adjacent oceanic waters (Schwamborn et al., 1999; Landeira et al., 2009), which result in a lack of adequate habitat for development and settlement. Once on the shelf, transport in northwesterly directions is carried out by the strong North Brazil Current, following the ARP. Along the NBC transport, a large number of larvae exported from coastal habitats northernmost of the Amazon River mouth, such as minor estuaries, are incorporated into the ARP and during the months of retroflexion these larvae are transported to the oceanic region beyond the shelf break through the NBC retroflexion (present study) (Fig. 2a).

Trends of an ontogenetic gradient can be observed for some groups of planktonic decapods in the study area. Coastal regions have concentrated higher abundances of early life history stages of holopelagic shrimps (sergestids, penaeids and carideans) that reproduce in coastal regions of lower salinity. These regions offer a greater supply of food and shelter for their larvae (Robertson and Duke, 1987; Lee et al., 1992; Krumme et al., 2004; Krumme, 2009).

A similar pattern was observed in the present study for the larvae of brachyuran crabs, the most abundant meroplanktonic decapods. Abundance of brachyuran zoeae decreased significantly from the coast towards oceanic areas, thus being more associated with the coastal regions. Crab larvae presented higher values within river plume areas than in adjacent habitats (Schwamborn et al., 1999, 2001; Brandão et al., 2015). Brachyuran zoeae were also recorded as the most abundant taxa within the planktonic community of ARP in the recent study of Araujo et al. (2017). However, the values of abundance and relative abundance of their advanced larval stages (i.e., brachyuran megalopae), did not vary greatly between the coastal and oceanic transect with ARP influence. Thus, the advanced stages may be more related to environments further from the coast, corroborating the hypothesis that typically coastal planktonic decapods are dragged by the NBC towards more distant oceanic regions. This explains the dominance of meroplanktonic organisms in transects influenced by the ARP.

#### 4.3. Comparing abundance between day and night

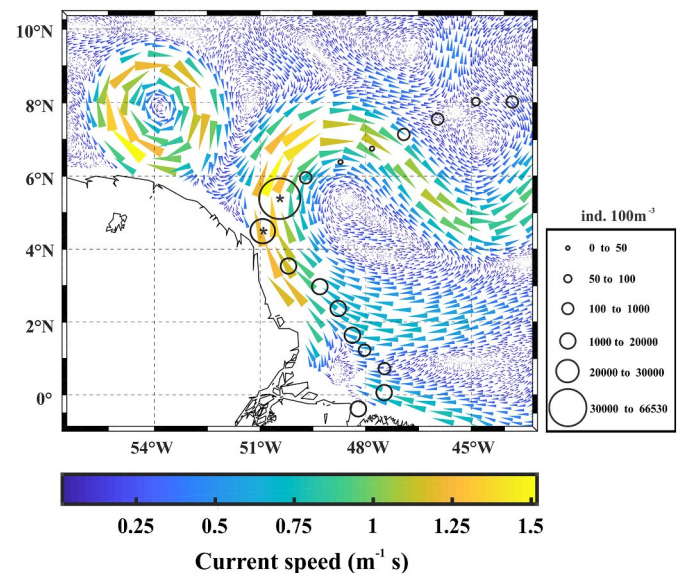
When compared to other studies on planktonic decapods, one striking difference in our results was the absence of any differences in abundance between day and night. Conversely, many studies showed that marine zooplankton, including decapods, conduct diel vertical migration (DVM) (Andersen and Sardou, 1992; Koettker et al., 2010; Lezama-Ochoa et al., 2014; Ivory et al., 2019). This is mostly thought to be a mechanism to avoid visual predators (Cohen and Forward Jr., 2009). This leads to higher abundances during the night in most studies, especially for nocturnal samplings near the surface in deep, oceanic waters (Brandao et al., 2013; Koettker et al., 2010; Ivory et al., 2019). However, non-migrating taxa and even inverted diel vertical migrations (i.e., aggregation at the surface during the day) have also been reported (Forward Jr., 1988; Queiroga and Blanton, 2005; Criales-Hernández et al., 2008; Landeira et al., 2017). Several factors may have

contributed to the absence of any significant differences between day and night in our data, including our sampling strategy that was not primarily aimed at that purpose.

In the shallow coastal waters and on the shelf, the water column was sampled almost entirely in an integrated way, so that DVM would not be detectable our data. At the deep oceanic stations, we sampled the upper 200 m. Thus, if the decapods analyzed in this study are vertically migrating, this happens mostly within this upper layer. Supporting this idea, previous studies in other geographic areas also showed zooplankton migration within the upper 200 m (Criales-Hernández et al., 2008; Bianchi et al., 2013). In the Ocean IARP transect the taxa that prevail in abundance are of mostly larvae coastal origin and probably remain in the surface layers that present favorable conditions for development and dispersal due to influences of the ARP, since physical-chemical barriers can limit the depth of the DVM (Ayón et al., 2008; Criales-Hernández et al., 2008; Bianchi et al., 2013; Lezama-Ochoa et al., 2014).

#### 4.4. Mesoscale processes influencing decapod distribution and assemblage structure

The peaks of planktonic decapod abundance at some stations at the NBC retroflexion and ARP (e.g., stations E09 and E10), provide good evidence of mesoscale processes enriching the plankton in this area. The presence of strong surface currents with an almost anticyclonic pattern and a warm pool in the region of the NBC retroflexion (Fratantoni and Glickson, 2002; Newinger and Toumi, 2015; Varona et al., 2019) may be related to these abundance peaks (Fig. 2a, b and Fig. 9), once coastal and oceanic transported decapods were crowding over the shelf break and slope stations (Fig. 9). Anticyclonic eddies are oceanographic phenomena known to cause disturbances that can increase productivity at their outer limits (McWilliam and Phillips, 1983). Higher abundances of planktonic decapods were recorded in waters surrounding warm-core eddies off southeastern Australia (McWilliam and Phillips, 1983) and in the Balearic Sea (Torres et al., 2014), the outer boundaries of the NBC ring apparently show the same pattern. In addition, low chlorophyll-a concentrations found in eddie cores (Fig. 2a, b, d and Fig. 3) that originated from the NBC retroflexion can be considered indicative of low abundances found at stations (stations



**Fig. 9.** Monthly variability of surface current dynamics at the Western Tropical Atlantic during October, evidencing the presence of eddies along the NBC retroflexion and NECC. Proportional spatial distribution of total decapods abundance in the sampling stations indicated by circles. \*: stations with maxima of planktonic decapod abundance (stations E09 and E10).

E11 and E12) located inside the warm pool (Fratantoni and Glickson, 2002).

Extremely high values of phytoplankton and zooplankton biomass were recorded for stations E09 and E10 by Araujo et al. (2017). High phytoplankton productivity rates were also recorded for the area of these stations during the retroflection period in 2014 by Otsuka et al. (2018), which related the high productivity of the retroflection region to the transition zone of the ARP, regions of abrupt variation of water transparency and high concentrations of nutrients, conditions that favor phytoplankton blooms. Huge numbers of diatoms and diazotrophic bacteria (such as *Trichodesmium* sp.) were recorded for the retroflection region, which may lead to greater abundance of planktonic organisms (Araujo et al., 2017; Otsuka et al., 2018).

In relation to the composition and structure of the community found in these environments, stations influenced by the ARP were dominated by large abundances of Luciferidae at different stages of development, and brachyuran zoeae. These organisms are grazers and their abundances have already been related to diatom and *Trichodesmium* sp. blooms, including in the study area (Lee et al., 1992; Schwamborn et al., 2002; Araujo et al., 2017; Conroy et al., 2017). Mesozooplankton grazing is high in the retroflection region and decreases with increasing salinity (Conroy et al., 2017). Therefore, the greater abundance of planktonic decapods in the retroflection area is also due to this greater availability of phytoplankton and micro/mesozooplankton as main food resources.

This cross-shelf gradient, with assemblages of planktonic decapods associated to benthic organisms near the most coastal and neritic areas, and holopelagic species associated with more oceanic regions, is a common pattern and has been described in several tropical and subtropical areas of the Atlantic Ocean (González-Gordillo and Rodríguez, 2003; Schwamborn et al., 1999; Lopes et al., 2006; Yoshinaga et al., 2010; Brandão et al., 2015). In most of the eastern continental shelf of South America, there is a trend of dominance in abundance of brachyuran zoeae, Luciferidae and caridean zoeae, respectively. However, we observed some marked differences at the North Brazilian shelf, in relation to this general pattern. Despite the significant contribution of meroplanktonic organisms in the neritic region, sergestid shrimps, mainly Luciferidae, showed abundances greater than the other taxa mentioned above. The dominance of Luciferidae was also observed in the Ocean transect influenced by ARP.

The community of decapods registered for the Amazonian coastal region was similar to other neritic regions of the Brazilian shelf, such as Schwamborn (1997) and Schwamborn et al. (1999), for the Itamaracá estuary in northeastern Brazil; Koettker and Freire (2006), in the Arvoredo Archipelago; Fernandes et al. (2002) in Guanabara Bay and Brandão et al. (2015) from the Cape of São Tomé to the Brazil - Uruguay border.

Generally, planktonic decapod abundance is low in the oligotrophic tropical Atlantic, but we recorded a very high abundance at station E31 that was at least two times larger than at the other sampling stations of the oceanic transect without ARP influence. Callianassid larvae dominated in abundance at this station. Adult callianassids are more related to sandy and muddy bottoms in coastal, shelf and upper slope areas, few being recorded on the ocean floor exceeding 2000 m depth (Manning and Felder, 1991; Dworschak, 2000; Fernandes et al., 2006). Decapod larvae related to continental shelf and slope have a wide distribution offshore (Miller and Morgan, 2013; Landeira et al., 2017), and the presence of sea mounts at shallower areas near station E31 are potential sites for parental stocks.

#### 4.5. Indicator indices and community structure

Since these environments are strongly connected, oceanic planktonic communities are present in both oceanic transects, which can be exemplified by the results of the analysis of indicator species, which did not categorize an indicator taxon for the Ocean IARP transect separately.

Thus, these distribution gradients, due to the influence of the ARP, may be responsible for the difference in community structure between the three transects. Therefore, it is possible to identify three assemblages of planktonic decapods: 1) Coastal ARP-influenced environments with a dominance of benthic, shallow water and holopelagic coastal taxa; 2) offshore ARP-influenced environments with a mixture of coastal and oceanic organisms, with a predominance of meroplankton; and 3) oceanic areas without ARP influence mostly dominated by holopelagic organisms.

The higher contribution of holoplanktonic decapods in oceanic areas is a commonly observed pattern in other areas of the Atlantic Ocean, as well as in coastal regions with high oceanic influence such as oceanic islands in the tropical Atlantic (Brandao et al., 2013), subtropical Atlantic (Landeira and Lozano-Soldevilla, 2018) and western Mediterranean (Torres et al., 2014), in addition to the southernmost Brazilian shelf (Brandão et al., 2015).

## 5. Summary and conclusions

The present study provides information on the abundance distribution, taxonomic composition and the relationship with oceanographic features of planktonic decapod communities in the western tropical Atlantic influenced by the Amazon River Plume. The coastal-oceanic gradient in abundance shows a similar trend as in other tropical coastal regions, but with considerably higher abundances. The planktonic decapod communities in the study area were mainly composed of larvae of benthic organisms in the coastal and oceanic areas with ARP influence. Conversely, Luciferidae was the most abundant taxon in areas influenced by the ARP and the contribution of holopelagic decapods was prominent in the oceanic transects, especially in oceanic waters without ARP influence. High abundances of brachyuran larvae and luciferid shrimps recorded in the present study are an indicative of the important contribution of planktonic decapods in the trophic transfer of energy to the macrozooplankton community of coastal and oceanic environments influenced by the ARP. Our results showed that complex current dynamics and mesoscale events can lead to offshore mixing of coastal and oceanic communities. However, it is unlikely that these advected coastal organisms could encounter a suitable settlement environment at deep oceanic areas or effectively return to coastal environments. The development of continuous long-term studies on the Amazon River retroflexion and plume is difficult due to the huge spatial scale of the ARP. Our results demonstrated that a coastal-oceanic sampling performed on the latitude of the retroflexion ring is an appropriate strategy to understand the influence and distribution of planktonic decapods directly related to the NBC advection processes without the need of long excursions beyond that region. Future studies covering the annual and seasonal of abundance and biomass variation shall clarify the distribution and biomass contribution of these organisms in the oceanic area during periods with and without the influence of the retroflection of the Amazon River Plume.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jmarsys.2020.103428>.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## References

- Andersen, V., Sardou, J., 1992. The diel migrations and vertical distributions of zooplankton and micronekton in the Northwestern Mediterranean Sea. 1. Euphausiids, mysids, decapods and fishes. *J. Plankton Res.* 14, 1129–1154. <https://doi.org/10.1093/plankt/14.8.1129>.
- Anderson, M.J., 2001. Permutation tests for univariate or multivariate analysis of variance and regression. *Can. J. Fish. Aquat. Sci.* 58, 626–639. <https://doi.org/10.1139/f01-004>.
- Araujo, M., Noriega, C., Hounsou-gbo, G.A., Veleda, D., Araujo, J., Bruto, L., Feitosa, F., Flores-Montes, M., Lefèvre, N., Melo, P., Otsuka, A., Travassos, K., Schwaborn, R., Neumann-Leitão, S., 2017. A synoptic assessment of the Amazon river-ocean continuum during boreal autumn: from physics to plankton communities and carbon flux. *Front. Microbiol.* 8, 1–18. <https://doi.org/10.3389/fmicb.2017.01358>.
- Ayón, P., Criales-Hernandez, M.I., Schwaborn, R., Hirche, H.J., 2008. Zooplankton research off Peru: a review. *Prog. Oceanogr.* 79, 238–255. <https://doi.org/10.1016/j.poceano.2008.10.020>.
- Bianchi, D., Galbraith, E.D., Carozza, D.A., Mislán, K.A.S., Stock, C.A., 2013. Intensification of open-ocean oxygen depletion by vertically migrating animals. *Nat. Geosci.* 6, 545–548. <https://doi.org/10.1038/NNGEO1837>.
- Boltovskoy, D., Gibbons, M.J., Hutchings, L., Binet, D., 1999. General biological features of the South Atlantic. In: *South Atl. Zooplankton*. vol. 2. Backhuys Publ. Leiden, pp. 1–41.
- Bourlès, B., Araujo, M., McPhaden, M.J., Brandt, P., Foltz, G.R., Lumpkin, R., Giordani, H., Hernandez, F., Lefèvre, N., Nobre, P., Campos, E., Saravanan, R., Trotte-Duhà, J., Dengler, M., Hahn, J., Hummels, R., Lübbecke, J.F., Rouault, M., Cotrim, L., Sutton, A., Jochum, M., Perez, R.C., 2019. PIRATA: a sustained observing system for tropical Atlantic climate research and forecasting. *Earth Space Sci.* 6, 577–616. <https://doi.org/10.1029/2018EA000428>.
- Brandao, M.C., Koettker, A.G., Freire, A.S., 2013. Abundance and composition of decapod larvae at Saint Paul's Rocks (equatorial Atlantic). *Mar. Ecol.* 34, 171–185. <https://doi.org/10.1111/j.1439-0485.2012.00531.x>.
- Brandão, M.C., Garcia, C.A.E., Freire, A.S., 2015. Large-scale spatial variability of decapod and stomatopod larvae along the South Brazil Shelf. *Cont. Shelf Res.* 107, 11–23. <https://doi.org/10.1016/j.csr.2015.07.012>.
- Brandao, M.C., Garcia, C.A.E., Freire, A.S., 2020. Meroplankton community structure across oceanographic fronts along the South Brazil Shelf. *J. Mar. Syst.* 208, 103361. <https://doi.org/10.1016/j.jmarsys.2020.103361>.
- Bray, J.R., Curtis, J.T., 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecol. Monogr.* 27, 325–349. <https://doi.org/10.2307/1942268>.
- Busalacchi, A.J., Picaut, J., 1983. Seasonal variability from a model of the tropical Atlantic Ocean. *J. Phys. Oceanogr.* 13, 1564–1588. [https://doi.org/10.1175/1520-0485\(1983\)013<1564:SVFAMO>2.0.CO;2](https://doi.org/10.1175/1520-0485(1983)013<1564:SVFAMO>2.0.CO;2).
- Calazans, D.K. de, 1993. Key to the Larvae and Decapodids of Genera of the Infraorder Penaeidea from Southern Brazilian Coast. Universidade Federal do Rio Grande. <http://repositorio.furg.br/handle/1/5572>.
- Calef, G.V., Grice, G.D., 1967. Influence of the Amazon River Outflow on the Ecology of the Western Tropical Atlantic: Zooplankton Abundance, Copepod Distribution, with Remarks on the Fauna of Low-salinity Areas. *J. Mar. Res.* 25, 84–92.
- Callède, J., Cochinneau, G., Alves, F., Guyot, J.-L., Guimarães, V., De Oliveira, E., 2010. Les apports en eau de l'Amazonie à l'Océan Atlantique. *Rev. des Sci. l'eau/Journal Water Sci.* 23, 247–273. <https://doi.org/10.7202/044688ar>.
- Carpenter, E.J., Montoya, J.P., Burns, J., Mulholland, M.R., Subramaniam, A., Capone, D.G., 1999. Extensive bloom of a N<sub>2</sub>-fixing diatom/cyanobacterial association in the tropical Atlantic Ocean. *Mar. Ecol. Prog. Ser.* 185, 273–283. <https://doi.org/10.3354/meps185273>.
- Carvalho, A.S.S., Nevis, A.B., Oliveira, D.B., Martinelli-Lemos, J.M., 2013. Larvas de Porcellanidae (Decapoda, Anomura) no plâncton de um estuário amazônico brasileiro. *Braz. J. Aquat. Sci. Technol.* 17, 7–15. <https://siaiap32.univali.br/seer/index.php/bjast/article/download/3549/2961>.
- Cavalcante, D.V., Bentes, B., Martinelli, J.M., 2012. Biodiversity of decapod crustaceans in the estuarine floodplain around the city of Belém (Pará) in Brazilian Amazonia. *Zoologia* 29, 203–209. <https://doi.org/10.1590/S1984-46702012000300003>.
- Chong, L.S., Berelson, W.M., McManus, J., Hammond, D.E., Rollins, N.E., Yager, P.L., 2014. Carbon and biogenic silica export influenced by the Amazon River Plume: patterns of remineralization in deep-sea sediments. *Deep Sea Res. Part I Oceanogr. Res. Pap.* 85, 124–137. <https://doi.org/10.1016/j.dsr.2013.12.007>.
- Clarke, K.R., Warwick, R.M., 2001. A further biodiversity index applicable to species lists: variation in taxonomic distinctness. *Mar. Ecol. Prog. Ser.* 216, 265–278. <https://doi.org/10.3354/meps216265>.
- Cohen, J.H., Forward Jr., R.B., 2009. Zooplankton diel vertical migration - a review of proximate control. *Oceanogr. Mar. Biol. Annu. Rev.* 47, 77–109.
- Conroy, B.J., Steinberg, D.K., Stukel, M.R., Goes, J.I., Coles, V.J., 2016. Meso-and microzooplankton grazing in the Amazon River plume and western tropical North Atlantic. *Limnol. Oceanogr.* 61, 825–840. <https://doi.org/10.1002/lno.10261>.
- Conroy, B.J., Steinberg, D.K., Song, B., Kalmbach, A., Carpenter, E.J., Foster, R.A., 2017. Mesozooplankton graze on cyanobacteria in the Amazon river plume and western tropical North Atlantic. *Front. Microbiol.* 8, 1436. <https://doi.org/10.3389/fmicb.2017.01436>.
- Cordeiro, R.T.S., Neves, B.M., Rosa-Filho, J.S., Pérez, C.D., 2015. Mesophotic coral ecosystems occur offshore and north of the Amazon River. *Bull. Mar. Sci.* 91, 491–510. <https://doi.org/10.5343/bms.2015.1025>.
- Criales-Hernández, M.I., Schwaborn, R., Graco, M., Ayón, P., Hirche, H.J., Wolff, M., 2008. Zooplankton vertical distribution and migration off Central Peru in relation to the oxygen minimum layer. *Helgol. Mar. Res.* 62, 85–100. <https://doi.org/10.1007/s10152-007-0094-3>.
- Csanady, G.T., 1985. A zero potential vorticity model of the North Brazilian Coastal Current. *J. Mar. Res.* 43, 553–579. <https://doi.org/10.5343/bms.2015.1025>.
- Dagg, M., Benner, R., Lohrenz, S., Lawrence, D., 2004. Transformation of dissolved and particulate materials on continental shelves influenced by large rivers: plume processes. *Cont. Shelf Res.* 24, 833–858. <https://doi.org/10.1016/j.csr.2004.02.003>.
- de Carvalho, A.S.S., Martinelli-Lemos, J.M., das Neves, A.B., Isaac, V., 2016. Spatio-temporal variation of the density of shrimp *Farfantepenaeus subtilis*, *Litopenaeus schmitti* and *Xiphopenaeus kroyeri* (Crustacea; Decapoda) in the Curuçá Estuary, North of Brazil. *Bol. Inst. Pesca, São Paulo* 42, 598–610. <https://doi.org/10.20950/1678-2305.2016v42n3p598>.
- de Oliveira, D.B., Silva, D.C., Martinelli, J.M., 2012. Density of larval and adult forms of the burrowing crustaceans *Lepidophthalmus siriboa* (Callinassidae) and *Upogebia vasquezii* (Upogebiidae) in an Amazon estuary, northern Brazil. *J. Mar. Biol. Assoc. United Kingdom* 92, 295–303. <https://doi.org/10.1017/S002531541100097X>.
- Décima, M., Landry, M.R., Rykaczewski, R.R., 2011. Broad scale patterns in mesozooplankton biomass and grazing in the eastern equatorial Pacific. *Deep. Res. Part II Top. Stud. Oceanogr.* 58, 387–399. <https://doi.org/10.1016/j.dsr2.2010.08.006>.
- Decima, M., Landry, M.R., Stukel, M.R., Lopez-Lopez, L., Krause, J.W., 2015. Mesozooplankton biomass and grazing in the Costa Rica Dome: amplifying variability through the plankton food web. *J. Plankton Res.* 38, 317–330. <https://doi.org/10.1093/plankt/fbv091>.
- Del Vecchio, R., Subramaniam, A., 2004. Influence of the Amazon River on the surface optical properties of the western tropical North Atlantic Ocean. *J. Geophys. Res.* Ocean 109, C11001. <https://doi.org/10.1029/2004JC002503>.
- D'Incao, F., Martins, S.T.S., 2000. Brazilian species of the genera *Acetes* H. Milne Edwards, 1830 and *Peisos* Burkenroad, 1945 (Decapoda: Sergestidae). *J. Crustac. Biol.* 20, 78–86. <https://doi.org/10.1163/1937240X-90000010>.
- Dos Santos, A., Rodriguez, A., González-Gordillo, J., 2004. Illustrated keys for the identification of the Pleocyemata (Crustacea: Decapoda) zoeal stages, from the coastal region of south-western Europe. *J. Mar. Biol. Assoc. U.K.* 84, 205–227. <https://doi.org/10.1017/S0025315404009075h>.
- Dufrène, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol. Monogr.* 67, 345–366. [https://doi.org/10.1890/0012-9615\(1997\)067\[0345:SAIIST\]2.0.CO;2](https://doi.org/10.1890/0012-9615(1997)067[0345:SAIIST]2.0.CO;2).
- Dworschak, P.C., 2000. Global diversity in the Thalassinidea (Decapoda). *J. Crustac. Biol.* 20, 238–245. <https://doi.org/10.1163/1937240X-90000025>.
- Epifanio, C.E., Garvine, R.W., 2001. Larval transport on the Atlantic continental shelf of North America: a review. *Estuar. Coast. Shelf Sci.* 52, 51–77. <https://doi.org/10.1006/eccc.2000.0727>.
- Fernandes, L.D. de A., Bonecker, S.L.C., Valentin, J.L., 2002. Dynamic of decapod crustacean larvae on the entrance of Guanabara Bay. *Brazilian Arch. Biol. Technol.* 45, 491–498. <https://doi.org/10.1590/S1516-89132002000600013>.
- Fernandes, E.V., Almeida, E.D., Peixoto, B.J.F.S., Souza, M.D., 2006. Larvas de Decapoda. In: Bonecker, S.L.C. (Ed.), *Atlas Do Zooplâncton Da Zona Econômica Exclusiva Brasileira*. Museu Nacional, Rio de Janeiro, pp. 101–164.
- Forward Jr., R.B., 1988. Diel vertical migration: zooplankton photobiology and behavior. *Oceanogr. Mar. Biol. Annu. Rev.* 26, 361–393.
- Fratantoni, D.M., Glickson, D.A., 2002. North Brazil Current ring generation and evolution observed with SeaWiFS. *J. Phys. Oceanogr.* 32, 1058–1074. [https://doi.org/10.1175/1520-0485\(2002\)032<1058:NBCRGA>2.0.CO;2](https://doi.org/10.1175/1520-0485(2002)032<1058:NBCRGA>2.0.CO;2).
- Giraldes, B.W., Coelho Filho, P.A., Smyth, D.M., 2015. Decapod assemblages in subtidal and intertidal zones-importance of scuba diving as a survey technique in tropical reefs, Brazil. *Glob. Ecol. Conserv.* 3, 163–175. <https://doi.org/10.1016/j.gecco.2014.11.011>.
- Giri, C., Ochieng, E., Tieszen, L.L., Zhu, Z., Singh, A., Loveland, T., Masek, J., Duke, N., 2011. Status and distribution of mangrove forests of the world using earth observation satellite data. *Glob. Ecol. Biogeogr.* 20, 154–159. <https://doi.org/10.1111/j.1466-8238.2010.00584.x>.
- Goes, J.I., do Rosário Gomes, H., Chekalyuk, A.M., Carpenter, E.J., Montoya, J.P., Coles, V.J., Yager, P.L., Berelson, W.M., Capone, D.G., Foster, R.A., 2014. Influence of the Amazon River discharge on the biogeography of phytoplankton communities in the western tropical north Atlantic. *Prog. Oceanogr.* 120, 29–40. <https://doi.org/10.1016/j.poceano.2013.07.010>.
- González-Gordillo, J.I., Rodríguez, A., 2003. Comparative seasonal and spatial distribution of decapod larvae assemblages in three coastal zones off the south-western Iberian Peninsula. *Acta Oecol.* 24, 219–233. [https://doi.org/10.1016/S1146-609X\(03\)00032-8](https://doi.org/10.1016/S1146-609X(03)00032-8).
- Gouveia, N.A., Gherardi, D.F.M., Wagner, F.H., Paes, E.T., Coles, V.J., Aragão, L.E.O.C., 2019. The salinity structure of the Amazon River plume drives spatiotemporal variation of oceanic primary productivity. *J. Geophys. Res. Biogeosci.* 124, 147–165. <https://doi.org/10.1029/2018JG004665>.
- Harper Jr., D.E., 1968. Distribution of *Lucifer faxoni* (Crustacea: Decapoda: Sergestidae) in neritic waters off the Texas coast, with a note on the occurrence of *Lucifer typus*. *Contrib. Mar. Sci.* 13, 1–16. <http://hdl.handle.net/1969.3/20603>.
- Herz, R., 1991. *Manguezais do Brasil*. USP, São Paulo.
- Hu, C., Montgomery, E.T., Schmitt, R.W., Muller-Karger, F.E., 2004. The dispersal of the

- Amazon and Orinoco River water in the tropical Atlantic and Caribbean Sea: observation from space and S-PALACE floats. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 51, 1151–1171. <https://doi.org/10.1016/j.dsr2.2004.04.001>.
- Ivory, J.A., Steinberg, D.K., Latour, R.J., 2019. Diel, seasonal, and interannual patterns in mesozooplankton abundance in the Sargasso Sea. *ICES J. Mar. Sci.* 76, 217–231. <https://doi.org/10.1093/icesjms/fsy117>.
- Johns, W.E., Lee, T.N., Schott, F.A., Zantopp, R.J., Evans, R.H., 1990. The North Brazil Current retroflection: seasonal structure and eddy variability. *J. Geophys. Res. Ocean* 95, 22103–22120. <https://doi.org/10.1029/JC095iC12p22103>.
- Judkins, D.C., 2014. Geographical distribution of pelagic decapod shrimp in the Atlantic Ocean. *Zootaxa* 3895, 301–345. <https://doi.org/10.11646/zootaxa.3895.3.1>.
- Kathiresan, K., Bingham, B.L., 2001. *Biology of mangroves and mangrove ecosystems*. *Adv. Mar. Biol.* 40, 84–254.
- Kjerfve, B., Perillo, G.M.E., Gardner, L.R., James, M., Dias, G.T.M., Mochel, F.R., 2002. Chapter twenty. Morphodynamics of muddy environments along the Atlantic coasts of North and South America. *Proc. Mar. Sci.* 4, 479–532. [https://doi.org/10.1016/S1568-2692\(02\)80094-8](https://doi.org/10.1016/S1568-2692(02)80094-8).
- Koeltker, A.G., Freire, A.S., 2006. Spatial and temporal distribution of decapod larvae in the subtropical waters of the Arvoredo archipelago, SC, Brazil. *Iheringia. Série Zool.* 96, 31–40. <https://doi.org/10.1590/S0073-4721200600100005>.
- Koeltker, A.G., Lopes, R.M., 2013. Meroplankton spatial structure and variability on Abrolhos Bank and adjacent areas, with emphasis on brachyuran larvae. *Cont. Shelf Res.* 70, 97–108. <https://doi.org/10.1016/j.csr.2013.10.004>.
- Koeltker, A.G., Freire, A.S., Sumida, P.Y., 2010. Temporal, diel and spatial variability of decapod larvae from St Paul's Rocks, an equatorial oceanic island of Brazil. *J. Mar. Biol. Assoc. UK* 90, 1227–1239. <https://doi.org/10.1017/S0025315409990890>.
- Kottek, M., Grieser, J., Beck, C., Rudolf, B., Rubel, F., 2006. World map of the Köppen-Geiger climate classification updated. *Meteorol. Z.* 15, 259–263. <https://doi.org/10.1127/0941-2948/2006/0130>.
- Krumme, U., 2009. Diel and tidal movements by fish and decapods linking tropical coastal ecosystems. In: *Ecological Connectivity among Tropical Coastal Ecosystems*. Springer, Dordrecht, pp. 271–324.
- Krumme, U., Saint-Paul, U., Rosenthal, H., 2004. Tidal and diel changes in the structure of a nekton assemblage in small intertidal mangrove creeks in northern Brazil. *Aquat. Living Resour.* 17, 215–229. <https://doi.org/10.1051/alr:2004019>.
- Kurata, H., 1970. *Studies on the life histories of decapod Crustacea of Georgia*. In: *Part III. Larvae of Decapod Crustacean of Georgia*. University of Georgia, Marine Institute, Sapelo Island, Georgia.
- Landeira, J.M., Lozano-Soldevilla, F., 2018. Seasonality of planktonic crustacean decapod larvae in the subtropical waters of Gran Canaria Island, NE Atlantic. *Sci. Mar.* 82, 119–134. <https://doi.org/10.3989/scimar.04683.08>.
- Landeira, J.M., Lozano-Soldevilla, F., Hernández León, S., Barton, E.D., 2009. Horizontal distribution of invertebrate larvae around the oceanic island of Gran Canaria: the effect of mesoscale variability. *Sci. Mar.* 73, 761–771. <https://doi.org/10.3989/scimar.2009.73n4757>.
- Landeira, J.M., Lozano-Soldevilla, F., Hernández-León, S., 2013. Temporal and along-shore distribution of decapod larvae in the oceanic island of Gran Canaria (NW Africa). *J. Plankton Res.* 35, 309–322. <https://doi.org/10.1093/plankt/fbs089>.
- Landeira, J.M., Brochier, T., Mason, E., Lozano-Soldevilla, F., Hernández-León, S., Barton, E.D., 2017. Transport pathways of decapod larvae under intense mesoscale activity in the Canary-African coastal transition zone: implications for population connectivity. *Sci. Mar.* 81, 299–315. <https://doi.org/10.3989/scimar.04599.06A>.
- Landry, M.R., Selph, K.E., Taylor, A.G., Décima, M., Balch, W.M., Bidigare, R.R., 2011. Phytoplankton growth, grazing and production balances in the HNLC equatorial Pacific. *Deep-Sea Res. II* 58, 524–535. <https://doi.org/10.1016/j.dsr2.2010.08.011>.
- Lee, W.Y., Omori, M., Peck, R.W., 1992. Growth, reproduction and feeding behavior of the planktonic shrimp, *Lucifer faxoni* Borradaile, off the Texas coast. *J. Plankton Res.* 14, 61–69. <https://doi.org/10.1093/plankt/14.1.61>.
- Legendre, P., Gallagher, E.D., 2001. Ecologically meaningful transformations for ordination of species data. *Oecologia* 129, 271–280. <https://doi.org/10.1007/s004420100716>.
- Lentz, S.J., 1995a. The Amazon River plume during AMASSEDs: subtidal current variability and the importance of wind forcing. *J. Geophys. Res. Ocean* 100, 2377–2390. <https://doi.org/10.1029/94JC00343>.
- Lentz, S.J., 1995b. Seasonal variations in the horizontal structure of the Amazon plume inferred from historical hydrographic data. *J. Geophys. Res.* 100, 2391–2400. <https://doi.org/10.1029/94JC01847>.
- Lezama-Ochoa, A., Irigoien, X., Chaigneau, A., Quiroz, Z., Lebourges-Dhaussy, A., Bertrand, A., 2014. Acoustics reveals the presence of a macrozooplankton biocline in the Bay of Biscay in response to hydrological conditions and predator-prey relationships. *PLoS One* 9, e88054. <https://doi.org/10.1371/journal.pone.0088054>.
- Loneragan, N.R., Bunn, S.E., Kellaway, D.M., 1997. Are mangroves and seagrasses sources of organic carbon for penaeid prawns in a tropical Australian estuary? A multiple stable-isotope study. *Mar. Biol.* 130, 289–300. <https://doi.org/10.1007/s002270050248>.
- Lopes, R.M., Katsuragawa, M., Dias, J.F., Montú, M.A., Muelbert, J.H., Gorri, C., Brandini, F.P., 2006. Zooplankton and ichthyoplankton distribution on the southern Brazilian shelf: an overview. *Sci. Mar.* 70, 189–202. <http://repositorio.furg.br/handle/1/2020>.
- Manning, R.B., Felder, D.L., 1991. Revision of the American Callinassidae (Crustacea: Decapoda: Thalassinidea). *Proc. Biol. Soc. Wash.* 104, 764–792. <https://decapoda.nhm.org/pdfs/10650/10650.pdf>.
- Martin, J., Olesen, J., Høeg, J.T., Høeg, J., 2014. *Atlas of Crustacean Larvae*. JHU Press, Baltimore.
- McConaughy, J.R., 1992. Decapod larvae: dispersal, mortality, and ecology. A working hypothesis. *Am. Zool.* 32, 512–523. <https://doi.org/10.1093/icb/32.3.512>.
- McWilliam, P.S., Phillips, B.F., 1983. Phyllosoma larvae and other crustacean macrozooplankton associated with Eddy J, a warm-core Eddy off south-eastern Australia. *Mar. Freshw. Res.* 34, 653–663. <https://doi.org/10.1071/MF9830653>.
- Meade, R.H., 1996. River-sediment inputs to major deltas. In: Milliman, J.D., Haq, B.U. (Eds.), *Sea-level Rise and Coastal Subsidence. Coastal Systems and Continental Margins. vol. 2*. Springer, Dordrecht, pp. 63–85.
- Melo, N.F.A.C., Neumann-Leitão, S., Gusmão, L.M.O., Martins Neto, F.E., Palheta, G.D.A., 2014. Distribution of the planktonic shrimp *Lucifer* (Thompson, 1829) (Decapoda, Sergestoidae) off the Amazon. *SciELO Bras* 74, S045–S051. <https://doi.org/10.1590/1519-6984.20612>.
- Miller, S.H., Morgan, S.G., 2013. Interspecific differences in depth preference: regulation of larval transport in an upwelling system. *Mar. Ecol. Prog. Ser.* 476, 301–306. <https://doi.org/10.3354/meps10150>.
- Moura, R.L., Amado-Filho, G.M., Moraes, F.C., Brasileiro, P.S., Salomon, P.S., Mahiques, M.M., Bastos, A.C., Almeida, M.G., Silva, J.M., Araujo, B.F., 2016. An extensive reef system at the Amazon River mouth. *Sci. Adv* 2, e1501252. <https://doi.org/10.1126/sciadv.1501252>.
- Muller-Karger, F.E., McClain, C.R., Richardson, P.L., 1988. The dispersal of the Amazon's water. *Nature* 333, 56–59. <https://doi.org/10.1038/333056a0>.
- Muller-Karger, F.E., Richardson, P.L., McGillicuddy, D., 1995. On the offshore dispersal of the Amazon's Plume in the North Atlantic: comments on the paper by A. Longhurst, "Seasonal cooling and blooming in tropical oceans". *Deep Sea Res. Part I Oceanogr. Res. Pap.* 42, 2127–2137. [https://doi.org/10.1016/0967-0637\(95\)00085-2](https://doi.org/10.1016/0967-0637(95)00085-2).
- Neumann-Leitão, S., Melo, P.A.M.C., Schwamborn, R., Diaz, X.F.G., Figueiredo, L.G.P., Silva, A.P., Campelo, R.P.S., Melo Júnior, M. de, Melo, N.F.A.C., Costa, A.E.S.F., 2018. Zooplankton from a reef system under the influence of the Amazon River Plume. *Front. Microbiol.* 9, 355. <https://doi.org/10.3389/fmicb.2018.00355>.
- Newinger, C., Toumi, R., 2015. Potential impact of the colored Amazon and Orinoco plume on tropical cyclone intensity. *J. Geophys. Res. Ocean.* 120, 1296–1317. <https://doi.org/10.1002/2014JC010533>.
- Nixon, S.W., Oviatt, C.A., Frithsen, J., Sullivan, B., 1986. Nutrients and the productivity of estuarine and coastal marine ecosystems. *J. Limnol. Soc. South. Africa* 12, 43–71. <https://doi.org/10.1080/03779688.1986.9639398>.
- Nóbrega, P.S.V. da, Bentes, B., Martinelli-Lemos, J.M., 2014. Population structure and relative growth of the Amazon shrimp *Macrobrachium amazonicum* (Heller, 1862) (Decapoda: Palaemonidae) on two islands in the fluvial-estuarine plain of the Brazilian Amazon. *Nauplius* 22, 13–20. <https://doi.org/10.1590/S0104-64972014000100002>.
- Omori, M., Ikeda, T., 1984. *Methods in Marine Zooplankton Ecology*. John-Wiley and Sons, Inc, New York.
- Otsuka, A., Feitosa, F., Araujo, M., Veleda, D., Cunha, M., Lefèvre, N., Gaspar, F., Montes, M., Borges, G., Noriega, C., 2018. Dynamics of primary productivity and oceanographic parameters under influence of the Amazon River Plume. *Open J. Ecol.* 8, 590–606. <https://doi.org/10.4236/oje.2018.811035>.
- Peel, M.C., Finlayson, B.L., McMahon, T.A., 2007. Updated world map of the Köppen-Geiger climate classification. *Hydrol. Earth Syst. Sci. Discuss.* 4, 439–473. <https://hal.archives-ouvertes.fr/hal-00298818>.
- Philander, S.G.H., Pacanowski, R.C., 1986. A model of the seasonal cycle in the tropical Atlantic Ocean. *J. Geophys. Res. Ocean* 91, 14192–14206. <https://doi.org/10.1029/JC091iC12p14192>.
- Queiroga, H., Blanton, J., 2005. Interactions between behaviour and physical forcing in the control of horizontal transport of decapod crustacean larvae. *Adv. Mar. Biol.* 47, 107–214. [https://doi.org/10.1016/s0065-2881\(04\)47002-3](https://doi.org/10.1016/s0065-2881(04)47002-3).
- Robertson, A.I., Duke, N.C., 1987. Mangroves as nursery sites: comparisons of the abundance and species composition of fish and crustaceans in mangroves and other nearshore habitats in tropical Australia. *Mar. Biol.* 96, 193–205. <https://doi.org/10.1007/BF00427019>.
- Santana, C.S.de., Schwamborn, R., Neumann-Leitão, S., Montes, M. de J.F., Lira, S.M. de A., 2018. Spatio-temporal variation of planktonic decapods along the leeward coast of the Fernando de Noronha archipelago, Brazil. *Braz. J. Oceanogr.* 66, 1–14. <https://doi.org/10.1590/s1679-87592018147206601>.
- Sasekumar, A., Chong, V.C., Leh, M.U., D'Cruz, R., 1992. Mangroves as a habitat for fish and prawns. In: Jaccarini, V., Martins, E. (Eds.), *The Ecology of Mangrove and Related Ecosystems. Developments in Hydrobiology*. Springer, Dordrecht, pp. 195–207. [https://doi.org/10.1007/978-94-017-3288-8\\_21](https://doi.org/10.1007/978-94-017-3288-8_21).
- Schwamborn, R., 1997. The influence of mangroves on community structure and nutrition of macrozooplankton in northeast Brazil. *ZMT Contrib* 4, 1–77. <https://epic.awi.de/id/eprint/13526/>.
- Schwamborn, R., Ekau, W., Silva, A.P., Silva, T.A., Saint-Paul, U., 1999. The contribution of estuarine decapod larvae to marine zooplankton communities in north-east Brazil. *Arch. Fish. Mar. Res.* 47, 167–182.
- Schwamborn, R., Neumann-Leitão, S., de Almeida, T., Silva, A.P., Werner, E., Saint-Paul, U., 2001. Distribution and dispersal of decapod crustacean larvae and other zooplankton in the Itamaracá estuarine system, Brazil. *Trop. Oceanogr.* 29, 1679–3013.
- Schwamborn, R., Ekau, W., Voss, M., Saint-Paul, U., 2002. How important are mangroves as a carbon source for decapod crustacean larvae in a tropical estuary? *Mar. Ecol. Prog. Ser.* 229, 195–205. <https://doi.org/10.3354/meps229195>.
- Shchepetkin, A.F., McWilliams, J.C., 2005. The regional oceanic modeling system (ROMS): a split-explicit, free-surface, topography-following-coordinate oceanic model. *Ocean Model.* 9, 347–404. <https://doi.org/10.1016/j.ocemod.2004.08.002>.
- Subramaniam, A., Yager, P.L., Carpenter, E.J., Mahaffey, C., Björkman, K., Cooley, S., Kustka, A.B., Montoya, J.P., Sañudo-Wilhelmy, S.A., Shipe, R., 2008. Amazon River enhances diazotrophy and carbon sequestration in the tropical North Atlantic Ocean. *Proc. Natl. Acad. Sci.* 105, 10460–10465. <https://doi.org/10.1073/pnas.0710729105>.
- Teodoro, S. de S.A., Negreiros-Fransozo, M.L., Simões, S.M., Lopes, M., da Costa, R.C., 2012. Population ecology of the planktonic shrimp *Lucifer faxoni* Borradaile, 1915

- (Crustacea, Sergestoidea, Luciferidae) of the southeastern coast of Brazil. *Brazilian J. Oceanogr.* 60, 245–253. <https://doi.org/10.1590/S1679-87592012000200014>.
- Torres, A.P., Dos Santos, A., Balbín, R., Alemany, F., Massutí, E., Reglero, P., 2014. Decapod crustacean larval communities in the Balearic Sea (western Mediterranean): seasonal composition, horizontal and vertical distribution patterns. *J. Mar. Syst.* 138, 112–126. <https://doi.org/10.1016/j.jmarsys.2013.11.017>.
- Varona, H.L., Veleda, D., Silva, M., Cintra, M., Araujo, M., 2019. Amazon River plume influence on Western Tropical Atlantic dynamic variability. *Dyn. Atmos. Ocean.* 85, 1–15. <https://doi.org/10.1016/j.dynatmoce.2018.10.002>.
- Woods, J., 1988. Scale upwelling and primary production. In: Rothschild, B.J. (Ed.), *Toward a Theory on Biological-Physical Interactions in the World Ocean*. Springer, Dordrecht, pp. 7–38. [https://doi.org/10.1007/978-94-009-3023-0\\_2](https://doi.org/10.1007/978-94-009-3023-0_2).
- Wu, K., Dai, M., Li, X., Meng, F., Chen, J., Lin, J., 2017. Dynamics and production of dissolved organic carbon in a large continental shelf system under the influence of both river plume and coastal upwelling. *Limnol. Oceanogr.* 62, 973–988. <https://doi.org/10.1002/lno.10479>.
- Yebra, L., Hernández-León, S., 2004. Aminoacyl-tRNA synthetases activity as a growth index in zooplankton. *J. Plankton Res.* 26, 351–356. <https://doi.org/10.1093/plankt/fbh028>.
- Yoshinaga, M.Y., Sumida, P.Y., Silveira, I.C., Ciotti, Á.M., Gaeta, S.A., Pacheco, L.F., Koettker, A.G., 2010. Vertical distribution of benthic invertebrate larvae during an upwelling event along a transect off the tropical Brazilian continental margin. *J. Mar. Syst.* 79, 124–133. <https://doi.org/10.1016/j.jmarsys.2009.07.007>.
- Zar, J.H., 1999. *Biostatistical Analysis*. Pearson Education India, Bangalore.