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FILIPPE GUILHERME RAMOS COSTA NEVES

**INFLUÊNCIA DA PLUMA ESTUARINA SOBRE A HERBIVORIA DO
ZOOPLÂNTON EM UM AMBIENTE RECIFAL (TAMANDARÉ, PERNAMBUCO)**

Recife

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Dissertação apresentada ao Programa de Pós-Graduação em Oceanografia da Universidade Federal de Pernambuco, como requisito parcial para a obtenção do título de Mestre em Oceanografia.

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Orientador: Prof. Dr. Pedro Augusto Mendes de Castro Melo.

Coorientador: Prof. Dr. Mauro de Melo Júnior.

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Aprovada em 09/06/2020.

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RESUMO

Nós objetivamos entender a influência estuarina sobre um ecossistema recifal a partir de três fatores: (i) comparação da estrutura da comunidade zooplanctônica entre a pluma e os recifes costeiros próximos, (ii) obtenção da prevalência do comportamento alimentar de copépodes, e (iii) identificação dos aspectos da teia alimentar recifal. O estudo foi conduzido na Área de Proteção Ambiental Costa dos Corais, a maior área de proteção marinha da costa sudoeste do Atlântico. O zooplâncton foi coletado com redes de dois tamanhos de malha para coleta de ambos o microzooplâncton e o mesozooplâncton, enquanto os dados ambientais foram coletados com o equipamento adequado. Foram requeridos dados da literatura para obter o comportamento alimentar dos copépodes. Nossos resultados demonstram a contribuição de famílias estuarinas, como Paracalanidae, Acartiidae e Oithonidae com seus náuplios e copepoditos, para os recifes costeiros tropicais. A abundância e biomassa do zooplâncton noturno foi bem maior que durante o dia e Copepoda foi o táxon mais abundante para ambos o microzooplâncton e o mesozooplâncton. A herbivoria foi o comportamento mais prevalente entre os copépodes sobre os recifes tropicais. Nossos dados também demonstram uma breve contribuição do microzooplâncton para a teia alimentar microbiana em ambientes sob influência de pluma, deixando o mesozooplâncton para a cadeia de pastagem. A maior parte dos herbívoros também demonstraram um comportamento onívoro.

Palavras-chave: Estuarino. Recifes de corais. Zooplâncton. Crustáceos. Teia alimentar.

ABSTRACT

We aimed to understand the estuarine influence on a reef ecosystem by comparing the zooplanktonic community structures between a plume and the nearby coastal reefs, by obtaining the prevalence of copepod's feeding behaviour, and identifying aspects of reef food web. The study was carried out in the Environmental Protection Area Costa dos Corais, the biggest marine protection area over the Southwestern Atlantic coast. Zooplankton was collected using nets of two mesh sizes for both microzooplankton and mesozooplankton sampling, whereas field data were collected with the proper equipment. Literature data was required to assess the feeding behaviour of copepods. Our results demonstrate the contribution of estuarine families, such as Paracalanidae, Acartiidae, and Oithonidae with their nauplii and copepodites to tropical coastal reefs. Nocturnal zooplankton abundance and biomass were higher than the day, and copepods were the most abundant taxa for both microzooplankton and mesozooplankton. Herbivory was the most prevalent feeding behaviour of copepods over tropical reefs. Our data also demonstrate a slight contribution of microzooplankton to microbial food web in environments under plume influence, leaving the mesozooplankton to the grazing one. The majority of herbivorous copepods also demonstrated an omnivorous behaviour.

Keywords: Estuarine. Coral reefs. Zooplankton. Crustaceans. Food web.

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1 INTRODUÇÃO

Plumas estuarinas são influenciadas pelo vento, pelas marés e pelas descargas fluviais (Morris, Allen, Howland, & Wood, 1995; Valle-Levinson, 2010). Elas são uma extensão dos estuários, mantendo características próprias de águas estuarinas. Os estuários apresentam baixa salinidade devido a descarga fluvial, porém isso não é regra já que há tipos em que há maior influência marinha do que a dos seus tributários. Assim, há regiões em que a salinidade é próxima a do mar adjacente, demonstrando uma grande influência marinha. Desse modo, os estuários apresentam uma grande variação de salinidade ao longo de um único dia.

Outra característica de estuários tropicais é sua grande produção de matéria orgânica graças a presença do manguezal nas suas margens. As marés empregam um importante papel na disponibilidade dessa matéria orgânica na coluna d'água, por isso, diz-se que os estuários são ambientes altamente produtivos, já que produzem uma grande quantidade de matéria orgânica. As plumas estuarinas detêm tais características, levando as condições estuarinas para a plataforma adjacente. Assim como as águas estuarinas, as plumas são altamente dinâmicas (Morris et al., 1995).

Ambientes recifais adjacentes a estuários podem ser influenciados pelas características estuarinas, ou seja, acúmulo de nutrientes e, conseqüentemente, alta produtividade primária e secundária. Os recifes são ambientes altamente produtivos e apresentam uma biodiversidade grande. Sua produtividade é especialmente o que conduz à alta biodiversidade do ecossistema. Uma grande quantidade de alimento permite que a comunidade recifal floresça, além de servir como berçário para um grande número de espécies, do mesmo modo que os estuários.

O zooplâncton apresenta uma grande importância em meio aos componentes da teia trófica marinha, pois serve de elo entre os produtores e demais consumidores, cabendo a eles o transporte da energia para níveis tróficos elevados, além de contribuírem com os ciclos biogeoquímicos dos elementos (Castellani & Edwards, 2017; Turner, 2004b). Entre esses metazoários planctônicos, os copépodes são geralmente os dominantes da comunidade, apresentando abundância de até 90% nos ecossistemas marinhos tropicais. Inclusive, eles são considerados os “insetos do mar” devido tamanha abundância nos biossistemas (Bjönberg, 1981; S. Neumann-Leitão, 1995; Schminke, 2007; A. P. Silva, Neumann-Leitão, Schwamborn, De Oliveira Gusmão, & De Almeida E Silva, 2004). Vale ressaltar ainda a importância dessa fauna como alimento para alguns peixes de interesse comercial (Irigoiien et al., 2002; Tseng, Souissi, Dahms, Chen, & Hwang, 2008). Percebe-se, portanto, o

zooplâncton como componente essencial para a dinâmica dos ecossistemas marinhos tropicais, como os estuários e também os recifes de corais.

O animais e protozoários do plâncton em ambientes recifais servem como fontes alimentares para os organismos ali presentes (Glynn, 1973). Inclusive, espécies de corais são conhecidas por ingerirem zooplâncton a uma faixa entre 20 a 80% de abundância da comunidade (Nascimento-Vieira, Neumann-Leitão, Porto-Neto, Silva, & Silva, 2010). Ayukai (1991) sugere que esforços devem ser empregados para compreender os padrões da comunidade zooplanctônica de modo a servir como base para futuros estudos da trofodinâmica do ambiente.

A matéria orgânica e os nutrientes são provenientes dos produtores bentônicos estuarinos como também da descarga fluvial. O florescimento da comunidade fitoplanctônica e, conseqüentemente, da comunidade zooplanctônica, é função desse aumento na concentração de nutrientes e matéria orgânica. O zooplâncton então se aproveita dessa quantidade de alimento e tende a aumentar sua abundância. No entanto, ao longo dos anos, a cadeia trófica clássica (fitoplâncton-zooplâncton-peixes) tem sido questionada por uma variedade de estudos. O zooplâncton, por sua vez, apresenta uma diversidade de tamanhos e hábitos alimentares. O microzooplâncton apresenta uma variedade de organismos pequenos menores que 200 μm , sendo capazes de se alimentar tanto de fitoplâncton quanto de ciliados. Estes, por outro lado, se alimentam tanto de fitoplâncton quanto da matéria orgânica suspensa. Assim, o conceito da alça microbiana foi criado, a fim de descrever a possibilidade do plâncton em reciclar a matéria orgânica que, de outro modo, seria transferida às comunidade bentônicas.

Os copépodes contribuem tanto para a cadeia trófica clássica quanto para a alça microbiana. Existem copépodes que apresentam hábitos herbívoros como *Pseudodiaptomus* spp. e outros que apresentam hábitos carnívoros como *Labidocera* spp. e *Calanopia americana*. A maioria apresenta hábitos onívoros como *Acartia* spp., *Oithona* spp., *Paracalanus* spp., *Parvocalanus crassirostris*, *Temora* spp. Os náuplios de copépodes podem, inclusive, apresentar hábitos detritívoros, alimentando-se de *pellets* fecais dos próprios copépodes e, assim, contribuir para a teia trófica detritívora.

A Área de Proteção Ambiental Costa dos Corais (APACC) apresenta ambientes recifais e estuarinos ao longo da sua extensão, que ocorre desde o estado de Alagoas a Pernambuco, com limite no litoral de Tamandaré. Esta cidade está localizada no litoral sul do estado de Pernambuco, onde há presença de recifes costeiros, que ocasionalmente encontram-se emersos na preamar. A região apresenta três linhas de recifes paralelos à praia, cuja terceira

linha determina o limite da Baía de Tamandaré. A pluma do estuário dos rios Mamucabas e Ilhetas pode banhar a região dos recifes. Suas águas podem ocasionar diminuição da salinidade como também aumento da turbidez das águas, devido as características estuarinas que carregam. Esses rios são costeiros e apresentam manguezais ao longo das suas bordas. Sendo assim, a presença da pluma estuarina pode apresentar implicações para o ecossistema recifal da região de Tamandaré, os quais podem apresentar quantidades significativas de material orgânico, por exemplo. A região litorânea de Pernambuco apresenta sazonalidade quanto ao regime de chuvas, sendo dividida em duas estações, uma chuvosa e uma seca, cujos períodos ocorrem entre abril e agosto e entre setembro e março, respectivamente (M. R. Da Silva, Silva-Cunha, Feitosa, & Muniz, 2005).

O foco dos estudos nos recifes de Tamandaré têm sido na estrutura e distribuição do plâncton e na biomassa e produtividades primária e secundária (Moura and Passavante, 1995; Silva *et al.*, 2005; Fidelis, 2014; Neumann-Leitão *et al.*, 2018). É essencial o entendimento da produção do zooplâncton nos ambientes marinhos a fim de permitir avanços nos planos de manejo de tais ecossistemas. Ainda mais relevante é a posição política dos recifes de Tamandaré, que estão dentro da APACC, a maior área de proteção ambiental marinha do país (Brasil, 1997).

Nesse contexto, o objetivo da presente dissertação é entender a influência que a pluma estuarina detém sobre os recifes tropicais presentes na Baía de Tamandaré. Para isso, três perguntas foram feitas: (i) há diferença na estrutura da comunidade entre a pluma e os recifes?, (ii) qual o comportamento alimentar mais prevalente entre os copépodes? e (iii) qual teia alimentar pode ser indicada para os recifes costeiros da região?

Para isso a presente dissertação está estruturada em um artigo intitulado “Distribution and prevalence of planktonic copepod feeding behaviour on reefs influenced by estuarine plume in Brazil”.

1.1 OBJETIVOS

Este trabalho apresenta os objetivos pautados na investigação da influência que a pluma estuarina pode apresentar para os recifes costeiros da baía de Tamandaré no sul do estado de Pernambuco. Essa região está inserida na Área de Proteção Ambiental Costa dos Corais, a maior área de proteção ambiental marinha do Brasil.

1.1.1 Objetivo geral

Avaliar a influência da pluma estuarina sobre a herbivoria do zooplâncton em um ambiente recifal da APA Costa dos Corais

1.1.2 Objetivos específicos

- a) Determinar os atributos da comunidade de copépodes mesoplanctônicos, predominantemente herbívoros, como composição, biomassa, abundância e diversidade;
- b) Determinar as taxas de ingestão diária das diferentes classes de tamanho dos copépodes herbívoros, em ambos horários do dia e períodos do ano;
- c) Estimar a herbivoria e o impacto alimentar dos copépodes mesoplanctônicos sobre a biomassa das diferentes frações do fitoplâncton recifal de Tamandaré, considerando a influência temporal das plumas estuarinas.

2 DISTRIBUTION AND PREVALENCE OF PLANKTONIC COPEPOD FEEDING BEHAVIOUR ON REEFS INFLUENCED BY ESTUARINE PLUME IN BRAZIL

Artigo submetido à revista **Marine and Freshwater Research**

ABSTRACT

We aimed to understand the estuarine influence on a reef ecosystem by comparing the zooplanktonic community structures between a plume and the nearby coastal reefs, by obtaining the prevalence of copepod's feeding behaviour, and identifying aspects of reef food web. The study was carried out in the Environmental Protection Area Costa dos Corais, the biggest marine protection area over the Southwestern Atlantic coast. Zooplankton was collected using nets of two mesh sizes for both microzooplankton and mesozooplankton sampling, whereas field data were collected with the proper equipment. Literature data was required to assess the feeding behaviour of copepods. Our results demonstrate the contribution of estuarine families, such as Paracalanidae, Acartiidae, and Oithonidae with their nauplii and copepodites to tropical coastal reefs. Nocturnal zooplankton abundance and biomass were higher than the day, and copepods were the most abundant taxa for both microzooplankton and mesozooplankton. Herbivory was the most prevalent feeding behaviour of copepods over tropical reefs. Our data also demonstrate a slight contribution of microzooplankton to microbial food web in environments under plume influence, leaving the mesozooplankton to the grazing one. The majority of herbivorous copepods also demonstrated an omnivorous behaviour.

Additional keywords: estuarine; coral reefs; zooplankton; crustaceans; food web

1 INTRODUCTION

In regard to the global income, reefs are recognized as the most valuable of all marine ecosystems. Numbers demonstrate they contribute about 1.8% of the biosphere value, which is between US\$16 and US\$54 trillion annually (Souter & Lindén, 2000). They can also support a variety of life forms, especially fish and corals (Bellwood, Hughes, & Nyström, 2004). Moreover, the ecosystem services that reefs provide to the human population are outstanding. They contribute to the people living within islands and coastal populations worldwide, which almost entirely depend on these coastal ecosystems for their income and daily protein, as well as their coastal protection (Woodhead, Hicks, Norström, Williams, &

Graham, 2019). Nowadays in the Anthropocene, in addition to natural threats reefs have been facing, there has been a strong concern for their protection against anthropogenic actions, such as overfishing, tourism and sedimentation (Bellwood et al., 2004; Sigrid Neumann-Leitão et al., 2018; Pauly & Zeller, 2014). Recently, the Brazilian coast suffered with an oil spill, which affected important and sensitive environments such as coastal reefs (Magris & Giarrizzo, 2020; Soares et al., 2020).

Coastal ecosystems such as woodlands, mangroves, and flood plains are required for the quality of the water reaching the reefs (Butler et al., 2013). They are important for the nutrient cycling within themselves together with spiralling in their streams (Newbold, Elwood, O'Neill, & Sheldon, 1963), which might decrease the rates that reefs are exposed to high amounts of nitrogen and phosphate compounds, for instance. Elevated nutrient concentrations can foster increases in alga productivity (Vallina et al., 2014), which may disturb reef communities later if estuarine waters reach these areas (Glasby, Gibson, & Cruz-Motta, 2017). However, plain management and policy actions can help the endeavour of maintaining reef ecosystem services (Glasby et al., 2017). Therefore, it is paramount that research should be done to provide effective information for both private and public stakeholders. The structure of the plankton community can be an indicative source of environmental health (Sigrid Neumann-Leitão et al., 2018), hence should be considered as one important step towards coastal marine management.

The zooplankton can play an important role in the flux of matter and energy in the pelagic systems (Sigrid Neumann-Leitão et al., 2018). The organisms are responsible for the resilience of marine ecosystems in times of disturbances, whether they are natural or anthropogenic. Copepods, for instance, can be herbivore, carnivore, omnivore and detritivore, hence comprising both kinds of food webs (Benedetti et al., 2016; Nakajima et al., 2017; Nakajima, Yoshida, Othman, & Toda, 2014). They can be responsible for transferring energy up the food chain to planktivorous fishes, and even corals and other zoanthids, for example (Jackson & Lenz, 2016; Nakajima et al., 2017). Performing the detritivore role, they recycle the matter that would be “lost” to sedimentation, bringing it back to the food chain to become available for higher levels, a process called microbial loop (Pomeroy, Williams, Azam, & Hobbie, 2007).

Due to high loads of nutrients and organic matter, estuarine food chains are detritivorous most of the time, although they demonstrate some pelagic grazing (Deegan & Garritt, 1997). Moreover, neritic waters with high loads of estuarine production can perform

the same activity despite decreases in oxygen content (Zhang et al., 2010). Nonetheless, reefs are highly productive ecosystems in terms of biodiversity. This coastal ecosystem is usually supported by herbivory most of the time (Steneck, Bellwood, & Hay, 2017). Productivity is high among algae, which fosters secondary productivity and an extremely diverse food web (Steneck et al., 2017). During the night, the zooplankton community may become more diverse and abundant as many individual zooplankters migrate upwards to graze on the phytoplankton production, which is driven either by physiological constraints or by avoiding predation (Lambert, 1989).

Estuaries are conspicuous worldwide, hence presenting a variety of characteristics in regard to their geomorphology and water flux (Ray, 2005). They are even recognised as exporters of organic matter to the adjacent continental shelf (Wösten, Willigen, Tri, Lien, & Smith, 2003). A study by Schwamborn, Voss, Ekau, & Saint-Paul (1999), conducted within tropical coastal ecosystems, demonstrated that the amount of carbon exported by mangroves, for instance, is negligible to offshore shelf, but is higher inshore until a nearby reef line. Due to their high loads of nutrients and organic matter together with a variety of habitats, estuaries present species that are strongly adapted to such a system, where they use the resources for their growth and development (Bible & Sanford, 2016; Courrat et al., 2009; David et al., 2016). There are certain copepods that present an omnivore state but a predominantly detritivore behaviour such as those within Ectinosomatidae and Oncaeidae (Benedetti et al., 2016) as well as the nauplii stages (Green, Harris and Duncan, 1992; Mauchline, 1998; Poulsen and Iversen, 2008; Nakajima, 2014). Understanding the ecological interactions of planktonic communities within estuaries could inform important data for the management of coastal environments influenced by them, such as coastal reefs.

On the tropical west coast of the Atlantic, there are many reef formations responsible for important ecosystem services to nearby human populations. Fishing, tourism, recreation and coastal protection are some of the services these reefs provide (ICMBio, 2012). These reefs present a diversity of environments such as mangroves and estuaries, whose production loads can reach the reefs (Araújo, Castiglioni, & Coelho, 2012; Lira, Falcão, Zapata, & Oliveira, 1978).

From this backdrop, we aimed to understand whether the reef formations of TB can be influenced by the estuarine environment nearby. The zooplankton community is a key factor in understanding this relationship, especially copepods and their feeding behaviour. Copepoda

was considered an object for this study due to their higher abundance in this area (Porto-Neto, 2003), representing more than 90% of the zooplankton community abundance (Silva et al., in review). We investigated (i) the spatial and temporal variation amongst the zooplankton, (ii) the prevalence of copepod's feeding behavior, and (iii) the food web most represented within the reef region.

2 MATERIALS AND METHODS

2.1 STUDY SITE

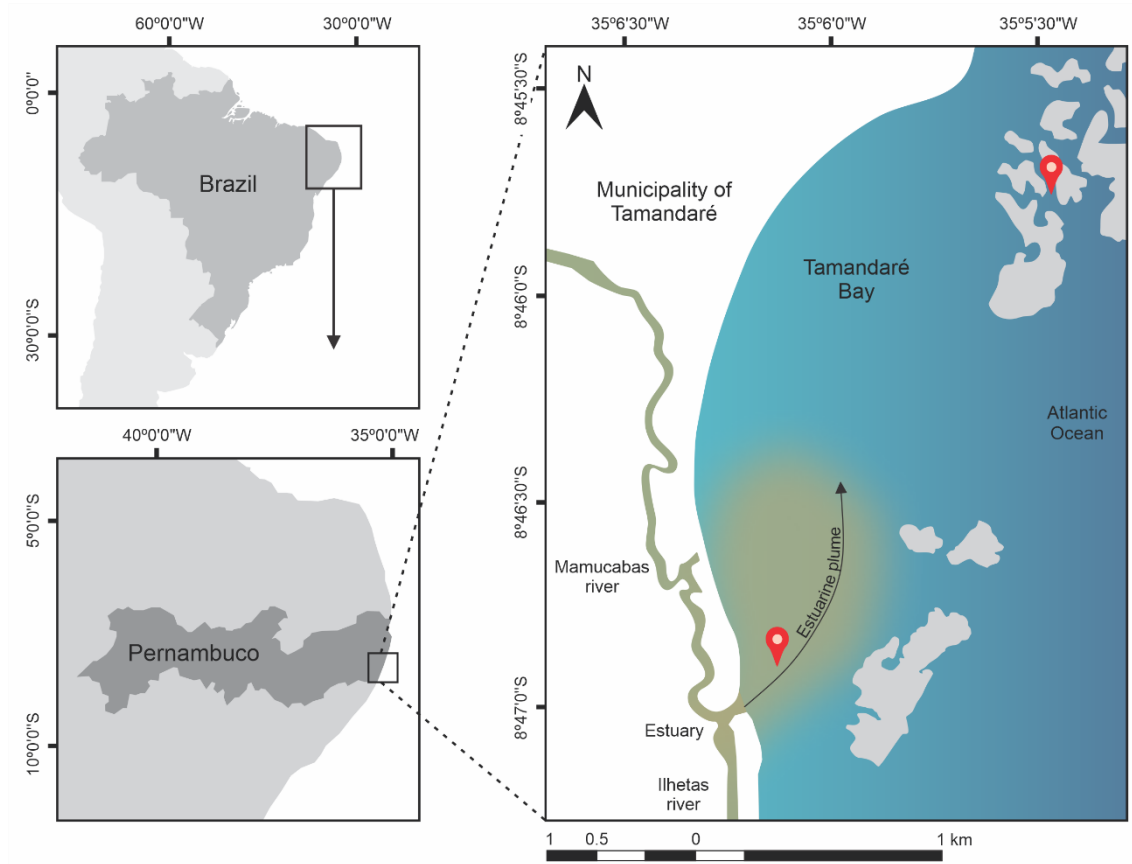
In the tropical coast of Northeast Brazil, one of these environments is the Mamucabas-Ilhetas estuary, located alongside Pernambuco state. This estuary disposes of its water onto a bay called Tamandaré Bay (TB), which presents reef formations at its eastward limit (Camargo, Araújo, Maida, & Ushizima, 2007; Fontes, Gomes, Vital, Ferreira, & Maida, 2020). These reefs are within the Costa dos Corais Environmental Protection Area (APACC), also presenting areas of forbidden human activities which are responsible for providing rehabilitation of marine species in the area (ICMBio, 2012).

The study was carried out on TB (Fig 01), which presents reef formations that are parallel to the coastline (Camargo et al., 2007; Fontes et al., 2020), and some estuaries nearby, such as the one of the Mamucabas-Ilhetas estuary (Araújo et al., 2012; Lira et al., 1978). Together they form one mouth towards the bay, where the rivers dispose of their discharge (Araújo, Tenório, & Castiglioni, 2014). The region presents a historical pluviometric precipitation of 2000 mm year⁻¹ on average (Araújo et al., 2012). The wet period happens from April to September, while the dry period goes from October to March (Portella, Santos, & Araújo, 2001).

Furthermore, this region is inside the APACC (Fontes et al., 2020), whose objective is to coordinate the activities of conservation and preservation with human activities, such as fishing, tourism and research in order to fulfill sustainability requirements (Ferreira, Maida, & Cava, 2001; ICMBio, 2012). According to the APACC plan, there are problems that pose issues regarding the sustainability of the Environmental Protection Area (ICMBio, 2012). For instance, non-managed fishing activities, disoriented coastal population increases and insufficient scientific knowledge are some threats to the management of the Area. The fishing production in the Area was some 2278 catches throughout the former decade of this century.

In addition, TB presents the exclusive area for the preservation of marine life where no human activity can be performed, except research.

Figure 01: Sampling sites at TB. The stations, reef and plume, are represented as the red points



Source: Silva, K.H.F.

2.2 SAMPLING STRATEGY

There were five campaigns performed from April 2018 to June 2019, during the dry (October 2018, December 2018) and rainy (April 2018, August 2018, June 2019) seasons. Two fixed stations were established: (i) over the reef area, and (ii) at the estuarine plume. During the day, the samples were collected at both stations, whereas during the night just the reefs were assessed. All samples were collected during the ebb tide, when the water flows from the estuary to the coast. Zooplankton samples were collected by horizontal subsurface hauls performed with two cylindrical-conical nets for three minutes. The two nets had 30 cm mouth diameters [64 μm (microzooplankton) and 200 μm (mesozooplankton) mesh sizes]. A total of 30 samples were collected for the study. To obtain the water volume filtered, a flowmeter was coupled at the mouth of the nets. After collection, the samples were transferred to plastic bottles and immediately preserved in formaldehyde solution (4%), buffered with sodium tetraborate.

Environmental data were assessed with a multiparameter equipment (Horiba U52) with sensors for temperature, salinity, transparency, turbidity, total dissolved solids, dissolved oxygen and pH. The local precipitation was also assessed through data collected from the Pernambuco State Agency of Water and Climate (APAC), considering 30 days of accumulated values.

2.3 LABORATORY PROCEDURE

In the laboratory, the samples were diluted in water solution to the identification and counting of zooplankton groups, and more specifically copepods considering their life stages (copepodites and nauplii). The mesozooplankton samples were split into small aliquots using a Motoda quarter (maximum 1/128 fraction), while microzooplankton samples were diluted with a volume [that varied from 20 mL to 100 mL] for a 2 mL subsample to be analysed in a Sedgewick-Rafter chamber. Each fraction or subsample was identified under either optical microscope (microzooplankton) or stereomicroscope (mesozooplankton). Specialized literature was used to obtain the taxa of the animals and of the heterotrophic protists as specific as possible (e.g., Bjönberg, 1981; Boltovskoy, 1999).

2.4 BIOMASS ESTIMATION OF COPEPODS

Copepods and their larval stages were measured (prosome length for adults and other copepodite stages, and the whole body length for nauplii) using a micrometer ruler on the lenses of microscopes. Then, the weight (μg) was obtained from regression equations (Table 01). For *Temora stylifera* the wet weight was converted in dry weight with a factor of 0.2 (Shmeleva, 1965). The dry weight was converted to carbon weight (μgC) according to Hirota (1981). The copepod biomass was given for each taxa by multiplying the correspondent carbon weight with the correspondent abundance.

TABLE 01: LENGTH-WEIGHT REGRESSION EQUATIONS FOR EACH TAXA. DW (DRY WEIGHT), WW (WET WEIGHT), L (PROSOME LENGTH IN μM), TL (TOTAL BODY LENGTH IN μM).

Taxa	Equation	Reference
All nauplii	$\text{Log}_{10} \text{DW (ngC)} = 2.94 \times \text{Log}_{10} \text{L} - 4.82$ ($\mu\text{mC} = \text{ngC} \times 0,001$)	Nakajima <i>et al.</i> , 2017
Benthic harpacticoid, Ectinosomatidae, and Miraciidae	$\text{Log}_{10} \text{DW} = 3.26 \times \text{Log}_{10} \text{TL} - 8.51$	Nakajima <i>et al.</i> , 2017

Clausocalanidae	$\ln DW = 2.78 \times \ln L - 16.52$	Webber and Roff, 1995
Corycaeidae	$\ln DW = 1.70 \times \ln L - 9.92$	Chisholm and Roff, 1990
Oncaeidae	$\ln DW = 2.10 \times \ln L - 11.63$	Webber and Roff, 1995
Paracalanidae	$\ln DW = 2.78 \times \ln L - 16.52$	Webber and Roff, 1995
Pontellidae	$DW = 3.770 \times 10^{-8} \times L^{2.837}$	Ara, 2001
Eucalanidae	$\log_{10} DW = 2.828 \times \log_{10} L - 5.408$	Ueda, Kobari and Steinberg, 2008
<i>Acartia lilljeborgi</i>	$DW = 6.177 \times 10^{-9} \times L^{3.029}$	Ara, 2001
<i>Acartia tonsa</i>	$DW = 9.662 \times 10^{-9} \times L^{2.931}$	Ara, 2001
<i>Calanopia americana</i>	$\ln DW = 2.67 \times \ln L - 15.47$	Chisholm and Roff, 1990
<i>Centropages</i> spp.	$\ln DW = 3.68 \times \ln L - 22.86$	Chisholm and Roff, 1990
<i>Euterpina acutifrons</i>	$\ln DW = 2.72 \times \ln L - 16.19$	Ara, 2001
<i>Labidocera</i> spp.	$DW = 1.666 \times 10^{-8} \times L^{2.837}$	Ara, 2001
<i>Macrosetella gracilis</i>	$\ln DW = 2.52 \times \ln L \times 16.03$	Webber and Roff, 1995
<i>Microsetella norvegica</i>	$\log_{10} DW = 3.26 \times \log_{10} TL - 8.51$	Nakajima <i>et al.</i> , 2017
<i>Microsetella rosea</i>	$\log_{10} DW = 3.26 \times \log_{10} TL - 8.51$	Nakajima <i>et al.</i> , 2017
<i>Oithona hebes</i>	$DW = 3.405 \times 10^{-10} \times L^{3.643}$	Ara, 2001
<i>Oithona nana</i>	$\log_{10} DW = 1.10 \times \ln L - 7.07$	Chisholm and Roff, 1990
<i>Oithona oswaldocruzi</i>	$DW = 2.513 \times 10^{-11} \times L^{4.113}$	Ara, 2001
Oithonidae (others)	$\ln DW = 1.10 \times \ln L - 7.07$ $\ln DW = 1.10$	Chisholm and Roff, 1990
<i>Paracalanus nanus</i>	$\ln DW = 2.78 \times \ln L - 16.52$	Webber and Roff, 1995
<i>Paracalanus parvus</i>	$\ln DW = 2.78 \times \ln L - 16.52$	Webber and Roff, 1995
<i>Paracalanus quasimodo</i>	$DW = 6.829 \times 10^{-11} \times L^{3.871}$	Ara, 2001
<i>Paracalanus</i> spp.	$\ln DW = 2.78 \times \ln L - 16.52$	Webber and Roff, 1995
<i>Parvocalanus crassirostris</i>	$DW = 1.945 \times 10^{-7} \times L^{2.582}$	Ara, 2001
Pseudodiaptomidae	$DW = 1.306 \times 10^{-9} \times L^{3.361}$	Ara, 2001
<i>Temora stylifera</i>	$\ln WW = 2.057 \times \log L - 4042$	Shmeleva, 1965
<i>Temora turbinata</i>	$\ln DW = 3.34 \times \ln L - 19.59$	Chisholm and Roff, 1990
Tisbidae	$\log_{10} DW = 3.26 \times \log_{10} TL - 8.51$	Nakajima <i>et al.</i> , 2017

Source: the author, 2020

2.5 FEEDING STRATEGIES

For each family of Copepoda, their main correspondent feeding behavior was assessed (Table 02; Benedetti et al., 2016; Boxshall & Halsey, 2004; Green, Harris, & Duncan, 1992; Mauchline, 1998; Nakajima et al., 2014; Pinto, Souza-Santos, & Santos, 2001; Poulsen & Iversen, 2008; Rieper, 1982). Copepods can behave as herbivores, carnivores, detritivores and/or omnivores (Benedetti et al., 2016; Nakajima et al., 2014). The abundance and biomass of omnivores were split between carnivore (50%) and herbivore (50%), as suggested by Nakajima et al. (2014). For families with mixed feeding behavior (e.g. Omnivore-herbivore), the abundance and biomass was first split between main feeding behaviors and then the omnivores were split as explained above.

TABLE 02: FEEDING BEHAVIOR OF COPEPOD FAMILIES.

All nauplii	Herbivore and detritivore	Green, Harris and Duncan, 1992; Mauchline, 1998; Poulsen and Iversen, 2008; Nakajima, 2014
Calanoida		
Paracalanidae	Omnivore-herbivore	Nakajima, 2014; Benedetti, 2016
Eucalanidae	Omnivore	Benedetti, 2016
	Omnivore-herbivore	Boxshall and Halsey, 2004; Nakajima, 2014; Benedetti, 2016
Clausocalanidae		
Centropagidae	Omnivore-herbivore	Nakajima, 2014; Benedetti, 2016
	Herbivore	Nakajima, 2014; Benedetti, 2016
Pseudodiaptomidae		
Temoridae	Omnivore-herbivore	Nakajima, 2014; Benedetti, 2016
Pontellidae	Carnivore	Boxshall and Halsey, 2004; Benedetti, 2016
Acartiidae	Omnivore-herbivore	Boxshall and Halsey, 2004; Nakajima, 2014; Benedetti, 2016
Cyclopoida		
Oithonidae	Omnivore	Nakajima, 2014; Benedetti, 2016
Oncaeidae	Omnivore-detritivore	Boxshall and Halsey, 2004; Benedetti, 2016
Corycaeidae	Carnivore	Boxshall and Halsey, 2004; Benedetti, 2016
Harpacticoida		

	Omnivore-detritivore	Nakajima, 2014; Benedetti, 2016
Ectinosomatidae		
Miraciidae	Omnivore-herbivore	Nakajima, 2014; Benedetti, 2016
Tachidiidae	Omnivore-herbivore	Nakajima, 2014; Benedetti, 2016
Tisbidae	Omnivore	Rieper, 1982; Pinto, 2001

Source: the author, 2020

2.6 DATA ANALYSIS

There was used a t test (when data is parametric; otherwise, the Mann-Whitney test was used) to analyze the first-order (non-interactive) effects of multiple independent variables: spatial (Estuarine plume *vs.* Reef area), seasonal (dry *vs.* wet), and time of day (day *vs.* night) on response variables: (1) total abundance and biomass of microzooplankton and (2) total abundance and biomass of mesozooplankton. The normality of the data was investigated through the Shapiro-Wilk test and the heterogeneity of variances was verified by the Levene test. When necessary, the data were Log (x+1) transformed. Parametric statistical analysis followed Zar (1996).

The structure of copepod assemblages was described using the diversity index (Margalef's richness index (d') and Shannon-Wiener diversity index (H')). Multivariate procedures included: (i) Permutational Multivariate analysis of variance (PERMANOVA) (Anderson, 2001; Mcardle and Anderson, 2001), which was performed (with 999 permutations) based on the dissimilarity of Bray-Curtis (data transformed with fourth root). This analysis was used to determine whether there were significant differences in the structure of the micro- and mesozooplankton community between the spatial, seasonal factors and time of day. The Monte Carlo P values were used for all analyses, and 9.999 random permutations were tested. In case of significant differences, a pairwise test (the multivariate version of the t statistic) between different levels of significant factor(s) was performed. The significance of the PERMANOVA was assessed by the P value. Only species that showed more than 2% of relative abundance were considered in this analysis; (ii) Multi-dimensional scaling (MDS), which was used to represent the Bray-Curtis matrix graphically in a two axis space (Sarmiento and Santos, 2012); (iii) In case of significant differences, SIMPER (Similarity of percentages) test was used to identify the taxa that contributed most to the dissimilarity between the groups.

The copepods' feeding behavior data were expressed as percentages for herbivore, carnivore, omnivore and detritivore, according to data obtained from section 2.4.

The Shannon-Wiener index, SIMPER analysis, MDS and PERMANOVA were applied using the software Primer_v.6 and R version 3.5.3. The t test (and in case of a Mann-Whitney test) was calculated using the software STATISTICA 7.0 and R version 3.5.3. The level of significance was set at $p < 0.05$ for all analyses.

3 RESULTS

3.1 ENVIRONMENTAL FACTORS

The mean in precipitation was 152 ± 121 mm throughout the period between March of 2018 and June of 2019, and ranged from 7 mm (October 2018) to 432 mm (April 2018) (Fig 2). The wet period presented a mean in precipitation of the order of 205 ± 119 mm (40 to 432 mm), whereas the dry period presented 64 ± 55 mm (7 to 135 mm) (Fig 2). Their values are of distinct seasonal periods ($p < 0.05$).

All variables were tested and no significant differences were detected (Fig 02; $p > 0.05$), suggesting a homogeneous condition between estuarine plume and reef areas for diurnal samples. The mean depth at the estuarine plume region was 1.98 ± 0.42 m (ranging from 1.70 to 2.70 m), whereas the depth at the reef region averaged 2.27 ± 0.47 m (ranging from 1.60 to 2.80 m). The sea-surface temperature was 27.98 ± 0.76 °C at the estuarine plume, ranging from 26.91 to 29 °C. Over the reef the sea-surface temperature was also 27.98 ± 0.50 °C, but ranged from 27.28 to 28.64 °C. The values for salinity were 28.59 ± 4.33 (ranging from 23.70 to 34.60) at the estuarine plume, and 32.90 ± 1.60 (ranging from 31.50 to 35.50) over the reef. The estuarine plume presented 27.53 ± 2.77 g L⁻¹ of total dissolved solids (from a minimum of 24.36 g L⁻¹ to a maximum of 31.50 g L⁻¹), whereas the reef area showed 30.44 ± 1.06 g L⁻¹ (29.50 to 32.20 g L⁻¹). For dissolved oxygen, the estuarine plume showed 5.81 ± 1.24 mg L⁻¹ (4.11 to 7.42 mg L⁻¹) and the reef, 6.23 ± 1.68 mg L⁻¹ (ranging from 4.45 to 8.16 mg L⁻¹). The pH was 7.75 ± 0.41 (7.19 to 8.29) at the estuarine plume area and 7.86 ± 0.46 (ranging from 7.28 to 8.51) at the reef region.

On the other hand, when comparing the day and night samples in the reef area, variables such as salinity, total dissolved solids, and pH were different from each other

($p < 0.05$). Salinity was 32.90 ± 1.50 during the day, whereas its nocturnal value was 31.65 ± 0.40 . Total dissolved solids during the day presented a mean value of the order of $30.43 \pm 0.99 \text{ g L}^{-1}$, whereas during the night it was $29.60 \pm 0.32 \text{ g L}^{-1}$. The pH showed a mean value of 7.85 ± 0.43 during the day, and 6.96 ± 1.02 during the night. In regards to the seasonal periods, only the sea-surface temperature presented values different from each other ($p < 0.05$). Its mean value in the dry period was 32.38 ± 1.94 , compared to 32.20 ± 0.52 in the wet season.

3.2 SPECIES COMPOSITION

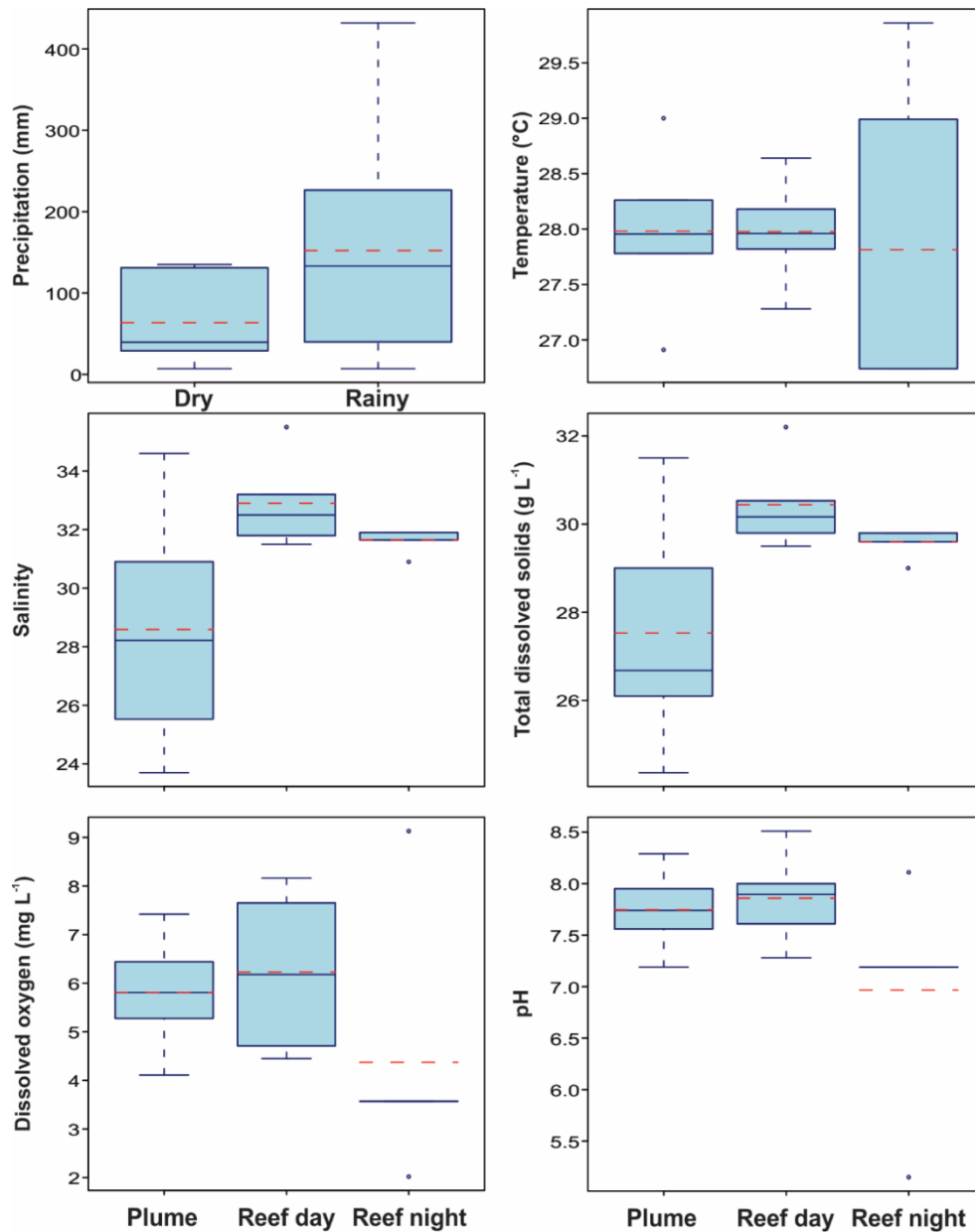
There were found 71 taxa, dominated by Copepoda (40 taxa). Heterotrophic protists were Dinoflagellata, Tintinnina, Foraminifera, and Radiozoa. The metazoan groups were Cnidaria (others), Hydrozoa, Siphonophorae, Gastropoda, Bivalvia, Polychaeta, Bryozoa, Nematoda, Cirripedia, Cladocera, Ostracoda, Copepoda, Amphipoda, Isopoda, Euphausiacea, Stomatopoda, Decapoda, Pycnogonida, Echinodermata, Chaetognatha, Appendicularia, Ascidiacea and Teleostei. Copepoda was represented by four orders and 24 species: Calanoida (Eucalanidae, Clausocalanidae, Centropagidae, Pseudodiaptomidae, Temoridae, Paracalanidae, Pontellidae and Acartiidae), Canuelloida (Longipediidae), Cyclopoida (Oithonidae, Oncaeidae and Corycaeidae) and Harpacticoida (Ectinosomatidae, Miraciidae, Tisbidae and Tachidiidae).

3.3 COPEPODA'S DIVERSITY AND EQUITABILITY

The microzooplankton revealed a diversity of $1.36 \text{ bits ind}^{-1}$ at the plume area, $1.45 \text{ bits ind}^{-1}$ at the reef during the day and $1.50 \text{ bits ind}^{-1}$ at the reef during the night (Fig 03). For the mesozooplankton, the diversity at the plume area was $1.00 \text{ bits ind}^{-1}$. The reef area showed a diversity of 1.32 and $1.29 \text{ bits ind}^{-1}$, during the day and the night, respectively. The equitability of the community at the plume area for the microzooplankton was 0.79 . The reef area presented an equitability of 0.85 during the day and 0.67 during the night. For the mesozooplankton, the equitability at the plume area was 0.53 . Over the reef, mesozooplankton's equitability was 0.66 during the day and 0.63 during the night. No statistical differences ($p > 0.05$) resulted in any distinction observed amongst the diversity and equitability between plume and reef during the day nor between reef during the day and the night.

FIGURE 02: ENVIRONMENTAL VARIABLES PER STATION/DAY-TIME. PRECIPITATION, TEMPERATURE, SALINITY, TOTAL DISSOLVED SOLIDS, DISSOLVED OXYGEN AND PH. THE LINE

OVER EACH BOXPLOT REPRESENTS THE MEDIAN VALUE, WHILE THE DASHED LINE SETS THE MEAN VALUE. THE SCALES ARE SPECIFIC FOR EACH PLOT.



Source: the author, 2020

3.4 TOTAL ABUNDANCE (IND. M⁻³) AND BIOMASS (μGC M⁻³) OF MICROZOOPLANKTON

The plume area showed an abundance (114961 ± 131731 ind. m⁻³) three times greater than the reef area (40640 ± 65020 ind. m⁻³; Fig 03). The most abundant group was Copepoda (95% on both locations), followed by Tintinnina (2%) in the plume and Gastropoda veligers on reef (2%) (Fig 04). Although there was not found any spatial effect on abundance ($p > 0,05$), the numeric values signalize an important plume contribution. Over the reef,

nocturnal zooplankton was 36328 ± 46290 ind. m^{-3} ($p > 0.05$). During the night, the dominant groups were Copepoda (89%), followed by Tintinnina (3%), Foraminifera (2%) and Cnidaria (2%). Considering seasonal periods, the zooplankton abundance in the rainy season presented 80385 ± 110588 ind. m^{-3} compared to 39364 ± 45913 ind. m^{-3} in the dry season ($p > 0.05$). Copepoda was abundant on both periods (94% and 93%, respectively), followed by Tintinnina (2%) in the wet season as well as Cnidaria (others) (2%) in the dry season.

The biomass at the estuarine plume area (10321 ± 10539 $\mu gC\ m^{-3}$) was four times greater than the reef area during the day (2873 ± 4459 $\mu gC\ m^{-3}$) (Fig 03). During the night, the biomass was three times greater than the day (7477 ± 8822 $\mu gC\ m^{-3}$). Copepodites of Oithonidae (23%) most represented the community biomass at the plume, followed by Acartiidae nauplii (12%), *Paracalanus quasimodo* (9%), copepodites of Paracalanidae (9%), and Clausocalanidae-Paracalanidae nauplii (9%) (Fig 04). At the reef region during the day, copepodites of Oithonidae (22%) most represented the community biomass as well, followed by Longipediidae nauplii (18%), Paracalanidae-Clausocalanidae nauplii (12%) and copepodites of Tachidiidae (9%). During the night, *Dioithona oculata* (33%) most represented the biomass of copepods. According to the seasonal periods, copepod biomass was two times greater in the rainy season (8278 ± 10274 $\mu gC\ m^{-3}$) than in the dry season (4809 ± 4208 $\mu gC\ m^{-3}$) ($p > 0.05$). Copepodites of Oithonidae (19%) were the most representative group in the wet season in regards to the biomass, and were followed by *Dioithona oculata* (14%), Paracalanidae-Clausocalanidae nauplii (10%), and copepodites of Tachidiidae (9%). In the dry season, the most representative group of the copepod biomass was Acartiidae nauplii (18%), followed by *Paracalanus quasimodo* (16%) and *Dioithona oculata* (15%). The multivariate analysis revealed that there are no differences regarding the spatial (PERMANOVA, pseudo- $F = 1.44$, $p > 0.05$) and temporal factors (PERMANOVA, pseudo- $F = 0.64$, $p > 0.05$). The MDS plots show the homogeneity of the community (Fig 05), though there is a slight separation of groups on reef between day and night.

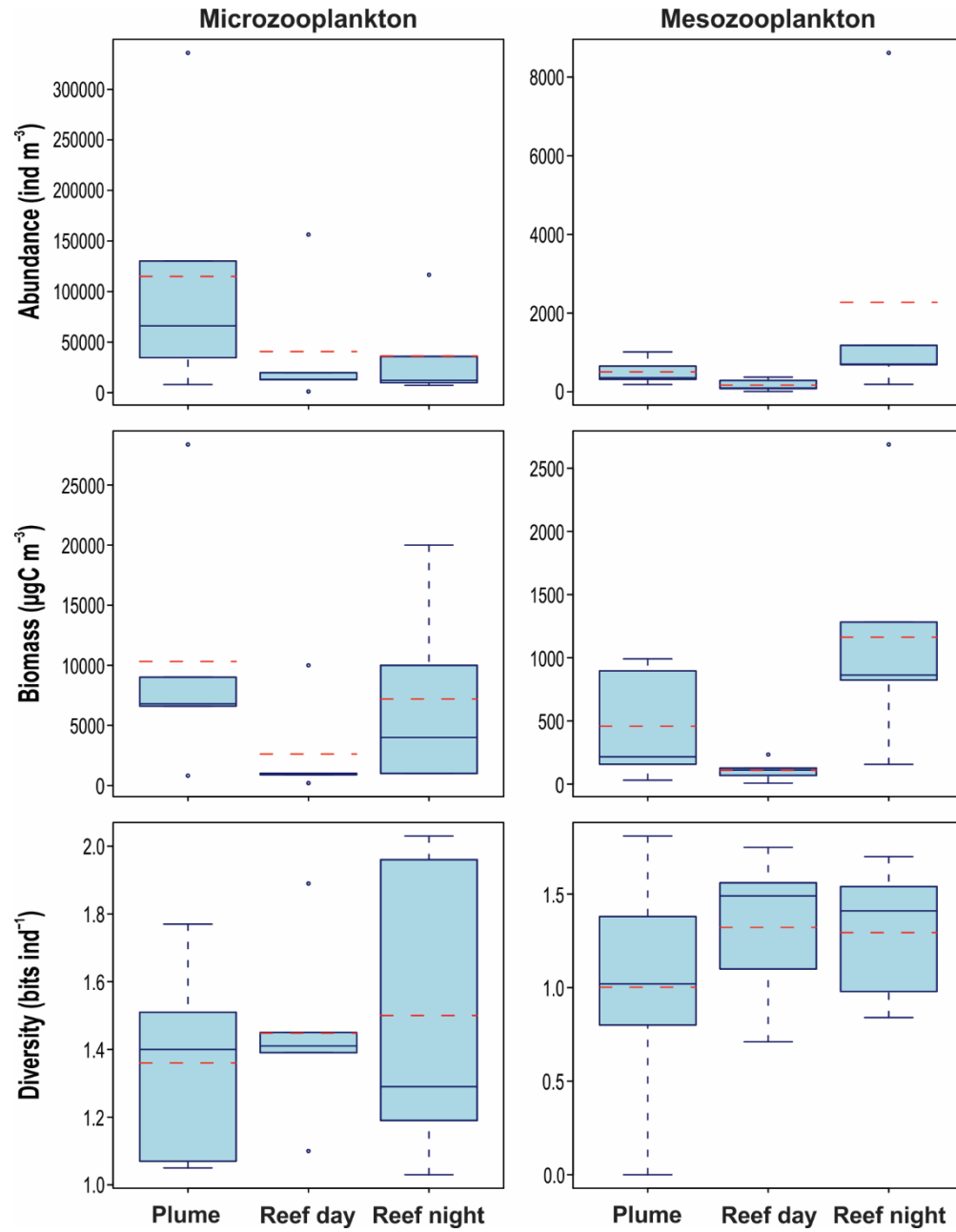
3.5 TOTAL ABUNDANCE (IND. M^{-3}) AND BIOMASS ($\mu GC\ M^{-3}$) OF MESOZOOPLANKTON

The estuarine plume area presented an abundance (507 ± 332 ind. m^{-3}) three times greater than the reef area during the day (172 ± 153 ind. m^{-3}) (Fig 03). Copepoda was the most dominant group (80% and 71%, respectively), followed by such groups as Brachyura (9% and 2%, respectively), Cirripedia (2% and 9%, respectively), and Appendicularia (4% and 6%, respectively) as well as fish larvae (9%) over the reef. At night the zooplankton

abundance was of the order of $2277 \pm 3560 \text{ ind. m}^{-3}$, which was 13 times greater than the day. The dominance was with Copepoda (91%), followed by Appendicularia (2%). The rainy and dry seasons showed abundances of the order of 1390 ± 2740 and $379 \pm 246 \text{ ind. m}^{-3}$, respectively, which represents 3.5 times the rainy over the dry season. Copepoda was also abundant on both seasons (90% and 77%, respectively), followed by Brachyura (2%) and Appendicularia (2%) in the rainy season, and these respective groups (2% and 6%, respectively) together with Cirripedia (3%) and fish eggs (3%) on the dry season.

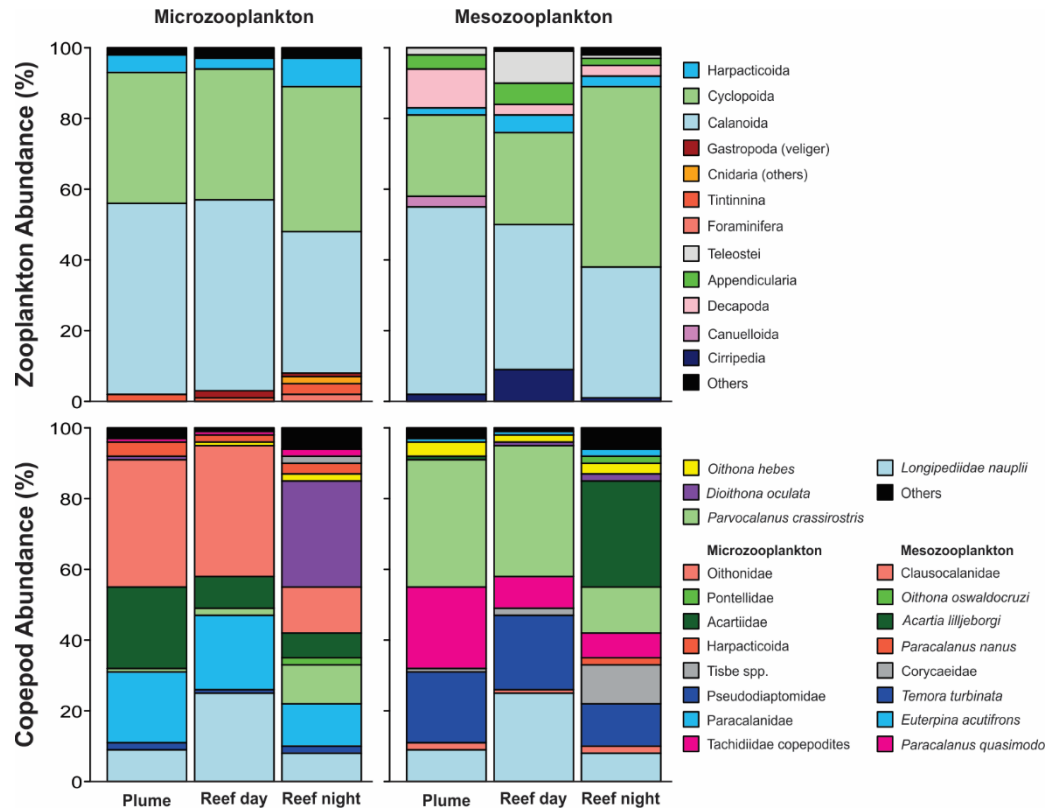
The biomass of copepods (Fig 03) at the estuarine plume area ($458 \pm 450 \mu\text{gC m}^{-3}$) was four times greater than the reef region ($109 \pm 83 \mu\text{gC m}^{-3}$). In contrast, biomass during the night was eleven times greater than the day ($1162 \pm 943 \mu\text{gC m}^{-3}$) ($p > 0.05$). *Paracalanus quasimodo* (62%) were found at the estuarine plume and *Acartia lilljeborgi* (29% and 35%) at the reef during the day and during the night, respectively. *Acartia lilljeborgi* represented 9% of the biomass at the plume area besides the species previously cited. The reef presented some other species/family with a biomass representation, which were *Paracalanus quasimodo* (14%), Pontellidae (12%), and Clausocalanidae (10%). During the night, *Dioithona oculata* represented 15% of the community biomass besides the species previously cited. According to the pluviometric seasons, the rainy season presented a biomass 1.6 times greater ($678 \pm 1401 \mu\text{gC m}^{-3}$) than the dry season ($424 \pm 692 \mu\text{gC m}^{-3}$) ($p > 0.05$). *Acartia lilljeborgi* (27%) most represented the biomass in the wet season and was followed by *Dioithona oculata* (15%) and *Paracalanus quasimodo* (11%). The dry season presented *Paracalanus quasimodo* (45%) as the most representative species in terms of biomass, followed by *Acartia lilljeborgi* (29%). The multivariate analysis demonstrated that there are no differences amongst the mesozooplankton considering the spatial (PERMANOVA, pseudo- $F = 0.58$, $p > 0.05$) and temporal factors (PERMANOVA, pseudo- $F = 1.74$, $p > 0.05$). The MDS plots demonstrate the homogeneity of the community (Fig 05).

FIGURE 03: ABUNDANCE (IND. M^{-3}), BIOMASS ($\mu\text{GC M}^{-3}$), AND DIVERSITY (BITS IND^{-1}) OF MICROZOOPLANKTON AND MESOZOOPLANKTON AT THE PLUME AREA AND AT THE REEF AREA DURING THE DAY AND NIGHT. THE SCALES ARE PROPER FOR EACH PLOT.



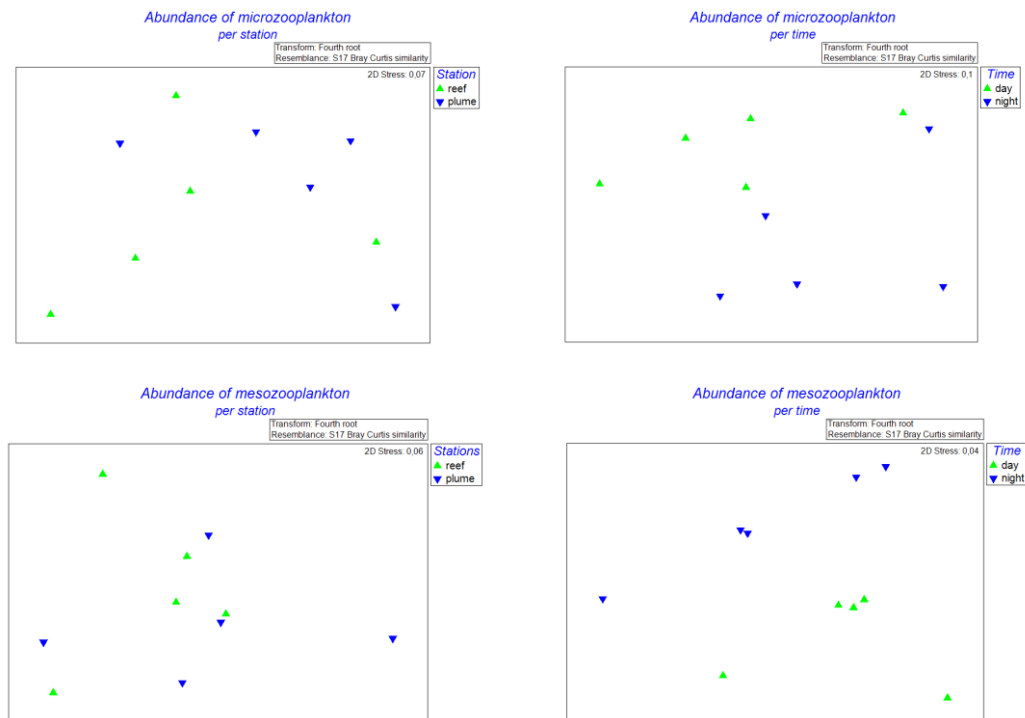
Source: the author, 2020

FIGURE 04: RELATIVE ABUNDANCE OF MESOZOOPLANKTON AND MICROZOOPLANKTON AT THE PLUME AREA AND REEF AREA. ABUNDANCE IS REPRESENTED ON THE LEFT AND BIOMASS ON THE RIGHT.



Source: the author, 2020

FIGURE 05: MDS PLOTS FOR MICROZOOPLANKTON AND MESOZOOPLANKTON ACCORDING TO THE STATIONS (REEF AND PLUME) AND THE TIME AT THE REEF STATION (DAY AND NIGHT). MICROZOOPLANKTON IS REPRESENTED ON THE TOP, AND THE MESOZOOPLANKTON BELOW.



Source: the author, 2020

3.6 COPEPODA'S FEEDING BEHAVIOUR

Copepods were represented by carnivores (Pontellidae and Corycaeidae), herbivores (Pseudodiaptomidae, Tisbidae, and all nauplii), omnivores (Paracalanidae, Subeucalanidae, Clausocalanidae, Centropagidae, Temoridae, Acartiidae, Oithonidae, Oncaeidae, Ectinosomatidae, Miraciidae, and Tachidiidae), and some omnivores with such a predominantly detritivore behaviour (Ectinosomatidae and Oncaeidae). The microzooplankton showed an abundance of carnivores, herbivores and detritivores of 14%, 51% and 35%, respectively, whereas the mesozooplankton appeared with 39%, 60% and 1%, respectively (Fig 06). Concerning their biomass, the microzooplankton presented 30%, 55% and 15% for carnivores, herbivores and detritivores, respectively. In contrast, the biomass of the groups for mesozooplankton were 61%, 30% and 9%, respectively (Fig 6).

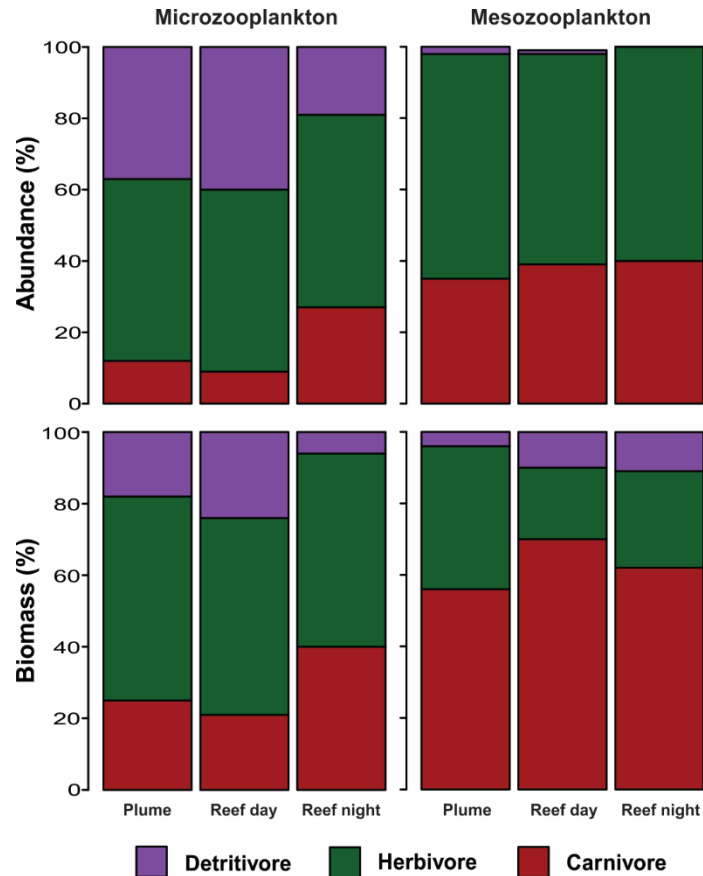
The microzooplankton abundance at the plume area showed 12% were carnivores (> Oithonidae Copepodites), 51% herbivores (> Acartiidae nauplii) and 37% detritivores (> Acartiidae nauplii). In contrast, the reef area during the day presented 9% of carnivores (> Oithonidae Copepodites), 51% herbivores (> Longipediidae nauplii), and 40% detritivores (> Longipediidae nauplii). This pattern changes during the night when the microzooplankton abundance reveals 27% of carnivores (> *Dioithona oculata*), 54% herbivores (> *Dioithona oculata*), and 19% detritivores (> Paracalanidae-Clausocalanidae nauplii). In regard to the microzooplankton biomass at the plume, 25% were carnivore (> Oithonidae Copepodites), 57% herbivore (> Oithonidae Copepodites), and 18% detritivore (ANMC). During the day at the reef, 21% of the community biomass were carnivore (> Oithonidae Copepodites), 55% herbivore (> Oithonidae Copepodites) and 24% detritivore (> Longipediidae nauplii). However, during the night, the representation of the groups were 40% (> *Dioithona oculata*), 54% (> *Dioithona oculata*) and 6% (> Pontellidae nauplii), respectively.

For the mesozooplankton abundance at the plume, 35% were carnivore (> *Paracalanus quasimodo*), 63% were herbivore (> *Paracalanus quasimodo*) and 2% were detritivore (> Longipediidae nauplii), and at the reef during the day, the carnivores totalled 39% (> *Dioithona oculata*), the herbivores, 60% (> *Dioithona oculata*), and the detritivores, 1% (> Oithonidae nauplii). The nocturnal sampling revealed 40% were carnivores (> *Dioithona oculata*), 60% were herbivores (> *Dioithona oculata*) and a considerably small amount were detritivores (> Oncaeidae). In terms of the biomass of mesozooplankton, the

plume appeared with 56% of carnivores, 40% of herbivores and 4% of detritivores (whose groups most contributing are the same for abundance). During the day, the mesozooplankton biomass was represented by 69% of carnivores (> *Acartia lilljeborgi*), 20% of herbivores (> *Acartia lilljeborgi*) and 11% of detritivores (> Pontellidae nauplii). In the night the biomass was represented by 63% of carnivores (> *Acartia lilljeborgi*), 27% of herbivores (> *Acartia lilljeborgi*) and 10% of detritivores (> Oncaeidae).

According to the pluviometric seasons, the microzooplankton abundance at the wet period was represented by 15% of carnivores (> Oithonidae Copepodites), 52% of herbivores (> Paracalanidae-Clausocalanidae nauplii), and 33% of detritivores (> Paracalanidae-Clausocalanidae nauplii). The dry period revealed 11% of carnivores (> Oithonidae Copepodites), 51% of herbivores (> Acartiidae nauplii) and 38% of detritivores (> Acartiidae nauplii). Regarding the microzooplankton biomass, at the wet period carnivores totalized 28% (> Oithonidae Copepodites), herbivores, 57% (> Oithonidae Copepodites), and detritivores, 15% (> Paracalanidae-Clausocalanidae nauplii), whereas the dry period presented carnivores with 53% (> *Dioithona oculata*), herbivores, 42% (> *Dioithona oculata* and Acartiidae nauplii), and detritivores with 5% (> Acartiidae nauplii). Besides, the mesozooplankton abundance at the wet period presented 39% of carnivores (> *Dioithona oculata*), 60% of herbivores (> *Dioithona oculata*), and 1% of detritivores (> Longipediidae nauplii), whereas the dry period showed 38% of carnivores (> *Paracalanus quasimodo*), 62% of herbivores (> *Paracalanus quasimodo*) and a considerably small amount of detritivores (> Oncaeidae). Regarding their biomass, mesozooplankton at the wet period showed 59% of carnivores (> *Acartia lilljeborgi*), 31% of herbivores (> *Acartia lilljeborgi*), and 10% of detritivores (> Oncaeidae), whereas at the dry period the group demonstrated 65% of carnivores (> *Paracalanus quasimodo*), 30% of herbivores (> *Paracalanus quasimodo*), and 5% of detritivores (> Oncaeidae).

FIGURE 06: RELATIVE ABUNDANCE OF CARNIVORE, HERBIVORE AND DETRITIVORE IN REGARD TO THEIR ABUNDANCE AND BIOMASS AT THE PLUME AND AT THE REEF REGION DURING THE DAY AND NIGHT.



Source: the author, 2020

4 DISCUSSION

The estuarine plume seems to comprise a source of zooplankton to the nearby reef system, demonstrated the contribution of typical estuarine families in the area (e.g., Paracalanidae, Acartiidae, Oithonidae, and their nauplii and copepodites). However, there was observed discrepancies amongst the zooplankton over the reef along the day, when nocturnal fauna appears to be higher in abundance at night. Among all planktonic organisms, Copepoda was the most abundant taxa in our study. This finding is similar to other studies done worldwide in environments such as reefs and estuaries (including plumes and fronts) (Cronin, Daiber, & Hulbert, 1962; Glynn, 1973; Hamner, Jones, Carleton, Hauri, & Williams, 1988; Kingsford & Suthers, 1994; Moore & Sander, 1976; Morgan, Robertis, & Zabel, 2005; Neumann-Leitão et al., 2018; Russell, Harrison, & Hunt, 1999; Suthers, Taggart, Kelley, Rissik, & Middleton, 2004; Zhou, Huang, Tan, Lian, & Li, 2015). Moreover, the most prevalent feeding behaviours of copepods were herbivory (> 55%) amongst omnivorous copepods.

Other groups were found together with the copepods on reefs, such as Gastropoda veligers, Brachyura, Cirripedia, Appendicularia and fish larvae. Veligers of Gastropoda are meroplanktonic molluscs that later migrate to the bottom of sand and rock habitats to start their settling. Additionally, they can serve as reef-builders, and contribute to the planktonic community as grazers (Vizzini, Colombo, Costa, & Mazzola, 2012). Brachyura, Cirripedia and fish larvae are also meroplanktonic. Brachyura larvae are predators that prey on smaller zooplankton within estuarine food webs (Staton & Sulkin, 1991). Cirripedia nauplii prey on different sources of carbon with adults feeding) on corals especially (Achituv, Brickner, & Erez, 1997). These groups accompanied the copepods in abundance, revealing the contribution of estuarine plumes as exporters, not only of organic matter but also of planktonic fauna, to nearby reefs.

The microzooplanktonic copepods demonstrate that the reef and plume contain similar groups. Although some groups demonstrate similar abundances regarding plume and reef (*Oithona hebes*, *Parvocalanus crassirostris*, and Longipediidae nauplii, for instance), some others indeed decreased their abundances (*Dioithona oculata*, copepodites of Oithonidae, Harpacticoida nauplii, Acartiidae nauplii, Oithonidae nauplii, Paracalanidae-Clausocalanidae nauplii, and Pseudodiaptomidae nauplii, for instance). Accordingly, the mesozooplanktonic copepods demonstrated the same tendency as microzooplankton (except Eucalanidae, which was found only on reefs): the copepod groups decreased their abundances as long as the waters reached the reefs. The estuarine influence on the reefs can be observed in two ways: (1) reef composition with typically estuarine species, and (2) higher abundance and biomass than other reefs far from the coast. The species within Oithonidae and Paracalanidae as well as their nauplii and copepodites are found abundantly in estuaries.

Oithona hebes, *Parvocalanus crassirostris* and Longipediidae can be found in estuaries, the former two being very abundant in these waters (Chew & Chong, 2011; Costa, Atique, Costa, & Pereira, 2011; Torres-Sorando, Zacarias, Roa, & Rodríguez, 2003). Longipediidae is a migrant oceanic family, hence their nauplii enjoy the estuarine waters for development (Chew & Chong, 2011). It is not surprising to find these groups on the reef due to the presence of the plume extending out to the reef. Groups that are more estuarine-dependent (*Dioithona oculata* and copepod nauplii) then decrease in abundance, which may reveal the near-ending of the plume. In other words, the influence of the plume may demonstrate a gradient from the estuary mouth towards the reef from a high estuarine influence at the estuary mouth to a low influence reaching the reefs.

As a matter of fact, the estuary is considered a way through which continental waters pass towards the ocean. As a result, it carries a significant amount of nutrients and organic matter washed from their tributaries and mangrove habitats. These nutrients foster the phytoplankton's primary productivity, which is the main source of carbon for copepods. Chew & Chong (2011) concluded that the main structuring parameters of the copepod community of estuaries and coastal waters are salinity and chlorophyll a. Furthermore, copepod biomass at the estuarine plume was dominated by estuarine species, some of which are also found in coastal waters (*Paracalanus quasimodo*, for example). Copepods may also be served with terrigenous sources of carbon as such demonstrated by Hu et al. (2015). These results may demonstrate the contribution of estuaries to occidental coasts of the oceans.

Interestingly, Longipediidae nauplii and copepodites of Tachidiidae (*Euterpina acutifrons*) peaked their biomass on the reef. Longipediidae is of oceanic origin which goes to estuaries to feed and breed. Moreover, Longipediidae can be found dwelling on the bottom of reef habitats (Fiers, 1984). This group can be found among the demersal zooplankton as well (Melo et al., 2010; Robichaux, Cohen, Reaka, & Allen, 1981). It is important to note that *Euterpina acutifrons* is an holoplanktonic, natant fauna (Coull & Vernberg, 1970). However, their nauplii and copepodites were abundantly found on the reef region. It may likely demonstrate the ongoing contribution of the plume to maintain estuarine conditions for the development of some planktonic fauna.

Our biomass data resembles that obtained in other coastal reef environments (Hamner & Carleton, 1979; Heidelberg, Sebens, & Purcell, 2004; Heidelberg, O'Neil, Bythell, & Sebens, 2010; McKinnon, Duggan, & De'ath, 2005; Nakajima et al., 2014; Roman, Furnas, & Mullin, 1990). Copepods tend to demonstrate relatively low biomass estimates over the reefs, but not as low as the estimates far from the coast (Nakajima, Yoshida, Othman, & Toda, 2008). Nonetheless, the plume indeed demonstrates higher biomasses than the reef itself. Thus, the ongoing contribution of the plume can be observed as a source of zooplankton biomass, mainly those of the families Paracalanidae, Acartiidae, Oithonidae and Longipediidae, whose abundances and biomass were similar and/or higher on reefs in comparison to the plume.

Herbivory species abundance was similar between plume and reef and was the most representative group in both places. According to the study of Putland & Iverson (2007), estuarine planktonic food web is most characterized by a microbial food web rather than the classical food web (phytoplankton-copepod-fish), i.e. smaller zooplankters feed upon the

phytoplankton, which presents higher biomasses in estuaries and coastal waters. In our study, nauplii were the main representative fauna for herbivory, in addition to *Paracalanus quasimodo* and *Dioithona oculata* copepodites. However, it is common for calanoid copepods to present an omnivorous feeding behaviour, feeding on smaller nauplii and zooplankters especially. This function gives them advantages over other groups for the acquisition of energy (Gifford & Dagg, 1988).

Mesozooplankton and microzooplankton also showed distinct abundance and biomass values from each other, the former being less abundant in the areas studied. Following Figueirêdo et al. (2018), the present paper studied both meso- and microzooplankton together, due to biases in juveniles and adults concentrations. Moreover, carnivory is more represented by the highest animals, which demonstrate a more predominant omnivore behaviour. Additionally, nauplii are considered to be omnivore-detritivore for they can also serve as faecal pellets feeders. This gives them another source of energy, together with phytoplankton (Green et al., 1992; Mauchline, 1998; Nakajima et al., 2014; Poulsen & Iversen, 2008). It is then observed that a more predominant detritivore behaviour occurs within the microzooplankton than the mesozooplankton. This is most likely due to the high abundance of nauplii in the smaller zooplanktonic group, which present a variety of feeding behaviours and could prey on both phytoplankton, protozooplankton (e.g. ciliates) and faecal pellets (Kiorboe, 1998). Importantly, the smaller and greater copepods are a food source for other higher-taxa, such as gelatinous zooplankters and fish larvae (Sun, Huo, & Yang, 2010; Turner, 2004a).

Thus, our results confirms the findings of Putland & Iverson (2007). These authors observed that herbivory is indeed an advantage for coastal microzooplankton, and this is due primarily to phytoplankton abundance, whose community takes advantage from the nutrients that come up from estuaries. However, studies with the phytoplankton abundance and biomass in contrast to potential secondary producers should be performed. Moreover, Turner (2004b) highlighted that smaller zooplankton are abundant at sea due to their wide range of feeding strategies, i.e. the presence of an omnivore state gives advantages to copepods. Amongst these advantages are the consumption of both phytoplankton and microbial fauna including nauplii (Gifford & Dagg, 1988). Indeed, carnivory is much more represented within mesozooplankton in terms of biomass. This is also described by Zöllner, Hoppe, Sommer, & Jürgens (2009), who demonstrated mesozooplankton to be predators not only on phytoplankton but on smaller zooplankters as ciliates, for example. The authors also discuss

trophic web views, as to not only consider the classical food web (phytoplankton-copepod-fish). Rather, the microbial food web should also be a factor to be taken into consideration.

This indicates the contribution of reef fauna to the nocturnal zooplankton biomass. In terms of what Heidelberg et al. (2004) discussed, the holoplanktonic fauna are potentially a source of energy to reefs. Moreover, out of these eight taxa, five potentially contribute to herbivory, including *P. parvus*, *P. acutus*, *T. turbinata*, and *Tisbe* spp., of which *P. acutus* exclusively feed on primary producers. In contrast, the mesozooplanktonic nocturnal groups were the copepodites of Acartiidae, Corycaidae and Temoridae, of which at least two taxa contribute to herbivory (Acartiidae and Temoridae).

The role in diel vertical migration (DVM) of zooplankton may follow two patterns: (1) predation avoidance and (2) food concentration, although environmental factors may also influence in certain ways (Liu, Sun, & Han, 2003). Within a food limiting body of water, copepods, for instance, can confront their predators in search for food. They can also stay afloat until they become satiated. Age can play a role in DVM, with adults being more experienced in avoiding predation, moving upwards to feed on their prey and moving downwards after feeding is completed. Nakajima et al. (2008) demonstrated that DVM is the cause of a high abundance and biomass of zooplankton at night. In addition, Yahel, Yahel, Herman, Jaffe, & Genin (2005) found a 10 times-concentration of zooplankton at night in a coral reef habitat of Red Sea, suggesting the role of DVM in changing the attributes of plankton during the night (Kramer, Bellwood, & Bellwood, 2013).

Despite the dominant groups, *Dioithona oculata* and *Acartia lilljeborgi* most represented the biomass during the night. It is observed that these dominant estuarine species can occur in coastal waters as well, especially within reefs (Mckinnon & Duggan, 2014; Melo et al., 2010; Silva, Neumann-Leitão, Schwamborn, Gusmão & Silva, 2004). *D. oculata* can form swarms, which are big aggregations of the fauna (Ambler, Ferrari, Fornshell & Buskey, 1999; Melo et al., 2010), a behaviour that helps the species to survive in reef areas (Mckinnon & Duggan, 2014). The species was also found to be the dominant form of potential carnivory in the reef. Melo et al. (2010) affirmed the presence of demersal fauna on the coastal reefs of TB, such as *P. acutus*, *C. americana* and *D. oculata*. The presence of *A. lilljeborgi* with a higher biomass at night could be indicative of what Gifford & Dagg (1988) have stated. The study of marine copepods' feeding behaviour can reveal much of their importance to coral reefs worldwide. Whereas some take advantage of swarms to dwell within

reefs, others are benefitted by their omnivore ability, hence contributing to the growth of reef-builders such as corals (Heidelberg et al., 2004).

It is paramount that climate influences the planktonic community, especially regarding the availability of resources to primary and secondary producers (Behrenfeld, 2014). Our findings demonstrate higher values of abundance and biomass within the rainy pluviometric period. The TB area is marked by an annually pluviometric regime of 2000 mm, most of which happens within the rainy season (Araújo et al., 2012). This likely contributes to the increase of nutrients in estuarine waters which adheres to what Rothlisberg & Jackson (1982) have discussed in their paper. Studying the planktonic community over the Gulf of Carpentaria in Australia (11–17.5°S) higher values of plankton biomass were found during the rainy period. The authors then emphasized the necessity of a hydrological study in the area to confirm the influence of nutrients on the planktonic community's high biomass. In contrast, Silva, 2019 studied TB during two pluviometric seasons, and found low values of Chlorophyll a in the dry period hence the dry period was found to be food limiting. This demonstrates that environmental variables affect the zooplanktonic community, especially in the availability of food and other limiting resources.

Overall, our findings demonstrate the ongoing influence of the estuarine plume over the coastal reef area as a source of zooplankton to the reefs, which appear to present its proper community dynamics. Copepoda was the most abundant zooplanktonic taxa in the reefs and their omnivore ability was found to be the main cause of their distribution over reefs, however further laboratory studies should confirm this hypothesis. Therefore the reefs are a source of zooplankton to the coastal community, adhering to research by Melo et al. (2010) which found that reefs can also be a nursing place to many zooplankters. The attributes of a zooplanktonic community over coral reef ecosystems can reveal much of the health of these systems in times of the abundant anthropogenic actions we see over marine habitats nowadays. Nonetheless, despite the ability of coastal systems with estuaries nearby to present a more predominant detritivore food web, herbivory is the most important role of pelagic copepods in these areas.

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3 CONSIDERAÇÕES FINAIS

Este estudo é o primeiro na costa do Nordeste brasileiro a apresentar o comportamento alimentar de copépodes marinhos em uma área de recifes costeiros tropicais. Tal trabalho pode servir de base para futuros estudos da ecologia trófica desses ambientes, que são altamente diversos.

Os copépodes foram os organismos mais abundantes tanto na pluma quanto nos recifes costeiros tropicais. Espécies estuarinas e costeiras dominaram a comunidade, como Paracalanidae, Acartiidae e Oithonidae juntamente com seus náuplios e copepoditos.

Alguns grupos zooplancônicos estuarinos acompanharam os copépodes na abundância sobre os recifes, embora não dominantes. Grupos como Gastropoda, Brachyura, Cirripedia, Appendicularia e larvas de peixe apresentaram maior abundância diante dos demais. A comunidade sobre os recifes apresentou composição similar à comunidade na pluma estuarina, embora a abundância e biomassa de alguns grupos diminuíssem no recife, com predominância de organismos costeiros.

A pluma estuarina apresentou abundância e biomassa de copépodes maior que os recifes costeiros tropicais adjacentes. No entanto, o zooplâncton noturno nos recifes apresentou uma abundância e biomassa bem maior que nas condições diurnas, revelando a importância da migração zooplancônica nos recifes costeiros tropicais para a dinâmica da comunidade.

A herbivoria é o hábito alimentar mais prevalente entre os copépodes sobre os recifes costeiros tropicais. Um achado importante é a maior presença de onívoros na comunidade, revelando que a herbivoria pode ser uma entre as demais habilidades desses copépodes para conseguir seu alimento.

O microzooplâncton, embora apresente comportamento alimentar relacionado à cadeia de pastagem, está mais integrado à cadeia detritívora que o mesozooplâncton. Este, por sua vez, está mais integrado à cadeia de pastagem. Contudo, o zooplâncton sobre os recifes de corais é mais integrante da cadeia de pastagem.

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ANEXO A - NORMAS DE SUBMISSÃO À REVISTA MARINE AND FRESHWATER RESEARCH

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- **PRESENTATION**
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- **CONFLICTS OF INTEREST**
- **ACKNOWLEDGEMENTS**
- **REFERENCES**
- **TABLES AND FIGURES**
- **SUPPLEMENTARY MATERIAL**
- **GUIDELINES FOR DATA ANALYSIS AND PRESENTATION**
- **UNITS, NOMENCLATURE AND FORMULAE**
- **ANIMAL AND HUMAN RESEARCH ETHICS**
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The work should be presented in clear and concise English. All text should be in Times New Roman, 12 point font, with double or 1.5-line spacing throughout, and with a margin of at least 3 cm on the left-hand side. **EVERY LINE OF EACH PAGE MUST BE CONSECUTIVELY NUMBERED IN THE LEFT-HAND MARGIN, STARTING FROM 1 TO THE HIGHEST NUMBERS NEEDED AS THIS GREATLY ASSISTS THE REFEREES.** All pages of the manuscript must be numbered consecutively, including those carrying references, tables and captions to illustrations, all of which are to be placed after the text. Follow the form of headings, tables and illustrations exemplified in recent issues of the Journal.

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ACKNOWLEDGEMENTS

The contribution of colleagues who do not meet all criteria for authorship should be acknowledged. Financial and material support should also be acknowledged. All sources of funding for the research and/or preparation of the article should be listed, and the inclusion of grant numbers is recommended. Authors should declare sponsor names along with explanations of the role of those sources if any in the preparation of the data or manuscript or the decision to submit for publication; or a statement declaring that the supporting source had no such involvement. If no funding has been provided for the research, please include the following sentence: "This research did not receive any specific funding".

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- *Journal article*
 Prince, J. D., Sellers, T. L., Ford, W. B., and Talbot, S. R. (1988). Confirmation of a relationship between localised abundance of breeding stock and recruitment for *Haliotis rubra* Leach (Mollusca: Gastropoda). *Journal of Experimental Marine Biology and Ecology* **122**, 91-104.
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