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Copepod Assemblages at the Base of Mangrove Food Webs during a Severe Drought

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Abstract: The effect of severe drought on the functional groups that sustain the base of the mangrove food webs in semi-arid areas is largely unknown. We therefore analyzed the intra-annual variation in the assemblages and functional groups of copepods in a shallow, low-inflow estuary of the Brazilian semi-arid coast when the most severe drought ever occurred. The lowest density was found in April (upstream region) and the highest in August (downstream region). Three main functional groups were identified, sorted by spawning strategy, and further subdivided according to feeding strategy, trophic regime, and diel vertical migration behavior. The community was significantly influenced by the extreme drought period, presenting a temporal homogenization in terms of composition, and an expressive and unexpected increase in density in the dry period, possibly due to phytoplankton blooms resistant to hypersalinity and the occurrence of copepod species adapted to stressful conditions. The few stress-tolerant species sustaining the food webs with seasonal variations were observed simplifying the trophic variability. The results indicate that hypersalinity can induce changes in the zooplankton community, increasing copepod mortality risk and, so, promoting alteration in the trophic estuarine dynamic.

Keywords: hypersalinity; climate change; zooplankton; estuarine systems; extreme weather events

1. Introduction

Copepods are an essential component of zooplankton in most of the water-based ecosystems and also in estuarine habitats, because of their abundance and biomass [1]. These small crustaceans prey on microorganisms such as phytoplankton and ciliates. They are considered a key group at the base of trophic pyramids, linking primary producers with higher trophic levels [2]. Describing their functional traits and the associated ecosystem biodiversity can aid in the understanding of their ecological roles [3].

Functional traits are phenotypic characteristics that indirectly affect the growth, reproduction, or survival of an organism, and consequently have a relevant role on the effects of ecosystem properties [4]. Copepod assemblages are taxonomically and functionally diverse [5], and their feeding type and reproduction strategies may vary depending on the environmental constraints [6–8]. Thus, studying species based on their functional characteristics can increase our knowledge of how ecosystems function more realistically than the taxonomic groupings alone [8,9].

Copepod assemblages have a temporally heterogeneous composition that changes based on intra-annual environmental modifications between the rainy and dry periods in tropical estuaries [10,11]. An understanding of this intra-annual variation is important in

order to describe and quantify the different estuarine communities [12] that alternate between seasons, and how each community survives unfavorable periods [13]. Precipitation has been recognized as a critical factor that causes seasonal variations in copepod communities in subtropical environments, and these freshwater/turbid inputs restrict their spatial distribution along the estuary [14]. The intensity and level of freshwater discharge can influence features such as salinity, temperature, nutrients, primary productivity and water residence time, affecting the temporal dynamics of estuarine assemblages [12].

A hypersaline regime can occur in estuaries where the hydrological deficit exceeds the evaporation rates from rainfall and river flow inputs. The resulting salinity exceeds that of coastal waters and increases further from the coastline [15]. This regime is common in semi-arid and arid estuarine regions [16,17]; however, hypersalinity is a phenomenon that has been intensifying worldwide. This phenomenon is caused by the combination of local human impacts, such as dams, weirs, irrigation [18], and climate change impacts, such as increasing sea surface temperature, sea-level rise, drought, and annual precipitation reduction [19]. This hypersalinity influences the spatial and temporal variation of estuarine organisms [20] and the functional groups at the base of estuarine food webs [2,14].

Copepod assemblage studies in tropical estuaries with large river flow revealed the highest abundance in the rainy season and the highest diversity during the dry season [21,22]. However, information on intra-annual dynamics in hypersaline mangrove ecosystems and the potential consequences for the food webs are scarce. Global climatic changes create more severe and prolonged droughts, especially in arid and semi-arid coastal regions [23,24]. The effect of drought on functional groups that sustain the base of mangrove food webs is unknown. Thus, the present study aimed to carry out a baseline study, evaluating the intra-annual distribution of assemblages and functional groups of copepods in a tropical low-inflow estuary in response to hypersalinity over one year (2015) considered the worst drought ever recorded in the Southwestern Atlantic (Brazil) [23]. Our hypothesis is that extremely high values of salinity can reduce the number of copepod species, over the course of a year, with few species sustaining the food webs.

2. Materials and Methods

2.1. Study Area

The Piranji Estuary is a mesotidal, semi-diurnal coastal system [25] located in the equatorial southwestern Atlantic (Northeast Brazil). It is a short (~20 km long) and shallow (~3 m) system where hypersalinity occurs naturally, making it an excellent model to evaluate the effects of hypersalinity on copepod assemblages (Figure 1); the salinity levels inside the estuary exceed the values generally found near the coastal ocean (sal. 34.5–36) [26]. The Piranji River is formed by tidal channels, extensive intertidal flats, shallow navigation channels, and low freshwater inflow [27,28]. Absence of salinity stratification in the water column is a feature of this low-inflow estuary [29]. There is a sandbar (spit type) at the river mouth parallel to the coastline, approximately 3.2 km long and 230 m wide [30]. The regional coastal climate is classified as a hot, semi-arid climate (BSh) according to the Köppen climate classification, and it is mainly influenced by the region's position in the intertropical convergence zone (ITCZ), which causes two distinct seasonal periods of precipitation. The rainy season runs from January to June, and the dry season runs from July to December (Figure 2).
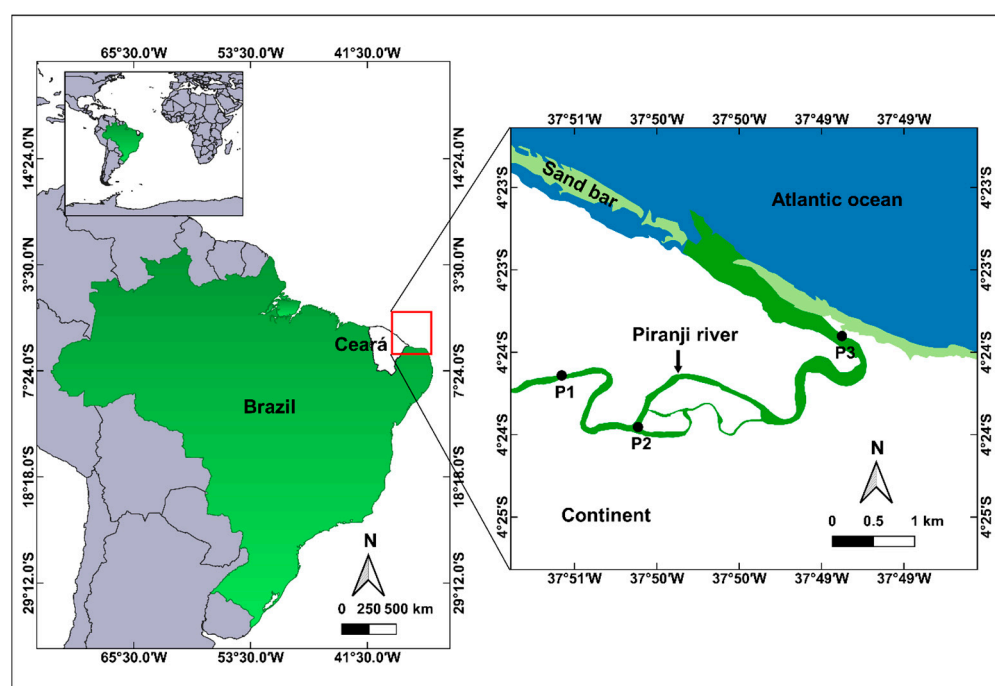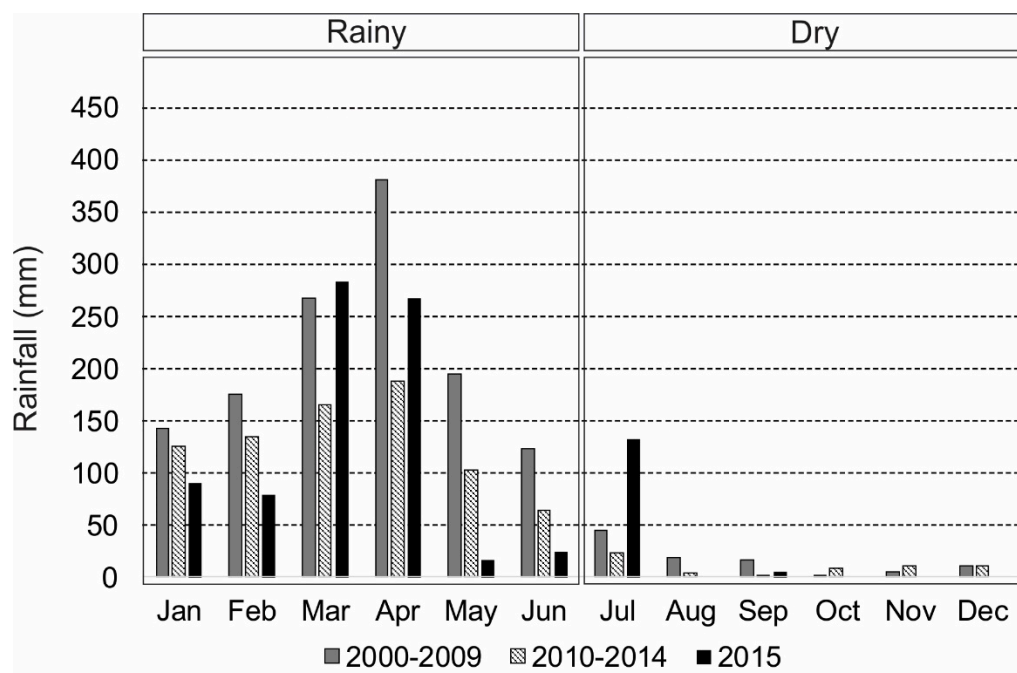
Figure 1. Piranji Estuary (equatorial Southwestern Atlantic, Brazil), and location of the P1–P3 sampling sites along the mangrove estuarine ecosystem during an intense drought period.
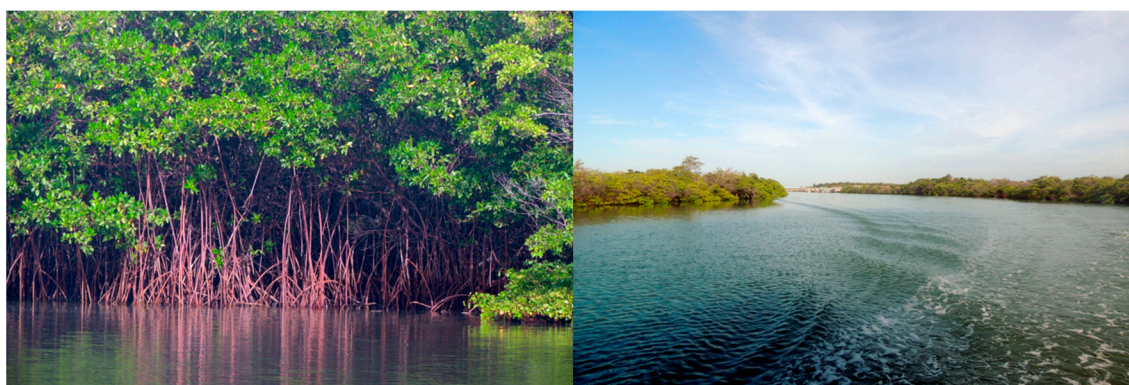
Figure 2. Piranji Estuary (equatorial Southwestern Atlantic, Brazil) with mangrove forests (**left** side) and the well-mixed shallow estuarine environment (**right** side).

Hypersaline conditions are related to several factors, such as climate (semi-arid region), the presence of multiple dams along the river basin [28], high evaporation rate and surface runoff [31] and shallow depth (mean 2.44 m) [27]. The Piranji Estuary also displays hyperthermal conditions (estuary water temperature approximately 2 °C above the coastal water temperature) [29] and decreasing fluvial discharge, related to intense droughts [27] and to the last drought cycle (2012–2016) in this location [23]. Intra-annual sampling was conducted in 2015 during this severe drought. The historical rainfall data (1988–2011) and data for the last drought cycle (including the sampling year, 2015) and the most recent years (2017–2020) are presented in Figure 3.

Figure 3. Mean precipitation (mm) of annual rainfall data (2000–2009), last drought cycle (2010–2014) [23] and collection date (2015) in Piranji Estuary (equatorial Southwestern Atlantic, Brazil) [32].

2.2. Intra-Annual and Spatial Sampling and Analysis

Intra-annual and spatial samplings were performed at three stations (P1, P2, and P3) along the river basin (P1, P2, and P3) to determine the spatial distribution of copepod assemblages. P1 was located upstream, P2 in an intermediate zone, and P3 was closest to the estuarine mouth in the downstream region (Figure 1). Six ebb tide campaigns were conducted in 2015; three in the rainy season (February, April, and June) and three in the dry season (August, October, and December).

The zooplankton samples were collected by horizontal trawls in the subsurface estuarine water layer with plankton netting (120 μm mesh) and equipped with a general oceanic flowmeter. Immediately after collection, samples were preserved in buffered formalin (10%) [33]. Samples were first analyzed under a stereomicroscope to identify copepods to the lowest possible taxonomic level using appropriate identification keys [5,34,35]. The samples were further sub-sampled (from 1/32 to 1/1024) using a Motoda splitter [33], and taxa were then counted. The abundance of copepod species was expressed as the number of individuals per cubic meter of filtered water (ind.m^{-3}).

2.3. Intra-Annual Environmental Analysis: Physicochemical Factors and Phytoplankton Pigments

Environmental variables (temperature, salinity, pH, dissolved oxygen, and depth) were measured in situ using a multi-parametric probe (YSI 6660). To determine chlorophyll a, aliquots of water were collected from the subsurface with a Van Dorn bottle and were filtered through 0.7 μm pore size glass-fiber filters (47 mm in diameter, type GF - 3, Macherey-Nagel, Düren, Germany) in triplicate. After filtration, the filters were kept frozen for subsequent spectrophotometric determination of chlorophyll *a* and pheophytin a using extraction in 90% acetone (method 10200H) [36].

To determine dissolved nutrients, samples were filtered in triplicate through 0.7 μm pore size glass-fiber filters (47 mm diameter, type GF-3, Macherey-Nagel, Düren, Germany). Some samples were excluded for determining silica and were filtered through membranes of mixed cellulose esters with a porosity of 0.45 μm (47 mm diameter, HATF, Millipore, Billerica, MA, USA). The analysis of dissolved nutrients (ammoniacal N, nitrite,

nitrate, phosphate, and silicate) was carried out according to the spectrophotometric methods described by [37] for marine and estuarine waters. Nitrite, nitrate and phosphate samples were kept refrigerated at 4 °C and analyzed within 48 h after the collection, ammoniacal N within 24 h and silicate samples were frozen to −20 °C and analyzed within a few weeks. The samples used to determine total nitrogen (TN) and total phosphorus (TP) were not filtered before analyzing using spectrophotometric methods [38]. For TN and TP, the unfiltered samples were previously oxidized after collection [38] and analyzed within a few weeks. After filtering the samples for nutrient determination, filtrations were also carried out with fiberglass filters with 1.2 μm porosity (Millipore APFC) that were previously dried in an oven at 105 °C and calcined in a muffle furnace at 480 °C, to determine total suspended solids (TSS) using gravimetry according to the 2540 D method [36].

2.4. Data Analysis

The abundance (ind.m^{-3}) of all copepod species was calculated at the sampled stations. Cluster analysis was used in conjunction with the Bray–Curtis similarity index to compare copepod assemblages during the sampling months. The data were log(x + 1) transformed. The cluster analysis was performed using the unweighted pair group method with arithmetic mean (UPGMA) based on the Bray–Curtis similarity index. The differences between cluster groups were tested using similarity profile analysis (SIMPROF) using PRIMER version 6. The species that contributed to each group were evidenced by similarity percentage (SIMPER) analysis. BEST (BIO-ENV stepwise) analysis was performed to determine the importance of environmental variables on intra-annual copepod assemblages under extreme drought conditions in 2015.

Finally, a literature review on copepod functional traits was performed (Supplementary Material SI). The functional traits were compiled into a matrix that included feeding type (active ambush feeding, passive ambush feeding, filter-feeding, cruise feeding, or mixed feeding), trophic group (herbivore, carnivore, omnivore, detritivore, herbivore-omnivore, omnivore-carnivore, or detritivore-carnivore), reproduction method (broadcast spawner or sac spawner), and diel vertical migration (DVM) activity. Six species (Harpacticoida sp1, Harpacticoida sp2, Harpacticoida sp3, *Parvocalanus* cf. *scotti*, *Pseudodiaptomus marshi* and *Pseudodiaptomus trihamatus*) were not included in this analysis because there were no data regarding their functional traits. Therefore, fourteen species were used to analyze the functional groups. These groups were based on the Euclidean distances assessed using the SIMPROF test at 5% significance.

3. Results

3.1. Intra-Annual and Spatial Variation: Environmental Data

The estuary showed a low depth (3.4 ± 1.1 m) throughout the 2015 year, with stable values for temperature (27.5 ± 0.9 °C), pH (8.0 ± 0.4) and dissolved oxygen (5.6 ± 0.5 mg/L) (Table 1). An increasing gradient of nutrients was observed throughout the year from the downstream station (P3) to the upstream station (P1) (Figure 1). The downstream site (P3) was more stable and had low nutrient concentrations dominated by oligotrophic marine waters (Figure 4). Chlorophyll *a* varied spatially, with values decreasing from the point furthest upstream of the river (P1) to the point closest to the mouth (P3). A clear spatial variation during the year was observed at points 1 and 2, where chlorophyll *a* was initially very low, but then increased significantly in the driest months of October (P1 = 41.31 μgL^{-1}) and December (P1 = 38.60 μgL^{-1}) (Figure 4G).
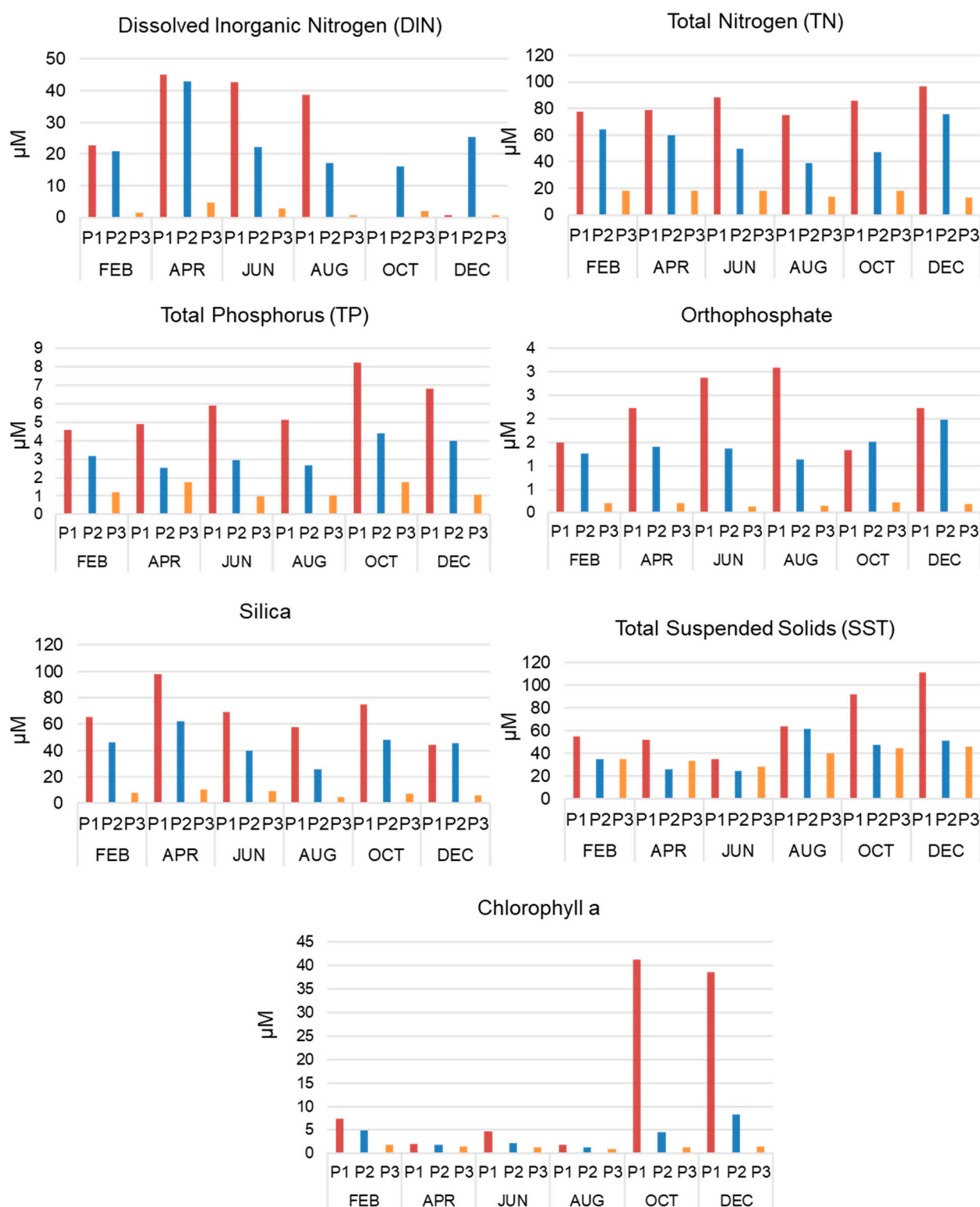
Figure 4. Nutrients in the Piranji Estuary (equatorial Southwestern Atlantic, Brazil, 2015). Point upstream of the river (P1) to the point closest to the estuarine mouth (P3).

Table 1. Intra-annual and spatial environmental variables in the Piranji Estuary (equatorial Southwestern Atlantic, Brazil, 2015). (T) temperature, pH, (OD) dissolved oxygen and (D) depth. Point upstream of the river (P1) to the point closest to the estuarine mouth (P3).

Month	Station	T	pH	OD	D
February	P1	29.15 ± 0.09	8.83 ± 0.02	3.79 ± 0.51	1.95 ± 0.63
	P2	29.06 ± 0.42	8.76 ± 0.49	3.84 ± 0.73	1.47 ± 0.47
	P3	28.07 ± 0.25	8.75 ± 0.09	5.55 ± 0.33	2.79 ± 1.40
April	P1	28.19 ± 0.06	7.30 ± 0.01	4.18 ± 0.59	2.87 ± 1.12
	P2	28.12 ± 0.03	7.62 ± 0.01	4.71 ± 0.11	2.28 ± 0.38
	P3	27.94 ± 0.01	7.81 ± 0.04	5.68 ± 0.06	3.08 ± 1.72
June	P1	28.42 ± 0.01	8.05 ± 0.01	4.77 ± 0.02	2.02 ± 0.44
	P2	28.07 ± 0.03	8.07 ± 0.01	4.58 ± 0.81	2.56 ± 0.73
	P3	27.15 ± 0.01	8.03 ± 0.07	5.48 ± 0.04	3.35 ± 1.06
August	P1	27.02 ± 0.01	7.92 ± 0.01	4.64 ± 0.04	1.59 ± 0.27
	P2	25.89 ± 0.01	8.18 ± 0.01	5.13 ± 0.10	1.65 ± 0.65
	P3	25.60 ± 0.01	8.13 ± 0.01	5.94 ± 0.03	3.30 ± 0.90
October	P1	27.58 ± 0.01	7.89 ± 0.01	6.01 ± 0.05	1.78 ± 0.45
	P2	27.02 ± 0.02	7.73 ± 0.01	4,65 ± 0.65	2.82 ± 1.07
	P3	26.15 ± 0.01	7.66 ± 0.01	5,73 ± 0.10	2.86 ± 0.93
December	P1	28.28 ± 0.02	8.60 ± 0.05	5.77 ± 0.80	1.82 ± 0.82
	P2	27.64 ± 0.20	8.48 ± 0.01	5.00 ± 0.94	1.59 ± 0.41
	P3	26.83 ± 0.05	8.47 ± 0.03	6.04 ± 0.01	2.81 ± 0.78

The values of salinity varied from 9.0 to 63.0 (Table 2). The hypersalinity condition increased toward the upstream station (P1) and occurred in most assessed months (February, June, August, October, and December) except April. The highest (62.2) and lowest (9.4) salinity values were obtained from the upstream station (P1) in December and April, respectively. A classic estuary, where salinity increases towards the downstream station (P1 < P2 < P3), was only observed in April. In other months, salinity values increased upstream (P1 > P2 > P3) (Figure 5), and the hypersaline estuary was classified as inverse during most parts of the year (Table 2).

Table 2. Salinity at the three sampling points (P1, P2, and P3) in Piranji Estuary (equatorial Southwestern Atlantic, Brazil, 2015). Point upstream of the river (P1) to the point closest to the estuarine mouth (P3). Hypersaline months are highlighted in red color and are common in this driest year.

	FEB	APR	JUN	AUG	OCT	DEC
P1	45	9	36	42	55	63
P2	45	26	37	39	46	52
P3	39	37	38	37	39	39
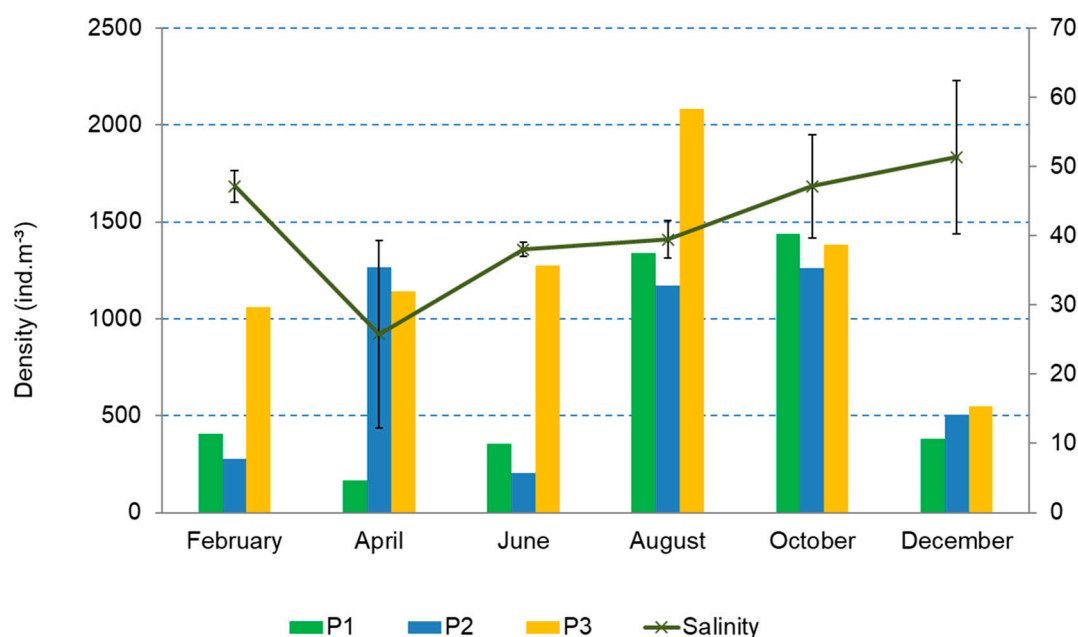
Figure 5. Copepod abundance (ind.m^{-3}) and salinity (mean with standard deviation) throughout the studied months in Piranji Estuary (equatorial Southwestern Atlantic, Brazil, year 2015). Point upstream of the river (P1) to the point closest to the estuarine mouth (P3).

3.2. Structure and Composition of the Copepod Assemblage

The estuarine assemblage consisted of 20 copepod species classified into three orders. The orders Calanoida, Harpacticoida, and Cyclopoida, were represented by ten, six, and four species, respectively. Species belonging to the Oithonidae family (juvenile copepodite): *Parvocalanus* cf. *scotti*, *Parvocalanus crassirostris*, *Oithona hebes*, and *Oithona oswaldocruzi*, had the highest abundances throughout the year (Supplementary Material SI).

The lowest density (166.34 ind.m^{-3}) was found in April (at P1) and the highest (2084.61 ind.m^{-3}) in August (at P3) (Figure 5). In general, at the P1 and P2 upstream points, copepod density increased when salinity values increased; however, there was a reduction in density when the highest salinity levels occurred (Figure 5). Changes in abundance at P3 were observed only at the highest salinity level (Figure 5).

Cluster multivariate analysis revealed the formation of two groups (Figure 6). The first group clustered downstream samples from P3 (closest to the estuarine mouth), and the second group clustered samples from P1 and P2 (upstream region of the estuary). SIMPER analysis showed the contribution of copepod species to both groups. In the group downstream, the species that contributed the most were *Parvocalanus crassirostris* (26.65%), *Parvocalanus* cf. *scotti* (21.31%), and *Oithona hebes* (14.49%). In the group upstream, *Oithona oswaldocruzi* (51.71%), *Parvocalanus crassirostris* (10.28%), and *Oithona hebes* (10.17%) contributed the most.
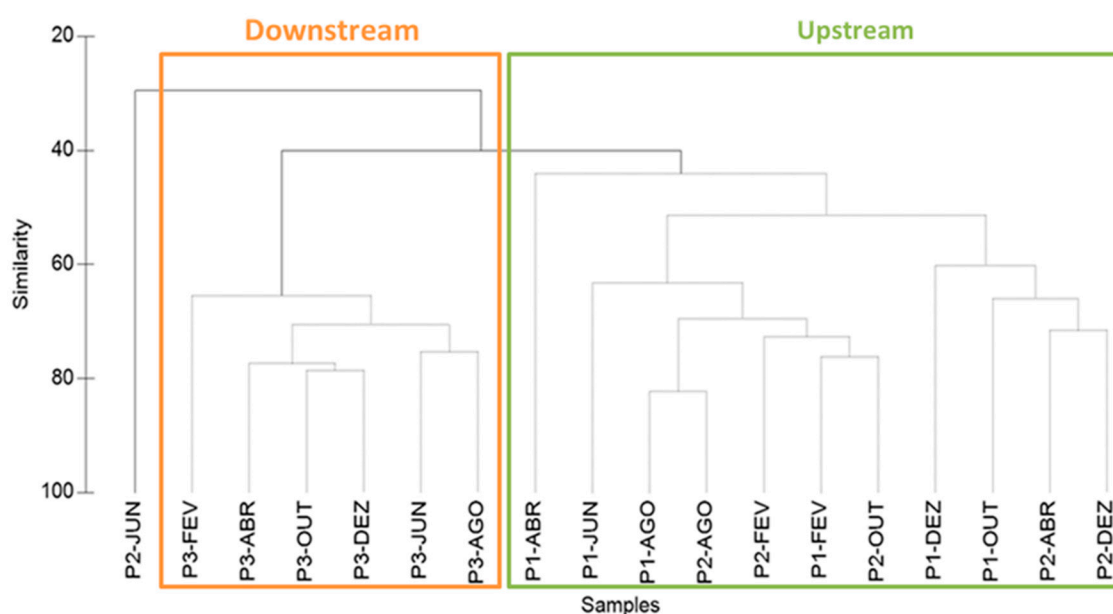
Figure 6. Copepod similarity analysis in Piranji Estuary (equatorial Southwestern Atlantic, Brazil, year 2015).

3.3. Copepod Assemblage and Environmental Factors

The BEST analysis showed that salinity, total nitrogen, silica, and chlorophyll a were the set of environmental factors that explained most of the variation in the copepod assemblages ($\rho = 0.58$; $p < 0.01$) (Table 3).

Table 3. BEST (BIO-ENV stepwise) test results in Piranji Estuary (equatorial Southwestern Atlantic, Brazil, 2015). Sal: salinity; P: depth; ammoniacal nitrogen: $N\text{-}NH_3$; total nitrogen: NT; total phosphorus: PT; total suspended solids: TSS; chlorophyll a: Chl *a*.

| Correlation	Number of Factors	Factors
0.576	**4**	**Sal, NT, silica e Chl-a**
0.564	5	Sal, $N\text{-}NH_3$, NT, silica and Chl-a
0.563	5	P, Sal, NT, silica and Chl-a
0.561	3	Sal, silica and Chl-a
0.559	7	P, Sal, $N\text{-}NH_3$, NT, PT, silica and Chl-a
0.559	6	P, Sal, $N\text{-}NH_3$, NT, silica and Chl-a
0.558	7	P, Sal, $N\text{-}NH_3$, NT, silica, SST and Chl-a
0.558	5	Sal, NT, silica, Chl-a and Feofitina-a
0.557	5	Sal, NT, PT, silica and Chl-a
0.555	6	Sal, $N\text{-}NH_3$, NT, silica, SST and Chl-a

3.4. Functional Groups of Copepods

Two primary characteristics based on the spawning strategy (sac spawner and broadcaster) were identified and sorted (Figure 7). According to the feeding strategy, followed by the trophic regime and diel vertical migration behavior (Supplementary Material SI), three functional groups were recognized (Figure 7).
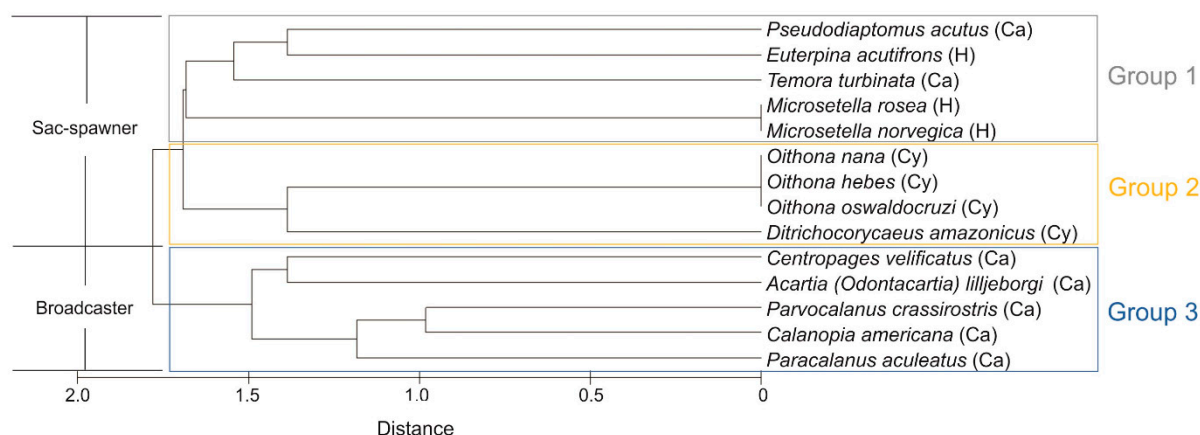

Figure 7. Identification of the functional groups of copepods in Piranji Estuary (equatorial Southwestern Atlantic, Brazil) during an intense drought period (year 2015). Groups 1 and 2: sac spawners. Group 3: broadcasters. Ca: Calanoida. Cy: Cyclopoida. H: Harpacticoida.

The mean abundance of groups ranged from 14.6 ± 23.6 ind.m⁻³ (Group 1—April) to 359.9 ± 48.5 ind.m⁻³ (Group 2). Group 1 consisted mainly of *Euterpina acutifrons* and Group 3 of *Parvocalanus crassirostris*. Group 2, characterized by the presence of stress-tolerant *Oithona oswaldocruzi* and *O. hebes,* had the highest abundance (Figure 8) throughout the year. The closer to the estuarine mouth, the greater the abundance of Groups 1 and 3 (P1 < P2 < P3). By contrast, the abundance of Group 2 was higher at the upstream stations (P2 > P1 > P3) (Figure 9).
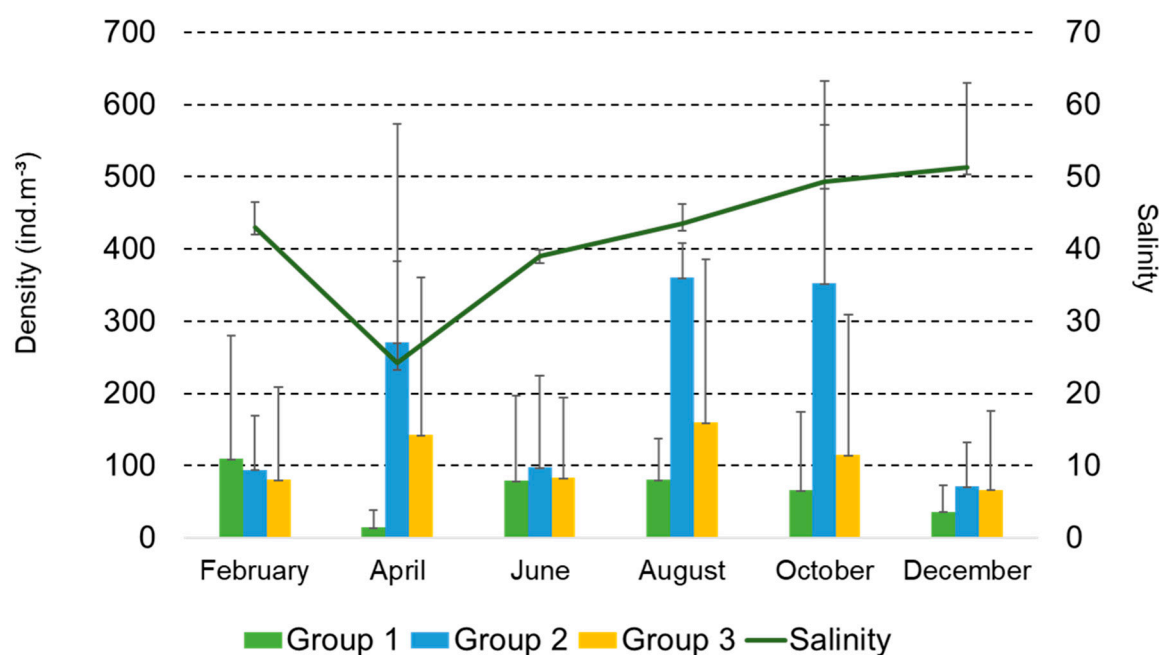
Figure 8. Copepod functional groups (ind.m⁻³) and salinity (mean and standard deviation) throughout the studied months in Piranji Estuary (equatorial Southwestern Atlantic, Brazil, 2015).
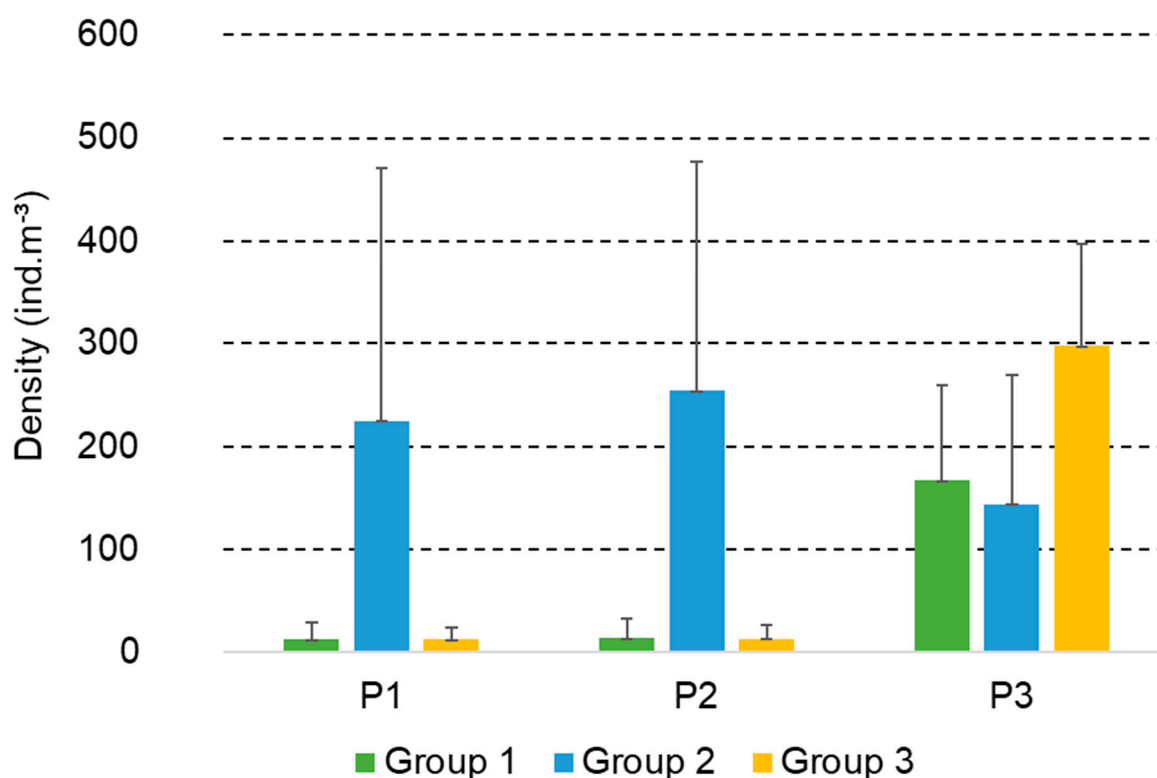
Figure 9. Spatial variation in abundance (ind.m^{-3}) of copepod functional groups in Piranji Estuary (equatorial Southwestern Atlantic, Brazil, 2015).

4. Discussion

The present study evaluated the spatial and intra-annual distribution of copepod assemblages in a well-mixed shallow-water estuary under the influence of hypersalinity during a period that was considered the worst drought on record in the tropical SW Atlantic (Brazil). The main factor affecting the estuarine conditions was salinity. In general, copepod abundance was low during the extreme salinity levels (lowest and highest levels). The estuary was markedly influenced by precipitation in an anomalous drought year, where rainfall (lower than the historical mean) was concentrated over three months, and nine months of the year had no precipitation. The precipitation brought a short-term regime of hyposalinity in April and was responsible for the acute salinity reduction in the upstream stations. In the following month, the precipitation reduced and then stopped, and hypersalinity returned to the estuarine system and reached a higher level in December.

A reduction in rainfall is a major problem in semi-arid regions, where phenomena such as El Niño can result in prolonged periods of drought. The El Niño event in 2015 and 2016 was one of the most severe since the first recorded event that occurred in 1950 [39], and it is forecast that the frequency of El Niño and La Niña events will increase and induce changes in the rainfall patterns of tropical semi-arid coasts, including Northeast Brazil [23,40]. The South Atlantic Ocean Dipole is another factor affecting precipitation values on a regional scale, including the semi-arid coast of Brazil [41]. Among the more recent droughts (1992, 1998, 2002, 2010, and 2012–2015), only droughts in 1998, 2002, and 2015 occurred during El Niño–Southern Oscillation (ENSO) years [40].

Although copepods occurred in reduced abundance under extreme salinity conditions, some species, such as Oithonidae, could survive actively, while others rest in periods of prolonged and/or extreme drought in the study area. It is known that salinity levels can influence various metabolic processes in copepods and the variation in the dominance of euryhaline species in estuaries depends on the selection of adapted individuals [42,43].

For this reason, salinity is recognized as an important key factor that regulates the structure of mangrove communities, although they have seldom been studied in hypersaline tropical estuaries [14,44–46]. Other environmental components such as nitrogen, silica, and chlorophyll *a* concentrations also directly or indirectly cause variations in estuarine copepod populations. Regarding the spatial variations in the nutrient content, we highlight that the total suspended solids, chlorophyll a, and pheophytin a, increased toward upstream stations far removed (~5 km) from the twice daily influence of tidal marine oligotrophic waters.

The taxa with the highest densities (*Parvocalanus* cf. *scotti*, *Parvocalanus crassirostris*, *Oithona hebes*, *Oithona oswaldocruzi*, and juveniles of Oithonidae) are commonly found in estuarine environments with similar salinity characteristics [21,47,48]. The occurrence of several juvenile copepodite stages suggests that these species can reproduce under higher salinity conditions (38–50), indicating the resistance of estuarine populations because an essential component of the density and secondary production is supported by copepodites [21,49,50].

In addition, a spatial pattern was observed in this well-mixed semi-arid estuary. *Parvocalanus crassirostris* and *Parvocalanus* cf. *scotti* had their highest densities near the mouth of the estuary and showed adaptation to the most marinized environment. They occur in coastal waters and open oceans, where they are concentrated mainly in waters close to the surface and may be dominant in plankton epipelagic communities [51]. *Oithona oswaldocruzi* and *Oithona hebes* were common in the upstream estuarine stations. *O. hebes* common in estuarine waters, is an indicative of mangrove areas, and is usually associated with *O. oswaldocruzi* [35]. The distinctive structures of the upstream and downstream assemblages also resulted from marine intrusion, and the increased residence time in the upper portions of the estuary [29] resulted in changes in phytoplankton productivity (P1 = 16.0 μgL^{-1}; P2 = 3.8 μgL^{-1}; P3 = 1.4 μgL^{-1}) [24]. In a simultaneous study conducted in the Piranji Estuary, phytoplankton biomass peaked in the middle and late dry seasons, when salinity reached maximum levels and water residence time was longer [24].

A particular feature of this tropical drought-prone estuary is the low number of species (n = 20) when compared to other estuaries in Brazil ([52] (n = 49); [53] (n = 30); [54] (n = 37)) and elsewhere in the world ([55] (n > 100); [56] (n = 47), [57] (n = 32)). Increased salinity can modify the structure and dynamics of planktonic communities through the selection of predominantly stress-tolerant marine species [58] and consequent simplification of planktonic communities, as observed in hypersaline estuaries, which have low numbers of species with high densities [14,59]. The lack of regular flow-through dams observed on this tropical coast induce an increase in hypersalinity in the mangrove estuarine ecosystem already affected by the drought effects [29] and may cause direct repercussions on species composition. Therefore, copepod assemblages were oversimplified in estuaries because of the low number of highly abundant species [14,60,61]. In this regard, hypersalinity and its effects can contribute to a less diverse and more stressed ecosystem [39].

It is important to highlight that the community under discussion in the Piranji Estuary is the active one. So, we did not consider resting eggs although some copepod genera such as *Pseudodiaptomus*, *Acartia*, *Centropages*, are well known for the production of resting stages which accumulate on the bottom during periods unfavorable for active swimming specimens. This aspect was not analyzed, but it should be explored in future research since the resting community, in the sediment of a hypersaline coastal lake, has the double species numbers of the sample collection in the water column [62,63].

In the multivariate analysis of the functional groups, we found a spatial distribution pattern of Groups 1 and 3 dominating the downstream and nearshore regions. These groups consisted of coastal and marine species, such as *Euterpina acutifrons* (Group 1) and *Parvocalanus crassirostris* (Group 3), which characterized the intrusion of marine and tolerant species into the mangrove ecosystem. Functional Group 2, consisting of stress-toler-

ant Oithonidae species, was clearly associated with estuarine waters (the upstream regions). Species of this family have biological strategies that contribute to their successful colonization, such as, for example, the feeding strategy. *Oithona* have low respiration rates and spend much of their time waiting to capture their prey through a quick jump [6,64]. Such a strategy allows the investment of more energy in reproduction [6]. Efficient feeding on small particles, including nanophytoplankton and cells > 50 mm, can also favor their dominance in eutrophic conditions [65]. *Oithona oswaldocruzi* and *Oithona hebes* were the dominant species in this group. This genus has been recognized as a colonizer of extreme environments, such as hypersaline areas in the upstream stations (P1 and P2), which may become more prevalent with ongoing climate change [18,20].

Two primary traits based on spawning strategy defined these functional groups, sac spawner (Group 1 and 2) and broadcaster (Group 3). The author of [66] mentioned that most pelagic copepods (mainly Calanoida) release their eggs freely into the sea or carry eggs in ovisacs attached to the genital segment, as is the case with other Copepoda orders. The latter method can be considered an adaptive advantage over co-occurring broadcast species [67,68]. This results in a sac spawner with comparatively low fecundity that is balanced by a higher abundance of specimens [69,69]. Female sac-spawner copepods have potentially higher mortality rates due to the presence of the ballast derived from their ovigerous sacs, which not only slows their movement but also acts as attractants for visual predators [70].

When comparing Cyclopoida and Calanoida Orders, the success of cyclopoids in extreme environments is related to the increased efficiency of some activities, for example, weight-specific respiration rates [64], low metabolic rates [71], feeding/swimming behavior [72], microbial food web exploitation [73,74], feeding strategies [65] and egg movement during embryo development [68]. These traits save energy that can be channeled into other essential functions, such as reproduction in stressful hypersaline environments [6,74]. Although Cyclopoids and Calanoids are common in estuarine water [35], the higher salinity levels (~50–60) in the upstream mangrove region create a more extreme and stressful environment that may not be suitable for certain groups or species. At the upstream station (P1), Group 2 (formed by only cyclopoids) may have benefited from the increase in salinity, although there are limits where they can no longer survive. Few copepod species could tolerate salinities > 100 [18], which could result in mass mortality and oversimplify the estuarine community and mangrove food webs in the coming decades. The occurrence and the density of species in hypersaline estuarine systems may thus change markedly in response to increased salinity levels.

5. Conclusions

In conclusion, one of the main results that we would like to highlight was that hypersalinity drives changes on copepod assemblages at the base of the mangrove food webs. The community was significantly influenced by the extreme drought period, presenting a temporal homogenization in terms of composition, and an expressive and unexpected increase in density in the dry period, possibly due to phytoplankton blooms resistant to hypersalinity and the occurrence of copepod species adapted to stressful conditions. These extreme salinity values can lead to few copepod species occurring across the year. The few stress-tolerant species sustaining the food webs with seasonal variations were observed simplifying the trophic variability. The results indicate that hypersalinity can induce changes in the zooplankton community, increasing copepod mortality risk and, so, promoting alteration in the trophic estuarine dynamic.

Long-term sampling over several years (interannual series) would be needed in further studies to verify the recovery of these copepod densities, since salinity decreases during years when precipitation is normal, and to specify if the recovery is fueled by germination of in situ resting stages or by a side supply of immigrating specimens from the sea. Increased siltation due to deforestation and dam construction, increased evaporation and

global temperatures, sea-level rise, and reduced rainfall tend to amplify the occurrence of hypersaline waters in many regions of the world [75,76].

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