

## Original Article

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# Factors affecting the seasonal variability of planktonic shrimps (Dendrobranchiata) along an estuary–ocean gradient on the Amazon continental shelf

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## Abstract

Dendrobranchiata shrimp taxonomic composition and spatial and temporal distribution on the Amazon continental shelf (ACS) were investigated along a transect between the sources of the Amazon and Pará Rivers, encompassing an extension of ~250 km towards the continental slope. Plankton was collected with oblique trawls (200 µm mesh size), and nine taxa were found; 59.4% were larvae (mysis or decapodid stages) and 40.6% were juveniles or adults. *Acetes* was negatively related to chlorophyll-*a* and temperature, and Luciferidae were positively correlated with months. This study provides novel information on the density distribution of dendrobranchiate shrimps, thus helping to pave the way to characterize a large-scale, hugely relevant area that is poorly studied. As in other tropical coastal areas, there is here an increase in number of taxa with increased distance from the coast. Luciferidae, Solenoceridae and Penaeidae were the most frequent families whereas Sicyoniidae and Sergestidae had the lowest frequency of occurrence nearer the slope. Despite the low larval density of penaeid shrimps, their presence in all months and at all sampling sites along the ACS proves the importance of this area for shrimps with socioeconomic relevance, as well as its importance as a nursery and growth habitat for dendrobranchiate shrimps.

## Introduction

Plumes of large rivers affect coastal and oceanic areas both at regional and continental scales, as well as at the global scale, and they play an important role in the hydrological cycle and thermodynamic stability of the ocean (Dagg *et al.*, 2004; Chérubin & Richardson, 2007). In northern Brazil, the tropical Atlantic receives the drainage from the Amazon River, which accounts for ~20% of the total global freshwater discharge, within a complex, megascale delta (Nittrouer *et al.*, 1986; Mikhailov, 2010). The interaction between river discharges from the Amazon system and the action of strong trade winds and surface ocean currents controls the pelagic processes in the northern coast of Brazil, affecting physico-chemical dynamics, as well as planktonic distribution and biomass on the Amazon continental shelf (Dagg *et al.*, 2004; Santos *et al.*, 2008; Moller *et al.*, 2010; Goes *et al.*, 2014; Conroy *et al.*, 2016; Santana *et al.*, 2020).

In large-scale tropical continental shelf environments, the diversity of organisms derives from an extensive coast with diverse marine and estuarine habitats (mangrove forests, marshes, coral reefs). In the north of Brazil, the junction of the outflowing rivers Amazon and Pará converts the ACS into an important nursery and growth area for marine and estuarine shrimps (Dall *et al.*, 1990; Dagg *et al.*, 2004; Nascimento *et al.*, 2013; Cordeiro *et al.*, 2015; Moura *et al.*, 2016).

Larval stages are the primary means for geographic dispersal of marine shrimps. During this phase, distribution is affected by temperature, salinity, rainfall, winds and currents, among others (Anger, 2001, 2006). These characteristics, together with food availability, competition and predation, are the major factors responsible for seasonal variation and recruitment levels in the adult population (Anger, 2001). Hence, a successful life history strategy depends mostly on the survival of planktonic larvae (Anger, 2006).

Shrimps represent an important group for marine ecosystems both in their larval phase, as a component of the plankton and trophic pyramid, and in their benthic/nektonic phase, where they act as omnivores or detritivores that play an important role in nutrient cycling and energy flow, serving as the main energy pathway from primary producers to higher trophic level organisms, such as fish. They obtain nutrients from dead organisms or part of them, making nutrients available to predators, constituting an important link in the aquatic trophic web. However, information on the distribution of shrimp larval stages or even of juveniles and adults as a component of zooplankton is scarce in the north Brazilian shelf.



There are 30 shrimp species of the suborder Dendrobranchiata reported on the Amazon continental shelf (ACS) and nearby estuarine areas: 5 Sergestoidea species (2 Luciferidae and 3 Sergestidae) and 25 Penaeoidea species (3 Aristeidae, 12 Penaeidae, 6 Sicyoniidae and 4 Solenoceridae) (D'Incao, 1997, 1998; Barros & Pimentel, 2001; Silva *et al.*, 2002a, 2002b, 2020; Costa & Costa, 2008; Melo *et al.*, 2014; Pimentel & Magalhães, 2014).

Luciferidae comprises holoplanktonic species that might account for up to 15% of planktonic biomass on tropical continental shelves due to their size (Longhurst, 1985), and all life stages are found on the ACS (Melo *et al.*, 2014; Conroy *et al.*, 2016; Neumann-Leitão *et al.*, 2018). Sergestidae includes pelagic or benthopelagic shrimps that inhabit estuaries and tropical, subtropical and temperate coastal waters, which have high abundance formed by aggregations in certain periods of the year (Omori, 1975; Xiao & Greenwood, 1993).

Penaeoidea are meroplanktonic with only larval stages found in zooplankton. In general, four types of migratory movements might be observed (based on Penaeidae): (1) migration of larvae and post-larvae to nursery areas (estuaries, mangroves, lagoons); (2) migration of juveniles outside the nursery area (towards the ocean, shelf); (3) migration of adults, generally towards deeper waters in the sea/ocean; and (4) migration only for spawning in some species (Dall *et al.*, 1990). Although penaeid larvae usually migrate from the ocean towards the estuary, where juveniles will develop until they return to the sea as adults (Dall *et al.*, 1990), the life cycles of Aristeidae, Solenoceridae and Sicyoniidae shrimps are exclusively marine (Gomez-Ponce & Gracia, 2003; Castilho *et al.*, 2008; Kapisiris & Thessalou-Legaki, 2009; Pezzuto & Coachman-Dias, 2009; Simões *et al.*, 2017; Garcia *et al.*, 2018).

Ecological studies about planktonic shrimps on the ACS are still scarce and have limited availability, as they consist of unpublished monographs, theses and dissertations, all of which are based on single cruises, with no seasonality reports. One of the only studies conducted about planktonic shrimp published as a manuscript was by Melo *et al.* (2014), who analysed the distribution of luciferid juvenile and adult shrimps along neritic and oceanic environments on the Amazon shelf, and recently Santana *et al.* (2020) analysed the abundance and composition of planktonic decapod communities along the Amazon River plume and its retroflexion. Therefore, nothing is known about the larval stages of dendrobranchiate on the ACS.

Based on the complexity of the ACS system and the dynamic character of the zooplankton, this study attempted to answer the following questions: which dendrobranchiate shrimps are found as the dominant planktonic components on the ACS? How are these four groups (penaeoid larvae and sergestoid larvae, juveniles and adults) spatially distributed in an area under the influence of the plumes of the Amazon and Pará rivers? Are there differences in the distribution of occurrence of shrimp larval stages? Which environmental factors primarily affect the spatial-temporal distribution of these groups?

Considering that freshwater supply in coastal areas depends on a highly variable estuarine plume, shrimp survival and development would be affected. This study hypothesized that there is a difference in the distribution of shrimp groups on the ACS related to seasonality and the coast–ocean gradient, since there are different migratory patterns depending on groups, and different tolerances to salinity variations. Thus, different distribution patterns of planktonic shrimp were expected.

## Method

### Study area

The Atlantic Ocean receives the discharges of the Amazon and Pará Rivers into a complex megascale delta (Nittrouer *et al.*,

1986). The Amazon River Basin, considered the largest in the world, extends from the Andes until the Atlantic Ocean and covers an area of  $\sim 7 \times 10^6 \text{ km}^2$  (Dagg *et al.*, 2004; Molleri *et al.*, 2010), discharging  $940 \times 10^6 \text{ t/year}$  of sediments and  $180,000 \text{ m}^3 \text{ s}^{-1}$  of fresh water into the Atlantic Ocean (Muller-Karger *et al.*, 1988; Mikhailov, 2010). In northern Brazil, the shelf break zone of the ACS is between 90 and 100 m depth (Nittrouer & DeMaster, 1996), and the inner shelf is limited by the 20-m isobath, with a deeply jagged coastline encompassing the largest continuous strip of mangrove forests in the world (Nascimento *et al.*, 2013).

The Amazon River outflow varies seasonally, ranging from  $\sim 220,000 \text{ m}^3 \text{ s}^{-1}$  in May (maximum flooding of the river) to  $100,000 \text{ m}^3 \text{ s}^{-1}$  in November (low flow period) (Geyer *et al.*, 1996; Silva *et al.*, 2009; Molleri *et al.*, 2010), and it forms a low-salinity surface plume that extends along the shelf, transported primarily north-westwards by the North Brazil Current (Muller-Karger *et al.*, 1988; Geyer *et al.*, 1996). There is only one rainy season in this region, from December to May (period of maximum flood of the Amazon River), and a less rainy season, from June to November (dry season or low flow period of the Amazon River) (Rao & Hada, 1990).

The North Brazil Current (NBC) transports warm surface waters to the north and flows along the ACS shelf break and slope (Richardson *et al.*, 1994). The NBC has a large annual cycle, concurrent with changes in wind speed, ranging from a maximum transport of  $36 \times 10^6 \text{ m}^3 \text{ s}^{-1}$  in July–August (maximum winds in the dry season) to a minimum transport of  $13 \times 10^6 \text{ m}^3 \text{ s}^{-1}$  in April–May (weak winds in the rainy season), with an annual mean transport of  $\sim 26 \times 10^6 \text{ m}^3 \text{ s}^{-1}$  (Johns *et al.*, 1998). It changes direction along the Brazilian northern coastline according to wind patterns and to position of the Amazon plume (Ffield, 2005). The predominance of the Amazon River plume near its mouth occurs in the first half of the year, coinciding with the higher river outflow and with weaker north-eastern trade winds. In the oceanic area, plume displacement is related to currents, moving north-eastwards via the NBC towards the Caribbean Sea. Near the State of Amapá, this current seasonally undergoes a large-scale eastward retroflexion towards Africa in the second semester, feeding the Equatorial North Counter-Current (ENCC) (Muller-Karger *et al.*, 1988; Ffield, 2005; Silva *et al.*, 2009).

### Sampling and sample processing

Samplings were performed seasonally, seven times in three-month intervals, from July 2013 to January 2015, along a transect with six sampling sites on the Amazon continental shelf, starting from the coastline (at Marajó Island) and going as far as  $\sim 250 \text{ km}$  off the coast on the slope, encompassing a full large-scale transect along an ocean–estuarine continuum (Figure 1). The distance from the sampling sites to the coast was  $\sim 23 \text{ km}$  (site 1),  $53 \text{ km}$  (site 2),  $83 \text{ km}$  (site 3),  $158 \text{ km}$  (site 4),  $198 \text{ km}$  (site 5) and  $233 \text{ km}$  (site 6). Samplings were conducted using a fishing boat equipped with radio, depth probe, GPS and a winch for plankton hauls. Before capturing the zooplankton, a CTD-probe (Hydrolab DS 5) was used to record the abiotic factors and make profiles of each parameter of the water column: temperature ( $^{\circ}\text{C}$ ), salinity and chlorophyll-*a* ( $\mu\text{g l}^{-1}$ ).

Samples were obtained with a conical-cylindrical plankton net (200  $\mu\text{m}$  mesh and 30 cm diameter), with a flow meter coupled to the net opening. The samplings were from surface to bottom, one sample per station, with oblique hauls down to 75% of local depth ( $\sim 10, 19, 34, 39, 53$  and  $80 \text{ m}$  depth), and at each depth they were hauled for 5 min. The total duration of the hauls varied from 10–20 min, at a speed of approximately 2 knots. Samples were

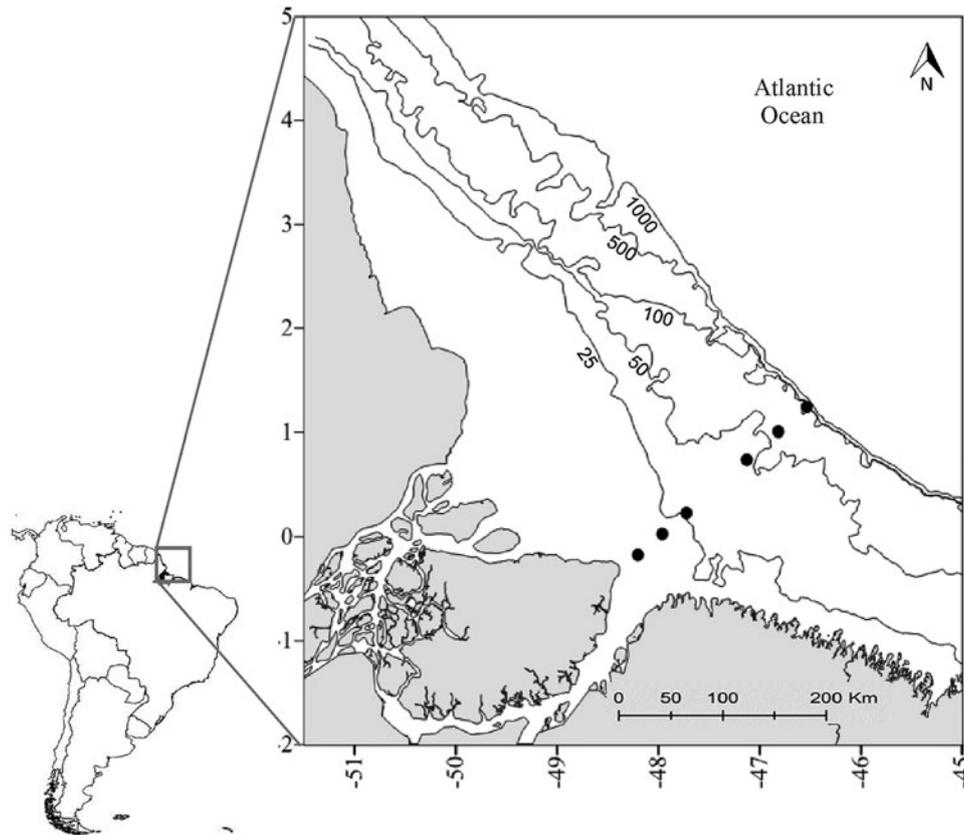


Fig. 1. Amazon continental shelf: the black dots represent the sampling sites in the period ranging from July 2013 to January 2015.

fixed in 4% formaldehyde, previously buffered with sodium tetraborate. In the laboratory, samples were fractionated with a Folsom sub-sampler, and a fraction of half of the initial sample was used to screen the shrimps. A total of 42 samples were analysed: 7 expeditions throughout 2 years (July/13, October/13, January/14, May/14, July/14, October/14, January/15)  $\times$  6 sites on the ACS.

Mysis larval stages, decapodids (post-larva), juveniles and adults (the latter two were only Sergestoidea) were identified using specialized references (Brooks, 1882; Cook, 1964; Boschi, 1981; Calazans, 1993; Oshiro & Omori, 1996; Dos Santos & Lindley, 2001). Nauplii and protozoa stages were not counted as the abundance of these small larvae was underestimated by the 200-micron net mesh. The organisms were counted and identified under an optical stereomicroscope (ZEISS StereoDiscovery v.12) and dissected using an optical microscope equipped with a micrometric disc.

#### Data analysis

Amazon River outflow data were obtained from the Brazilian Hidroweb service (<http://www.snirh.gov.br/hidroweb/>) based on data from the Óbidos-Pará station provided by the Brazilian National Water Agency (ANA). Due to the huge scale of the Amazon basin, river discharge seasonality at the river mouth is mostly affected by rain in upstream areas, and not by the seasonal timing of rainfall on the coast. The variables 'outflow' ( $\text{m}^3 \text{s}^{-1}$ ), 'temperature' ( $^{\circ}\text{C}$ ), 'salinity' and 'chlorophyll-*a*' ( $\mu\text{g l}^{-1}$ ) were tested using Shapiro-Wilk ( $k$  samples) and Levene's tests, and did not have normality and homoscedasticity, respectively. Thus, variation in outflow between months could be compared using Kruskal-Wallis ANOVA, as well as other abiotic factors among distance to the coast and months, all of which were followed by Student-Newman-Keuls (SNK) post hoc test.

Spatial variation in temperature ( $^{\circ}\text{C}$ ), salinity and chlorophyll-*a* ( $\mu\text{g l}^{-1}$ ) was represented by contour maps, elaborated using Surfer<sup>®</sup> 9.0 (Golden Software Inc., 2005). The krigage interpolation method was used due to its higher precision, because it is more faithful to the data, and due to its better curve smoothness compared with other methods (Landim, 2003). Isolines related to the environmental factors mentioned above were highlighted, and salinity was categorized according to Seidel *et al.* (2015) in salinity ranges ( $S$ ) that characterize the Amazon River plume: inner or estuarine plume ( $0 < S \leq 20$ ), intermediate plume ( $20 < S \leq 31$ ), outer plume ( $31 < S \leq 36$ ), and ocean waters ( $S > 36$ ).

The number of shrimps found in the aliquoted volumes was multiplied by the corresponding subsampling factor and the shrimp density was estimated in number of individuals per  $\text{m}^3$  ( $\text{ind m}^{-3}$ ). Frequency of occurrence was calculated considering the number of samples in which each taxon occurred compared with the total number of samples, and taxa were grouped in four categories: very frequent ( $>70\%$ ), frequent ( $\leq 70$  and  $\geq 40\%$ ), infrequent ( $< 40$  and  $\geq 10\%$ ) and rare species ( $< 10\%$ ) (Melo, 2004 adapted from Mateucci & Colma, 1982). The frequency of occurrence of shrimps was also calculated according to distance from the coast and was compared using the chi-square test, testing the hypothesis of increasing ( $A > 0$ ) or decreasing tendency ( $A < 0$ ) in the proportion of these frequencies, using BioEstat<sup>®</sup> 5.0 (Ayres *et al.*, 2007).

Even after transformation, shrimp densities did not meet the criteria to perform parametric tests. Therefore, Kruskal-Wallis ANOVA was used to compare the variation in shrimp density among months and distances from the coast. Shrimp density was compared between years and periods with higher vs lower Amazon River outflow using pairwise Mann-Whitney tests. These univariate analyses were performed using Statistica<sup>®</sup> 12.7 (Statsoft Inc., 2015), with a significance level of 5%.

A Redundancy Analysis (RDA) was performed according to Borcard *et al.* (2011), using the 'vegan' package in R (Oksanen *et al.*, 2017), to analyse shrimp assemblage distribution concerning explanatory variables (environmental factors, months and distance from the coast). For this analysis, the environmental data matrix (outflow, salinity, temperature and chlorophyll-*a*) was transformed using the 'Standardization' method, and shrimp density matrix (per development stages and families) was transformed using the Hellinger method. The latter is recommended for species abundance data clusters or ordinations, since it is not influenced by matrix zeros and it lowers the importance of more abundant groups (Legendre & Birks, 2012). Subsequently, a permutation ANOVA (PERMANOVA) was performed to test the significance of the RDA model, with 999 permutations, adopting the significance level of 5%.

## Results

### Abiotic factors

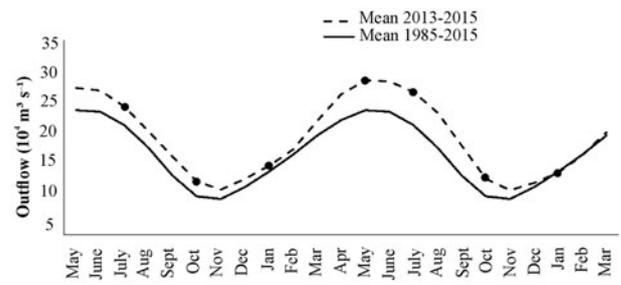
The highest Amazon River outflow ( $291,900 \text{ m}^3 \text{ s}^{-1}$ ) was in May (2014) and the lowest ( $\sim 110,000 \text{ m}^3 \text{ s}^{-1}$ ) was in October (2013 and 2014). River outflow significantly differed among months ( $H_{(df=6; N=217)} = 195.75; P < 0.01$ ); May and July 2014 had the maximum river discharges, and the outflow in May 2014 was significantly higher than the rest of the study period. October (2013 and 2014) showed the lowest discharges, the beginning of the river level descent process occurred in July 2013, and discharge started to increase in January (2013 and 2014). Only January (both years) showed values within the historical mean from 1985 to 2015, while the other months showed somewhat higher discharges (Figure 2).

Sea temperatures ranged from 22–30 °C and remained above 27 °C on the majority of the shelf. Temperature also differed according to coast–ocean distance ( $H_{(5; 1434)} = 748.30; P < 0.01$ ). The lowest temperatures were recorded starting 200 km away from the coast and only at the deepest sites (Figure 3). Temperature significantly varied among months ( $H_{(6; 1434)} = 287.89; P < 0.01$ ); July (2013 and 2014), with high discharge, had the highest mean temperatures and January and October/14 had the lowest, coinciding with low river discharge (Figure 4).

Salinity varied from 2 to 38; the lowest values were recorded in May (mean value of  $30.93 \pm 8.89$  SD), along with the period of highest Amazon River outflow, and the highest values were recorded in October ( $37.02 \pm 2.79$ ) ( $H_{(6; 1407)} = 674.66; P < 0.01$ ), the period with the lowest river outflow (Figure 4). Regarding coastal-offshore gradients, the lowest mean salinities were recorded near the shore, at a 23 km distance from the coast ( $H_{(5; 1407)} = 314.08; P < 0.01$ ) (Figure 4). The shelf was under the influence of low-salinity plume waters in all months, which was evident as far as 150 km distance. Farther than 150 km, salinity was  $>36$  during most of the sampling period. Low-salinity plume waters showed a longer extension in May/2014, exceeding 200 km of distance on the ACS, and a shorter extension in October, where the plume reached as near as  $\sim 60$  km (Figure 3).

Chlorophyll-*a* varied from  $0.3 \mu\text{g l}^{-1}$  ( $\sim 41$  m depth, 233 km from coast) to  $85.1 \mu\text{g l}^{-1}$  ( $\sim 0.5$  m depth, 53 km from coast), both in January 2014, in the onset of the rainy season. Mean chlorophyll-*a* values were significantly higher in July 2013 and January 2014 ( $15.2$  and  $10.5 \mu\text{g l}^{-1}$ , respectively) ( $H_{(6; 1383)} = 288.60; P < 0.01$ ), while they were higher in the more superficial layers in January 2014 ( $0.5$ – $6.5$  m depth at 53 km from the coast).

Overall, chlorophyll-*a* showed a similar spatial extent along the low-salinity plume, with significant variations along the coast–ocean distance ( $H_{(5; 1383)} = 567.65; P < 0.01$ ). The largest spatial extent of remarkably high chlorophyll-*a* values occurred in July



**Fig. 2.** Mean daily Amazon River outflow in the study period (July 2013 to January 2015) and in the last 30 years (1985–2015). The black dots indicate the sampling months on the Amazon continental shelf.

2013 and May 2014, along the entire water column, reaching farther than 200 km and with very high values ( $>20 \mu\text{g l}^{-1}$ ). In the other months, it remained more concentrated near the coast (as near as  $\sim 100$  km) and in more superficial layers (only down to 20 m depth). The lowest values ( $<5 \mu\text{g l}^{-1}$ ) occurred far away from the coast and at deep layers (Figures 3 and 4).

### Abundance and distribution of Dendrobranchiata shrimps

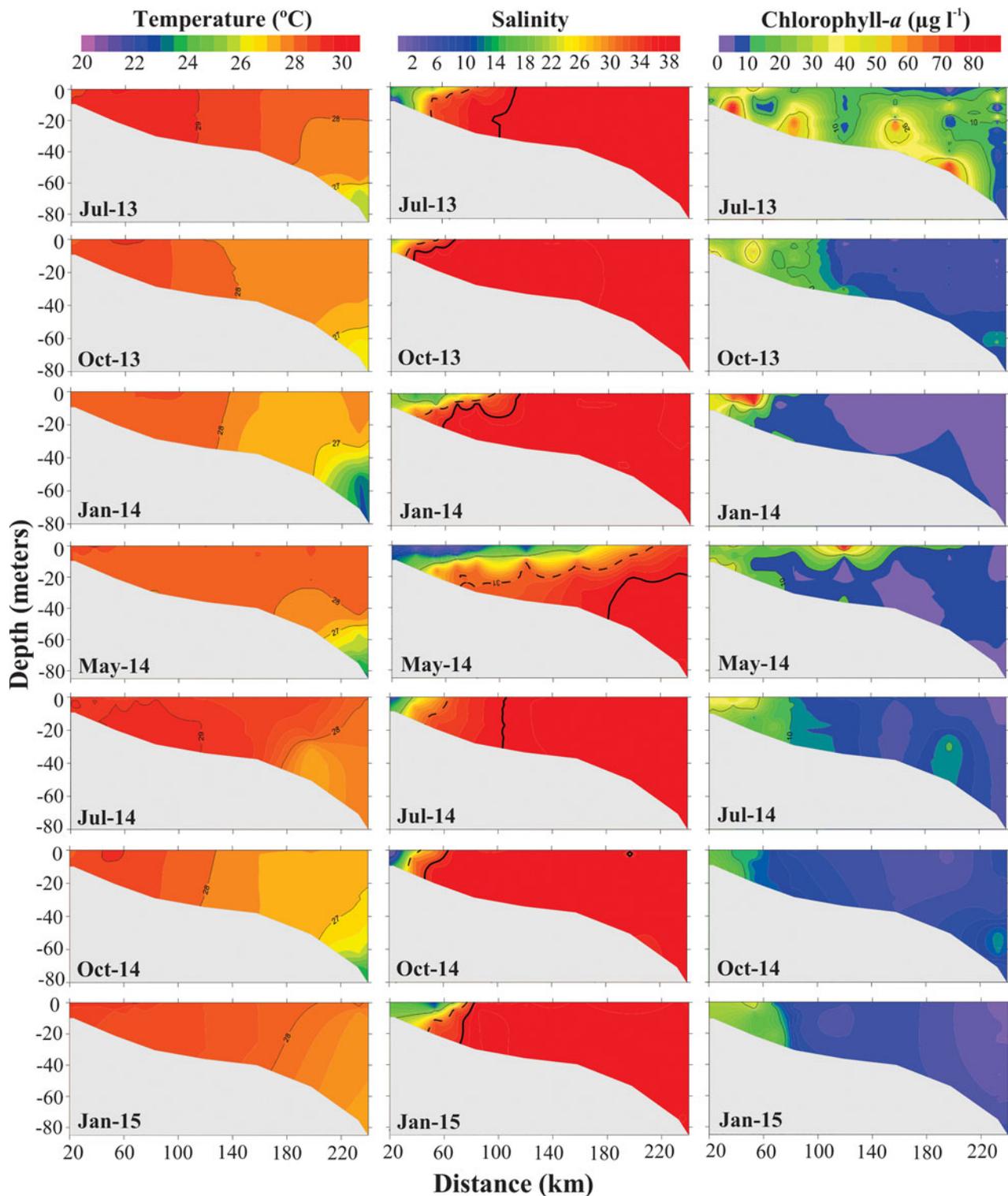
In the present study 14,057 specimens of dendrobranchiate planktonic shrimps were analysed, belonging to five families and nine taxa (Supplementary Table S1). Luciferidae shrimps (13,065 specimens) and the mysis stage (8078 larvae) were the most abundant among the dendrobranchiate shrimps. The total density of shrimps presented a mean of  $2.18 \pm 6.26 \text{ ind m}^{-3}$ . They were present throughout the study period with higher mean in May 2014 ( $9.09 \pm 15.37 \text{ ind m}^{-3}$ ) followed by October 2013 ( $2.11 \pm 3.15 \text{ ind m}^{-3}$ ). The lowest mean density was in July 2013 ( $0.16 \pm 0.2 \text{ ind m}^{-3}$ ). Regarding the distance from the coast, the shrimp were present in all the extension of the platform, with the highest mean density at 158 km ( $5.58 \pm 14.27 \text{ ind m}^{-3}$ ) and lower at 233 km ( $0.54 \pm 0.67 \text{ ind m}^{-3}$ ).

### Abundance and distribution of sergestoid shrimps

Shrimps of the Luciferidae family were the most abundant among dendrobranchiates, accounting for 92.85% of total shrimps with the highest densities (maximum:  $37.88 \text{ ind m}^{-3}$ ; mean:  $2 \pm 6.28 \text{ ind m}^{-3}$ ), followed by Sergestidae ( $3 \text{ ind m}^{-3}$ ;  $0.19 \pm 0.59 \text{ ind m}^{-3}$ ), accounting for 3.53% of total dendrobranchiate abundance on the ACS. In terms of frequency of occurrence, Luciferidae (86%) were very frequent ( $>70\%$ ) and Sergestidae were infrequent in the samples (33%).

Luciferidae was present with high densities throughout the study period; the highest density was during maximum discharge in May 2014 ( $54.36 \text{ ind m}^{-3}$ ), yet the lowest density was during high discharge in July 2013 ( $0.79 \text{ ind m}^{-3}$ ). This family was also present throughout the continental shelf, with the highest densities between 80 and 200 km ( $72.30 \text{ ind m}^{-3}$ ) (Figures 5 and 6). A significant increasing trend ( $A > 0$ ) was found in the proportion of luciferid shrimps ( $\chi^2 = 296.69; P < 0.01$ ) with increased distance from the coast.

Among luciferid shrimps, *Belzebub faxoni* was dominant on the ACS, with the highest density both in mysis and in post-larval stages (7580 larvae, mean density:  $1.13 \pm 3.61 \text{ ind m}^{-3}$ ) and in juveniles–adults (5454 individuals,  $0.80 \pm 2.79 \text{ ind m}^{-3}$ ). *Belzebub faxoni* was found in all months, and throughout the shelf, whereas *Lucifer typus* had low densities (28 individuals,  $0.08 \text{ ind m}^{-3}$ ), represented only by juveniles and adults, collected as far as  $\sim 190$  km from the coast.



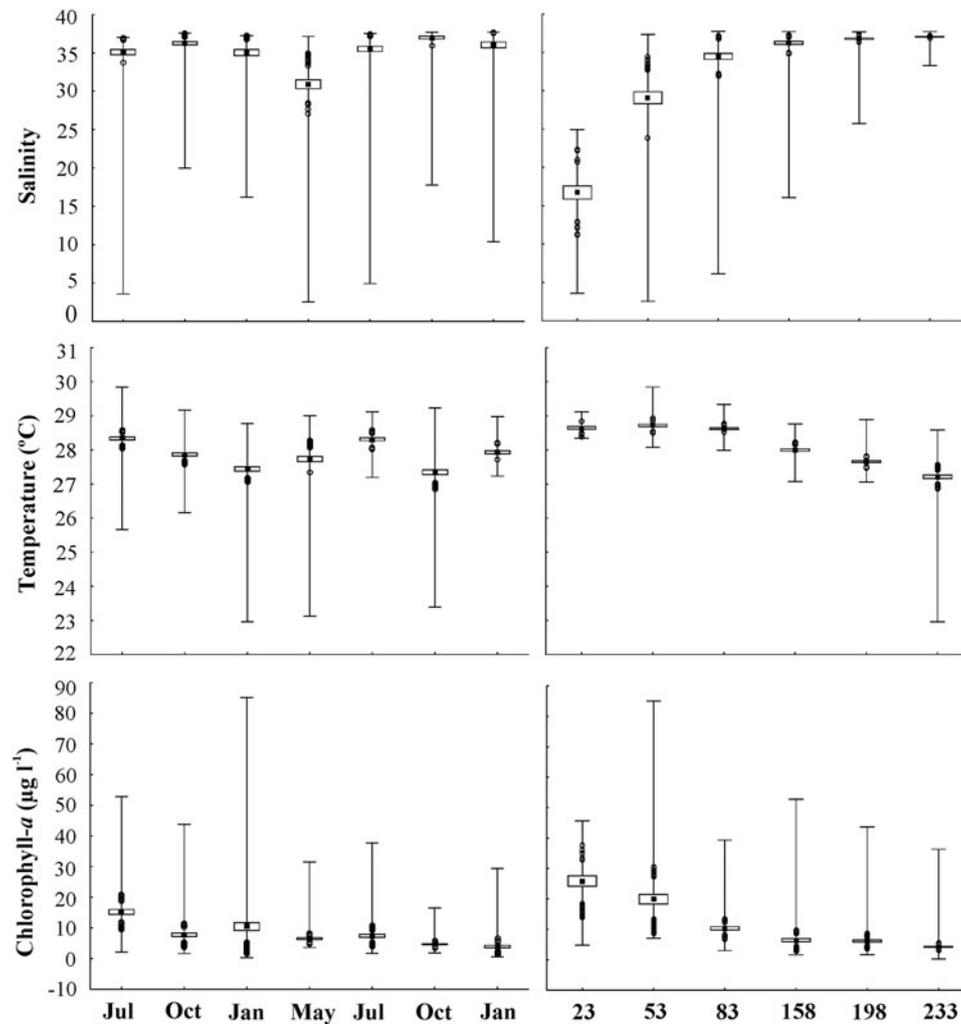
**Fig. 3.** Temperature ( $^{\circ}\text{C}$ ), salinity, and chlorophyll- $a$  ( $\mu\text{g l}^{-1}$ ) in the water column of the Amazon continental shelf (2013–2015). For salinity: estuarine range (up to the full line), inner plume range (between the full line and the dashed line), outer plume range (between the dashed line and the thicker line), and oceanic range (from the thicker line onwards).

Sergestid shrimps were present in all months with lower densities than luciferids. However, they were not present throughout the shelf, having higher densities up to 55 km from the coast (497 individuals;  $7.58 \text{ ind m}^{-3}$ ) and low densities farther than this distance (Figures 5 and 6). A significant decreasing trend ( $A < 0$ ) was found in the proportion of sergestid shrimps ( $\chi^2 = 378.65$ ;  $P < 0.01$ ) with increased distance from the coast.

Among sergestids, there was predominance of *Acetes* spp. on the ACS, with the highest densities up to 55 km from the coast (depth

$\sim 20$  m), where development stages ranging from mysis II to adults were found: mysis II (36 larvae, total density:  $0.84 \text{ ind m}^{-3}$ ), post-larvae (PL) (247 larvae,  $3.67 \text{ ind m}^{-3}$ ), and juveniles–adults (211 individuals,  $3.21 \text{ ind m}^{-3}$ ), including 10 males and 12 females of *A. americanus* (Figure 5). *Sergestes* sp. were also found: 1 mysis II and 2 post-larvae ( $0.02 \text{ ind m}^{-3}$ ), with low densities collected at the 100-m isobath, starting  $\sim 200$  km away from the coast.

Distribution of dendrobranchiate shrimp density was significantly correlated with explanatory variables. The RDA model



**Fig. 4.** Minimum and maximum values, outliers, mean and standard error of abiotic factors in relation to months and distance from the coast on the Amazon continental shelf (2013–2015).

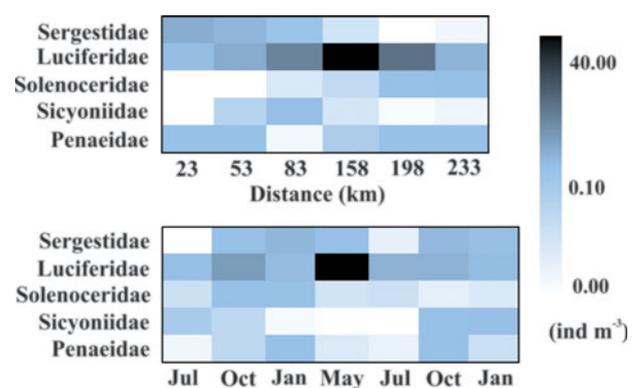
explained ~18% ( $R^2_{\text{non-adjusted}} = 30.74\%$ ;  $F = 2.44$ ;  $P = 0.001$ ) of the total variation in shrimp assemblages. The two first RDA axes together explained 81.45% of variability; the first axis explained 58.8% of variability and was positively related to salinity (0.78) and negatively related to chlorophyll-*a* (−0.72). The second axis explained 22.6% of variability and was positively correlated with distance from the coast (0.78) and negatively correlated with temperature (−0.84) (Table 1; Figure 7).

Among sergestoid shrimps, *Acetes* spp. were negatively correlated with chlorophyll-*a* and Luciferidae were positively correlated with the temporal variable (month), both on axis 1. On axis 2, *Acetes* spp. was also negatively correlated with temperature (Figure 7, Supplementary Table S2).

#### Abundance and distribution of penaeoid shrimps

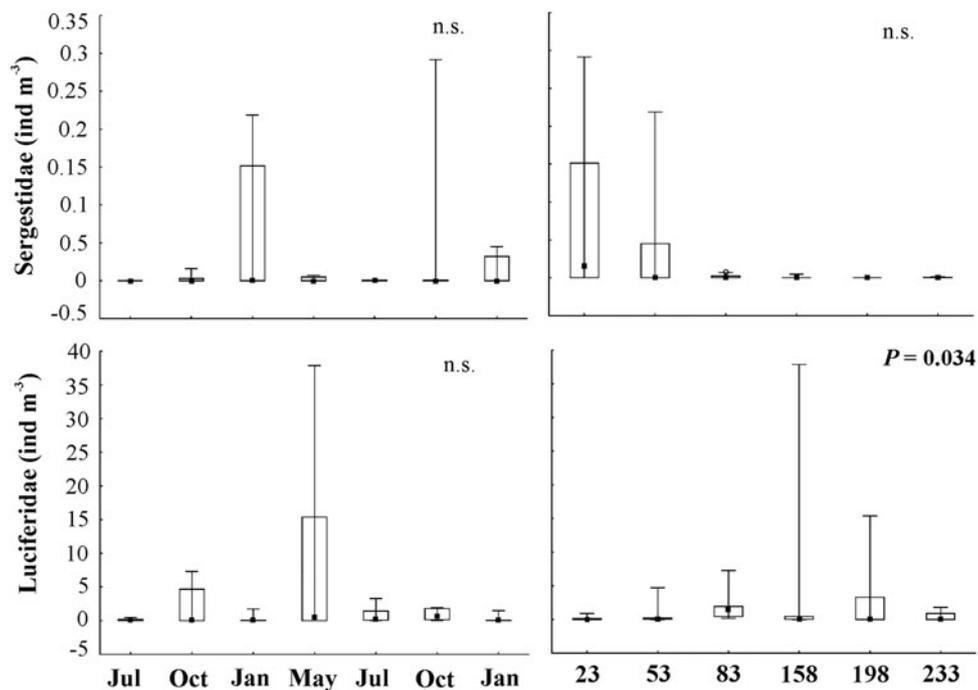
Penaeoid shrimps represented only 3.62% of the total individuals collected on the ACS; however, they were very frequent (76%). They were represented by Solenoceridae (infrequent: 33%), Sicyoniidae and Penaeidae (frequent: 40 and 57%, respectively). All three families had low densities, and Sicyoniidae shrimps had the highest mean density (0.52 ind m<sup>−3</sup>).

Larvae of sicyoniid shrimps were represented by few specimens (total: 304 larvae), with higher density in phases MI and MII of the mysis stage (239 mysis larvae, total density: 0.62 ind m<sup>−3</sup>) compared with post-larvae. Sicyoniidae density peaked in



**Fig. 5.** Heatmap showing the total density distribution (ind m<sup>−3</sup>) of the dendrobranchiate shrimp assemblage in relation to months and distance from the coast on the Amazon continental shelf (2013–2015).

January 2015 in the onset of the rainy season (262 individuals, 0.52 ind m<sup>−3</sup>) and this family was not present in May and July 2014 (peak river discharge). Regarding distribution on the ACS, Sicyoniidae was present only offshore, beyond 50 km, with higher density 83 km away from the coast (282 individuals; 0.64 ind m<sup>−3</sup>, Figures 5 and 8) and a significant decreasing trend in the frequency of occurrence with increased distance from the coast ( $A < 0$ ;  $\chi^2 = 15.41$ ;  $P < 0.01$ ).



**Fig. 6.** Minimum and maximum values, medians and 25% and 75% quartiles of density ( $\text{ind m}^{-3}$ ) of sergestoid shrimps considering months and distance from the coast on the Amazon continental shelf (2013–2015). n.s., not significant.

**Table 1.** Coefficients of correlation resulting from the Redundancy Analysis (RDA) between explanatory variables and densities of dendrobranchiate shrimp families on the Amazon continental shelf (2013–2015)

Variables	Code	Axis 1	Axis 2
Distance from the coast (km)	DC	0.55	<b>0.78</b>
Months	Mo.	0.37	−0.08
Temperature ( $^{\circ}\text{C}$ )	T( $^{\circ}\text{C}$ )	−0.13	<b>−0.84</b>
Salinity	Sal	<b>0.78</b>	0.25
Chlorophyll- <i>a</i> ( $\mu\text{g l}^{-1}$ )	Chlo	<b>−0.72</b>	−0.43
Outflow ( $\text{m}^3 \text{s}^{-1}$ )	Outfw	0.13	−0.24
$R^2 = 0.31$ ; $R^2_{\text{adjusted}} = 0.18$			
Explanation ratio		58.81%	22.64%

Values in bold indicate correlations higher than 0.7.

Few solenocerid shrimps were found on the shelf ( $N = 115$  larvae) and most were in the mysis III stage (88 larvae,  $0.58 \text{ ind m}^{-3}$ ). Mysis II stages were absent in July 2013 and post-larvae were present only in October 2013 (4 larvae,  $0.02 \text{ ind m}^{-3}$ ). Overall, solenocerid shrimps were present in all months, with the highest density in the onset of the rainy season in January 2014 (39 larvae,  $0.40 \text{ ind m}^{-3}$ ). Solenoceridae was present only farther than 80 km from the coast, with higher densities as far as 200 km (74 individuals;  $0.49 \text{ ind m}^{-3}$ ) (Figures 5 and 8), and a significant increasing trend in the frequency of occurrence on the ACS with increased distance from the coast ( $A > 0$ ;  $\chi^2 = 63.50$ ;  $P < 0.01$ ).

Penaeid shrimp densities were homogeneous (90 individuals;  $0.62 \text{ ind m}^{-3}$ ), with higher densities of mysis stages compared with post-larvae (53 mysis,  $0.51 \text{ ind m}^{-3}$ ). They were present in all months, with higher density in the dry season, October 2014 ( $0.22 \text{ ind m}^{-3}$ ), which was related to the low Amazon River outflow ( $Z = -3.23$ ;  $P = 0.001$ ). Penaeidae were present throughout the shelf (Figures 5 and 8), with a significant increasing trend

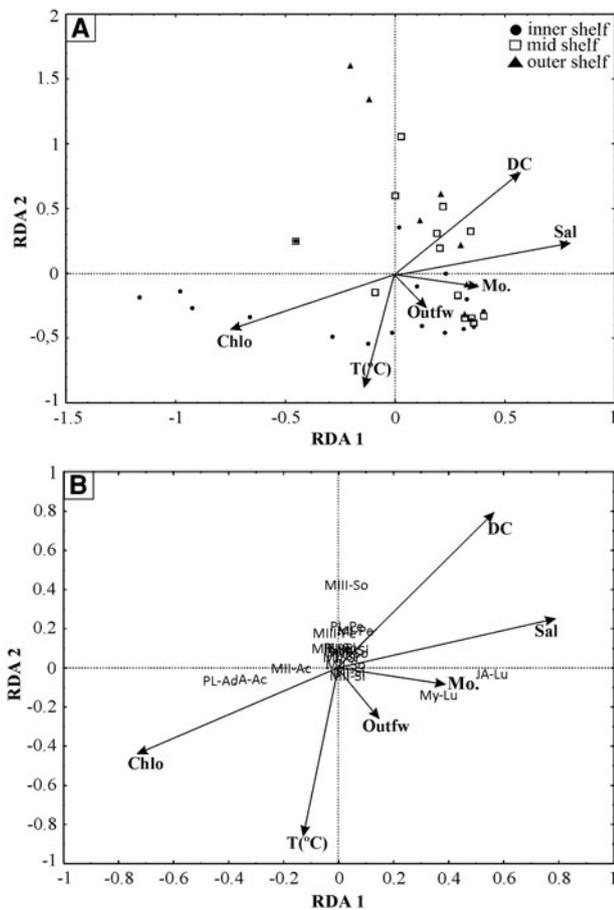
in the frequency of occurrence ( $A > 0$ ;  $\chi^2 = 12.74$ ;  $P < 0.01$ ) with increased distance from the coast.

Density distribution of penaeoid shrimps was significantly correlated with the explanatory variables in the RDA model; however, few taxa had correlations higher than 0.1 with the RDA axes. Therefore, solenocerid and penaeid mysis III stages were positively correlated with distance from the coast on axis 2 (Figure 7, Supplementary Table S2).

## Discussion

This study provides novel information on density distribution of dendrobranchiate shrimps (superfamilies Sergestoidea and Penaeoidea) in the plankton of the Amazon Continental Shelf, with information on seasonal variations, thus helping to pave the way to understanding this large-scale, hugely relevant ecosystem that remains poorly studied. The hypothesis that the distribution of shrimps groups on the ACS is heterogeneous was accepted, and this study revealed different migratory patterns depending on groups, and different tolerances to salinity variations. Previous studies on planktonic shrimps in this region have been based on one single cruise only and analysis were performed to luciferid species (Melo *et al.*, 2014) and mainly by families (Santana *et al.*, 2020), not distinguishing the groups as presented here. Thus, this is the first study to reveal the temporal variability of these key organisms on the ACS (see summarized data in Supplementary Table S1).

In tropical coastal areas, the zooplankton species diversity increases towards outer shelf and open ocean waters (Boltovskoy *et al.*, 1999; Lopes *et al.*, 2006). In ACS, an effect of the Amazon river plume is a local drop in the diversity of most oceanic planktonic groups (Boltovskoy *et al.*, 1999), due to the dominance of an immense low-salinity plume ( $<20$ ) from the inner shelf to mid-shelf areas, as also shown by Santana *et al.* (2020) who found that the major contributions of marine holopegagic decapods (e.g. penaeid shrimps) occurred in the oceanic area without plume influence.



**Fig. 7.** Representation of the density dispersal of dendrobranchiate shrimps according to explanatory variables on the Amazon continental shelf (2013–2015), produced using Redundancy Analysis (RDA). A: scores of samples with vectors. B: scores of taxa with vectors. Explanation ratio: RDA1: 58.8%; RDA2: 22.6%. Mo.: months, Chlo: chlorophyll- $\sigma$  ( $\mu\text{g l}^{-1}$ ),  $T(^{\circ}\text{C})$ : temperature, Outfw: water outflow, Sal: salinity, DC: distance from the coast (km), My-Lu: Luciferidae mysis, JA-Lu: Luciferidae juveniles and adults, MII-Ac: mysis II of *Acetes* spp., PL-Ac: post-larvae of *Acetes* spp., JA-Ac: juveniles and adults of *Acetes* spp., MIII-So: mysis III of Solenoceridae, MIII-Si: mysis III of Sicyoniidae, MIII-Pe: mysis III of Penaeidae, PL-Pe: post-larvae of Penaeidae.

Aside from reflecting the environmental requirements of each family, the different patterns among shrimps also reflect the complexity of the ACS environment. During our study, the low-salinity plume reached as far as 200 km from the shore, in May. All other months had a more restricted plume (less than  $\sim 100$  km from the shore), and this allowed observation of shrimp assemblage distribution both at sites under direct influence of the Amazon plume and at sites with more oceanic characteristics.

We observed higher frequency and abundance of Sergestoidea in areas under the influence of the Amazon River plume. Planktonic shrimps densities obtained in this study were similar to those in the Arvoredo Archipelago (Koettker & Freire, 2006), and São Tomé Cape to Brazil (Brandão *et al.*, 2015). The only study that covered a large extent in the western tropical Atlantic influenced by the Amazon River plume was Santana *et al.* (2020), who reported the huge abundance of planktonic decapods, mostly *Brachyura* larvae and luciferids shrimps in coastal and oceanic areas under the influence of the plume of the Amazon River.

The sergestoid shrimp stages that were present ranged from larvae to adults, with emphasis on the high density of *B. faxoni*, which along with *Acetes* spp. plays an important role in the food web and produces high biomass in continental shelf environments (Longhurst, 1985). The holoplanktonic shrimp *Lucifer typus* was

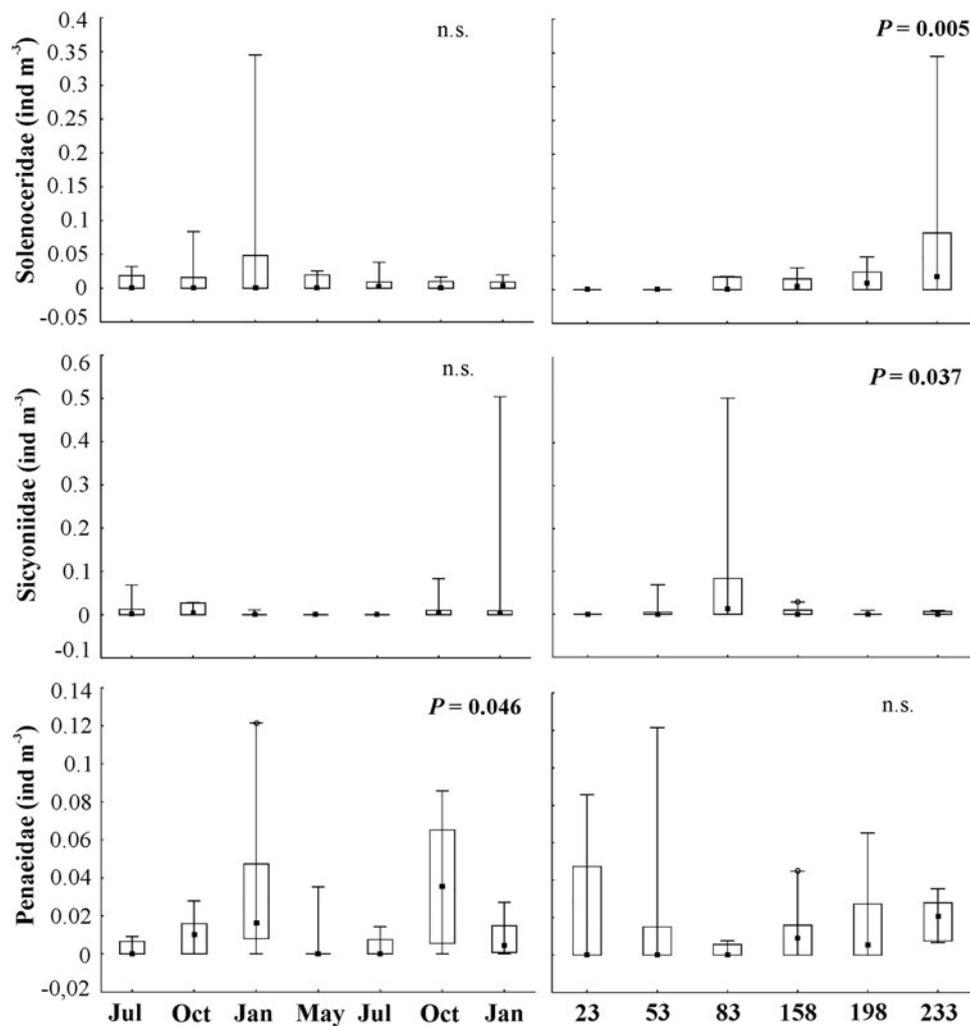
confirmed as an oceanic tropical water shrimp (Bowman & McCain, 1967; Xu, 2010; Melo *et al.*, 2014; Marafon-Almeida *et al.*, 2016) while *B. faxoni* proved to be typically coastal, with the highest densities among all the shrimp taxa in this study (Bowman & McCain, 1967; Longhurst, 1985; Arshad *et al.*, 2011), thus corroborating Melo *et al.* (2014), who reported its high-density pattern on the ACS.

The positive correlation of Luciferidae with months was associated with the dynamics of the Amazon River outflow and salinity on the ACS. This indicates that Luciferidae shrimps, dominated by *B. faxoni*, were associated with the shortest distance from the coast and highest outflow, which is corroborated by their high densities on the inner-mid shelf ( $<150$  km, present study) and the high abundance of luciferid in the coastal and oceanic areas under Amazon river plume influence seen by Santana *et al.* (2020). They appear to have a continuous recruitment, with a peak that might be associated with species reproductive and spawning periods (Fugimura *et al.*, 2005; Cavalcante-Braga, 2017 unpublished); however, this aspect needs to be further investigated on the ACS.

Among Sergestidae, *Sergestes* sp. seems to be an oceanic tropical water species ( $\geq 36$ ), as *Neosergestes edwardsi* (previously *Sergestes edwardsi*), which has been a good indicator of these water masses (Brandão *et al.*, 2013). On the other hand, *Acetes* spp. was found to be a coastal species with its entire life cycle occurring in the inner part of the ACS. Two species of the genus *Acetes* might occur on the ACS: *A. americanus*, which is distributed on the continental shelf of Brazil and is likely associated with coastal water masses, and *A. marinus*, which does not have a known larval development and is endemic to the influence area of the Amazon River mouth (D'Incao & Martins, 2000; Vereshchaka *et al.*, 2015). Due to the difficulty in differentiating between the larval stages of these two species, it was not possible to determine if they are concurrent or if they have different distributions on the ACS.

Seasonality of congeners of *Acetes* spp. is well known; however, this was not evident on the ACS. Overall, recruitment is continuous throughout the year in tropical and subtropical regions, with spawning peaks occurring during hotter seasons (Xiao & Greenwood, 1993; Simões *et al.*, 2013a, 2013b; Santos *et al.*, 2015). *Acetes* spp. distribution was primarily associated with higher temperatures and chlorophyll-*a*. *Acetes americanus* is known to have higher abundance in the months with high chlorophyll-*a* concentration (Santos *et al.*, 2015) and it occurs in shallower sites with high temperatures and lower salinity values (Simões *et al.*, 2013b); these patterns are similar to those found for *Acetes* spp. on ACS.

Penaeoid larvae were less abundant and were represented by Solenoceridae, Sicyoniidae and Penaeidae. With little variation, all larval stages were present, from mysis I to post-larva, which is in line with the reproductive behaviour of the benthic adult population. Penaeoid distribution might be explained by different factors; this taxon had the highest number of species recorded on the ACS (Barros & Pimentel, 2001; Silva *et al.*, 2002a, 2002b, 2020), and is expected to have a wider niche. Its low larval density can be explained by different migratory movements (see Dall *et al.*, 1990, who identified four patterns for penaeid shrimps' life cycle). It is also likely that penaeoid larval densities reflect diel migrations, especially post-larvae that tend to concentrate at deeper levels during the day, while moving towards the surface at night (Gomez-Ponce & Gracia, 2003, 2007, 2008). *Solenocera* larvae tend to remain in the middle of the water column, while *Sicyonia* larvae have wider dispersal in the column and Penaeidae tend to concentrate near the surface between 0 and 10 m depth (Gomez-Ponce & Gracia, 2008). Efforts should be taken for vertical sampling on the PCA at different depths, to throw some light on this issue.



**Fig. 8.** Minimum and maximum values, medians and 25% and 75% quartiles of density ( $\text{ind m}^{-3}$ ) of penaeoid shrimps considering months and distance from the coast on the Amazon Continental Shelf (2013–2015). n.s., not significant.

Solenoceridae species inhabit deeper layers ( $>80$  m), and their reproduction occurs on the outer shelf (Dall *et al.*, 1990; Gomez-Ponce & Gracia, 2003). In previous studies, mysis stages of *Solenocera* spp. were usually found from mid- to outer shelf (Gomez-Ponce & Gracia, 2003, 2007). In the present study, solenocid larvae were found at mid- to outer shelf stations, as well; this explains the correlation found with distance on the ACS and reflects the reproductive behaviour of adults.

Larval distribution of sicyoniid shrimps occurs from mid- to inner ACS since larval stages of *Sicyonia* spp. predominated on the ACS  $\sim 80$  km from the coast. Sicyoniid shrimp adults are usually distributed on the continental shelf at sites deeper than 200 m (D'Incao, 1995). *Sicyonia dorsalis*, *S. laevigata* and *S. parri* reproduction is known to be continuous, with variable juvenile recruitment and two to three peaks a year, one of which occurs with higher intensity (Bauer & Rivera-Vega, 1992; Castilho *et al.*, 2008). Sicyoniidae larvae was not strongly correlated with any explanatory variable addressed in this study. There is little information available on Sicyoniidae and studies on *S. dorsalis* and *S. typica* larvae, which are species that occur on the ACS, are non-existent. According to Costa *et al.* (2005), *S. dorsalis* occurs in areas with salinity values above 30. Although the larvae found here on the ACS were not identified at the species level, all of them were found in saline waters.

Penaeidae occurrence was homogeneous throughout the ACS, ranging from mysis to post-larvae; this has also been observed for

their counterparts in other regions of the world (Price *et al.*, 1993; Rogers *et al.*, 1993; Vance *et al.*, 1996, 1998; Castilho *et al.*, 2008; Galindo-Bect *et al.*, 2010; Pham *et al.*, 2012). Penaeid shrimp larvae distribution on ACS was associated with high salinity, and consequently, these larvae are located further from the coast, which proves the hypothesis of higher occurrence far from the plume. The highest penaeid larvae densities occur in the periods with the lowest Amazon River outflow, thus reflecting seasonality from October to January, which is also related with migratory behaviour (e.g. *Farfantepenaeus subtilis*, according to Aragão *et al.*, 2015). The continuous presence of penaeid larvae in all sampling months and at all sites throughout the ACS proves the importance of this area as a nursery habitat for these shrimps, where juveniles and adults have been captured every year since the 1960s.

This study has shown that the Amazon River outflow has a great influence on the dynamics of Amazon continental shelf salinity and chlorophyll-*a*, thus explaining shrimp assemblage distribution, as is expected in large river plumes (Dagg *et al.*, 2004; Santos *et al.*, 2008; Goes *et al.*, 2014; Conroy *et al.*, 2016). Overall, the highest densities occurred nearer the coast, which reinforces the presence of species that endure high variations in environmental factors on the ACS. Our data suggest that *Acetes* spp. (Sergestidae) is strongly affected by higher temperatures and chlorophyll-*a*, and *B. faxoni* shrimps (Luciferidae) are associated with shorter distance and higher outflow. On the other

hand, Solenoceridae and Penaeidae distribution is explained by a larger distance from the coast and high salinity.

In conclusion, the planktonic shrimps on the inner shelf were associated with chlorophyll-*a*, temperature and outflow, and shrimps on the mid-outer shelf were related to salinity and distance from the coast. This study shows information on the distribution of density of Dendrobranchiata shrimps on the Amazon continental shelf for the first time, with a seasonal approach over two years, and helps to pave the way towards characterizing the distribution of these shrimps in a wide area which has been poorly studied so far, serving as a base for future comparisons. Finally, it is worth noting that the Amazon continental shelf is an extremely high priority conservation area as it serves as a nursery and growth area for at least five shrimp families.

**Supplementary material.** The supplementary material for this article can be found at <https://doi.org/10.1017/S0025315421000308>

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