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Population dynamics of *Oikopleura dioica* (Tunicata: Appendicularia) in a tropical estuary: Spatiotemporal patterns and environmental drivers

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ABSTRACT

Oikopleura dioica, a dominant appendicularian in coastal and estuarine ecosystems, plays an important role in trophic dynamics and carbon fluxes. Despite its ecological relevance, data on its population dynamics and secondary production remain scarce in Amazonian estuaries. This study presents the first estimates of trunk length, biomass, and daily secondary production of *O. dioica* in the Emboraí Velho estuary, a macrotidal system on the eastern Amazon coast (Brazil). Zooplankton and environmental data were collected over multiple months and tidal phases. Results revealed significant spatiotemporal variations in abundance, biomass, and production rates, with higher values recorded during dry periods, when increased salinity and pH were observed. Spearman correlation analyses indicated that salinity and turbidity were key predictors of *O. dioica* distribution, while temperature showed no significant correlation. Trunk length varied with tidal phase and environmental conditions, with smaller individuals dominating in turbid, mesohaline waters. These findings highlight the species' sensitivity to salinity and its preference for marine-influenced conditions, emphasizing its potential as an indicator of estuarine hydroclimatic variability. The study provides essential data on appendicularian ecology in tropical estuaries and supports the inclusion of *O. dioica* in estuarine monitoring and conservation frameworks.

1. Introduction

Brazil has one of the longest coastlines in the world, extending approximately 8500 km, 35 % of which is occupied by the Brazilian Amazon Coast (BAC). This region harbors the largest continuous mangrove belt on the planet, covering around 7591 km^2, and encompasses numerous rivers, bays, islands, and tide-dominated estuaries (Souza-Filho, 2005). These environments sustain highly complex and productive ecosystems, whose biological dynamics are shaped by the interplay between local climate and the physical–chemical properties of the water (Giarrizzo and Saint-Paul, 2008; Magalhães et al., 2015; Leite et al., 2023). The high biological productivity of these areas is largely supported by waters enriched with particulate organic matter, with mangrove forests serving as a primary carbon source for estuarine and coastal consumers, including benthic, planktonic, and nektonic organisms (Koch and Wolff, 2002; Brenner and Krumme, 2007; Arumugam et al., 2016).

Appendicularians are planktonic tunicates that inhabit both coastal and oceanic environments. They are recognized as key players in carbon cycling because (i) their productivity can match or even exceed that of dominant planktonic crustaceans, such as copepods and euphausiids (Tomita et al., 1999); (ii) their grazing impact on primary producers is substantial (López-Urrutia et al., 2003a); and (iii) they play an important role in the oceanic biological carbon pump (Taucher et al., 2024). These organisms are filter feeders that build and inhabit a mucopolysaccharide-cellulose structure called a "house" that captures and concentrates a wide range of food particles, including bacterioplankton, phytoplankton, heterotrophic protists, dissolved organic

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matter (DOM), and even viruses (Bedo et al., 1993; Fernández et al., 2004; Lawrence et al., 2018). Once the house becomes clogged with debris and fecal pellets, it is abandoned and replaced by a new one. The renewal rate varies from 2 to 40 houses per day, depending on environmental conditions such as temperature (Hansen et al., 1996), salinity (Sato et al., 2001), and food availability (Lombard et al., 2009). Both appendicularians and their discarded houses serve as important food sources for carnivorous zooplankton, such as medusae, chaetognaths, and ctenophores (Capitanio et al., 2018).

Due to their ability to feed on pico- and nanoplankton, appendicularians occupy a central position in the microbial food web, acting as a direct trophic link between small microbial prey and larger predators (Touratier et al., 2003; Dadon-Pilosof et al., 2023). They also play an important role in the classical food web, preyed upon by invertebrates and several fish species, including larvae of pleuronectiforms and scombrids, juvenile and adult forage fish (e.g., herrings, sand lances, capelins, smelts, and gadiforms), as well as top predators such as marine birds, mammals, and Pacific salmon (Purcell et al., 2005; Suca et al., 2018; Kume et al., 2021; Ruiz et al., 2024). Furthermore, there is growing evidence that appendicularians significantly contribute to pelagic secondary production in oligotrophic to mesotrophic coastal and oceanic environments, due to their high carbon assimilation efficiency at low to moderate food concentrations (Lombard et al., 2010; Berline et al., 2011; Katija et al., 2017; Jaspers et al., 2015, 2023).

Despite their ecological importance, few studies have estimated appendicularian secondary production, especially in tropical and subtropical waters. Such estimates are crucial for understanding energy fluxes and trophic dynamics in marine systems and can provide important indicators of environmental changes and anthropogenic impacts (e.g., ocean warming and acidification), given their high sensitivity to such disturbances (Bouquet et al., 2018). Along the Brazilian coast, several studies have addressed the composition and structure of appendicularian communities (Vega-Pérez et al., 2011; Carvalho and Bonecker, 2010; Carvalho et al., 2016; Neumann-Leitão et al., 2018; Rocha et al., 2024), but knowledge regarding their population dynamics remains limited (Miyashita and Lopes, 2011). This knowledge gap is especially evident in the BAC estuaries, where data on the secondary production of these organisms are lacking. Influenced by a hot, humid equatorial climate, semidiurnal macrotidal regimes, and elevated concentrations of dissolved nutrients and organic matter from extensive mangrove forests, these environments display distinctive physico-chemical and biological traits (Dittmar and Lara, 2001; Magalhães et al., 2015; Cavalcanti et al., 2022). These characteristics distinguish them from other tropical estuarine systems worldwide (Veríssimo et al., 2017; Balqis et al., 2022; Bhavan et al., 2025).

In the Amazonian estuaries, two appendicularian species have been identified: *Oikopleura (Vexillaria) dioica* Fol, 1872, and *Oikopleura (Coecaria) longicauda* (Vogt, 1854). Although primarily marine, these species can be found in estuaries under polyhaline conditions, with *O. dioica* being dominant due to its high abundance and frequency of occurrence (Costa et al., 2008; Andrade et al., 2022). Given this context, the present study aimed to describe the temporal variation in biomass and secondary production of *O. dioica* in the Emboraí Velho estuary, testing the hypothesis that this species plays a key role in secondary production in this and other Amazonian coastal and marine systems (Hopcroft et al., 1998a; Capitanio et al., 2018). The results offer new insights into zooplankton dynamics in tropical estuarine ecosystems and provide a basis for comparing secondary production across similar systems in Brazil and other regions of the world.

2. Materials and methods

2.1. Study area

The field survey was conducted at a fixed station in the main channel of the Emboraí Velho estuary (Fig. 1a-c). This estuary is situated on the

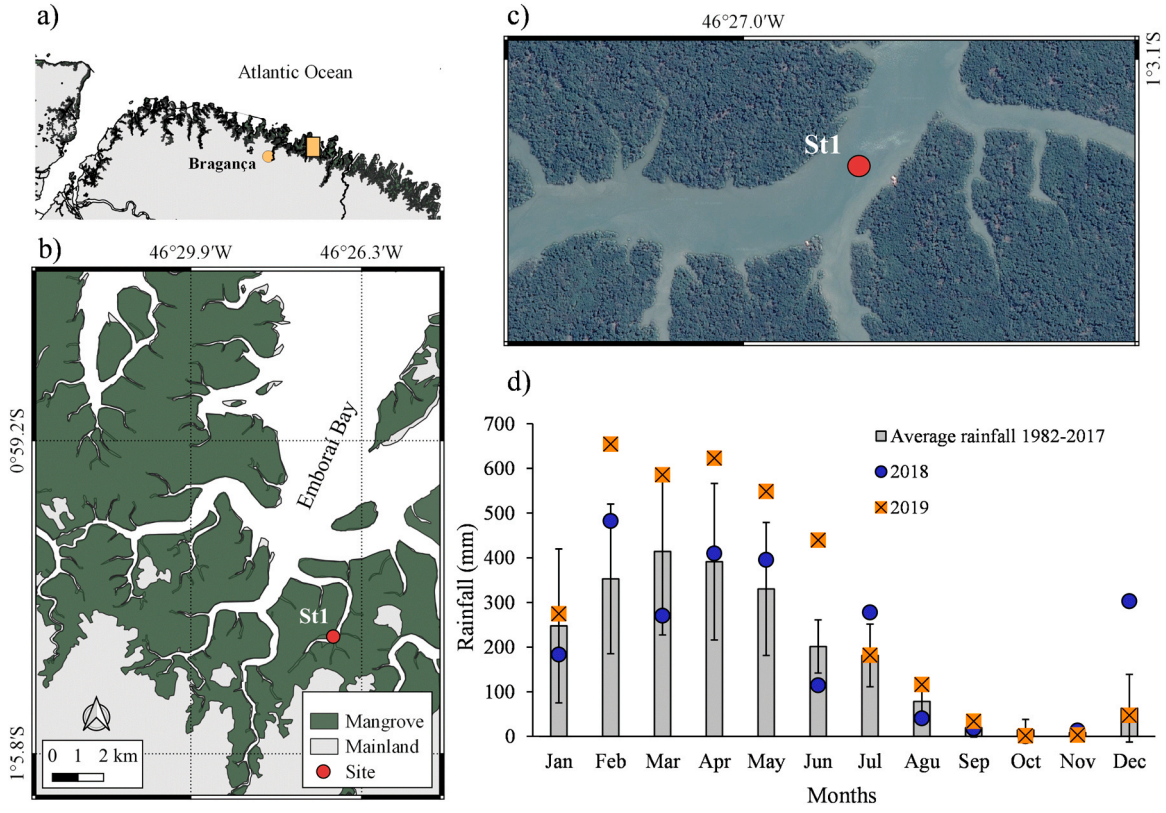


Fig. 1. Study area: (a) Location of the Emboraí Velho estuary on the Brazilian Amazon Coast (BAC); (b, c) Sampling station in the inner sector of the estuary (46°26'51.14" W, 1°03'16.37" S); (d) Historical average (1982–2017) and total monthly rainfall during the study period (2018–2019).

Urumajó coast, in the northern Brazilian state of Pará, approximately 200 km southeast of the mouth of the Amazon River. It is classified as a permanently open estuary, characterized by a broad salinity gradient (8.3–39.3) and high turbidity levels (17.4–409.2 NTU), as well as shallow waters (maximum = 5 m), and strong tidal currents reaching up to 5 m s^{-1} (Sousa et al., 2013; Barros et al., 2019, Carvalho Neto et al., 2023). From a hydrodynamic standpoint, the system is dominated by semidiurnal meso- to macrotidal regimes, with tidal ranges averaging approximately 5 m, reaching up to 6 m during equinoctial spring tides and 3–4 m during neap tides (DHN, 2020).

The region is influenced by a hot and humid equatorial climate, with a pronounced rainy season from January to July, and a dry (or less rainy) season from August to December (Moraes et al., 2005; Fig. 1d). Interannual variation in rainfall patterns may occur, but approximately 75–85 % of the total annual precipitation is typically concentrated in the first half of the year. This seasonal distribution is primarily regulated by latitudinal shifts of the Intertropical Convergence Zone (ITCZ), which induces intense convective activity during the rainy season (Marengo, 1995). The rainfall data used in this survey were acquired from the Tracuateua station of the National Meteorological Institute, which is located at 01°06'S, 46°87'W, approximately 56 km from the study area (Fernandes et al., 2023). Air temperatures remain high and stable throughout the year, with a mean annual value of approximately 27 °C, while mean annual precipitation exceeds 2000 mm (INMET, 2020). Wind regimes also exhibit seasonal variability, with stronger northeasterly winds, often exceeding 10 m s^{-1} , prevailing during the dry season (CPTEC/INPE, 2018).

The estuary is part of the Araí-Peroba Marine Extractivist Reserve (MMA, 2025), where renewable natural resources (e.g., crabs, fishes, and mollusks) are sustainably harvested by traditional communities residing within the reserve's boundaries (Costa and Soares, 2021). The surrounding landscape includes a mosaic of coastal ecosystems, especially well-developed mangrove forests (Silva et al., 2025). As observed in other Amazonian estuaries and adjacent coastal habitats (Dittmar and Lara, 2001; Goes et al., 2014), the export of nutrients and organic matter from mangroves regulates both primary and secondary production in the estuarine environment.

2.2. Samplings and study design

To understand the influence of environmental variables on population dynamics of *O. dioica* in the Emboraí Velho estuary, their temporal variation was investigated at a fixed station (1º03'16,37" S, 46º26'51,14" W) located in the inner sector of the estuary (Fig. 1b). A total of four campaigns were conducted in January and April 2018 (rainy season), and September and December 2019 (dry season), during two tidal cycles in spring tide periods.

The hydrological variables (salinity, turbidity, temperature and dissolved oxygen [DO] concentrations) were measured *in situ* at the subsurface (~ 1 m in depth), with readings taken every 10 min over a 25-hour sample period using a CTDO equipped with a turbidity sensor (RBR Maestro). For temperature, the CTDO was accurate to ± 0.002 °C, while for conductivity, it was accurate to ± 0.0003 S m^{-1}. Additionally, water samples (500 mL) were collected every 3 h from the subsurface with a 5L Niskin oceanographic bottle (General Oceanics Inc.) for laboratory analysis of pH and chlorophyll-a concentrations. These samples were preserved in a cooler at 4 °C for transportation to the laboratory.

During the study period, zooplankton samples were collected using conical plankton nets (200 µm mesh size, 0.50 m mouth diameter, and 1.5 m in length) towed horizontally for 3 min in the subsurface layer. The nets were equipped with mechanical flowmeters (General Oceanics 2030 R) to estimate the volume of water filtered. Samplings were conducted at 3-hour intervals over a 25-hour period, using a small powerboat running at an average speed of 1.5 knots, resulting in a total of 36 samples (9 samplings x 1 station x 4 months). After the samplings, the organisms were stored in 600 mL plastic bottles and fixed in a 4 % formalin solution (final concentration) neutralized with sodium tetraborate (5 g L^{-1}).

2.3. Laboratory procedures

The pH was measured using a pH meter (Labmeter, pH 2—Hs—3B). The water samples collected for the determination of chlorophyll-a (phytoplankton biomass) were vacuum-filtered through glass-fiber filters (Macherey-Nagel GF-5, 47 mm, Carvalhaes) and the filters were then freeze-dried for further analysis. Chlorophyll-a was extracted with 90 % acetone *v/v* and determined spectrophotometrically, according to the protocol of Parsons and Strickland (1963) and UNESCO (1966). A Thermo Scientific 220 Evolution UV-Vis spectrophotometer was used to analyze the chlorophyll-a concentrations. This spectrophotometer was calibrated with deionized water (mixed bed deionizer Q-380 M), and the detection limit (DL) established for the analysis of chlorophyll-a was 0.02 mg m^{-3}. To ensure quality control, the linearity of the chemical method ($R^2 > 0.998$) was determined using an individual calibration curve compiled from standard solutions of known concentrations of the respective substances.

The preserved zooplankton samples were rinsed to remove the formalin buffer and subdivided into aliquots into one to five aliquots using a Folsom splitter, and all the specimens of *O. dioica* were then identified (Esnal, 1999), quantified and measured in squared Petri dishes, using a stereomicroscope (Zeiss, Stemi 2000) containing a micrometric ruler attached to one of its eyepieces. To obtain the total estimate of organisms per sample, the specimens count was multiplied by the subsampling factor (1−5).

The quantitative data obtained for each sample were used to calculate density (ind m^{-3}), relative abundance (%), biomass (mg m^{-3}), daily production rate (mg m^{-3} d^{-1}), and the frequency of occurrence (FO) of *O. dioica*. The relative frequency of occurrence was determined by the proportion of samples in which organisms were recorded. Biomass was estimated by multiplying the density of species by the mean carbon weight, which was derived from the trunk length employing a weight-length regression equation (López-Urrutia et al., 2003b). The daily production rate (*Pc*, mgC m^{-3} d^{-1}) was calculated by:

$$Pc = Bc * g_s$$

where *Bc* = biomass in carbon (mgC m^{-3}) and g_s = somatic growth rates (d^{-1}). The values of g_s were estimated using the equation of López-Urrutia et al. (2003b): $g_s = 0.21e^{0.0815\,T}$, where T (°C) is the water temperature.

2.4. Statistical analysis

The effects of the study month, season (rainy/dry), tide phase (flood/ebb) and circadian period (day/night) on environmental variables (salinity, turbidity, temperature, pH, dissolved oxygen and chlorophyll-a concentrations) and on the biological attributes of *O. dioica* (biomass and productivity) were evaluated using the nonparametric Mann-Whitney *U* test and Kruskal-Wallis *H* test. When the Kruskal–Wallis test indicated significant differences, a *post hoc* Dunn's (software Rstudio R 3.6.0 +) multiple comparison test based on rank sums was applied to identify pairwise differences among treatments (Zar, 2013). Spearman rank correlation analysis was used to investigate relationships between environmental and biological variables. All these analyses were run in PAST (version 4.16), with a 5 % significance level (α = 0.05).

Principal Component Analysis (PCA) was applied to identify potential relationships among environmental variables throughout the study period, using RStudio (R version 3.6.0 +) and the Factoextra and FactoMineR packages (Kassambara, 2017). The data were range-transformed to standardize all variables, scaling each variable from zero to one.

3. Results

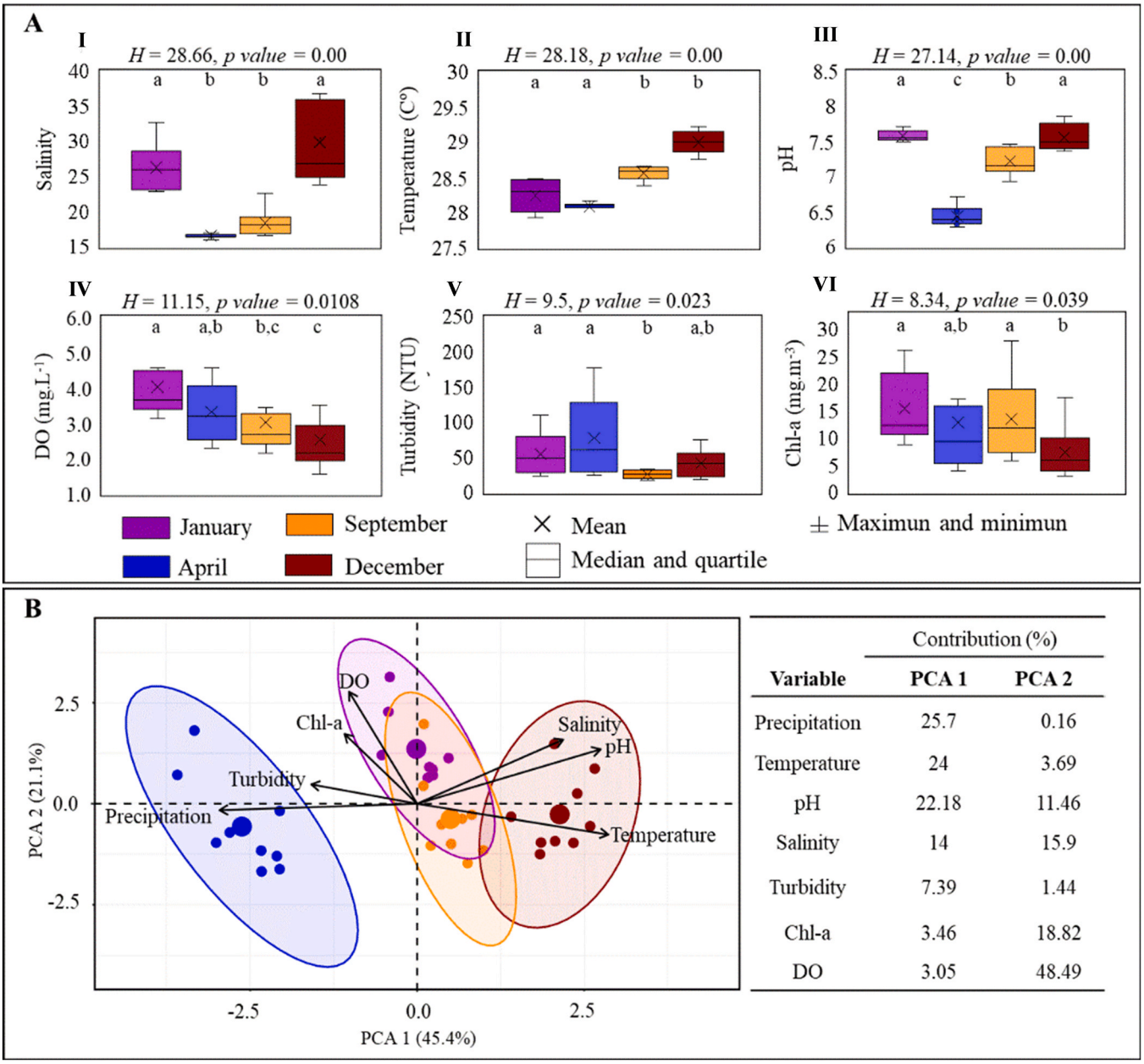
3.1. Precipitation

During the study period, precipitation rates varied when compared to the 35-year historical average (1982–2017). These variations had clear effects on the temporal fluctuations of hydrological variables, such as salinity and chlorophyll-a concentrations, among others. The relationships between these variables are shown in Fig. 2 A, B.

Fig. 1d illustrates the changes in precipitation levels during the study period, comparing them with the historical average. In 2018, total annual precipitation was 2510 mm, representing a reduction of approximately 40 % compared to the total recorded in 2019, which reached 3512 mm. The former (2018) was characterized as a hot year, with precipitation levels below the historical average during the first half of the year. In January 2018, monthly, rainfall was 25.5 % below the historical average, while in April of that same year, an increase of 4.5 % above the average was observed. Toward the end of 2019, fluctuations in precipitation were recorded in September and December. In September, precipitation increased by 70 % relative to the historical average, whereas in December, a 25 % decrease was recorded (Fig. 1d).

3.2. Environmental variables and chlorophyll-a concentrations

To assess temporal patterns, environmental variables and biological attributes of *O. dioica* (i.e., biomass and production rate) were pooled and reported as means ± standard deviation, considering both monthly (referring to the specific sampled months) and seasonal (dry *vs.* rainy season) timescales. On a seasonal basis, salinity (21.3 ± 5.3–24.1 ± 7.2; $U = 112$, $p > 0.5$), pH (7.0 ± 0.6–7.4 ± 0.3; $U = 132$, $p > 0.5$), and



Variable	Contribution (%) PCA 1	PCA 2
Precipitation	25.7	0.16
Temperature	24	3.69
pH	22.18	11.46
Salinity	14	15.9
Turbidity	7.39	1.44
Chl-a	3.46	18.82
DO	3.05	48.49

Fig. 2. (A) Boxplots and results of the Kruskal–Wallis test for environmental variables (salinity, temperature, pH, dissolved oxygen [DO], turbidity, and chlorophyll-a) measured in January, April, September, and December in the Emboraí Velho estuary. Different letters denote statistically significant differences between months, as determined by Dunn's post hoc test; (B) Principal Component Analysis (PCA) biplot showing the ordination of monthly samples based on environmental variables. The relative contribution of each variable to the formation of PCA axes is indicated by vector length and direction.

water temperature (28.2 ± 0.2 °C to 28.8 ± 0.3 °C; $U = 6$, $p = 0.00$) were slightly lower during the rainy season than in the dry season. These decreases are likely linked to enhanced freshwater input resulting from precipitation-driven runoff, particularly intense during the first half of the year (Fig. 1d).

Throughout the study period, mesohaline to polyhaline conditions prevailed, with mean salinity values ranging from 16.6 ± 0.3 in April 2018–30.0 ± 0.2 in December 2019 ($H = 28$, $p < 0.01$). The pH remained predominantly alkaline and exhibited a strong positive correlation with salinity (Fig. 2 A, III), with monthly means varying from 6.4 ± 0.1–7.6 ± 0.1 ($H = 27$, $p < 0.001$). Water temperature was relatively stable, showing only minor short-term fluctuations (<1 °C), ranging from 28.1 ± 0.1 °C in April 2018–29.0 ± 0.2 °C in December 2019—an expected trend for estuarine systems in tropical regions. Despite the overall subtle temporal variability (on both monthly and seasonal scales), significantly higher temperatures were observed during the dry season months ($H = 28.6$, $p < 0.05$; Fig. 2 A, II).

Temporal variations in dissolved oxygen (DO), chlorophyll-a concentrations, and turbidity showed inverse patterns compared to salinity and other physicochemical variables. A significant decline in DO was observed during the dry season (2.8 ± 1.0 mg L^{-1}; $U = 69$, $p < 0.001$), with mean monthly values rising from 2.5 ± 1.0 mg L^{-1} in December 2019–4.0 ± 1.0 mg L^{-1} in January 2018 ($H = 11$, $p < 0.05$; Fig. 2 A, IV). Chlorophyll-a concentrations followed a similar trend to DO, exhibiting lower values during the dry season (10.5 ± 6.7 mg m^{-3}) compared to the rainy season (14.0 ± 9.3 mg m^{-3}), although seasonal differences were not significant ($p > 0.5$). However, pronounced monthly variability was detected ($H = 8$, $p < 0.05$), with the lowest chlorophyll-a concentration recorded in December 2019 (7.4 ± 4.6 mg m^{-3}; Fig. 2 A, VI). Turbidity displayed significant seasonal variation ($U = 74$, $p < 0.001$), with markedly higher values during the rainy season (April 2018: 77.4 ± 59.9 NTU) relative to the dry season (September 2019: 25.8 ± 6.0 NTU), likely attributable to increased inputs of organic and inorganic material derived from mangrove runoff associated with high precipitation levels. The Principal Components Analysis (PCA) confirmed a clear temporal structuring of environmental variables, revealing distinct seasonal patterns in estuarine conditions over the sampling period (Fig. 2B). The first two principal components explained 66.5 % of the total variance related to the environmental-precipitation dynamics, with PC1 accounting for 45.4 % and PC2 for 21.1 %. Although both axes were significant ($p < 0.001$), interpretation focused on PC1 due to its higher explanatory power. This axis effectively discriminated between rainy season samples (blue and purple circles) and dry season samples (red and orange circles). Dry season months were associated with higher

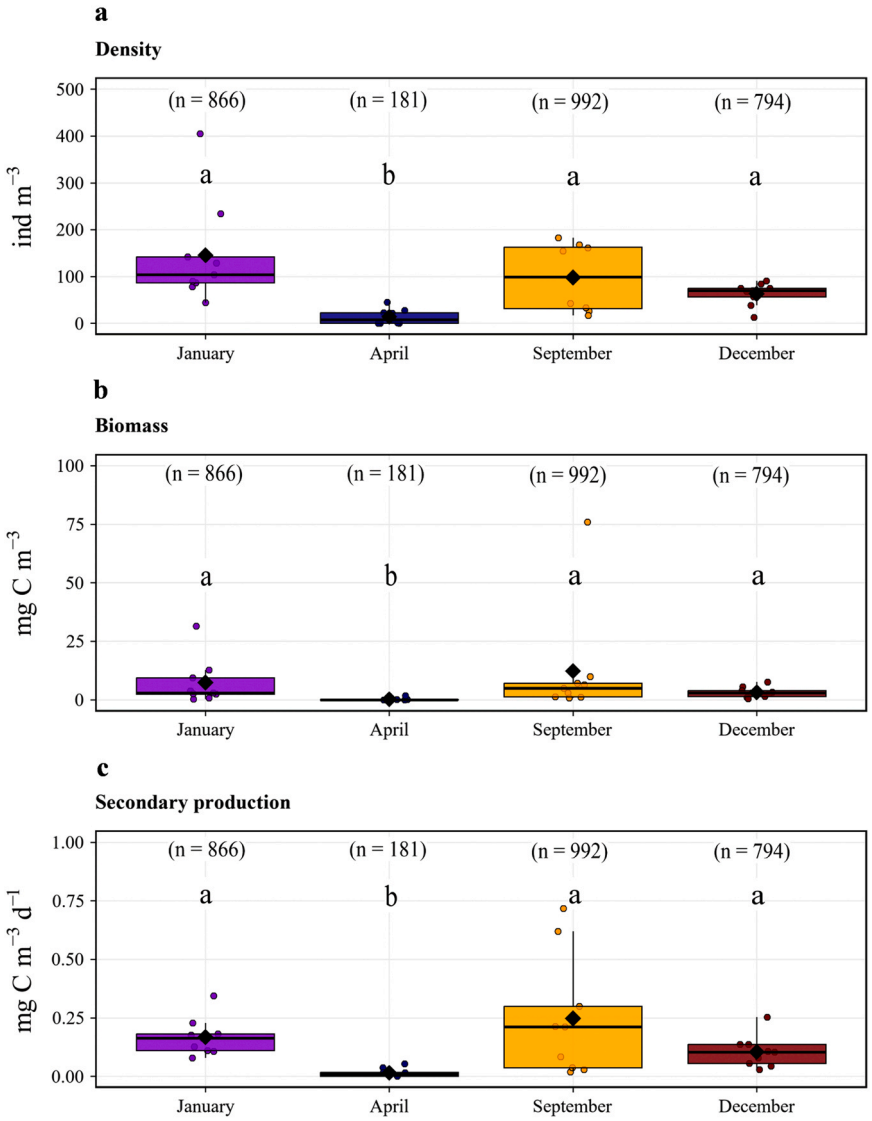


Fig. 3. Mean values (+SD) of (a) density, (b) biomass (mg C m^{-3}), and (c) production rate (mg C m^{-3} d^{-1}) of *O. dioica* obtained for the months studied in the Emboraí Velho estuary (Pará, Brazil). Note differences in scale.

salinity, temperature, and pH, whereas negative scores on PC1—typical of rainy season months—corresponded to increased levels of DO, chlorophyll-a, and turbidity. The contribution of each environmental variable to the PCA axes is illustrated in Fig. 2B.

3.3. Temporal distribution of the density, biomass and secondary production of O. dioica

Although no clear seasonal pattern in *Oikopleura dioica* density was detected ($p>0.05$), significant differences among months were observed ($H = 19.1$, $p < 0.001$; Fig. 3a). Mean density ranged from 14.1 ± 16.2 ind m^{-3} in April to 158.3 ± 111.5 ind m^{-3} in January 2018—months characterized by high precipitation levels—representing 4 % and 35 % of the total species abundance, respectively. In contrast, during drier months, mean densities ranged from 63.3 ± 24.3 ind m^{-3} in December to 190.3 ± 284.8 ind m^{-3} in September 2019, accounting for 15 % and 46 % of total abundance, respectively. These findings suggest a marked influence of precipitation on *O. dioica* density, as evidenced by the negative and significant correlation between these variables (Table 1).

In contrast, *O. dioica* biomass exhibited significant seasonal variation, increasing from 3.8 ± 7.7 mg C m^{-3} during the rainy season to 7.7 ± 17.2 mg C m^{-3} in the dry season ($U = 89$, $p < 0.05$). On a monthly scale, both biomass ($H = 17.9$, $p < 0.001$) and production rate ($H = 18.3$, $p < 0.001$) followed a similar trend, with the lowest values recorded in the rainy month of April 2018 and the highest in the dry month of September 2019 (Fig. 3b, c). These results indicate that the productivity of *Oikopleura dioica* increases during periods of reduced precipitation and high salinity (Table 1).

3.4. Trunk length of the O. dioica population

The trunk length data of *O. dioica* were organized monthly according to tidal phases, allowing the construction of temporal size-frequency distributions (Fig. 4). Throughout the study period, trunk length showed significant temporal variation, with pronounced monthly heterogeneity ($H = 37.5$, $p < 0.001$).

Regarding variation by tidal phase within each month, the longest trunk lengths were recorded during flood tide in January 2018 ($p<0.001$; Fig. 4A). In September 2019, individuals collected during low and flood tides exhibited greater trunk lengths compared to those sampled during high and ebb tides. In December 2019, trunk lengths observed during high and ebb tides differed significantly from each other and from those recorded during low and flood tides.

At a finer temporal resolution (Fig. 4B), significant differences in trunk length were detected during low tide events ($H = 38.1, p < 0.001$). Individuals with mean trunk lengths of approximately 260 μm predominated in January and April 2018, whereas larger individuals (~300 μm) were more frequent in September and December 2019. During high tide, the largest trunk lengths were observed in December 2019, with values reaching up to 340 μm (Fig. 4B). No significant differences in trunk length were observed during flood and ebb tide events.

Table 1
Results of Spearman's rank correlation analysis assessing the relationships between the density, biomass, and secondary production of *O. dioica* and environmental variables in the Emboraí Velho estuary, northern Brazil.

Variables	Prec	pH	Sal	°C	NTU	Chl-a	DO
O. dioica (ind m^{-3})	-0.38*	0.47*	0.29	0.13	-0.21	0.24	0.15
O. dioica (mg C m^{-3})	-0.56*	0.45*	0.38*	0.34*	-0.35*	0.17	-0.03
O. dioica (mg C m^{-3} d^{-1})	-0.49*	0.48*	0.35*	0.30	-0.36*	0.14	0.04

Prec: precipitation, Sali: Salinity, Turb: turbidity, Temp: Temperatura (°C). * The correlations were significant at $p \leq 0.05$.

These results suggest that tidal dynamics, combined with monthly variability, significantly influence the size distribution of *O. dioica* populations.

3.5. Relationships between environmental variables and O. dioica

The relationships between the density, biomass, and production of *O. dioica* and environmental variables—including precipitation, salinity, temperature, turbidity, dissolved oxygen, and chlorophyll-*a* concentrations—were assessed using Spearman correlation analysis (Table 1). Among the variables analyzed, precipitation and salinity exerted the strongest influence on the distribution patterns of *O. dioica*. A positive and significant correlation with salinity was observed, which likely explains the high biomass and production recorded in September 2019, a month characterized by low precipitation and meso-polyhaline conditions (Table 1).

In addition to salinity, biomass and production were also positively correlated with pH (Table 1; Fig. 5), while turbidity exhibited a significant negative correlation with these parameters. These patterns are further supported by Fig. 5, which illustrates the preference of *O. dioica* for environments with salinity values around 18 and pH ranging from 6.9 to 7.0. Temperature was positively and significantly correlated with biomass ($r_s = 0.34$, $p<0.05$), but no significant associations were found between temperature and either density or production. No significant correlations were detected between the ecological attributes of *O. dioica* and either dissolved oxygen concentrations or chlorophyll-*a* levels.

4. Discussion

Seasonal variability in precipitation plays an important role in shaping the biogeochemical characteristics of Amazonian estuaries, directly influencing the abundance and production of planktonic communities (Lam-Hoai et al., 2006; Leite et al., 2023). The interaction between macrotidal regimes and hydrological variables—particularly salinity and temperature—regulates key ecophysiological processes, including growth rate and metabolism in planktonic organisms (Basu et al., 2022; Procópio et al., 2024). As a result, temporal fluctuations in plankton structure and dynamics largely reflect changes in water properties and tidal conditions (Souza-Júnior et al., 2013; Leite et al., 2016; Srichandan et al., 2021).

During the first half of 2018 (January–June), precipitation levels in the study area showed marked variability compared to historical averages, likely due to the southward migration of the Intertropical Convergence Zone (ITCZ) and the presence of the Upper-Level Cyclonic Vortex, which intensified cloud formation in April–June 2018 (INMET, 2024). Despite the peaks observed in February and May 2018, rainfall was lower than in the first half of 2019 (Fig. 1d), likely reflecting anomalous sea surface temperatures (SST) in the Pacific and Atlantic oceans induced by the La Niña event of 2018 (Santos et al., 2024).

Barros et al. (2019) reported that euhaline conditions prevailed in the estuary during the dry season, primarily due to reduced freshwater inflow. Conversely, salinity decreased during the rainy season, as observed in nearby estuaries such as Taperaçu (Magalhães et al., 2013; Pereira et al., 2023) and Caeté (Diele and Simith, 2006; Andrade et al., 2025). Although January 2018 is commonly classified as part of the rainy season (Moraes et al., 2005), the precipitation levels (Fig. 1d) and changes in hydrological variables (e.g., salinity and pH; Fig. 2 A) indicate transitional characteristics for this period.

Appendicularians, planktonic tunicates, are considered the second most abundant group of mesozooplankton globally, surpassed only by copepods (Gorsky and Fenaux, 1998; Hopcroft et al., 1998a; Jaspers et al., 2023). During population peaks, their abundance may even exceed that of copepods (Questel et al., 2013). Their distribution is influenced by multiple environmental factors, including temperature, salinity, food availability (Acuña and Anadón, 1992; Nakamur et al., 1997; Tomita et al., 2003; Sato et al., 2008), tides (Costello and Stancyk,

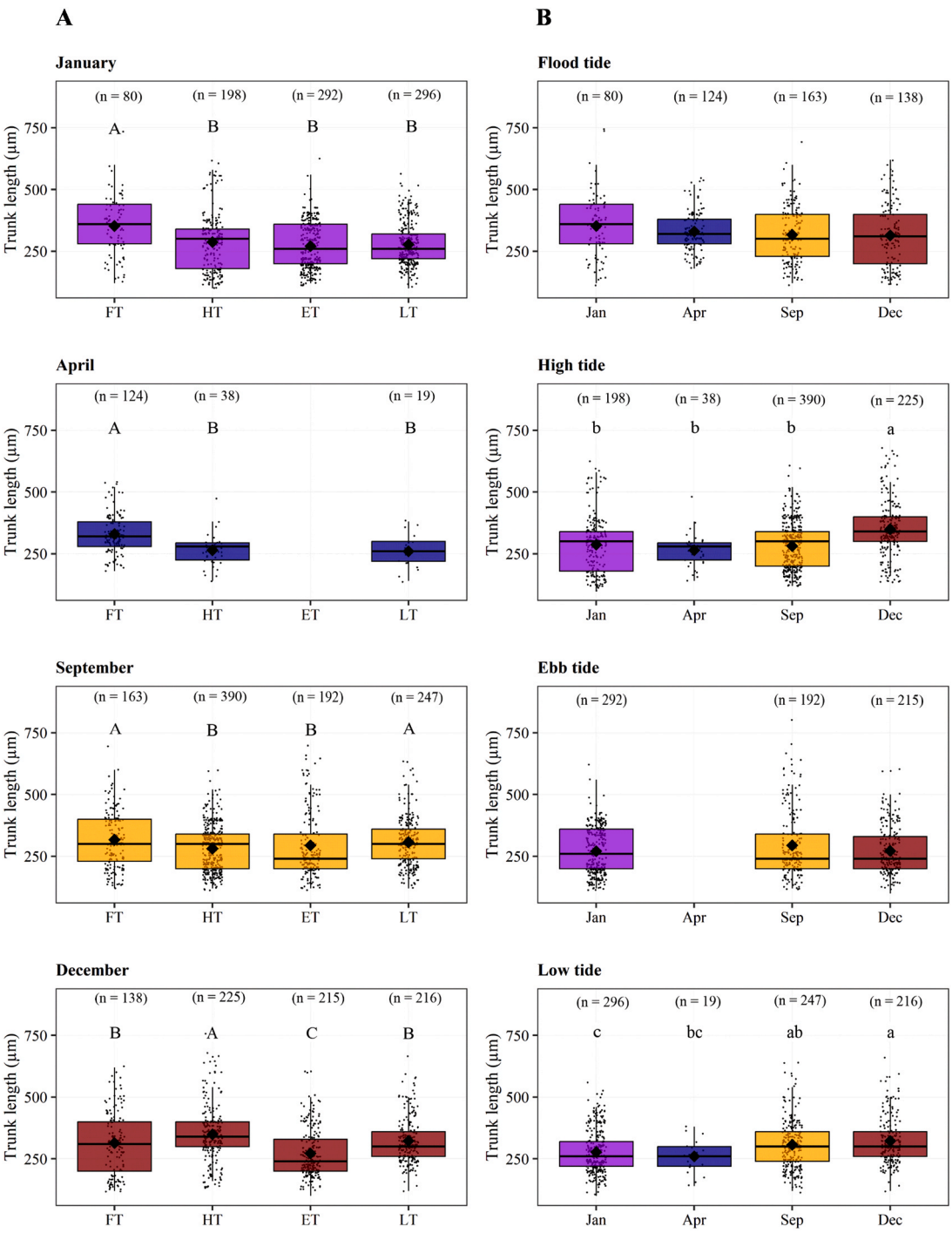


Fig. 4. Trunk length distributions of *O. dioica* according to tidal phase (flood, high, low, and ebb tides) in monthly samples collected with 200 µm mesh nets in the Emboraí Velho estuary, northern Brazil.

1983), predation (Shiganova, 2005; Sommer et al., 2003), and synergistic effects (Bouquet et al., 2009). Coastal regions often host dense appendicularian populations due to nutrient inputs and turbulent mixing zones, as previously documented in the Pacific (e.g., Shiga, 1985; Uye and Ichino, 1995; Sato et al., 2001) and Atlantic (Forneris, 1965; Tundisi, 1970; Capitanio, 1995; Aravena and Palma, 2002). Despite the nutrient-rich nature of Amazonian estuaries, precipitation and salinity appeared to be the main drivers of *O. dioica* population stability in the Emboraí Velho estuary.

While *O. longicauda* is also common in the region (Barros et al., 2019; Fernandes et al., 2023), this study focuses on the ecological dynamics of *O. dioica*, the most abundant species. This distribution pattern mirrors global observations in brackish ecosystems from temperate (Brunetti et al., 1990; Spinelli et al., 2009; Dolgner et al., 2021), subtropical (Du et al., 2011; Liu et al., 2013; Nascimento et al., 2021), and tropical regions (Hopcroft et al., 1998a; Hoover et al., 2006; Andrade et al., 2022). While *O. longicauda* displays oceanic affinities and is commonly found on the inner continental shelf off Brazil (Esnal and Castro, 1977; Tundisi, 1970; Miyashita and Lopes, 2011), *O. dioica* is typically associated with neritic and estuarine environments (Neumann-Leitão et al., 2003; Andrade et al., 2022), prevailing in brackish ecosystems (Carvalho and Bonecker, 2010; Nogueira et al., 2018; Fernandes et al., 2023).

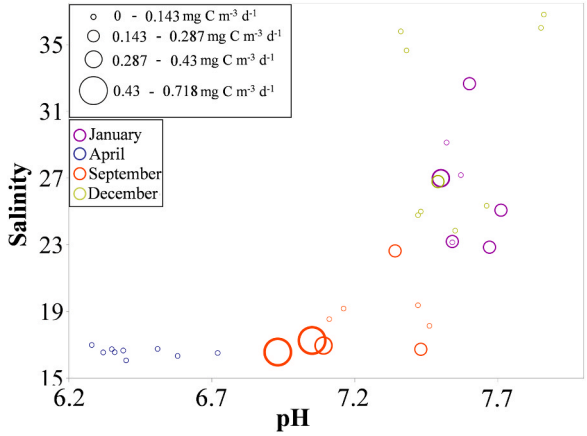


Fig. 5. Influence of salinity and pH on the secondary production rate of *O. dioica* throughout the sampling months in the Emboraí Velho estuary, northern Brazil. Note the differences in scale across graphs.

In the Emboraí Velho estuary, rainfall variability and associated hydrological changes significantly influenced the abundance, distribution, and secondary production of *O. dioica* (Figs. 2–3; Table 1). Higher abundance in September 2019 (dry season) compared to April 2018 (rainy season) suggests that reduced precipitation favors the species, in agreement with findings from other Amazonian estuaries (Leite et al., 2016; Andrade et al., 2022). Tidal fluctuations also affected recruitment and retention, with larger and more abundant individuals recorded at flood tide in April 2018. In contrast to findings by Costello and Stancyk (1983) and Srichandan et al. (2021), which documented high *O. dioica* densities during high tides, Esnal et al. (1985) observed greater densities during low tides in the Potengi estuary, highlighting the influence of site-specific hydrodynamic conditions.

Appendicularians are ecologically important due to their rapid growth, high reproductive output, and contribution to marine snow via discarded houses (Gorsky and Fenaux, 1998; Onuma and Nishida, 2022). House turnover increases with decreasing salinity, with up to 53 houses produced per individual for a salinity drop from 35 to 25. Daily house production (130–290 % of individual biomass) is notably high in estuarine environments (Sato et al., 2001), contributing significantly to trophic dynamics. Jaspers et al. (2023) also highlighted the role of this process in sustaining planktonic biomass and ecosystem function.

The obtained results indicate that *O. dioica* biomass and secondary production peaked during low-precipitation periods, reflecting its preference for marine-influenced conditions. While previous studies have linked rainfall-driven hydrological changes to phytoplankton and copepod dynamics (Andrade et al., 2016; Oliveira et al., 2023), data on appendicularians in Amazonian estuaries remain scarce, reinforcing the ecological importance and originality of the present contribution.

Secondary production estimates provide key insights into energy and carbon flow within planktonic food webs (Omori and Ikeda, 1992). Comparing these metrics across tropical coastal regions remains challenging due to methodological discrepancies (e.g., mesh size, sampling frequency) and lack of standardization (Harris et al., 2000; Leite et al., 2020). The present findings provide an important baseline for improving the quantification of appendicularian contributions to ecosystem functioning in tropical estuarine environments.

Trunk length in *O. dioica* exhibited tidal modulation, reaching its highest values at flood tide. Small individuals lacking gonads or bearing undeveloped gonads predominated, consistent with the observations reported by Spinelli et al. (2015) in the North Patagonian frontal system. In April 2018, individuals measuring 80–600 μm were primarily found in meso-polyhaline waters with high turbidity, dissolved oxygen and chlorophyll-a concentrations (Figs. 2–4), while larger specimens (>600 μm) occurred in clearer, more saline conditions in December 2019. The persistence of immature individuals across months suggests continuous reproduction, influenced by high temperatures that reduce generation time (Deibel and Lowen, 2012). According to Uye and Ichino (1995), warmer temperatures lead to smaller trunk sizes in *O. dioica*, a trend corroborated by several other studies (Hopcroft et al., 1998a; Sato et al., 2001; Bouquet et al., 2018). In addition to temperature, trunk length is also influenced by salinity (Uye and Ichino, 1995), pH (Bouquet et al., 2018), and predation pressure (Liang and Vega-Pérez, 1995; Purcell et al., 2005). During the reproductive phase, individuals discard their houses and exhibit vividly colored gonads, increasing vulnerability to predators (Alldredge, 1982; Gorsky and Palazzoli, 1989; Fenaux, 1998). Despite their small size, *O. dioica* individuals exhibit high biomass and play a key role in trophic food webs due to their rapid growth rates (Hopcroft and Roff, 1998b; Jaspers et al., 2023). Trunk length measurements recorded in this study are consistent with those reported for the Patagonian frontal system (Spinelli et al., 2015) and European coastal waters (López-Urrutia et al., 2005), the latter including individuals exceeding 1000 μm, likely reflecting the influence of lower temperatures on growth. Similar size patterns have been documented in Jiaozhou Bay, China (Li et al., 2020), and Kingston, Jamaica (Hopcroft et al., 1998a).

The salinity increase associated with lower precipitation levels positively influenced *O. dioica*, resulting in higher density, biomass, and secondary production. An opposite trend was observed in April 2018, when a decline in salinity coincided with reduced abundance. The species also appears to prefer higher pH levels, as reported by Barros et al. (2019) and Andrade et al. (2022). Although some studies (e.g., Winder et al., 2017; Bouquet et al., 2018) suggest that low pH may favor appendicularians by increasing fecundity and shortening generation time, laboratory experiments suggest that high pH is suboptimal for *Oikopleura* (Troedsson et al., 2013). Therefore, it remains unclear whether lower pH acts as a positive regulator or whether increased pH has a negative effect. Further research is required to clarify the influence of pH on appendicularian ecology in estuarine environments, particularly in the context of ongoing climate change and ocean acidification (Troedsson et al., 2013). The variations observed among the serial samples are consistent with patterns commonly reported in zooplankton surveys, which naturally exhibit considerable variability due to the intrinsic dynamics of the organisms. Such fluctuations may include periods of relative stability, as well as pronounced patchiness or even the absence of individuals in some tows. This spatial–temporal heterogeneity is a well-documented characteristic of plankton communities, particularly within the zooplankton. Therefore, despite the inherent variability, the dataset can be regarded as robust and representative of the conditions that typically occur in the environment.

Although no significant correlations were observed between the density and production of *Oikopleura dioica* and water temperature, this variable remains a key ecological driver influencing the species' development and distribution. As noted by Paffenhöfer (1976), its preference for warmer water layers is associated with shorter generation times and higher growth rates. According to the ecophysiological model proposed by Lombard et al. (2010), *O. longicauda* exhibits better performance than other appendicularian species under oligotrophic conditions. This trend may explain the lack of dominance of *O. longicauda* in the present study, whereas *O. dioica* remained dominant throughout the sampling period—likely due to its affinity for eutrophic environments with elevated temperatures, contrasting with patterns reported in other systems (e.g., Acuña and Anadón, 1992; Lombard et al., 2010). The absence of significant correlations between *O. dioica* and concentrations of chlorophyll-*a* and dissolved oxygen, coupled with its negative association with turbidity, strongly suggests that food availability is not a limiting factor for the species in the Emboraí Velho estuary. This pattern is consistent with the observations of Leite et al. (2016) in the Taperaçu estuary, where high autotrophic and heterotrophic productivity sustains robust Oikopleuridae populations.

This study provides a valuable contribution to the understanding of

Oikopleura dioica dynamics in the Amazon coastal region, particularly within the Emboraí Velho estuary. By presenting the first estimates of biomass, secondary production, and trunk size distribution for this species in the area, it provides essential baseline data for understanding its population dynamics and ecological role in comparable estuarine environments across Brazil and globally. These findings underscore the importance of including *O. dioica* in estuarine monitoring and management strategies, given its potential role in biodiversity maintenance and trophic sustainability.

We recognize that this study represents an initial temporal assessment based on a single year of observations. Although extending the monitoring period would provide a stronger basis for evaluating long-term patterns, the data already reveal consistent variability linked to tidal conditions and monthly changes. Even with the limited duration, the results offer robust preliminary evidence of the processes influencing the size structure of *O. dioica* populations in this estuarine environment. Continued future research will be essential to further clarify the ecological significance of this species within tropical coastal ecosystems.

5. Conclusions

This study highlights the complex relationships between environmental variables and the population dynamics of *Oikopleura dioica*, underscoring the central roles of rainfall seasonality, salinity, and tidal regime in shaping its ecological attributes. Rainfall-driven salinity variation emerged as a key driver of both density and secondary production, with low-rainfall periods favoring population growth. Tidal dynamics also influenced the transport and spatial distribution of individuals along the estuary. Temporal patterns in salinity and pH suggest that deviations beyond the species' tolerance range may reduce its occurrence, revealing both vulnerability and resilience to climatic variability. Food availability was likely not a limiting factor for *O. dioica*, given the species' high filtration efficiency and the abundance of suspended organic matter—characteristic of turbid Amazonian estuaries—comprising pico- and nanoplankton, diatoms, bacteria, and detritus. Production estimates presented here reinforce the ecological importance of *O. dioica* as a secondary producer, particularly during drier periods, highlighting the influence of regional seasonality on its population dynamics. Populations were largely dominated by immature individuals, and population metrics showed negative correlations with precipitation and positive associations with salinity and tidal regime. This study provides the first estimates of biomass, secondary production, and body size distribution for *O. dioica* in the Amazon coastal zone, offering valuable insights into its ecological role and population behavior in tropical estuarine systems. These findings emphasize the need to include *O. dioica* in estuarine monitoring and management efforts, as part of integrated strategies to sustain biodiversity and ecological integrity. Incorporating this knowledge into conservation planning will be essential to anticipate and mitigate the impacts of climate change on these vulnerable environments.

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Author Statement

All authors contributed to the conception and design of the study. The manuscript adheres to the publisher's Ethical Guidelines.

CRediT authorship contribution statement

André Magalhães: Writing – review & editing, Supervision, Data curation, Conceptualization. **Silva Thaynara Raelly Costa:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Data curation. **Penha Sânia Maria Ribeiro da Penha Ribeiro da Penha:** Writing – review & editing, Methodology, Investigation. **Farley Darlan dos Santos Fernandes:** Writing – review & editing, Methodology, Investigation. **Silva Elton:** Writing – review & editing, Software, Data curation. **Aráujo Ályssa:** Conceptualization. **Costa Rauquírio Marinho da:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition, Conceptualization. **Pereira Luci Cajueiro Carneiro:** Writing – review & editing, Resources, Methodology.

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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Data availability

Data will be made available on request.

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