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GLEICE DE SOUZA SANTOS

CONTRIBUIÇÃO DO MEROPLÂNCTON PARA AS COMUNIDADES ZOOPLANCTÔNICAS DOS RECIFES DE TAMANDARÉ (PERNAMBUCO, BRASIL) E NOVAS METODOLOGIAS PARA AMOSTRAGEM E ESTIMATIVA DE BIOMASSA DO ZOOPLÂNCTON TROPICAL

Recife
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RESUMO

A composição e biomassa do zooplâncton dos recifes de Tamandaré (PE, Brasil) foram investigadas com o objetivo de caracterizar esses ecossistemas como fontes ou sumidouros de zooplâncton para o ambiente pelágico. Foram desenvolvidos dois novos sistemas de redes estacionárias: a *Channel Midwater Neuston Net* (CMNN) e a *Reef Edge Net* (REN), adaptadas para a coleta de zooplâncton em pontos fixos próximos aos recifes. Também foram desenvolvidos fatores de conversão para o cálculo da biomassa do zooplâncton, através da análise de imagens, com base nos dados de comprimento, diâmetro esférico equivalente, área e biovolume do zooplâncton de ambientes costeiros tropicais. As coletas foram realizadas durante noites de lua nova de 19 a 22 março e de 10 a 12 de novembro de 2015 e de 7 a 11 de março de 2016. A camada subsuperfícial da água foi amostrada através de arrastos subsuperficiais com rede cônica (300 µm), com duração de 13 minutos, após o pôr do sol. As novas redes estacionárias (300 µm) coletaram durante 4 horas, contra o fluxo de corrente das marés vazantes. A REN foi ancorada na borda dos recifes e amostrou o zooplâncton "lavado" do topo recifal. A CMNN coletou os organismos que estavam sendo transportados para a plataforma continental em canais entre os recifes. Os dados obtidos com o uso da CMNN e a REN em comparação com a rede cônica mostraram que as novas redes são eficientes na coleta de zooplâncton de recifes rasos. A REN mostrou uma melhor performance na coleta de larvas de peixes e invertebrados bentônicos quando comparada com a CMNN e a rede cônica, provavelmente pela sua posição e profundidade em relação ao recife. As correlações entre os dados de tamanho e biomassa do zooplâncton mostraram que o biovolume foi o parâmetro mais adequado para mensurar a biomassa do zooplâncton de ambientes costeiros tropicais. No tocante às assembleias zooplanctônicas dos recifes de Tamandaré, a abundância do zooplâncton foi significativamente maior na subsuperfície da água e nas bordas dos recifes quando comparada aos canais. A abundância alta de zooplâncton registrada na borda recifal sugere que existe uma baixa predação desses organismos no topo dos recifes, o que pode ser explicado também pela baixa cobertura de corais escleractíneos e alta cobertura de macroalgas dos recifes do Tamandaré. Esses resultados sugerem que ao invés de sumidouros, esses ecossistemas podem ser classificados como fontes importantes de zooplâncton para o ambiente pelágico. O meroplâncton foi mais abundante em relação ao holoplâncton na borda dos recifes e canais. O grupo mais abundante do meroplâncton foi representado pelas larvas de decápodes. Náuplios

de cirrípedes, larvas de estomatópodes e ovos e larvas de peixes também foram importantes. O meroplâncton contribuiu com mais de 50% para a biomassa do zooplâncton dos recifes de Tamandaré. Esse estudo mostra a relevância do meroplâncton nos sistemas pelágicos ao entorno de um recife tropical e sugere que a influência de larvas e ovos produzidos por peixes e invertebrados bentônicos residentes dos recifes tem sido subestimada em estudos que abordam a produtividade desses ecossistemas.

Palavras-chave: Zooplâncton recifal. *Channel Midwater Neuston Net*. *Reef Edge Net.* Biovolume. Biomassa zooplanctônica. Meroplâncton.

ABSTRACT

The composition and biomass of the zooplankton of the reefs of Tamandaré (Pernambuco state, Brazil) were investigated aiming to characterize theses ecosystems as sources or sinks of zooplankton for pelagic systems. Two new systems of passive nets suitable for sampling zooplankton at fixed stations close to patch reefs were created: the Channel Midwater Neuston Net (CMNN) and the Reef Edge Net (REN). Factor conversions were created to estimate zooplankton biomass through image analysis based on length, equivalent spherical diameter, body area and biovolume of zooplankton from coastal tropical waters. Sampling was carried out during new moon nights from March 19 to 22 (2015), from November 10 to 12 (2015), and from March 7 to 11 (2016). A conical plankton net (300 µm) sampled the subsurface of the water in tows carried out for 13 minutes after sunset. The new passive nets (300 µm) sampled for 4 hours against the local current flow of ebb tides. The REN was deployed at the reef edge and sampled the zooplankton "washed" from reef tops. The CMNN sampled the organisms transported to the continental shelf through channels between reefs. The CMNN and REN were efficient for sampling zooplankton assemblages in shallow reefs when compared to the results obtained using a common conical plankton net. The REN showed a better performance for sampling eggs and larvae of fish and benthic invertebrates compared to the CMNN and the plankton net, probably due to its position and depth in relation to reefs. The correlation between body size and biomass of zooplankton showed that the biovolume is the best parameter to infer the biomass of zooplankton from tropical coastal waters. Regarding the zooplankton assemblages of the reefs of Tamandaré, the abundance of these organisms was higher at subsurface and reef edges compared to the channels. The high abundance record at the reef edges suggests that there is a low predation pressure on zooplankton, which may also be explained by the low coverage of scleractinian corals and high coverage of macroalgae on the reefs of Tamandaré. These results suggest that these reefs are sources instead of sinks of zooplankton. The meroplankton showed higher abundances than holoplankton reef edges and channels. Decapod larvae was the most abundant group regarding the meroplankton composition but cirripedian nauplii, stomatopod larvae, fish eggs and larvae were also important. The meroplankton composed more than 50% of zooplankton biomass in the reefs of Tamandaré. This study shows the relevance of meroplankton in pelagic systems adjacent to a tropical reef and suggests that the influence of eggs and larvae released by reef resident benthic

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Key-words: Reef zooplankton. Channel Midwater Neuston Net. Reef Edge Net. Biovolume. Zooplankton biomass. Meroplankton.

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1 INTRODUÇÃO

Os recifes costeiros tropicais de águas rasas são ambientes rochosos utilizados como habitat por uma grande variedade de espécies marinhas. As assembleias zooplanctônicas de águas que banham recifes costeiros tropicais são caracterizadas pela abundância de larvas e ovos de animais bentônicos e pelágicos que residem nos recifes. A produção e a dispersão desses organismos são essenciais para o estabelecimento das comunidades recifais. Além disso, larvas e ovos recém eclodidos são considerados uma fonte de alimento importante para vários organismos planctívoros (Holzman e Genin, 2003).

Os recifes tropicais são reconhecidos como ecossistemas produtivos, onde o que é produzido e importado de áreas adjacentes (ex. região oceânica) é consumido de forma rápida pelos organismos residentes dos recifes (Odum e Odum, 1955; Hamner *et al.*, 2007; Nakajima *et al.*, 2014; Nakajima *et al.*, 2017). Por exemplo, os recifes de coral verdadeiros apresentam uma cobertura coralínea alta e uma abundância relevante de peixes recifais que causam uma pressão predatória intensa sobre a comunidade zooplanctônica. Os peixes planctívoros são predadores ativos de zooplâncton próximo à superfície do recife, principalmente durante o período diurno. Durante a noite, os corais abrem os seus tentáculos para se alimentarem dos organismos planctônicos (Holzman *et al.*, 2005; Yahel e Yahel, 2005; Yahel *et al.*, 2005; Hamner *et al.*, 2007; Heidelberg *et al.*, 2010). Por isso, esses ambientes representam verdadeiros sumidouros de zooplâncton.

Outra característica importante desses ecossistemas é a dominância de copépodes no mesozooplâncton ao entorno dos recifes (Heidelberg *et al.*, 2004; Nakajima *et al.*, 2008; Alldredge e King, 2009; Heidelberg *et al.*, 2010; Nakajima *et al.*, 2014). Embora exista uma abundância relevante de espécies bentônicas e pelágicas residentes dos recifes tropicais e que liberam suas larvas e ovos no ambiente pelágico (como por exemplo, decápodes e peixes), a captura desses organismos em estágios iniciais de desenvolvimento, em amostras de zooplâncton coletadas com redes tradicionais, pode não retratar o verdadeiro potencial desses ecossistemas como produtores de meroplâncton.

A distribuição espacial e temporal de larvas e ovos de peixes e invertebrados em ambientes marinhos está diretamente relacionada ao regime de correntes, temperatura, salinidade, concentração de organismos fitoplanctônicos na água do mar, tempo de vida das larvas no ambiente pelágico, taxas de mortalidade, habilidades sensoriais das larvas, presença

de locais apropriados para o assentamento, característica demográficas das populações de adultos, momento e local de desova, etc. (Williams *et al.*, 1984; Forward, 1987; Anger, 2001; Sale e Kritzer, 2003; Fernandes *et al.*, 2012; Kough *et al.*, 2013; Kough e Paris, 2015; Epifanio e Cohen, 2016; Mactavish *et al.*, 2016).

Em ambientes costeiros o meroplâncton vem sendo estudado com ênfase na distribuição vertical e temporal de larvas de poliquetas, bivalves, cirrípedes, braquiúros, camarões decápodes e peixes em função de mudanças nas variáveis ambientais (Ziadi *et al.*, 2015; Mactavish *et al.*, 2016) e em relação às marés, fases da lua, regime de ventos e outras variáveis (Criales *et al.*, 2002; Criales *et al.*, 2003; Criales *et al.*, 2010; Ayata *et al.*, 2011; Roura *et al.*, 2013; Blake, 2017). Entretanto, pouco se sabe sobre a contribuição do meroplâncton produzido pelos recifes nesses processos.

No nordeste do Brasil, poucos estudos têm enfatizado a quantificação do meroplâncton de ambientes pelágicos no entorno de recifes costeiros. Alguns registros desses organismos são encontrados em estudos desenvolvidos nos recifes de Tamandaré (PE) que abordaram: a análise do zooplâncton demersal dos recifes (Silva, 2003; Melo *et al.*, 2010), a influência dos estuários nos ambientes costeiros ao entorno dos recifes (Porto Neto, 2003; Nascimento-Vieira *et al.*, 2010), a composição do séston da baía de Tamandaré (Silva, 2016) e a distribuição espaço-temporal de larvas de peixes (Silva-Falcão *et al.*, 2012). O estudo da biomassa sestônica e da estrutura da comunidade zooplanctônica dos recifes de Maracajaú (RN) também revelaram a importância do meroplâncton nesses ecossistemas (Mayal *et al.*, 2009). Todavia, as estratégias de amostragem de zooplâncton utilizadas nos trabalhos anteriormente citados não são apropriadas para um estudo quantitativo do meroplâncton produzido pelos recifes.

Nos bancos dos Abrolhos (BA), Koettker e Lopes (2013) descreveram uma comunidade abundante e diversa de larvas de invertebrados no ambiente pelágico sobre e no entorno dos recifes, com ênfase em larvas de decápodes braquiúros de espécies residentes dos recifes. Entretanto, pouco se sabe sobre o potencial dos recifes como ecossistemas produtores de ovos e larvas em momentos de desova de peixes e invertebrados bentônicos, bem como a importância desses eventos no aporte de biomassa para os ambientes pelágicos.

Quantificar, de forma precisa, a presença de larvas e ovos de peixes e invertebrados bentônicos em ambientes recifais é um grande desafio. A maioria dos organismos bentônicos e pelágicos residentes desses ecossistemas liberam larvas e ovos durante a noite (Forward, 1987;

Samoilys, 1997; Nanami *et al.*, 2013), preferencialmente em dias de lua nova (Forward, 1987; Nolan e Danilowicz, 2008), o que torna a navegação próxima aos recifes, bem como a manipulação de redes tradicionais de coleta de zooplâncton, um trabalho perigoso.

Outro problema é a hora exata e duração dos momentos desova, que varia para cada espécie (Forward, 1987), visto que uma amostragem realizada em um horário "inadequado" poderia subestimar a verdadeira contribuição do meroplâncton recifal para os ambientes pelágicos ao entorno dos recifes. A falta de conhecimento sobre padrões de correntes, dispersão, mecanismos de retenção e distribuição em manchas de larvas nesses ambientes também dificultam uma quantificação confiável do meroplâncton.

Métodos tradicionais de coleta de zooplâncton também podem subestimar a quantificação da produção do meroplâncton de origem recifal nos ambientes pelágicos de águas rasas, umas vez que as malhas e design de redes comumente usadas em estudos realizadas nesses ecossistemas são mais apropriadas para a captura de organismos com pouca mobilidade, como é o caso de bombas de sucção usadas na coleta de zooplâncton em recifes (Heidelberg *et al.*, 2004; Holzman *et al.*, 2005; Heidelberg *et al.*, 2010). Outros métodos de coleta usados nesses ecossistemas são mais adaptados para a captura de pós-larvas de decápodes e peixes, que é o caso das *channel nets* (Shenker *et al.*, 1993; Thorrold *et al.*, 1994; Doherty e Mcilwain, 1996; Nolan e Danilowicz, 2008; Criales *et al.*, 2010) e das armadilhas luminosas (Brogan, 1994; Hickford e Schiel, 1999; Chan *et al.*, 2016).

Outra dificuldade metodológica para o estudo do zooplâncton dos ecossistemas recifais tropicais está relacionada às estimativas precisas da biomassa dos organismos através de métodos não destrutivos de amostras. O método do peso úmido do plâncton vem sendo utilizado como uma alternativa para o estudo da biomassa do séston marinho (Wiebe *et al.*, 1975; Postel *et al.*, 2000; Pitois e Fox, 2006; Melo Júnior *et al.*, 2007; Silva, 2016). Entretanto, não é possível, através desse método, estimar de forma precisa, a biomassa dos grandes grupos do zooplâncton. Devido à forte correlação existente entre o tamanho e a biomassa dos organismos marinhos, é possível obter fatores de conversão confiáveis para o cálculo do peso seco, massa de carbono e nitrogênio do zooplâncton baseados em medições do comprimento dos organismos obtidas com o uso de ocular micrométrica em estereomicroscópios (Uye, 1982).

Todavia, essas medições demandam um grande tempo de análise em laboratório. Por isso, muitos equipamentos ópticos e softwares têm sido desenvolvidos para a obtenção de dados

de tamanho do zooplâncton, *in situ* e em laboratório, de uma forma mais rápida e automatizada. Alguns exemplos desses equipamentos são o UVP (Underwater Vision Profile), o LOPC (Laser-Optical Plankton Counter), o Coulter Counter, a FlowCam e o ZooScan (Sheldon *et al.*, 1972; Grosjean *et al.*, 2004; Schultes e Lopes, 2009; Gorsky, G. *et al.*, 2010; Forest *et al.*, 2012; Álvarez *et al.*, 2014).

Nesse contexto, alguns estudos têm enfatizado a elaboração de fórmulas para calcular a biomassa do zooplâncton a partir de dados de área corpórea e biovolume dos organismos obtidos por análises de imagens medidas com ocular micrométrica (Alcaraz *et al.*, 2003; Hernández-León e Montero, 2006; Lehette e Hernández-León, 2009). Entretanto, os fatores de conversão disponíveis na literatura, até o presente momento, foram elaborados em ambientes antárticos e subtropicais. Logo, o uso dessas fórmulas pode ser inapropriado para as estimativas de biomassa do zooplâncton de origem tropical.

A área escolhida para a realização dessa tese foi o complexo recifal de Tamandaré, localizado dentro dos limites da Área de Proteção Ambiental Costa dos Corais (ICMbio - Instituto Chico Mendes de Conservação e Biodiversidade - http://www.icmbio.gov.br/apacostadoscorais), no município de Tamandaré, litoral sul do estado de Pernambuco (8º 45'36" e 8º 47'20" S e 35º 03'45" e 35º 06'45" W). Esses recifes são caracterizados pela baixa cobertura de corais escleractíneos e alta cobertura de macroalgas e zoantídeos (Costa, 2013; Santos *et al.*, 2015). Representam um habitat importante para o desenvolvimento de várias espécies de peixes que realizam migrações de estuários para regiões da plataforma continental adjacente (Silva-Falcão *et al.*, 2012; Aschenbrenner *et al.*, 2016). Esses ambientes são considerados uma fonte importante de sustento para várias famílias que vivem no município de Tamandaré e realizam atividades relacionadas à pesca e ao turismo (Ferreira e Maida, 2001). Apesar da sua proximidade com a região costeira, as águas que banham os recifes de Tamandaré não estão em processos de eutrofização (Silva, 2015).

Diferente dos recifes de corais localizados em regiões tropicais oligotróficas do Caribe e Indo-Pacífico, os recifes de águas rasas de ambientes costeiros do Nordeste do Brasil recebem uma grande influência de regiões estuarinas, o que aumenta consideravelmente a turbidez das águas que banham esses recifes (Silva *et al.*, 2013). Esse fator é uma das principais razões pelas quais os recifes da costa brasileira apresentem uma alta cobertura de macroalgas e uma baixa cobertura de corais escleractíneos (Leão e Dominguez, 2000; Leão e Kikuchi, 2005).

Provavelmente, esses recifes apresentam uma produção alta de organismos planctônicos que estão sob uma menor pressão predatória, quando comparados às assembleias zoooplanctônicas que habitam recifes com uma cobertura alta de corais escleractíneos.

Para testar uma das hipóteses propostas na presente tese foram incialmente desenvolvidos dois capítulos voltados à metodologia de coleta e análise da biomassa do zooplâncton tropical. O primeiro capítulo teve como objetivo principal apresentar dois métodos novos apropriados para a amostragem de zooplâncton em pontos fixos próximos aos recifes, visando uma quantificação precisa de larvas e ovos, recém eclodidos, de peixes e invertebrados. O segundo capítulo teve o objetivo de apresentar fatores de conversão para o cálculo da biomassa do zooplâncton de regiões tropicais e comparar as fórmulas propostas no presente estudo com as fórmulas da literatura. O terceiro e último capítulo teve o objetivo de investigar se os recifes de Tamandaré podem ser considerados sumidouros ou fontes de zooplâncton para o ambiente pelágico, bem como destacar qual o grupo do mesozooplâncton mais relevante para o aporte de biomassa para os ambientes pelágicos.

Pela primeira vez no Brasil é realizada uma coleta de zooplâncton com o uso de redes estacionárias durante o período noturno, em pontos fixos próximos aos recifes, em potencial momentos de desova de invertebrados bentônicos e peixes. O principal objetivo é avaliar a real contribuição e o papel de ambientes recifais tropicais, de uma área protegida marinha, no aporte de meroplâncton para os sistemas pelágicos. Também é relevante, no presente trabalho, a investigação das assembleias de zooplâncton de uma área recifal completamente fechada ao uso, onde são proibidas práticas como a pesca e o pisoteio. Vale salientar que também é executado, pela primeira vez, um estudo comparativo da análise de imagens de zooplâncton com o uso do ZooScan e da composição elementar (porcentagem de carbono e nitrogênio) desses organismos, em um ambiente tropical costeiro, que culminará na elaboração de fórmulas para calcular, de forma mais precisa, a biomassa do zooplâncton de uma região tipicamente tropical.

2 HIPÓTESES

2.1 Redes estacionárias são apropriadas para uma estimativa confiável do meroplâncton de origem recifal;

2.2 A biomassa do zooplâncton de origem tropical não é estimada, de forma precisa, com o uso de modelos elaborados com o tamanho de organismos de ambientes subtropicais e antárticos;
2.3 Os recifes de Tamandaré são fontes ricas de biomassa zooplanctônica para o ambiente pelágico durante períodos de desova de peixes e invertebrados bentônicos.

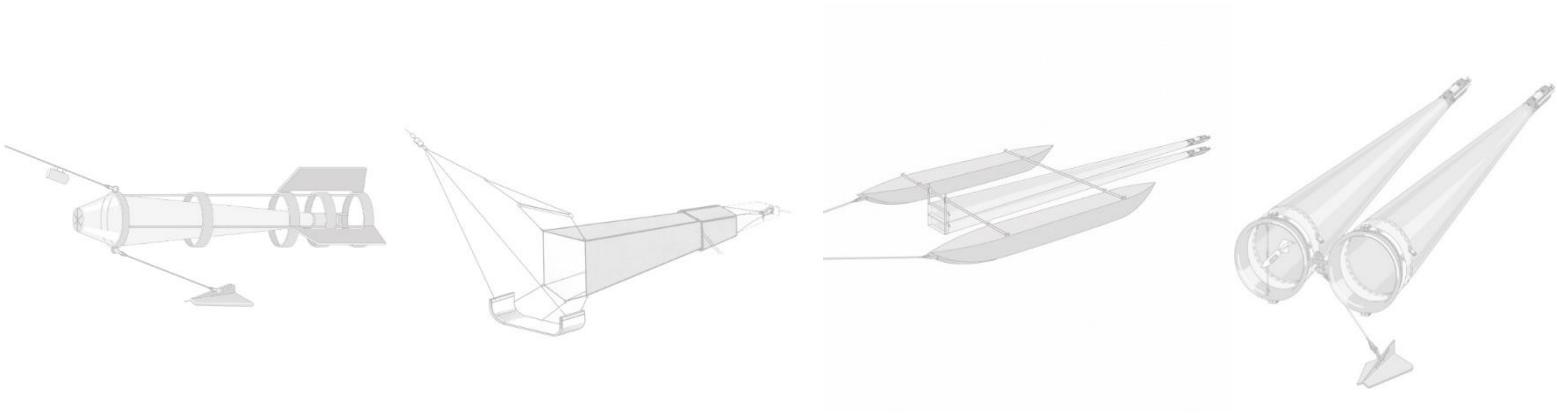
3 OBJETIVOS

3.1 Objetivo geral

Desenvolver novas metodologias para a amostragem e estimativa de biomassa do zooplâncton tropical e investigar a contribuição do meroplâncton na composição e biomassa do zooplâncton dos recifes de Tamandaré (PE, Brasil).

3.2 Objetivos específicos

3.2.1 – Criar redes eficazes e de fácil manuseio para a coleta do zooplâncton em pontos fixos próximos à recifes rasos;
3.2.2 - Comparar os resultados obtidos usando os novos métodos de coleta com dados obtidos com o uso de rede tradicional de amostragem de zooplâncton;
3.2.3 – Elaborar fórmulas para o cálculo da biomassa do zooplâncton (peso seco, carbono e nitrogênio) em função de dados de comprimento (mm), diâmetro esférico equivalente (ESD) (mm), área (mm^2) e biovolume (mm^3);
3.2.4 – Comparar as fórmulas criadas no presente para o cálculo da biomassa do zooplâncton com fórmulas existentes na literatura;
3.2.5 – Descrever, a nível de grandes grupos, a comunidade zooplanctônica dos recifes de Tamandaré através da análise de imagens obtidas com o uso do ZooScan;
3.2.6 – Quantificar ovos e larvas recém eclodidas de peixes e invertebrados bentônicos nos recifes de Tamandaré;
3.2.7 – Calcular a biomassa do zooplâncton e estimar a contribuição de ovos e larvas recém eclodidas de peixes e invertebrados na biomassa total das assembleias zooplanctônicas dos recifes de Tamandaré;
3.2.8 – Avaliar se os recifes de Tamandaré podem ser classificados como fontes ou sumidouros de zooplâncton para o ambiente pelágico.



4 TWO NEW METHODS FOR SAMPLING ZOOPLANKTON AND LARVAL ASSEMBLAGES IN TROPICAL REEF ECOSYSTEMS

Abstract

Sampling mobile zooplankton on reefs is a major challenge, mainly due to the problems faced when towing plankton nets inside complex reef mosaics. This study presents two new systems that permit precise point sampling of micro- and mesozooplankton and larvae of invertebrates and fish: the Channel Midwater Neuston Net (CMNN) and the Reef Edge Net (REN). Both are moored systems that are equipped with 64- and 300-micron mesh nets. The CMNN system was designed for continuous sampling in tidal channels between reef patches. It samples at three precise depth layers (epineuston: 0 m to 0.075 m, hyponeuston: 0.075 m to 0.0225 m, 1 m layer: 0.925 m to 1.075 m depth). The REN system allows sampling at precise, adjustable depths at given distances from the reef edge. The objective of the REN is to collect organisms that are washed from reef tops and reef edges with the ebb flow. The performance of these two new systems was evaluated and compared with results obtained by using common Ring nets in horizontal subsurface tows. Fieldwork was performed at two reef patches of the Tamandaré reef system (Brazil) in November 2015. The CMNN and REN showed similar performance in comparison with Ring net tows, capturing microzooplankton communities as well as veliger, polychaete, decapod and barnacle larvae in similar abundances. For the mesozooplankton, the REN presented a similar performance to the Ring net tows, efficiently capturing decapod crustacean and fish larvae as well as fish eggs. The CMNN showed lower abundance of decapod larvae and fish eggs but showed a good performance for the quantification of fish larvae. The two new passive nets showed a high effectiveness in collecting larvae and advantages over tows

with Ring nets since they stay for several hours continuously capturing larval aggregations during spawning events. This high capturing efficiency is probably related to the avoidance of sample reflux in the long nets that sink and close at slack tide for the CMNN, and due to the long, trap-like design with funnel-shaped internal “anti-reflux” nets, for the REN. Navigation safety and easy handling are further advantages of these moored systems, as compared to towing plankton nets at nighttime between reefs. CMNN and REN may become useful tools for the study of zooplankton and larval ecology and for integrated long-term studies in marine protected areas and reefs under multiple human impacts.

Key words: Channel Midwater Neuston Net - Reef Edge Net - passive net systems - meroplankton - ichthyoplankton - larval production

4.1 INTRODUCTION

Tropical reefs harbor diverse communities of benthic and pelagic organisms. Larval dispersal plays a key role in population dynamics and connectivity in these ecosystems (Oliver et al., 1992; Sheppard et al., 2009; D’Agostini et al., 2015; Kough and Paris, 2015). In shallow tropical reefs, spawning events have been recorded mainly during nocturnal ebb tides (Samoilys, 1997; Francini et al., 2002). Several species of fish and invertebrates have shown this behavior as a strategy to increase the chances of survival. Furthermore, many fish and invertebrates spawn during new moon periods (Babcock, 1984; Williams et al., 1984; Francini et al., 2002; Padilla-Gamiño et al., 2011) to hinder the visualization of larvae by planktivores and other predators (Nolan and Danilowicz, 2008).

To design an appropriate sampling strategy for surveys of larval production and dispersal is a considerable challenge. In tropical regions, several species spawn during the dry season, when temperature is higher and winds, currents and turbidity are fainter. Clearly, temperature and primary production have an influence on spawning and meroplankton (larvae and eggs) abundance in coastal waters (Williams et al., 1984; Anger, 2001; Mwaluma et al., 2011; Fernandes et al., 2012; Ziadi et al., 2015).

Many studies recorded that spawning events in nearshore ecosystems have occurred at night (Jokiel et al., 1985; Forward, 1987; Francini et al., 2002; Nanami et al., 2013). However, it is a challenge to identify the right time to capture newly hatched larvae, and thus to design appropriately timed sampling strategies. Standard plankton net tows have been extensively used

to study zooplankton communities and larval abundance (Harding, 2001; Castro et al., 2005; Hernandez Jr et al., 2011; Mwaluma et al., 2011; Fernandes et al., 2012; Koettker and Lopes, 2013; Ziadi et al., 2015; MacTavish et al., 2016). However, tows at given times of the night may underestimate the larval production if they are not conducted exactly during specific spawning events. Plankton patchiness is another serious concern for the assessment of larval abundance (Omori and Hamner, 1982; White et al., 2014).

Several plankton trap and pump systems have been developed to obtain new insights into reef plankton, such as the horizontal in situ plankton pump sampler (Rützler et al., 1980), several types of light traps (Brogan, 1994; Hickford and Schiel, 1999), cone-shaped plankton traps to collect organisms on reef tops (Porter and Porter, 1977; Ohlhorst, 1982; Yahel and Yahel, 2005; Melo et al., 2010) and zooplankton pump samplers (Heidelberg et al., 2004; Holzman et al., 2005; Yahel and Yahel, 2005; Heidelberg et al., 2010).

However, it is still a considerable challenge to study the production of larvae during spawning and hatching events. Pump samplers are unable to collect vagile organisms due to their escape behavior. The destruction of fragile organisms in pumps is a further serious drawback. Light traps are not quantitative, and their efficiency depends on moon regime, turbidity, the animal's sensory capacity, behavioral response and swimming speed, etc. (Hickford and Schiel, 1999). Common channel nets (mesh size: 1 to 3 mm) are, such as light traps (Shenker et al., 1993; Thorrold et al., 1994; Criales et al., 2010; Chan et al., 2016) and crestnets (Doherty and Mcllwain, 1996; Nolan and Danilowicz, 2008) mainly designed for the capture of large pre-settlement stages of fish and shrimp, and are not useful for the study of spawning events and larval production. Thus, in spite of the vast literature on this subject, there is still a lack of appropriate methods that are specifically designed to collect newly hatched larvae of invertebrates and fish.

The design of the two new systems described in the present study was based on several requirements to accurately quantify nocturnal larval release on reefs.

There are several issues in quantitatively sampling larvae and zooplankton on shallow reefs: (I) Spawning occurs at discrete, often very narrow time spans, which are hard to predict, with a high risk of missing these peak events in standard plankton tows. (II) Towing plankton nets in between reef patches is often dangerous and in some situations simply impossible, even with a very small boat. This is especially critical in nighttime sampling and under rough weather

conditions and new moon, when reefs may not be well perceived during navigation in complete darkness. (III) Tows will always have to be conducted at a safe distance from the reef edge, thus the association of the samples with the reefs is weak, if any. (IV) Tows cover large stretches, and thus cannot be associated to a specific sampling point or to a specific reef patch.

The aim of this study was: (I) to characterize and evaluate the performance of two new passive net systems in shallow coastal reef areas; (II) to integrate data obtained with the two new passive nets and standard plankton net tows for sampling micro- and mesozooplankton (64 and 300 µm mesh sizes, respectively), with emphasis on larvae of fish and invertebrates; (III) to describe and test two new tools for sampling zooplankton and improve our ability to detect, quantify and understand the dynamics of larval production in reef ecosystems.

4.2 MATERIALS AND METHODS

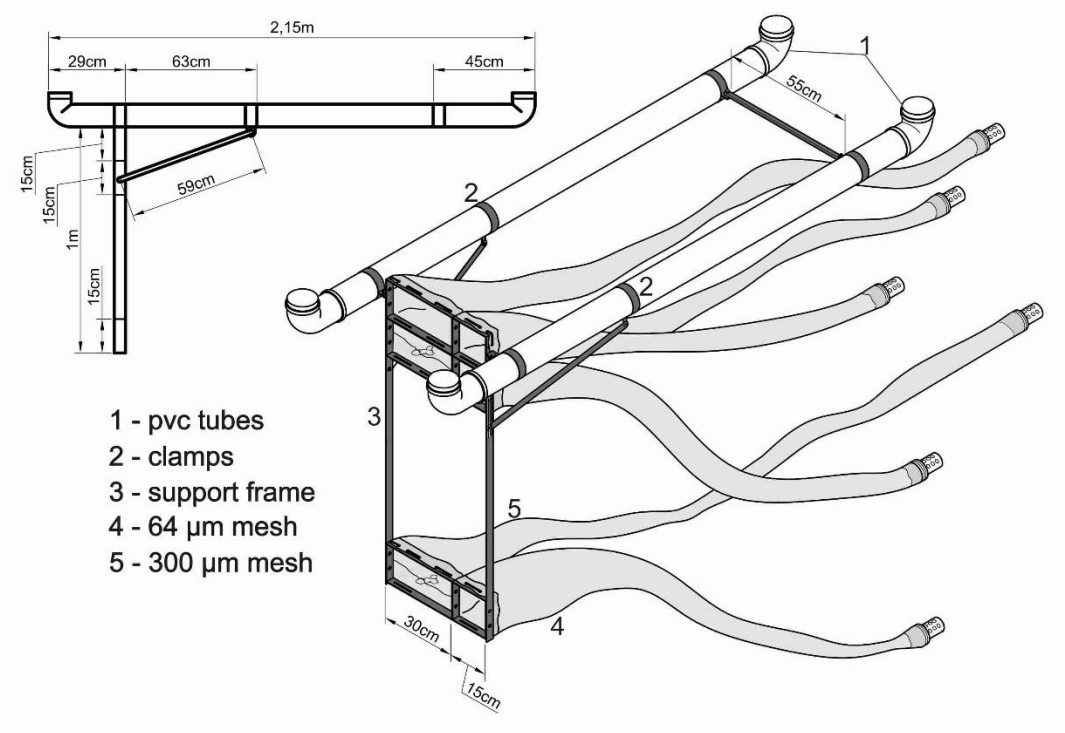
4.2.1 Description of the two new passive net systems

Channel Midwater Neuston Net (CMNN) – A lightweight mini-catamaran equipped with six rectangular-conical plankton nets attached to two floating tubes (two PVC tubes with 2.15 m length and 100 mm diameter). Three depth layers are sampled: 1.) Epineuston: air-water interface, 0 m to 0.075 m, 2.) Hyponeuston: 0.075 m to 0,0225 m, 3.) 1 m layer: 0.925 to 1.075 m (Fig. 1). Each depth layer of the CMNN contains two nets with different mesh sizes: 64 µm mesh for microzooplankton (mouth area: 15 cm x 15 cm, i.e., 0.022 m^2, length: 1.5 m) and 300 µm mesh for meso-, macrozooplankton and fish larvae (mouth area: 30 cm x 15 cm, i.e., 0.045 m^2, length: 2.5 m). The 300 µm mesh nets of the hyponeuston and 1 m layers were equipped with calibrated flowmeters (Hydro-Bios, Kiel, Germany) to measure filtered volume. The CMNN was designed to stay for several hours at a fixed station and sample during maximum ebb flow in tidal channels between reefs patches. The whole system is allowed to move freely according to the main current flow (Fig. 1).

Reef Edge Net (REN) – A lightweight moored system composed of two slim, long, double-conical plankton nets, each net being equipped with an internal “anti-reflux net”. It contains a 64 µm mesh net for microzooplankton (mouth area: 15 cm x 15 cm, i.e., 0.022 m^2) and a 300 µm mesh net for meso- and macrozooplankton and ichthyoplankton (mouth area: 30 cm x 15 cm, i.e., 0.045 m^2). Both nets have a length of 2 m (Fig. 1). The nets have an internal layer of the same mesh, an “anti-reflux net”, designed to hold back the return of vagile

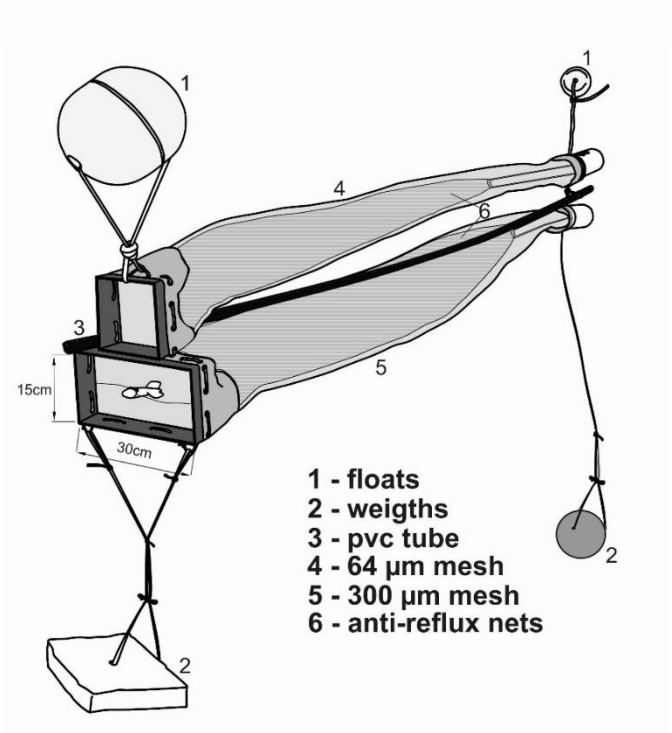
organisms. The length of the inner anti-reflux net is 1.35 m, with an internal opening diameter of 8 cm, being considerably narrower than the opening diameter (11 cm) of the external net towards the net bucket (Fig. 2). The internal net is hold permanently stretched and open by two straps at the distant end (Fig. 2). At the front of the collector bucket of the 64 µm net, a sieve (1 mm mesh size) was loosely attached to prevent the entrance of large predators. The REN was firmly moored with two weights (20 kg of concrete at the front and 3 kg lead at the cod end) and maintained stretched out with a slim PVC tube that was placed alongside the net between the cod end and the mouth (Fig. 2). Two floats (5 and 0.5 liters buoyancy) kept the net in a fixed position in the water column. Ropes were adjusted as to have the net mouth exactly aligned with the upper reef edge and as to have the whole system always completely submerged. The 300 µm mesh net was equipped with a Hydro-Bios (Kiel, Germany) calibrated flowmeter to measure filtered volume. The REN was designed to stay for several hours at a fixed station, thus sampling as close as possible to the reef edge during maximum ebb flow. The central objective of the REN is to collect organisms that are washed from the reef tops and reef edge with the ebb flow. It was designed to be as lightweight and small as possible, to be deployed manually and handled and transported in any small boat. Diving or snorkeling may be necessary for fine adjustments of the ropes that define position and depth of the REN, at least during the first use at a given location.

Figure 1 – The Channel Midwater Neuston Net (CMNN).



Fonte: o autor.

Figure 2 – The Reef Edge Net (REN).



Fonte: o autor.

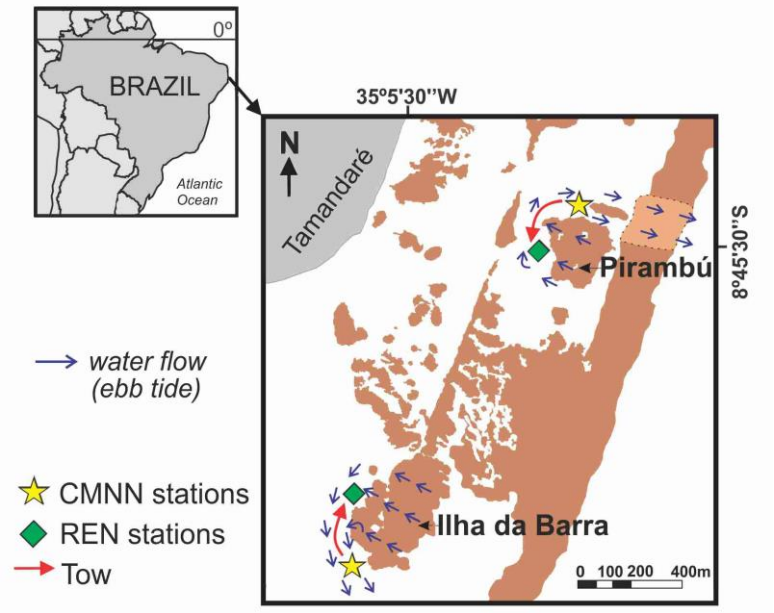
4.2.2 Case study: Tamandaré reefs

The new sampling systems were tested in the Tamandaré reefs, Brazil (Fig. 3). This reef complex is part of the "Costa dos Corais" Marine Protected Area (Pernambuco State, Brazil). This MPA was created to preserve the biodiversity and sustainable use of natural resources on shallow coastal reefs. In April 1999, through a federal decree, a reef patch known as "Ilha da Barra" and its surrounding waters were permanently closed to any fishing and visiting (Fig. 3).

Two sampling areas were chosen for this study: "Ilha da Barra" (closed area) and "Pirambu" (open-access area, with moderate fishing and visiting). In each area, two fixed stations were determined for the mooring of CMNN and REN systems: one station in a tidal channel (for the CMNN) and one station at the downstream side (at ebb tide) of the reef patch (for the REN).

Sampling was carried out during three consecutive nights, from November 10 to 12, 2015 (new moon). Tidal amplitude was 1.9 m. CMNN and REN systems were deployed during high tide, in the afternoon (3:00 pm to 4:50 pm) and recovered after approximately four and half hours (at low tide, during the night).

Figure 3 - Map of the study area in the Tamandaré reef system (Pernambuco State, northeastern Brazil) showing the sampling stations and current fields. CMNN: Channel Midwater Neuston Net. REN: Reef Edge Net. Blue arrows: current fluxes at maximum ebb tide, showing the currents washing the reef tops towards the edges and then towards the inlets between reefs. Red arrow: track for Ring net tows.



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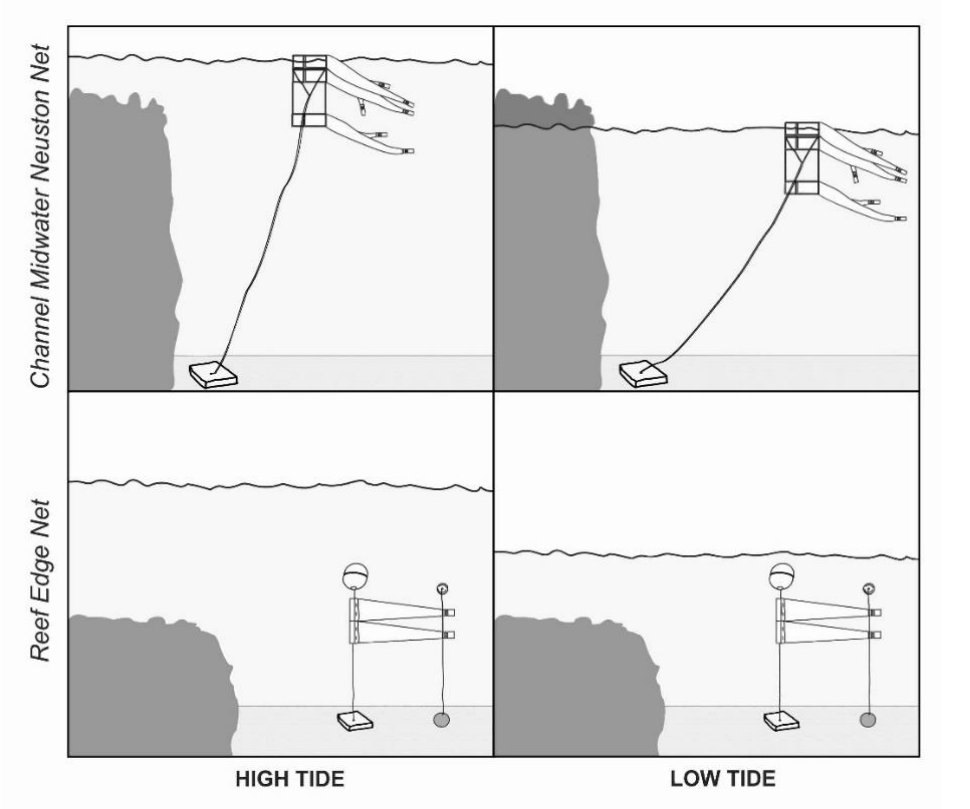
Average water temperature and salinity ranged from 28.4°C to 29.0ºC and from 35.3 to 36.3, respectively, measured at the beginning and at the end of each sampling with a YSI CastAway CTD (SonTek, San Diego, CA, USA). Maximum current speed during new moon spring tides at the Ilha da Barra tidal channel (depth: 7 to 9 m according to the tides) varied from 3 to 5.8 cm s^{-1}, measured in March and October 2015, 1.5 m above the bottom with a S4 current meter (InterOcean Systems LLC, San Diego, CA, USA).

At the sandy bottom adjacent to the reef edges, where the RENs were deployed, local depth was 4 to 5 m at high tide. Sampling depths of the two RENs (at Ilha da Barra and Pirambú reefs) were adjusted by divers as to be aligned with the upper edge of each reef. RENs thus stayed 2.2 m and 1.9 m above the bottom at Ilha da Barra and at Pirambu, respectively and stayed approximately 5 m distant from the reefs (Fig. 4). This resulted in an effective sampling depth of approximately 2.2 to 2.7 m (during deployment at high tide) to 0.5 to 1.4 m at the end of the sampling (at retrieval during low tide).

At the tidal channels where the two CMNNs were deployed, local depth was 8.1 to 9.8 m during high tide (Fig. 4). The three sampling depth layers of the CMNNs (center of each net) were constant at 0.0375 m, 0.1875 m and 1 m.

Additionally to deploying REN and CMNN systems (Fig. 5), horizontal subsurface tows were conducted with two standard conical-cylindrical Ring nets (64 and 300 µm mesh nets, with 0.3 m and 0.6 m diameters, i.e., 0.07 and 0.282 m^2 mouth area, respectively). These tows were performed at 1.5 to 2 knots between both stations during nocturnal ebb tide in each area, covering the distance between both fixed stations (Fig. 3). Mean sampling depth of the Ring nets was 0.15 m for the 64 µm mesh (0.3 m diameter, 1 m length) and 0.3 m for the 300 µm mesh (0.6 m diameter, 2.5 m length). Ring net tows were conducted immediately after sunset for thirteen minutes, starting at the CMNN station towards the REN station (towing against the ebb current flow).

Figure 4 – Schematic illustration of tidal levels and positions of sampling systems during deployment (high tide) and retrieval (low tide). Not to scale.



Fonte: o autor.

All 20 nets (2 x 6 CMNN, 2 x 2 REN, and 2 x 2 Ring nets) sampled simultaneously during each night.

In the 64 and 300 µm mesh sizes of the 1 m depth layer of the CMNN, filtered volume ranged from 8.03 to 20.85 m^3 and from 16.07 to 41.71 m^3, respectively. In the REN, filtered volume ranged from 3.07 to 7.78 and from 6.15 to 15.56 m^3 for 64 and 300 µm mesh nets, respectively. Ring net tows yielded larger filtered volumes, from 12.09 to 31.92 m^3 for the 64 µm mesh and from 48.39 to 127.68 m^3 for the 300 µm mesh nets.

An unexpected influence of strong winds on the epineuston and hyponeuston nets (CMNN) was observed at both channel stations. This happened when the wind direction was against the surface current flows. Hence, an entanglement of the 64 µm nets of the two upper (epineuston and hyponeuston) layers occurred occasionally, as could be observed in low flowmeter rotations. Therefore, only relative abundance composition and length frequency

distribution data of the micro- and mesozooplankton from epineuston and hyponeuston nets were presented in this study.

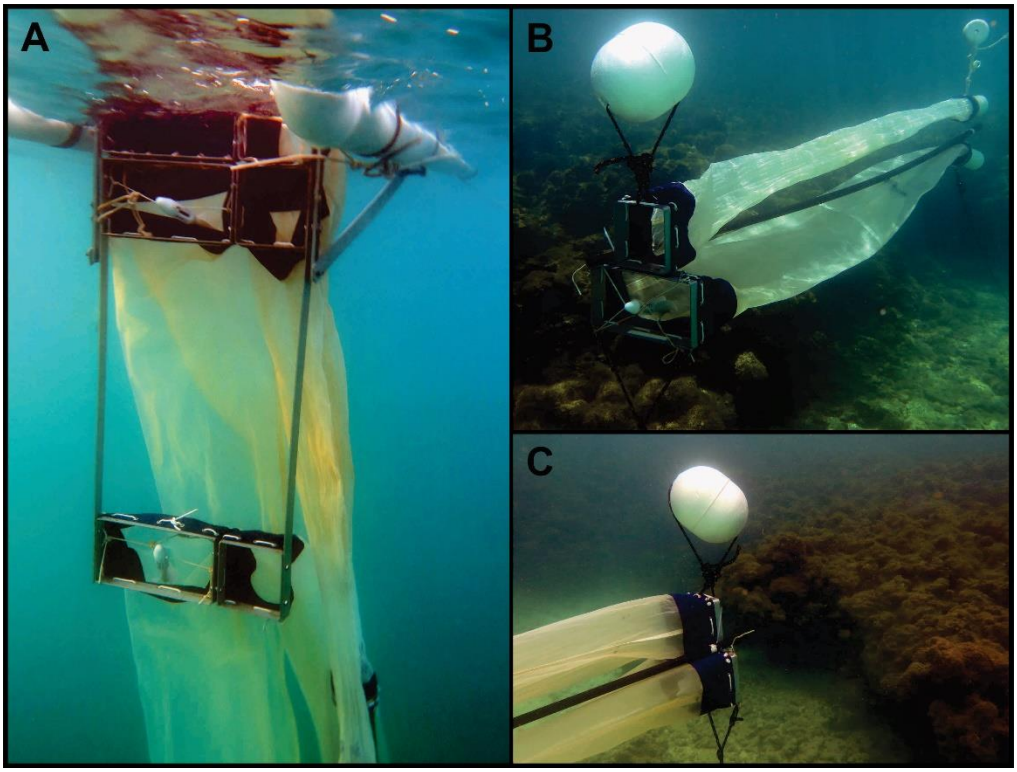
All samples were preserved in 4% formaldehyde buffered with 0.05% sodium tetraborate (final concentrations in seawater). Any large organisms trapped on the 1 mm sieve of the 64 µm REN were preserved separately. In this study, 60 samples (30 for each mesh size) were analyzed (three nights x 20 nets).

4.2.3 Laboratory methods

Seston biomass ($mg.m^{-3}$) was measured as wet weight (Wiebe et al., 1975). First, samples were accumulated on sieves (20 and 200 µm sieves for 64 and 300 µm mesh samples, respectively). Then, sieves were placed on absorbant paper towels to remove excess water before weighing on a balance with 0.01 g precision. Microzooplankton samples (64 µm mesh) were analyzed under a Zeiss Axiostar plus binocular microscope, using a Sedgewick-Rafter counting chamber. Aliquots of 1 ml were taken from a diluted microzooplankton sample (varying from 1 to 1000 ml, depending on total abundance).

These subsamples were used to count, measure and identify 100 to 300 organisms per sample. Thirty individuals per sample were measured with a calibrated ocular micrometer. The 300 µm mesh samples (mesozooplankton and ichthyoplankton) were scanned at 2400 dpi resolution using a ZooScan equipment (Hydroptic, France). Two size fractions (>1 mm and <1 mm) were thus scanned for each sample. Aliquots were splitted with a Motoda splitter (Motoda, 1959) to obtain 1000 to 1500 objects per scan. Objects were manually separated for 20 minutes prior to scanning.

Figure 5 – Underwater photographs of the two new systems at the Tamandaré reefs. A: the Channel Midwater Neuston Net. B and C: the Reef Edge Net.



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After scanning and image processing (with the ZooProcess software), each image was converted, processed and had its vignettes (small images of each object) extracted and loaded into the Plankton Identifier software (Gorsky et al., 2010). All objects were measured prior to semi-automated classification of vignettes, based on the Random Forest algorithm, followed by manual identification and validation by an experienced zooplankton taxonomist (Grosjean et al., 2004; Gorsky et al., 2010).

4.2.4 Data Analysis

To test possible differences in seston biomass ($mg.m^{-3}$), organism abundance ($ind.m^{-3}$) and size distribution among the sampling systems, Kruskal-Wallis ANOVA was used with Mann-Whitney tests for post-hoc comparisons at $\alpha = 0.05$ (Zar, 1996). The relative frequencies of specific size classes were compared between gears (i.e., percentage of organisms < 2 mm and > 2 mm for the 64 µm samples and percentage of organisms < 3 mm and > 3 mm for 300

µm samples) using Mann-Whitney tests at $\alpha = 0.05$. Meroplankton / holoplankton abundance ratios were also tested between gears using Mann-Whitney tests at $\alpha = 0.05$ (Zar, 1996).

4.3 RESULTS

4.3.1 *Quantification of spawning and hatching events on reefs*

The new sampling systems proved to be very useful for the study of spawning events on reefs. For instance, very large amounts of fish eggs where sampled in the 300 µm mesh net (7.35 ± 8.3 ind. m^{-3} and 19.8 ± 35.49 ind. m^{-3} for CMNN and REN, respectively). Larvae of reef macroinvertebrates were also very abundant in these samples, for example, zoea-stage larvae of brachyuran crabs (1.66 ± 1.39 ind. m^{-3} and 7.43 ± 5.91 ind. m^{-3} for CMNN and REN, respectively) and larvae of other decapods (2.78 ± 2.5 ind. m^{-3} and 9.56 ± 8.38 ind. m^{-3} for CMNN and REN, respectively), mainly larvae of caridean shrimps, hermit crabs and lobsters. Larvae of reef fishes were even more abundant than decapods (1.1 ± 1.18 ind. m^{-3} and 10.96 ± 11.26 ind. m^{-3} for CMNN and REN, respectively). Among these fish larvae, recently hatched early stages (preflexion) were clearly dominant, while among decapod larvae, early zoea-stage larvae were dominant, indicating the capture of freshly hatched larval communities that were directly obtained from the reefs.

4.3.2 Comparing sample composition between gears

The new net systems and the towed Ring nets yielded highly diverse communities of reef plankton organisms. Overall, nineteen groups were identified in the 64 µm samples and twenty-one in the 300 µm samples (Table 1). Copepods (nauplii and adults) were the most abundant group in all sampling systems and in both mesh sizes (Table 1 and Fig. 6).

In the microzooplankton (64 µm), copepod nauplii dominated by abundance in all gears. Furthermore, foraminiferans and appendicularians were also very abundant in microzooplankton samples (Table 1 and Fig. 6). Composition and density of the microzooplankton community was very similar between gears, indicating a similarly efficient capture for these organisms, in spite of much lower net current speeds for passive systems than for towed nets.

In contrast to the microzooplankton, the large organisms caught in 300 µm samples displayed considerable differences in composition and density between gears. In the 300 µm

samples, fish eggs were the second most important group (after copepods), representing on average 16.2% abundance in the epineuston and 1 m layer (CMNN) and in REN samples. Decapods were the second most abundant group in the 300 μm Ring net samples, representing on average 22.6% of the total abundance (Table 1 and Fig. 6).

Additionally to the small early-stage larvae and copepods, many groups of organisms larger than 3 cm were effectively quantified in this study, such as polychaetes, isopods of the genus *Excorallana* spp., juveniles of the penaeid shrimp *Rimapenaeus* spp., unidentified juveniles of Penaeidae, megalopae and juveniles of portunid crabs and puerulus-stage lobsters of the genus *Palinurus* spp.

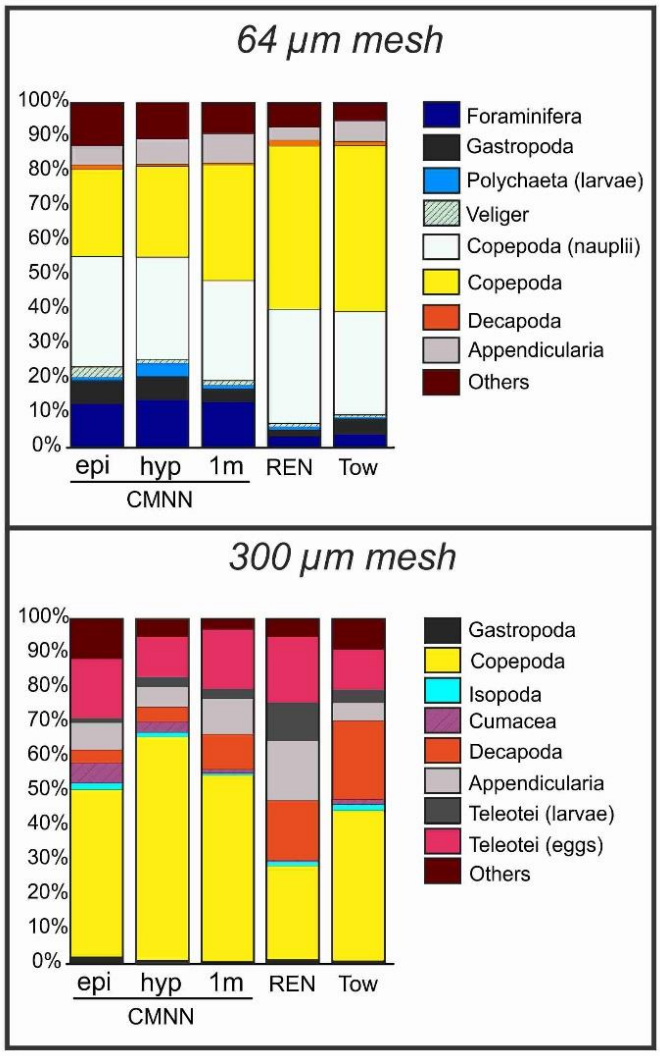
4.3.3 Comparing size structure between gears

The length-frequency distribution of the organisms captured by the different sampling systems showed very similar patterns, with higher abundances in smaller size classes followed by a rapid decrease in abundance towards larger animals. The organisms captured in 64 μm nets ranged from 0.07 to 3.6 mm, and 95% of them were in the 0.01 to 2 mm size range in all gears. Organisms captured by 300 μm mesh nets ranged from 0.42 to 67.4 mm, and 72% were in the 0.01 to 2 mm size range for all gears tested (Fig. 7). The relative contribution of the organisms captured in 64 μm nets with < 2 mm and > 2 mm did not show differences between gears. However, the samples obtained with the 300 μm mesh Ring net tows presented a significantly higher contribution of large organisms (> 3 mm) when compared to the passive nets (Mann-Whitney tests, $p<0.001$).

4.3.4 Comparing seston biomass and abundance between gears

The seston biomass and total abundance of the microzooplankton community did not show differences among the CMNN, REN and towed Ring nets (Table 2; Fig. 8), in spite of much lower current speeds for passive systems than for towed nets. Similarly, abundances of veliger larvae, polychaetes, decapods (i.e., caridean early-stage zoea larvae), brachyuran larvae (zoeae and megalopae) and cirripede nauplii did not show significant differences among the nets, for the microzooplankton.

Figure 6 - Relative abundance (%) of major groups of the micro- and mesozooplankton sampled with the Channel Midwater Neuston Nets (CMNN), the Reef Edge Nets (REN) and the Ring nets (Tow). Epi: epineuston, Hyp: hyponeuston. 1m: 1 m layer nets of the CMNN.

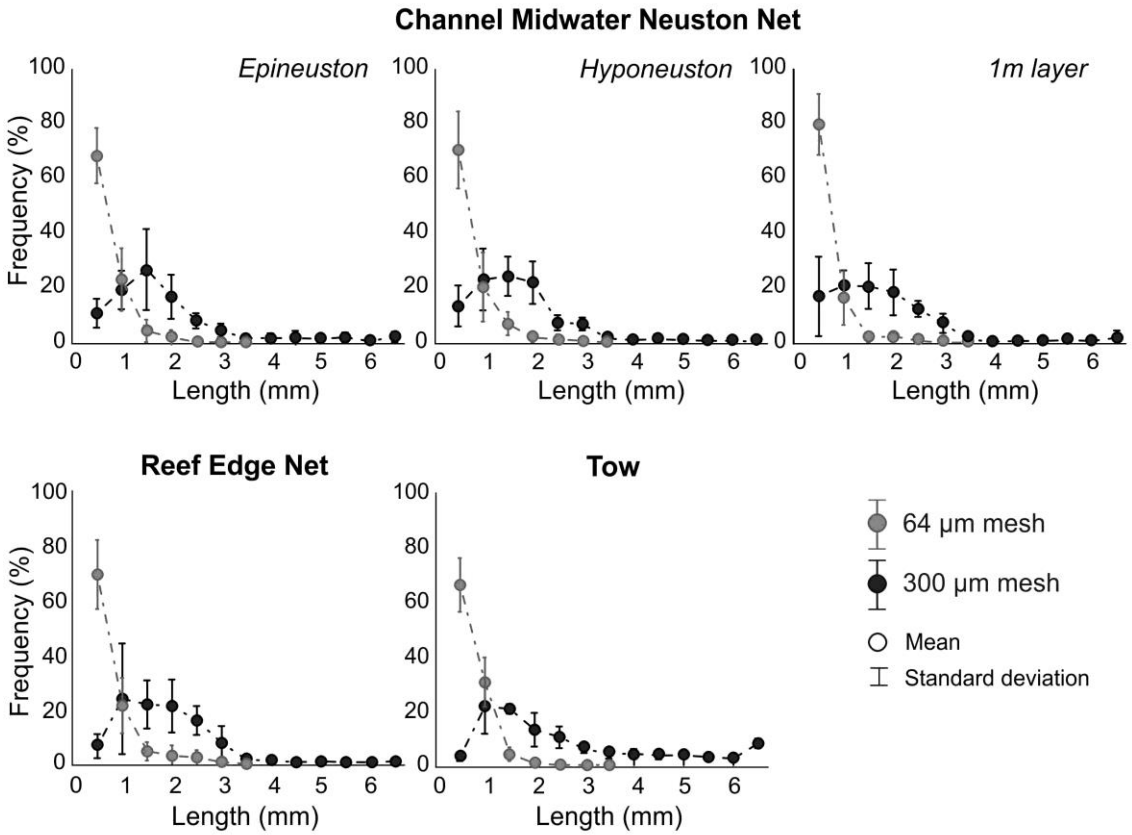


Fonte: o autor.

However, seston biomass and abundance of the mesozooplankton were markedly lower in the passive nets than in the Ring net, but no significant differences were found between CMNN and REN (Table 2 and 3; Fig. 8). The abundance of decapods, i.e., larvae of caridean shrimps (zoea I), early phyllosoma-stage larvae of *Palunirus* (stage I), porcellanid crabs and unidentified decapods, brachyurans (zoeae and megalopae) and fish eggs did not show any significant differences between the two new systems, but presented differences between CMNN and Ring nets, except for early stage (preflexion) fish larvae, that were captured in similar

densities in CMMN and Ring nets (Table 2 and 3; Fig. 9). No differences were observed between REN and Ring nets in all four groups analysed (Table 2 and 3; Fig. 9), in spite of very low effective current speeds for the REN.

Figure 7 – Length-frequency distribution (%) of organisms captured by the 64 and 300 µm mesh nets of the Channel Midwater Neuston Net (CMNN), the Reef Edge Net (REN) and the Ring nets (Tow).



Fonte: o autor.

Table 1 – Relative abundance (%) of the main groups of the micro- and mesozooplankton captured using the Channel Midwater Neuston Nets (CMNN), the Reef Edge Nets (REN) and the towed Ring nets (Tow). For the 64 µm samples the others contains: Ostracoda, Amphipoda, *Lucifer faxoni,* Isopoda, Cumacea, Mysidacea, Echinodermata (larvae) and Chaetognata; For the 300 µm samples, the others contains: Hydrozoa, Siphonophorae, embryos and juveniles of Mysidacea, Euphausiacea, Echinodermata (larvae), Tanaidacea, Cirripedia (cypris) and Ostracoda.

64 µm mesh	**Channel Midwater Neuston Net** (%)			**Reef Edge Net** (%)	**Tow** (%)
	Epineuston	*Hyponeuston*	*1m layer*		
Tintinida	0.65	0	0.95	0.39	0.46
Foraminifera	12.29	13.56	12.98	2.99	3.44
Veliger	2.91	1.06	1.26	0.93	0.61
Gastropoda	6.79	6.78	3.67	1.77	4.54
Bivalvia	2.91	1.75	0.68	0.29	0.28
Polychaeta (larvae)	1.04	3.81	1.23	1.03	0.66
Copepoda (nauplii)	32.13	29.87	29.02	33.11	29.89
Copepoda (adults)	25.34	26.27	33.7	47.43	48.33
Decapoda (larvae)	1.29	0.64	0.57	1.69	1.19
Cirripedia (nauplii)	1.62	0.79	0.38	3.38	1.23
Appendicularia	5.71	7.42	8.5	3.88	5.91
Teleostei (eggs)	0.97	2.07	0.38	0.88	0.5
Teleostei (larvae)	0.65	0.64	0	0.59	0.28
Others	5.7	5.34	6.68	1.64	2.68
300 µm mesh	**Channel Midwater Neuston Net** (%)			**Reef Edge Net** (%)	**Tow** (%)
	Epineuston	*Hyponeuston*	*1m layer*		
Gastropoda	1.9	1.11	0.65	1.19	0.83
Polychaeta	1.28	1.25	0.29	0.52	0.9
Copepoda	48.55	64.61	53.95	27.27	43.66
Isopoda	1.87	1.37	0.51	1.08	1.66
Mysidacea	0.7	0.06	0.05	0.02	3.02
Cumacea	5.8	3.05	1.14	0.63	1.58
Amphipoda	7.15	0.36	0.96	0.83	1.48
Decapoda (larvae)	2.41	1.4	6.29	9.37	12.99
Brachyura (zoea)	1.01	1.52	3.97	7.68	9.6
Brachyura (megalopa	0.38	1.37	0	0.04	0.13
Stomatopoda	0.38	1.49	0.8	2.06	1.88
Chaetognatha	1.06	0.87	0.92	0.59	0.19
Appendicularia	8.05	5.82	10.45	17.44	5.34
Teleostei (larvae)	1.19	2.84	2.83	11	3.71

The continuation of Table 1…		11.65	17.08	19.11	11.62
Others	1.07	1.22	0.12	1.16	1.41

Fonte: o autor.

Table 2 – Abundance (mean ± standard deviation) of the main groups of the micro- and mesozooplankton captured using the Channel Midwater Neuston Nets (CMNN), the Reef Edge Nets (REN) and the towed Ring nets (Tow). For the 64 µm samples the others contains: Ostracoda, Amphipoda, *Lucifer faxoni*, Isopoda, Cumacea, Mysidacea, Echinodermata (larvae) and Chaetognata; For the 300 µm samples, the others contains: Hydrozoa, Siphonophorae, embryos and juveniles of Mysidacea, Euphausiacea, Echinodermata (larvae), Tanaidacea, Cirripedia (cypris) and Ostracoda.

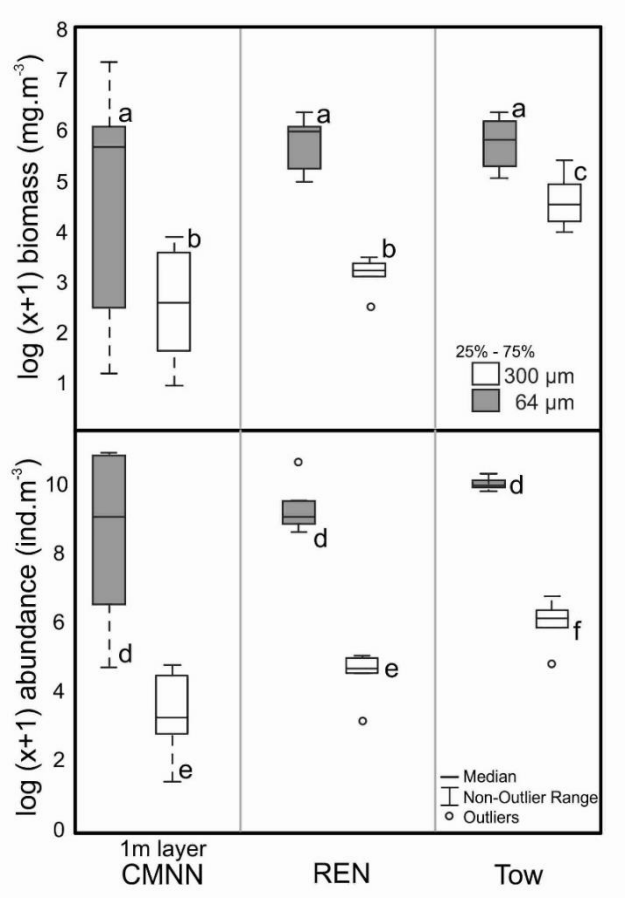
64 µm mesh	**CMNN** (ind. m^{-3})	**REN** (ind. m^{-3})	**Tow** (ind. m^{-3})
	1m layer		
Tintinida	138 ± 182	24 ± 30	53 ± 73
Foraminifera	246 ± 255	448 ± 232	698 ± 546
Veliger	149 ± 245	132 ± 80	112 ± 86
Gastropoda	540 ± 485	21 ± 53	896 ± 581
Bivalvia	124 ± 146	20 ± 23	55 ± 33
Polychaeta (larvae)	215 ± 257	111 ± 155	132 ± 125
Copepoda (nauplii)	10,302 ± 14,447	7,553 ± 12,518	10,544 ± 4,667
Copepoda (adults)	8,291 ± 11,375	4,613 ± 1,392	6,750 ± 1,985
Decapoda (larvae)	54 ± 98	114 ± 176	76 ± 63
Cirripedia (nauplii)	11 ± 19	212 ± 47	188 ± 292
Appendicularia	2,398 ± 3,686	486 ± 539	1,293 ± 1,022
Teleostei (eggs)	30 ± 46	24 ± 59	98 ± 91
Teleostei (larvae)	0	54 ± 101	17 ± 29
Others	242 ± 262	242 ± 122	349 ± 228
Total	22,988 ± 31,774	14,303 ± 16,104	21,617 ± 10,131
300 µm mesh	**CMNN** (ind m^{-3})	**REN** (ind m^{-3})	**Tow** (ind m^{-3})
	1m layer		
Gastropoda	0.39 ± 0.39	1.17 ± 0.9	2.66 ± 3.16
Polychaeta	0.14 ± 0.11	0.53 ± 0.48	4.09 ± 2.86
Copepoda	21.15 ± 25.31	29.69 ± 19.38	191.7 ± 108.7
Isopoda	0.2 ± 0.2	1.03 ± 0.6	7.23 ± 3.99
Mysidacea	0.04 ± 0.08	0.02 ± 0.04	11.81 ± 7.79
Cumacea	0.58 ± 0.81	0.8 ± 1.39	6.53 ± 4.25
Amphipoda	0.64 ± 0.86	0.8 ± 0.73	5.53 ± 6.76
Brachyura (zoea)	1.66 ± 1.39	7.43 ± 5.91	55.71 ± 79.74
Brachyura (megalopa)	0	0.03 ± 0.08	0.43 ± 0.5

The continuation of Table 2…

Other Decapoda (larvae)	2.78 ± 2.5	9.56 ± 8.38	60.24 ± 55.58
Stomatopoda	0.43 ± 0.28	2.15 ± 2.37	11.23 ± 16.3
Chaetognatha	0.37 ± 0.46	0.47 ± 0.59	0.74 ± 0.69
Appendicularia	5.7 ± 8.96	13.3 ± 18.92	21.75 ± 10.48
Teleostei (larvae)	1.1 ± 1.18	10.96 ± 11.26	14.98 ± 17.95
Teleostei (eggs)	7.35 ± 8.3	19.8 ± 35.49	49.22 ± 33
Others	0.08 ± 0.18	1.16± 1.21	5.9 ± 3.67
Total	42.61 ±51.07	98.89±107.8	449.76±355.54

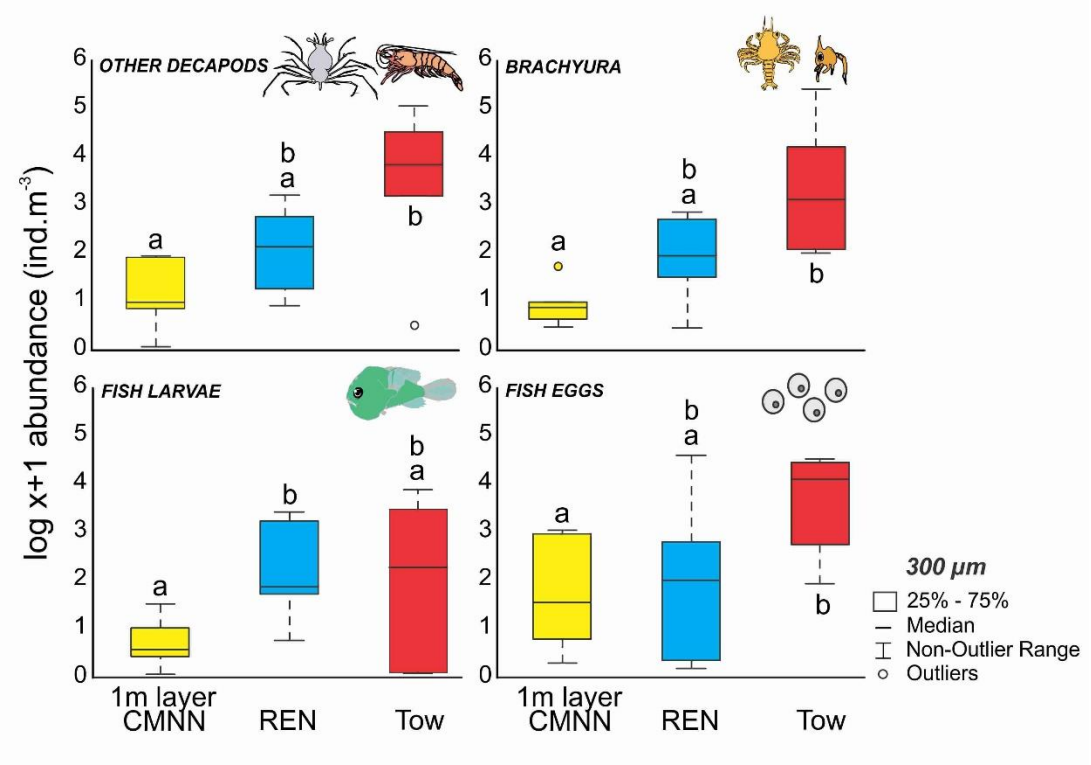
Fonte: o autor.

Figure 8 - Log (x+1) seston biomass and log (x+1) abundance in the 64 µm and 300 µm samples from the 1 m layer of the Channel Midwater Neuston Net (CMNN), the Reef Edge Net (REN) and the Ring nets (Tow). Significantly different groups (marked with different letters) were detected by the Mann-Whitney tests.



Fonte: o autor.

Figure 9 - Log (x+1) abundance of the most abundant larvae of the mesozooplankton captured by the 1 m layer of the Channel Midwater Neuston Net (CMNN), the Reef Edge Net (REN) and the Ring nets (Tow). Significantly different groups (marked with different letters) were detected by the Mann-Whitney tests. Decapoda: caridean, peneidean, rock lobster and unidentified decapod larvae. Brachyura: zoeae and megalopae stages.



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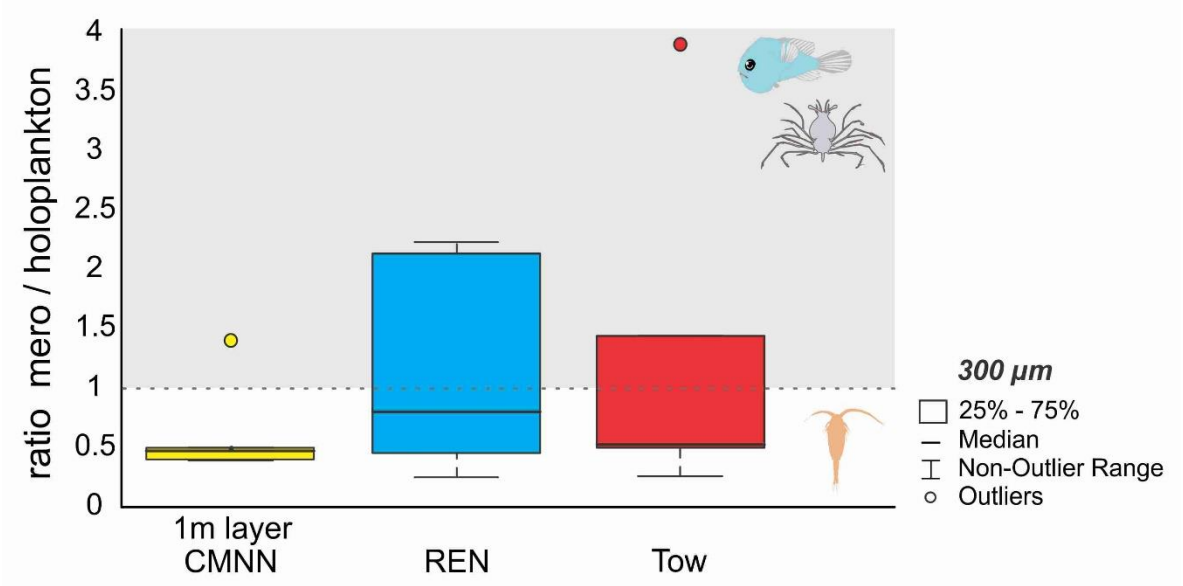
For the 64 µm mesh nets, the meroplankton : holoplankton ratio in CMNN (1 m layer), REN and Ring nets were always less than 1 (mean: 0.03, 0.05 and 0.03, respectively), indicating a dominance of holoplankton (i.e., copepods) in the microzooplankton. Conversely, for the 300 µm mesh nets, meroplankton : holoplankton ratios included values above 1 (mean: 0.62, 1.12 and 1.2, respectively). Thus, for 300 µm mesh REN and Ring nets, holoplankters (e.g. copepods) were less abundant than larvae (Fig. 10). No differences in meroplankton / holoplankton ratios were recorded between gears, for both mesh sizes, indicating that the new systems and standard nets sample similar communities.

Table 3 - Results of Mann-Whitney tests ("p"-values) comparing different sampling methods. The following parameters are compared between gears: seston biomass (mg.m^{-3}), total abundance (ind.m^{-3}), Decapoda (ind.m^{-3}), Brachyura (ind.m^{-3}), fish larvae (ind.m^{-3}) and fish eggs (ind.m^{-3}). CMNN: 1 m layer of the Channel Midwater Neuston Net. REN: Reef Edge Net. Tow: towed Ring net. Only samples obtained with 300 µm mesh nets were considered. ^{T}: Higher values for the towed Ring net, ^{R}: Higher values for the REN.

	Mann-Whitney test / p-*value* / 300 µm mesh		
	CMNN vs REN	CMNN vs Tow	REN vs Tow
Seston Biomass	n.s.	0.0022^{T}	0.0022 ^{T}
Total Abundance	n.s.	0.0022 ^{T}	0.0087 ^{T}
Decapoda	n.s.	0.0411 ^{T}	n.s.
Brachyura	n.s.	0.0022 ^{T}	n.s.
Fish larvae	0.0087^{R}	n.s.	n.s.
Fish eggs	n.s.	0.026 ^{T}	n.s.

Fonte: o autor.

Figure 10 - Ratio of meroplankton : holoplankton abundance in the mesozooplankton captured by the 1 m layer of the Channel Midwater Neuston Net (CMNN), the Reef Edge Net (REN) and the Ring nets (Tow). Mero: meroplankton; Grey area (ratio > 1): samples with higher abundance of meroplankton (larvae and eggs) than holoplankton.



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4.4 DISCUSSION

This study presents two new systems that were designed to quantify zooplankton and larval production during spawning events on shallow reefs. Even under the weak tidal current regime of the study area, the passive systems presented in this study (CMNN and REN) showed to be clearly suitable for investigations that require punctual and accurate sampling, thus opening new perspectives for research on tropical reefs.

The high density of early life history stages of invertebrates, fish larvae and fish eggs in the passive nets indicates freshly released organisms (Forward, 1987; Nanami et al., 2013) and shows the usefulness of the two new systems for sampling larval assemblages at shallow reef ecosystems during spawning and hatching events.

The Channel Midwater Neuston Net and the Reef Edge Net showed a high efficiency in sampling holoplankton and meroplankton (larvae and eggs), similarly to the results of Rützler et al. (1980), who used a complex motor-driven horizontal net (HOPLASA) with 250 µm mesh size for 5 to 8 hours of sampling on the shallow tropical reefs of Belize. However, the target of the sampler of Rützler et al. (1980) was on small, less mobile larvae of invertebrates such as larval sponges, cnidarians and echinoderms, while this is the first study to present a method to capture highly vagile crustacean and fish larvae on reefs.

The 64 µm nets showed the same microzooplankton capturing performance among the three sampling techniques used, with good agreement in seston biomass, total abundance and abundance of larvae.

The new passive net systems yielded a good representation of the composition of major groups of the micro- and mesozooplankton as compared to results obtained with towed Ring nets, in spite of much lower effective current speeds. This high capturing efficiency is probably due to the avoidance of sample reflux due the long nets that sink and close at slack tide for the CMNN, and to the long, trap-like design with funnel-shaped internal anti-reflux nets, for the REN.

4.4.1 Filtered volume and sample size

Several factors have been described in previous studies as having a strong influence on zooplankton sampling efficiency, such as net design, mouth diameter, mesh size, towing speed, plankton patchiness and sampling depth (Fleminger and Clutter, 1965; Cassie, 1968; Clutter

and Anraku, 1968; Tranter and Smith, 1968; Barkley, 1972; Cook and Hays, 2001; Holzman et al., 2005; Tseng et al., 2011; Skjoldal et al., 2013; Chan et al., 2016; Pitois et al., 2016).

The most important factor to understand the differences in filtered volumes between passive and towed gears used in the present study are the weak currents at all fixed sampling stations. Ring net tows filtered a considerable volume of water, due to the constant and high speed during the hauls (1.5 to 2 knots) and their much larger mouth area (3 and 6 times larger than the mouth areas of the passive nets for the 64 and 300 µm meshes, respectively). Thus, the filtered volume recorded in the CMNN and REN was 4 and 8 times lower than in the Ring net tows, respectively.

There is a sense that longer tows increase the chances of encountering patches of plankton (Cassie, 1968) and larval retention may be an important source of patches around reefs zones (Mwaluma et al., 2011). Large volumes of filtered water by plankton gears increase the chances to capture mobile as well as rare animals (Dixon and Robertson, 1986). This may partially explain the higher abundance in the 300 µm mesh Ring nets. The shape and size of samplers also have a strong influence on filtering performance and zooplankton avoidance (Fleminger and Clutter, 1965; Tranter and Smith, 1968). It is relevant to consider that the design of the mouth of the new passive nets and their apertures are three and six times smaller than the 64 and 300 µm Ring nets, respectively.

The filtered volume was much lower in the CMNN and REN than in the Ring nets, although the passive nets sampled for more than four hours (vs 13 minutes of towing for the Ring nets). The same patterns have also been observed in previous intercomparisons of various zooplankton trap net systems, which recorded the volume of water filtered, the zooplankton abundance as well as the abundance of specific mobile species inside the plankton trap systems. These parameters were much lower than those recorded in standard tows (Dixon and Robertson, 1986; Cook and Hays, 2001; Pitois et al., 2016).

Probably, the higher filtering efficiency of the Ring net tows and shallower sampling depth (compared to the 1 m layer of the CMNN and the deep REN) at least partially explains the higher total abundance in 300 µm mesh samples in the tows datasets compared to the results obtained by the passive nets described in the present study. In coastal areas, most zooplankton organisms and fish eggs tend to accumulate and disperse at the surface, especially during the night (Hardy et al., 1987; Yannicelli et al., 2006; Irisson and Lecchini, 2008), which would

explain higher densities and biomasses in subsurface Ring net tows as compared to REN samples and 1 m layer samples of 300 µm meshes.

4.4.2 Gear avoidance

Several groups of zooplankton have been described as active swimmers, showing response mechanisms to vibrational stimuli and hydrostatic pressure waves, which may influence their avoidance to any samplers (Fleminger and Clutter, 1965; Clutter and Anraku, 1968).

Towing speed has a huge influence on capture in two different ways: by extrusion, when smaller animals escape through the mesh or, by avoidance, when mobile species escape from the sampler. At high-speed tows, the pressure of the water filtered through the mesh is higher when compared to low-speed tows, which strongly influences the evasion of smaller plankton species through the sampler by extrusion. In contrast, larger animals with swimming mechanisms may increase their chances of escaping by avoidance in tows performed at lower speeds (Cook and Hays, 2001; Fleminger and Clutter, 1965).

The effects of zooplankton escaping by extrusion and avoidance from samplers observed in previous intercomparasions (Dixon and Robertson, 1986; Pitois et al., 2016) have not influenced the size structure of the communities sampled by 64 µm nets in this study since the organisms collected by the three gears used in the current study showed a similar percentage of contribution by the size intervals approached. Conversely, for 300 µm mesh nets, higher gear avoidance against passive nets may explain the higher contribution of large organisms (> 3 mm) to Ring net tow samples.

The 64 µm mesh size of the 1 m layer of the CMNN, REN and the Ring net had the same capturing performance with no differences in total abundance of microzooplankton, veliger, Polychaeta, Decapoda and Cirripedia larvae, although the new passive net systems presented lower filtration efficiency compared to the Ring net. On the other hand, animals captured with the 300 µm nets presented higher total abundance in the Ring net samples when compared to the CMNN and REN samples.

Pitois et al. (2016) described Decapoda as contributing 24% more to the Ring net samples than to the Continuous Semi-Automatic Sampler (CALPS) samples and the authors attributed their findings to the ability of Decapoda and other larger zooplankton groups to

escape from the CALPS. Dixon and Robertson (1986) recorded higher abundance of mobile animals such as chaetognaths, polychaetes and larvaceans in traditional towns compared to pump sampling systems. Holzman et al. (2005) also noted that the use of some traps in coral reef ecosystems such as pumps underestimate the abundance of large zooplankton, e.g. decapods and larvaceans due to the fact that those groups avoid capture using their swimming abilities.

Similarly, the 300 µm nets at the 1 m layer (CMNN) presented lower abundances of decapod larvae and fish eggs, as compared to 300 µm Ring net samples. This is probably due to the difference in sampled depth (1 m vs subsurface). Eggs of innumerous coastal fish species have been known to accumulate close at surface (Hardy et al., 1987), as do many decapod larvae (Yannicelli et al., 2006). Additionally, the weak currents at CMNN stations may have facilitated sampler avoidance by agile decapods. Conversely, the 1 m layer of the CMNN recorded the same fish larvae abundance as the Ring net. It seems that nocturnal gear avoidance and sampling depth had no effects on fish larvae captured by the 1 m layer of the CMNN.

The REN showed a much better performance for capturing decapod larvae and fish eggs, as compared to the CMNN. These differences may be related to the production of these organisms at the reefs, and that the REN sampled them right at their dispersal source. Decapod larvae and fish eggs are probably washed directly from the reefs and are then captured at the edge, indicating the existence of intense spawning activities of reef fish and high densities of decapods on these reefs.

The two new methodologies described in the current study for sampling micro-, meso- and macrozooplankton, combined with standard tows, may be applied for further studies aiming at a more comprehensive picture of larval ecology in shallow tropical reefs.

4.5 CONCLUSIONS

The Channel Midwater Neuston Net and the Reef Edge Net provide a collection of robust scientific data with reliable representation of micro, meso-, and macrozooplankton, as well as fish eggs and fish and invertebrate larvae. The Reef Edge Net showed a better performance for the quantification of fish and invertebrate larvae, although it presented a lower filtered volume compared to the CMNN and Ring nets. It seems that the fixed depth and position in relation to the reefs during the sampling period are the main factors to explain the REN larvae

capture performance, together with the anti-reflux net inside the REN, which functions as a larval trap.

The main advantage of using the new passive net systems described in the present study over Ring nets is that they stay longer *in situ*, capturing larval aggregations during spawning events. In addition, the safety of navigation and easy handling are big advantages of these moored systems, as compared to towing plankton nets at nighttime between the reefs.

The integrated use of traditional plankton nets with novel passive gears may optimize larval monitoring and spawning records in integrated long-term studies in tropical coastal environments, emphasizing larval production, connectivity, trophic interactions, and the role of larval supply from marine protected areas to damaged reefs.



5 FROM IMAGES TO ELEMENTS: USING BODY DIMENSIONS TO INFER CARBON AND NITROGEN MASS IN TROPICAL COASTAL ZOOPLANKTON

Abstract

The biomass of zooplankton is one of the key parameters for any marine ecosystem models. However, there are only few non-destructive methods available to measure this biomass, and none of them is intended to coastal tropical marine zooplankton. This study proposes conversion factors to predict the biomass (i.e., dry weight, carbon and nitrogen mass) of tropical zooplankton based on the body size data of organisms obtained through semi-automatic image analysis. Biomass estimates of the zooplankton from a coastal tropical area of Brazil are compared to previously published conversions for zooplankton from subtropical and Antarctic waters. Length (mm), equivalent spherical diameter (mm), body area (mm^2) and ellipsoid biovolume (mm^3) of zooplankton were significantly correlated with dry weight, carbon and nitrogen mass ($p < 0.001$ for all correlations). Ellipsoid Biovolume showed the best correlation coefficients for all biomass measurements ($r = 0.93$, 0.96 and 0.96, respectively). Comparisons between tropical zooplankton biomass estimations using formulas proposed in the present study with other conversion factors showed significant differences (Mann-Whitney test, $p < 0.001$) in dry weight, carbon and nitrogen measurements. Tropical zooplankton biomass was underestimated up to 54% and overestimated up to 254% using the conversion factors proposed in previous studies. The use of regression equation parameters suggested in the present study will help researches to prevent such errors in biomass estimations of pelagic organisms of coastal tropical areas, when using image analysis tools.

Key words: zooplankton biomass, factor conversions, equivalent spherical diameter, body area, ellipsoid biovolume

5.1 INTRODUCTION

The study of biomass is essential to understand key aspects of marine life such as growth, production, community structure, the efficiency of energy transfer through trophic levels, etc. (Rodriguez and Mullin 1986; Sprules and Munawar 1986; Zhou 2006; Andersen et al. 2016). Several analytical techniques have been used to measure dry weight, carbon and nitrogen mass for assessing zooplankton biomass (Omori 1969; Hopkins 1982; Schram and Schmitz 1983; Froneman 2001; Puelles et al. 2003; Yahel et al. 2005). However, these methods implicate in the complete destruction of organisms, thus hampering the use of samples for further taxonomic studies (Postel et al. 2000).

Instead of that, analyses of wet mass have been used as a nondestructive method to estimate the total sestonic biomass of plankton samples, since there is a consistent linear relationship between dry and wet mass (Wiebe et al. 1975; Postel et al. 2000; Pitois and Fox 2006; Kiørboe 2013). Nevertheless, a proper measurement of biomass of specific zooplankton major groups through this method is not achievable, and sestonic mass may contain large contributions of detritus. Other concern regarding to biomass measurements is that formalin-fixed samples may have their zooplankton biomass underestimated as suggested by Alcaraz et al. (2003) due to organism biomasses loss after the formalin fixation of samples.

Only few studies have yet suggested methods for measurements of zooplankton biomass through images analysis. For example, Alcaraz et al. (2003) studied the relationship between biovolume and carbon and nitrogen mass of zooplankton, through the analysis of images obtained under a stereomicroscope. They proposed allometric regression equations to estimate carbon and nitrogen mass of the bulk zooplankton, without considering the variability of organism body shapes and group-specific elemental composition. Lehette and Hernández-León (2009) published compiled data of the relationships between dry mass and digitized body area of zooplankton (obtained by using stereomicroscope images) from subtropical and Antartic waters. Gorsky et al. (2010) recorded the relationship between ZooScan image metrics and elemental composition of zooplankton from the California Current, in an upwelling area, but the authors only provided conversion factors to assess the biomass (in carbon and nitrogen units) for three groups (copepods, euphausiids and chaetognats) from an upwelling ecosystem.

There is still a large gap concerning biomass conversion factors, mainly in relation to body size vs carbon and nitrogen contents of group-specific zooplankton data for tropical areas.

Information on elemental composition of zooplankton of tropical waters is limited to Beers (1966) and Ikeda and Mckinnon (2012), who studied organisms from the Sargasso Sea and the Great Barrier Reef, respectively, but the relationship between carbon and nitrogen mass and body size was not in the scope of these studies.

The current use of current conversion factors that were intended to estimation of biomass of zooplankton from subtropical and Antarctic environments can increase the error in biomass measurements of planktonic groups from tropical areas, given the high variability of body size of pelagic organisms around the world (Acevedo-Trejos et al. 2015; Brun et al. 2017). Thus, the elaboration of specific conversion factors to estimate biomass of zooplankton from tropical waters, through image analyses, may help researches to provide more reliable biomass measurements of specific-groups of pelagic organisms from these regions.

This study addresses four main objectives: i) to provide carbon and nitrogen contents, and dry mass data of zooplankton major groups from tropical coastal waters of northeastern Brazil; ii) to compare the percentage of carbon and nitrogen in the dry mass of the organisms in fresh and formaline- preserved samples; iii) to integrate dry, carbon and nitrogen mass to length, equivalent spherical diameter (ESD), body area and biovolume of the zooplankton and create reliable conversion factors to measure zooplankton biomass through image analyses; iv) to compare the conversion factors proposed in the present study with formulas published in the literature. The application of the regression equations proposed in this study as well as the comparison of these formulas with those published in the literature aim to contribute to a more precise assessment of zooplankton biomass of tropical regions, based on size measurements.

5.2 MATERIALS AND METHODS

Field activities were carried out in two coastal areas: Bacia do Pina estuary (08°03’S; 34°52’W – Recife city) and in the reefs of Tamandaré (8°45’S; 35°06’W – Tamandaré city), both located in Northeastern Brazil. Samplings were performed from November 2016 to January 2017 (dry season) using standard ring nets with 200, 300 and 500 µm mesh sizes, which were towed horizontally at subsurface (at 1.5 to 2 knots).

Fresh samples were stored in 5L-bottles filled with ambient seawater at 6 to 10ºC for up to 12 hours to have the organisms immobilized (cold-shock) in order to obtain images. Each sample was splitted into two aliquots: the first one was used to analyze fresh organisms

(fresh samples) and the second to perform further analyses with organisms preserved in formalin at 4% final concentration (preserved samples). The acquisition of zooplankton images and the analytical procedures performed in this study (details explained hereafter) were carried out with fresh samples approximately 12 hours after the sampling. Fixed samples were analyzed after 2 months.

Fresh and fixed zooplankton samples were sorted into two fractions: < 0.5 mm and > 0.5 mm. All organisms were quickly washed with distilled water to remove detritus and phytoplankton on zooplankton body surface. In order to obtain group-specific relationships between body size and elemental composition of the zooplankton, the organisms were sorted into major groups (copepods, decapods, mysids, polychaets and fish larvae) under a stereomicroscope. After that, each group (varying from 1 to 294 organisms belonging to the same group) was scanned at 2400 dpi resolution, using a ZooScan (Hydroptic, France). The organisms of each scanning were then stored in tin capsules and dried at 60ºC for 24 hours. Each capsule was weighed in a microbalance and the carbon (C) and nitrogen (N) mass were measured by using a EuroVector elemental analyzer (model Euro EA 3000-Single).

The percentage of carbon and nitrogen in the zooplankton dry mass (%) were transformed (log x+1) and normality and homoscedasticity were tested using Kolmogorov-Smirnov and Bartlett tests, respectively. To compare the percentage of carbon and nitrogen contents in fresh and fixed organisms, Mann-Whitney tests were used. Only copepods (12 and 10 capsules for fresh and fixed samples, respectively) and planktonic decapods (18 and 10 capsules for fresh and fixed samples, respectively) were used for these comparisons.

The images obtained with the ZooScan were analyzed in the Plankton Identifier (PkID) software (Gorsky et al. 2010). The length of organisms was measure based on the "major" metric that represents the largest linear axis of the particle in an image. The body area (mm^2) of zooplankton was considered based on the "area excluded" metric, which represents the 2-D area of the particle (surface area) on the image, i.e., the sum of pixels of the scanned particle (Gorsky et al. 2010; Vandromme et al. 2012). The sum of pixels of an organism in an image, was converted to a sphere and the ESD was estimated as the diameter of this sphere. The ellipsoid biovolume (mm^3) was calculated based on "major" and "minor" (major and minor axes of the particle) metrics, i.e., as Biovolume = $4/3*\pi*(major/2)*(minor/2)^2$ (Vandromme et al. 2012).

Data of biomass (dry, carbon and nitrogen mass) and size (length, ESD, body area and biovolume) of the zooplankton were transformed into their natural logarithms and parameters of exponential regressions ($y = a * x^b$) were obtained to calculate the linear regressions that correlate organisms biomass and size. The regressions were determined from $Biomass\ (\mu g) = exp(a).Size^b$, where the *a* and *b* are the intercept and the slope of the regressions, respectively. The *Biomass* may be measure as dry, carbon or nitrogen mass (in µg) while the *Size* represents the length (mm), ESD (mm), body area (mm^2) and biovolume (mm^3) of the zooplankton.

Five zooplankton groups were analyzed: mysids (n = 6), polychaetes (n = 5), copepods (n = 22), planktonic decapods (n = 28) and fish larvae (n = 13). Due to the fact that mysids and polychaetes were only sporadically captured in plankton samples, the n was insufficient to derive group-specific regression equations for these groups. Thus, data on these taxa were only included in the general regression equations for the whole zooplankton community.

The conversion factors created in the present study to estimate biomass (dry, carbon and nitrogen mass) were compared, through Mann-Whitney tests, with biomass measurements performed with the formulas published by Uye (1982), Alcaraz et al. (2003) and Lehette and Hernández-León (2009) (Table 4), in order to access prospective errors in biomass measurements of tropical zooplankton using formulas generated with organisms of subtropical and Antarctic waters. The biases related to biomass measurements (in percentage) using the formulas created in this study and other from literature was estimated as bias = 100*(this study – reference)/this study. All statistical analysis was performed by using Matlab R2017.b at a level of significance of 0.05 (Zar 1996).

5.3 RESULTS

The carbon and nitrogen contents of dry mass (%) of the zooplankton sampled in tropical waters of Northeastern of Brazil varied within a consistent, narrow range, from 39.1% to 47.58% and from 8.38% to 15.27%, respectively (Fig. 11 and Table 5). The copepods analyzed in the present study were mainly represented by *Temora turbinata, Acartia lilligeborgii* and *Labidocera fluviatilis* and the decapods by *Belzebub faxoni*, brachyuran larvae and other decapod larvae. The pairwise comparisons between fresh and fixed samples of copepods and

planktonic decapods did not show any significant differences in the percentage of carbon or nitrogen contents of zooplankton dry mass (Mann-Whitney test, $p > 0.05$), thus indicating that there was no significant carbon or nitrogen loss due to fixation. Thus, both fresh and fixed samples were used together to elaborate the conversion factors to estimate zooplankton biomass.

Copepods showed the smallest individual dry mass compared to the other zooplankton groups and varied from 1.75 to 26.6 µg with a median of 12.9 µg. The carbon and nitrogen mass of copepods varied from 0.78 to 14.6 µg and from 0.31 to 4.04 µg, with median values of 6.52 and 1.4 µg, respectively. Copepods metrics are described at (Table 6). The fish larvae composed the largest individual dry mass, ranging from 35.6 to 2397 µg and showed a median of 100 µg. Carbon and nitrogen values of fish larvae ranged from 17 to 1160 µg and from 4.74 to 262.9 µg, with median values of 53.9 and 13.57 µg, respectively. Fish larvae metrics are described at (Table 6).

The total length, ESD, body area and biovolume of the total zooplankton were significantly correlated with dry, carbon and nitrogen mass ($p < 0.001$ for all correlations) (Table 7; Fig. 12 and 13). Conversion factors to estimate the biomass for total zooplankton and for zooplankton major groups (copepods, planktonic decapods and fish larvae) are shown in Table 7.

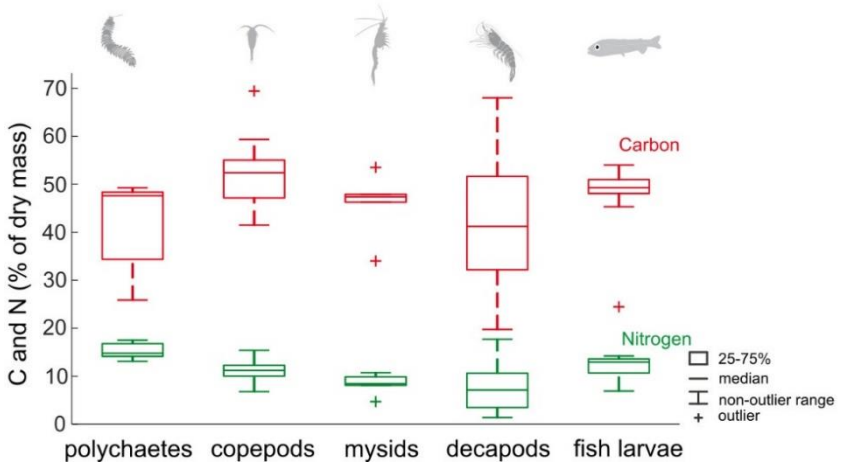
The comparison of the conversion factors proposed in the present study with those published by Uye (1982), Alcaraz et al. (2003) and Lehette and Hernández-León (2009) showed significant differences (Mann-Whitney test, $p < 0.001$) in their resulting biomass estimates. While estimates using the equations of Alcaraz et al. (2003) were several orders of magnitude lower than the present results (by up to 54%), the tropical zooplankton biomass was overestimated by up to 254% using the conversion factors proposed by Lehette and Hernández-León (2009), as compared to the present results. Additionally, biomass measurements of tropical zooplankton using the conversion factors proposed by Uye (1982) showed errors of biomass estimation around 50% (Table 6).

Table 4 – Previously published factor conversions to estimate the biomass (in µg) of zooplankton based on length (µm), biovolume (mm^3) and body area (mm^2) of organisms. "exp" is the exponential function. *DM*: dry mass; *C*: carbon mass; *N*: nitrogen mass.

Biomass (ug)	Factor conversions	Group	Reference
dry mass	$\exp(\log_{10} DM) = 3.13\ \log(\text{length}) - 8.18$	copepods	Uye (1982)
carbon	$\exp(\log_{10} C) = 3.07\ \log(\text{length}) - 8.37$		
nitrogen	$\exp(\log_{10} N) = 3.12\ \log(\text{length}) - 9.10$		
carbon	$C = 0.165 + 0.0695$ biovolume	zooplankton major groups (general equation)	Alcaraz et al. (2003)
nitrogen	$N = 0.0546 + 0.0137$ biovolume		
dry mass	$DM = 43.38\ Body\ Area^{1.54}$	zooplankton major groups (general equation)	Lehette and Hernández-León (2009)

Fonte: o autor.

Figure 11 – Carbon (C) and nitrogen (N) percentage of dry mass (%) of the zooplankton sampled in the Brazilian tropical waters.



Fonte: o autor.

Table 5 – Means of carbon (C) and nitrogen (N) content (%) of zooplankton in different parts of the world. "x" indicates that information is not available.

Source	Beers (1966)		Omori (1969)		Uye (1982)		Davis and Wiebe (1985)		Ikeda and Mckinnon (2012)		Present study	
	North Atlantic (Sargasso Sea)		*North Pacific (Open Sea of Japan)*		*North Pacific (Inland Sea of Japan)*		*North Atlantic (Warm-core Gul Stream)*		*South Pacific (Australia)*		*Tropical Atlanti (Northeastern Brazil)*	
	C	N	C	N	C	N	C	N	C	N	C	N
Polychaetes	29.9	8.9	x	x	53.2	13	35	x	x	x	41.6	15.27
Copepods	41.6	9.6	53.3	9.4	45.5	11.8	47	x	38.4	9.8	41.43	10.63
Mysids	40.7	9.9	42.4	11	40.6	11.1	x	x	43.8	11	46.08	8.38
Planktonic decapods	36.9*	7.8*	41.1	9.3	37.2	8.8	42	x	41.25	11.5	39.1	10
Fish larvae	37.9	9.6	42	11.2	42.2	11.2	44	x	x	x	47.58	11.95

Fonte: o autor.

Table 6 – Individual dry, carbon and nitrogen mass (µg), length, ESD, body area (mm^2) and ellipsoid biovolume (mm^3) of zooplankton of coastal tropical areas of Brazil.

	Copepods		Polychaetes		Mysids		Planktonic decapods		Fish larvae	
	range	median	Range	median	range	median	range	median	range	median
dry mass (µg)	1.75 - 26.6	12.9	14.0 - 94.6	30.0	34.2 - 440.2	82.2	5.31 - 2814	34.6	35.6 - 2397	100
carbon (µg)	0.78 - 14.6	6.52	3.62 - 46.9	14.7	16.76 -244.3	38.8	1.52 - 227.7	15.9	17.0 - 1160	53.9
nitrogen (µg)	0.31 - 4.04	1.4	1.83 - 19.0	4.34	4.78 - 67.2	9.43	0.07 - 1088.2	3.28	4.74 - 262.9	13.57
length (mm)	0.71 - 1.76	1.54	2.58 - 5.37	3.52	2.20 - 5.57	3.08	0.91 - 6.7	2.0	3.46 - 10.1	5.8
ESD (mm)	0.47 - 1.16	1.02	1.45 - 2.62	1.72	1.63 - 3.66	2.0	0.61 - 5.1	1.38	1.93 - 6.3	2.63
body area (mm^2)	0.18 - 1.10	0.87	1.66 - 5.79	2.38	2.24 - 10.5	3.37	0.30 - 20.1	1.61	3.19 - 31.5	5.58
biovolume (mm^3)	0.04 - 0.65	0.45	0.92 - 5.55	1.69	2.37 - 19.4	3.9	0.08 - 51.2	1.34	3.14 - 84.9	5.82

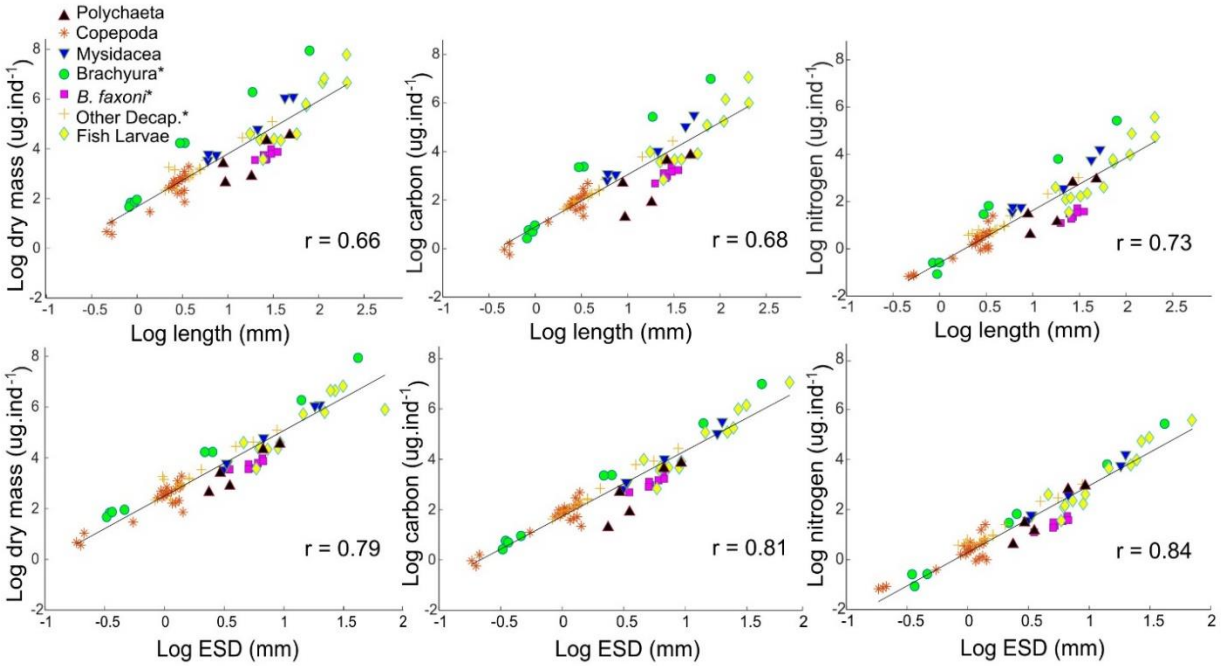
Fonte: o autor.

Table 7 – Regression parameters obtained with the relationship between length (mm), ESD (mm), body area (mm2) and biovolume (mm3) vs dry, carbon and nitrogen mass (µg) of zooplankton from tropical waters of Brazil. a, b and r2 are the intercept, the slope (and standard error) and the coefficient of determination of the regression, respectively. "exp" is the exponential function.

	Length (mm)			ESD (mm)			Body area (mm^2)			Biovolume (mm^3)		
Dry mass	exp (*a*)	*b*	*r2*	exp (*a*)	*b*	*r2*	exp (*a*)	*b*	*r2*	exp (*a*)	*b*	*r2*
Copepods	4.29	2.45 ± 0.1(	0.91*	11.5	2.40 ± 0.07	0.89*	14.5	1.20 ± 0.08	0.89*	23.0	0.79 ± 0.12	0.88*
Planktonic decapods	8.08	1.77 ± 0.2(	0.76*	15.3	2.55 ± 0.10	0.94*	18.8	1.20 ± 0.09	0.90*	31.5	0.83 ± 0.08	0.93*
Fish larvae	0.73	3.25 ± 0.7(	0.91*	4.67	3.43 ± 0.36	0.96*	5.96	1.77 ± 0.32	0.96*	15.1	1.19 ± 0.27	0.95*
General zooplankton**	5.33	2.12 ± 0.1	0.89*	12.2	2.58 ± 0.06	0.95*	15.6	1.29 ± 0.05	0.95*	27.3	0.90 ± 0.06	0.95*
Carbon mass	exp (*a*)	*b*	*r2*	exp (*a*)	*b*	*r2*	exp (*a*)	*b*	*r2*	exp (*a*)	*b*	*r2*
Copepods	2.12	2.59 ± 0.0(	0.93*	6.05	2.54 ± 0.06	0.92*	7.72	1.27 ± 0.07	0.92*	12.6	0.84 ± 0.10	0.92*
Planktonic decapods	2.95	2.00 ± 0.2	0.82*	6.45	2.84 ± 0.03	0.99*	7.84	1.31 ± 0.01	0.94*	13.7	0.91 ± 0.01	0.97*
Fish larvae	0.41	3.13 ± 0.7(	0.91*	2.52	3.31 ± 0.38	0.95*	3.17	1.71 ± 0.34	0.95*	7.78	1.16 ± 0.27	0.95*
General zooplankton**	2.44	2.15 ± 0.1	0.90*	5.65	2.60 ± 0.06	0.95*	7.27	1.31 ± 0.04	0.95*	12.7	0.91 ± 0.04	0.96*
Nitrogen mass	exp (*a*)	*b*	*r2*	exp (*a*)	*b*	*r2*	exp (*a*)	*b*	*r2*	exp (*a*)	*b*	*r2*
Copepods	0.58	2.14 ± 0.1	0.88*	1.39	2.08 ± 0.07	0.86*	1.69	1.04 ± 0.08	0.86*	2.53	0.68 ± 0.12	0.85*
Planktonic decapods	0.60	2.04 ± 0.3(	0.79*	1.79	2.56 ± 0.05	0.98*	1.64	1.34 ± 0.04	0.91*	2.93	0.93 ± 0.04	0.94*
Fish larvae	0.09	3.23 ± 0.7(	0.92*	0.60	3.36 ± 0.37	0.95*	0.77	1.74 ± 0.33	0.95*	1.93	1.17 ± 0.28	0.95*
General zooplankton**	2.21	0.55 ± 0.1	0.90*	1.33	2.66 ± 0.06	0.95*	1.72	1.34 ± 0.04	0.95*	3.07	0.93 ± 0.05	0.96*

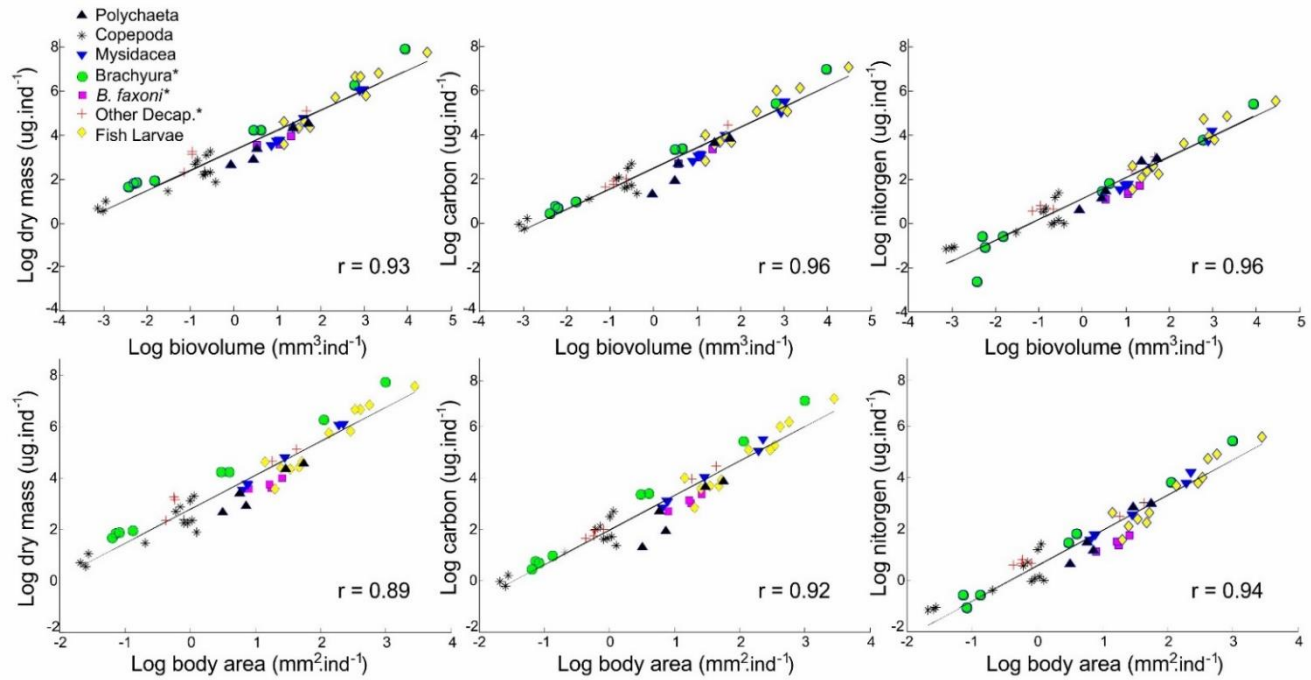
Fonte: o autor.

Figure 12 – Natural logarithm of the length and ESD vs log dry, carbon and nitrogen mass of the zooplankton sampled in the Brazilian tropical waters. *: planktonic decapods. r: correlation coefficient.



Fonte: o autor.

Figure 13 - Natural logarithm of the biovolume and body area vs log dry, carbon and nitrogen mass of the zooplankton sampled in the Brazilian tropical waters. *: planktonic decapods. r: correlation coefficient.



Fonte: o autor.

Table 8 - Means and standard deviations of zooplankton biomass measurements from coastal tropical waters of Brazil by using factor conversions proposed in the present study and others. The error of biomass measurements using the factor conversions of the literature are also show. All comparisons of biomass measurements between the present study and previous studies were highly significant ($p < 0.001$, Mann-Whitney test). Bias = 100*(this study – reference)/this study.

	Biomass estimates (µg)		Group	Bias (%)
	Present study	Uye (1982)		
dry mass	12.38 ± 8.72	5.63 ± 2.4		- 54%
carbon	6.6 ± 4.88	3.84 ± 1.61	copepods	- 43%
nitrogen	1.42 ± 0.89	2.17 ± 0.92		+ 53%
	Present study	Alcaraz et al. (2003)		
carbon	10.04 ± 21.25	0.22 ± 0.15	zooplankton major groups	- 98%
nitrogen	2.44 ± 5.43	0.06 ± 0.03	(general equation)	- 98%
	Present study	Lehette and Hernández-León (2009)		
dry mass	22.63 ± 43.7	80.25 ± 225.8	zooplankton major groups (general equation)	+ 254%

Fonte: o autor.

5.4 DISCUSSION

The present study provides new carbon and nitrogen content data for common zooplankton major groups found in coastal tropical areas of Brazil and shows that the individual biomass of these organisms can be precisely estimated based on data of the length, ESD, body area, and biovolume measurements obtained through image analysis. Carbon and nitrogen percentages of dry mass of tropical zooplankton are similar to those observed in other parts of the world (Table 5). However, our results show that dry, carbon and nitrogen mass of zooplankton from tropical waters of Brazil are not precisely estimated using the current conversion factors from subtropical and polar areas.

Our dataset did not detect any significant carbon and nitrogen losses in copepods and decapods from fixed samples in comparison with carbon and nitrogen contents of organisms in fresh samples. These results suggest that these groups preserve the elemental composition of their dry mass at least until two months after fixation. In contrast, Omori (1978) detected losses of organic weight in chaetognaths and copepods sampled in Suruga Bay (Japan) after one week of sample preservation. Alcaraz et al. (2003) analyzed the zooplankton community from the Mediterranean Sea and the Galician shelf (North Atlantic) and recorded differences in C and N contents of organisms comparing fresh and fixed samples after two months of fixation.

One possible explanation is the gentle procedure of low-speed sampling and careful handling of the samples taken in shallow waters, which prevented any significant physical damage to these fragile organisms, and thus avoided loss of tissue and liquids in subsequent fixation and storage in this study. In contrast, the above mentioned studies were based on common offshore sampling from research vessels, which may be more destructive, leading to carbon as nitrogen loss from damaged organisms. Therefore, we suggest that any such studies should be conducted with slow sampling and careful handling of these fragile organisms.

Also, the different patterns recorded in Alcaraz et al. (2003) in comparison to the present study may be due to the fact that those authors analyzed the whole zooplankton community (copepods, cladocerans, ostracods appendicularians, other tunicates, cnidarians, chaetognaths and invertebrate larvae), while we analyzed pairwise samples of copepods and decapods. Probably, rates of carbon and nitrogen losses of the plankton samples, after

fixation, may be different for each specific groups. Other possibility is that zooplankton obtained in different regions (upwelled subtropical and tropical waters) may be different biomass losses after fixation.

Investigations on body size and elemental composition of zooplankton elucidate important ecological traits of pelagic organisms such as metabolism rates and ecosystem productivity (Ikeda and Skjoldal 1989; Kimmel et al. 2006; Ikeda and Mckinnon 2012). Due to the difficulties to analyze zooplankton body mass in carbon and nitrogen units, several studies on zooplankton ecology approaching analyses of ZooScan images have focused on ellipsoid biovolume of organisms to assess the size spectra of zooplankton communities (Gilabert 2001; Zhou 2006; Zhou et al. 2009; Basedow et al. 2010; Dai et al. 2016).

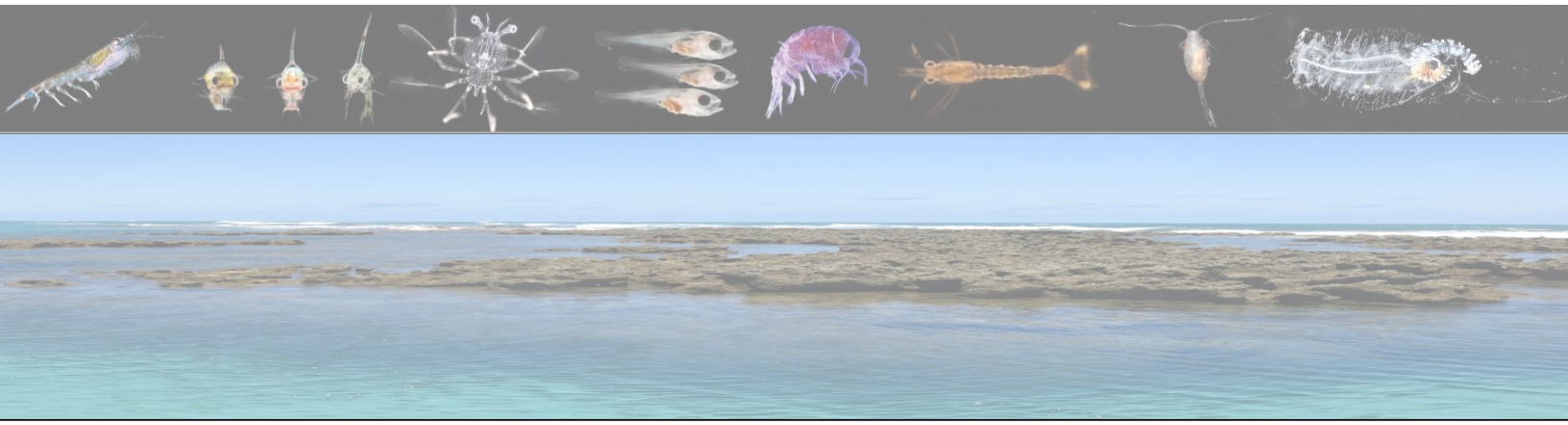
On the other hand, Hernández-León and Montero (2006) suggested that the body area of zooplankton is a better parameter, in comparison to biovolume, to create conversion factors to estimate biomass through image analysis, since the ellipsoid shape sometimes does not represent the real morphology of some zooplankton taxa. However, the results of the present study showed that the relationship between the biovolume and the dry mass showed the best correlation coefficients compared to the body area, length and ESD, indicating that the ellipsoid biovolume may be more useful for such assessments.

Alcaraz et al. (2003) documented the correlation between carbon and nitrogen contents and the ellipsoid biovolume of zooplankton (for the all community, in general, and for salps) by analyzing silhouette photographs obtained using a camera attached to stereomicroscope. The present study is the first to describe the same relationship by using the ZooScan for specific zooplankton groups and corroborate with Alcaraz et al. (2003) results, since we observed a strong correlation between carbon and nitrogen mass and biovolume for the organisms investigated in Brazilian tropical waters.

Only few studies have used the conversion factors proposed by Alcaraz et al. (2003) to estimate biomass (using carbon and nitrogen units) for whole zooplankton community (Frangoulis et al. 2010; Frangoulis et al. 2017). However, the use of the formulas presented in this study will help future researchers to convert, length, ESD, body area or biovolume data into carbon and nitrogen mass when the biomass of specific-groups of zooplankton be the interest of future studies on zooplankton ecology.

Currently, most studies on zooplankton biomass, using data of ZooScan images, have applied the conversion factors proposed by Hernández-León and Montero (2006) and Lehette and Hernández-León (2009) to achieve the dry mass of zooplankton. In order to calculate the carbon and nitrogen mass of major groups, other data sources from literature (Beers, 1966, Uye 1982, Cabel and Wiebe 1985, etc.) have been commonly used (Vandromme et al. 2012; Schultes et al. 2013; Vandromme et al. 2014; Marcolin et al. 2015).

In conclusion, the present study provides conversions factors to the direct measurement of carbon and nitrogen mass of zooplankton major groups from the tropical Atlantic. It also shows that the use of conversion equations to estimate zooplankton biomass based on organisms of subtropical and polar waters provides unreliable data in biomass estimation of zooplankton from tropical waters. Thus, we expect to prevent such errors in biomass estimates using size measurements on further studies about the ecology of tropical pelagic communities.



6 ARE TROPICAL COASTAL REEFS SINKS OR SOURCES OF ZOOPLANKTON? A CASE STUDY IN A BRAZILIAN MARINE PROTECTED AREA

Abstract

In spite of the paramount ecological and socio-economic relevance of tropical reefs ecosystems, the dynamics of their larvae abundance remain poorly characterized. The small-scale distribution and detailed analysis of individual biomass of zooplankton were studied in the coastal reefs of Tamandaré (Brazil). Zooplankton samples were collected during nocturnal ebb tides at new moon, using three different devices to sample at three different environments: a standard ring net that was towed at subsurface, the Channel Midwater Neuston Net that collected at midwater in channels between patch reefs and the Reef Edge Net, that captured organisms that are washed by ebb currents from reef tops towards the reef edge. Zooplankton was analyzed using a ZooScan to obtain abundances and biovolume of each taxonomic groups. Specific biomass measurements were done to obtain allometric equations used to calculate zooplankton biomass from biovolume. Zooplankton were significantly more abundant at subsurface and at the reef edge compared to channel environments. The high abundance of organisms at reef edges suggests a low predation pressure on zooplankton at near-bottom areas, since the reefs of Tamandaré present a low coverage of planktivorous corals, being dominated by macroalgae. These results show that rather than sinks these ecosystems may be considered important sources of zooplankton available for planktivorous species. Regarding zooplankton composition, we found large amount of initial stages of meroplanktonic larvae and newly hatched fish eggs, which presented consistently greater abundances compared to holoplankton and emergent benthic taxa. Decapod larvae were the most abundant group of the meroplankton, but cirripedian nauplii, stomatopod larvae, fish larvae and fish eggs were also abundant. More than 50% of the total zooplankton estimated biomass was due to meroplankton taxa, mainly

composed by decapod larvae. This study shows that the contribution of meroplankton on pelagic productivity of tropical reefs has been underestimated.

Key words: meroplankton, zooplankton biomass, Channel Midwater Neuston Net, Reef Edge Net, coastal reefs

6.1 INTRODUCTION

Zooplankton is an important source of carbon within food webs of tropical reef ecosystems (Odum e Odum, 1955; Hobson, 1991; Sheppard *et al.*, 2009). In coral reefs, the top down control on these pelagic organisms has a particular diel feature: numerous species of planktivorous fishes are active predators at near-bottom zones during the day (Hamner *et al.*, 1988; Hobson, 1991; Motro *et al.*, 2005; Hamner *et al.*, 2007) while most scleractinian corals feed on zooplankton at night (Odum e Odum, 1955; Sebens e Deriemer, 1977; Sebens *et al.*, 1998). This intensive predation causes a severe depletion of zooplankton on reefs with a high coverage of corals (located in oligotrophic waters far from coastal areas and estuarine influence), which can be observed as a near-bottom depletion of pelagic organisms (Holzman *et al.*, 2005; Yahel e Yahel, 2005; Yahel *et al.*, 2005; Hamner *et al.*, 2007; Alldredge e King, 2009; Heidelberg *et al.*, 2010). These patterns have led to the general characterization of reef ecosystems as sinks of zooplankton, a steadfast paradigm in reef ecology.

Conversely, tropical reefs located along the Brazilian coastline present a high cover of macroalgae and a low coverage of corals (Maida e Ferreira, 1997; Barbosa *et al.*, 2009; Francini-Filho *et al.*, 2013; Feitosa e Ferreira, 2015; Santos *et al.*, 2015) mainly due to the high levels of sedimentation (from estuarine discharges) in reef areas, which interferes on scleractinian development (Leão e Dominguez, 2000; Leão e Kikuchi, 2005).

Studies on zooplankton ecology in waters surrounding Brazilian reefs have recorded the numerical dominance of copepods (Mayal *et al.*, 2009; Melo *et al.*, 2010) and its high contribution for biomass in zooplankton assemblages (Marcolin *et al.*, 2013). Copepoda is also the most important group of typical coral reefs systems (Heidelberg *et al.*, 2004; Nakajima *et al.*, 2008; Alldredge e King, 2009; Heidelberg *et al.*, 2010; Nakajima *et al.*, 2014). Due to their high abundances, copepod swarms have been considered a relevant carbon source available to higher trophic levels of coral reefs (Hamner e Carleton, 1979).

In addition, the presence of a diverse sessile macrofauna in tropical reefs provides a relevant supply of meroplankton in pelagic systems since several benthic invertebrates and pelagic vertebrates spend the initial phase of theirs lives (eggs and larvae) carried by local currents in pelagic environment (Williams *et al.*, 1984; Anger, 2001; Sheppard *et al.*, 2009). Thus, production, retention and transport of larvae play an important role in population dynamics and connectivity in reef ecosystems (D'agostini *et al.*, 2015; Kough e Paris, 2015).

In tropical regions, spawning and hatching events are common during the dry season, when temperature and wind are high and currents and turbidity are weaker (Williams *et al.*, 1984; Anger, 2001). Several species of benthic and pelagic organisms release their eggs and larvae during nocturnal high and ebb tides (Forward, 1987; Francini *et al.*, 2002; Nanami *et al.*, 2013) especially during new moon (Williams *et al.*, 1984; Morgan e Christy, 1995; Samoilys, 1997). This helps to avoid visual predation of larvae and eggs (Nolan e Danilowicz, 2008). However, the influence of spawning and hatching events on zooplankton abundance of tropical reefs has probably been underestimated, since assessing peaks of larvae release is not a trivial task, because I) the navigation around shallow reefs at night is dangerous, II) there are few information regarding to duration (minutes, hours) of spawning events and III) methodological problems (Santos *et al.*, 2017).

Although copepods are considered numerically dominant in zooplankton assemblages of coral reefs and other marine systems, they are smaller than meroplankton forms (i.e., decapods, fish larvae etc) and contributes little for total zooplankton biomass of tropical reefs (Heidelberg *et al.*, 2010). However, the relevance of larvae and eggs for the input of biomass in pelagic systems around tropical reefs has not been properly approached. Thus, information on meroplankton abundance is essential to understand the potential contribution of larvae and eggs biomass in food webs of shallow tropical reefs.

The reefs of Tamandaré are within the largest Marine Protected Area of Brazilian coastal waters called "APA Costa dos Corais" (created in 1997). In April 1999 through a federal decree a patchy reef within the Tamandaré reef complex known as "Ilha da Barra" and its surrounding waters were permanently closed to any fishing and visiting activities. Nowadays, this no-take area provides great opportunities to investigate a tropical system without anthropogenic activities. The reef tops of the Ilha da Barra closed area are mainly covered by the zoanthid *Zoanthus sociathus* (Ellis, 1768) (30.5%) and by macroalgae (30%), being

dominated by the Rhodophyta *Palisada perforta* (Bory) KW Nam. In spite of complete closure for more than a decade, these reef tops have a very low coverage of corals (less than 1%) (Santos *et al.*, 2015).

The present study intends to test the hypothesis that coastal tropical reefs characterized by low coverage of scleractinian corals are sources of zooplankton for pelagic systems, by addressing the question whether zooplankton shows a significant near-bottom depletion compared to adjacent channels and subsurface environments.

If the shallow reef tops of Tamandaré are sinks of zooplankton, samples taken in the waters that are washed from the reef tops towards the reef edge should have lower abundances of zooplankton compared to samples taken in open waters (channels and subsurface environments). If the reef tops are sources of zooplankton, no numerical differences should be detected between organisms taken in the waters washed from the reef tops and samples taken in open waters. Furthermore, this study investigates the relative importance of meroplankton to holoplankton and emergent benthic organisms (bottom-dwelling species, which are suspended by waves or perform vertical migration) in these ecosystems.

6.2 MATERIAL AND METHODS

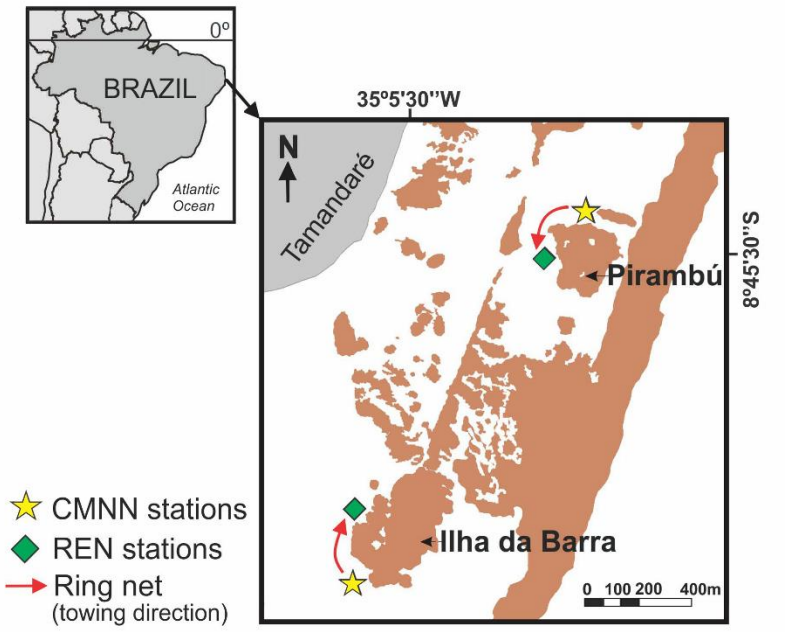
6.2.1 *Study area*

The reefs of Tamandaré (8º 45'36'' and 8º47'20'' S and 35º03'45'' and 35º06'45'' W) are located in the state of Pernambuco in northeast of Brazil (Fig. 14) under a tropical climate with high precipitation (ranging from 81 mm^3 to 526 mm^3 in summer and winter per season, respectively) and average air temperature ranging from 26ºC in the winter to 30ºC in the summer (Maida e Ferreira, 1997). This reef system is an important habitat for different life stages of fishes that use the estuary as a nursery and perform cross-shelf ontogenetic migrations (Silva-Falcão *et al.*, 2012; Aschenbrenner *et al.*, 2016). This ecosystem provides livelihood to many families through fishing (octopus, crabs, lobsters, fishes, etc) and tourism activities.

At the period of this study Chlorophyll *a* was analyzed using the spectrophotometric method (Unesco, 1966) and ranged from 0.01 to 1.27 mg m^{-3}. Temperature and salinity were measured using a YSI CastAway CTD (SonTek, San Diego, CA, USA) and ranged from 28.56 to 30.45 ºC and from 35.46 to 35.84, respectively. The current speed was measured in Ilha da Barra channel (depth varying from 7 to 9 m according to the tides) using a S4 current meter

(InterOcean Systems LLC, San Diego, CA, USA) in March and October 2015 and varied from 3 to 5.8 cm s^{-1}.

Figure 14 - Map of the study area in the reefs of Tamandaré (northeastern Brazil) showing the sampling stations. CMNN: Channel Midwater Neuston Net. REN: Reef Edge Net. Red arrow: track for ring net tows direction.



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6.2.2 *Sampling strategy*

Zooplankton samples were obtained in two reef areas with extensive shallow reef tops: "Ilha da Barra" (fishing prohibited reef) and "Pirambú" (fishing regulated reef), during three campaigns: I) from March 19 to 22 (2015), II) from November 10 to 12 (2015) and III) from March 7 to 11 (2016) in consecutive nights of new moon, during the dry season. Three different devices were used for zooplankton sampling: a common ring net, the Channel Midwater Neuston Net (CMNN) and the Reef Edge Net (REN) (Fig. 14 and 15).

The CMNN is a set of 6 passive nets (3 nets with 64 µm and 3 with 300 µm mesh sizes) adapted to be deployed in channels between patch reefs (Fig. 15) and samples 3 layers: the epineuston (air-water interface) at 0 m to 0.075 m, the hyponeuston at 0.075 m to 0.225 m (CMNN-neuston) and the 1 m layer (at midwater of channels) at 0.925 m to 1.075 m. The

CMNN sampled the zooplankton transported from reefs towards continental shelf (Santos *et al.*, 2017).

The REN is a set of 2 passive nets (one with 64 µm and another with 300 µm mesh sizes) that allows the adjustment of sampling depth at sandy bottom adjacent to reefs (Fig. 15). The RENs were deployed approximately 5 m away distant from the reef (to assure safe nocturnal navigation) and aligned with the upper edge of each patchy reef (Ilha da Barra and Pirambú) studied. The RENs stayed 2.2 m and 1.9 m above the bottom at Ilha da Barra and at Pirambú, respectively and sampled the zooplankton washed from near-reef areas (Santos *et al.*, 2017).

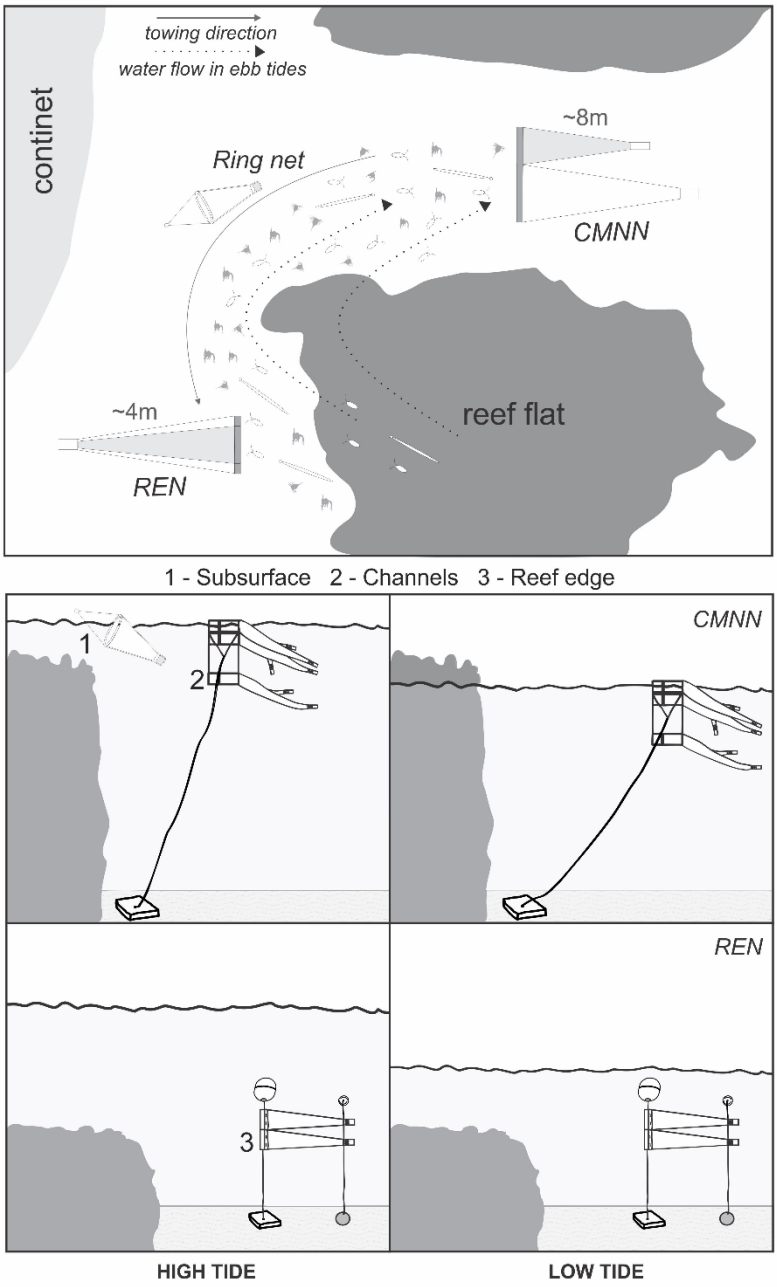
The tidal amplitude during surveys was 1.85 m. The vertical position of nets from CMNN regarding to patch reefs changes according to tidal regime, but all CMNN nets sampled similar depth during all ebb tide. In contrast, the position of REN does not changes close to edges of patch reefs during ebb tides but the sampling depth changes and showed an average of 2.1 m in the beginning (at high tide) and 0.4 m in the end of sampling period (late ebb tide).

Each passive net (CMNN and REN) was deployed before dusk in fixed stations close to Ilha da Barra and Pirambu patch reefs (Fig. 14) in high tide regime. They sampled during nocturnal ebb tides for approximately 4 hours. In the northeast of Brazil, the sunset occurs approximately at 6:00 pm during summer season.

Subsurface horizontal tows were carried out using a ring net with a 300 µm mesh size (against the local current flow) after sunset, from CMNN stations towards the REN stations, during 13 minutes (Fig. 14 and 15).

These devices sampled specific environments around the reefs: subsurface (CMNN-neuston and ring net), channels (the 1 m layer of the CMNN) and the reef edge (REN) (Fig. 15). All samples were preserved in 4% formaldehyde buffered with 0.05% sodium tetraborate (final concentration in seawater). The present study will present only results obtained from the 300 µm mesh size nets.

Figure 15 - Schematic illustration of sampling stations and current fluxes at maximum ebb tides, showing the currents washing the reef tops towards the edges of reefs and then towards the inlets between reefs. Tidal levels and positions of sampling systems during deployment (high tide) and retrieval (low tide). Not to scale.



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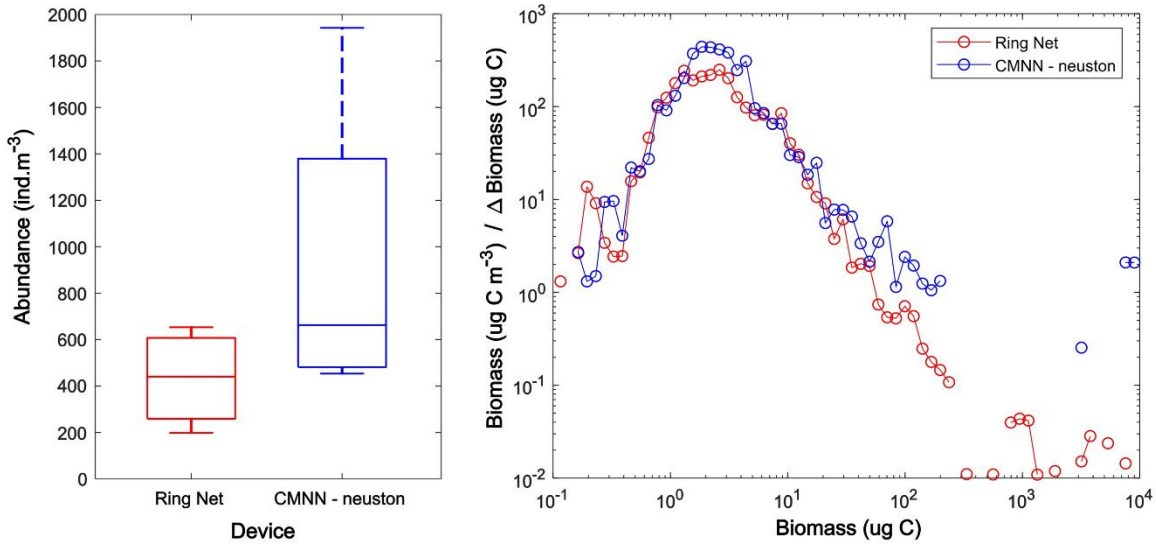
During fieldwork the CMNN showed operational problems in epineuston and hyponeuston nets (entanglement of nets caused by strong winds), which caused unreliable flowmeter readings on some sampling days. The abundances in ring nets and CMNN-neuston (epineuston and hyponeuston) were compared from samples of days that we did not have problems with entanglement of nets (n = 4). The zooplankton abundance between the ring net and the CMNN-neuston did not show differences (Mann-Whitney, p = 0.3429) and the Two-sample Kolmogorov-Smirnov test showed that the carbon weight distribution of zooplankton in both nets are from the same continuous distribution (h = 0, p = 0.5759). Thus, we considered the ring net samples (from all campaigns) to appropriately characterize the subsurface environment (Fig. 15 and 16), in an overall comparable way to the stationary nets. In the present manuscript, only data from the 1 m layer of the CMNN (channels) will be considered, additionally to the REN (reef edges) and ring net (subsurface) samples.

Figure 16 - Abundance (ind.m-3) and Normalized Biomass Size Spectra (NBSS) of the zooplankton sampled at subsurface using a standard ring net (in red) and the epineuston and hyponeuston (neuston, in blue) of the Channel Midwater Neuston Net (CMNN).



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6.2.3 *Laboratory methods*

Samples were divided into two size fractions: > 1 mm and < 1 mm. Aliquots of each fraction were split (when necessary) using a Motoda splitter (Motoda, 1959) and scanned using a ZooScan (Hydroptic, France) at 2400 dpi resolution (Grosjean *et al.*, 2004; Gorsky, Gaby *et*

al., 2010). Some samples were scanned completely (without fractioning) due to their low amount of particles. Touching objects were manually separated (for 20 minutes) prior to scanning. Each image (containing from 1000 to 1500 objects) created by the scanning was processed in ZooProcess software, i.e., vignettes were created of each particle scanned for each aliquot. The data set of vignettes was uploaded in the Ecotaxa Plataform (http://ecotaxa.obs-vlfr.fr) and all vignettes were classified into zooplankton major groups.

Additionally, fresh organisms were scanned and C and N contents were analyzed using a EuroVector elemental analyzer (model Euro EA 3000-Single). Using the major and minor axis of each image scanned, the ellipsoid biovolume of zooplankton was calculated using the following formula $(4/3*\pi*(major/2)*(minor/2)^2)$. From comparing pairwise measurements of individuals C and N content and biovolume, allometric regression equations were developed to measure zooplankton biomass.

6.*2.4 Data analysis*

Total abundance (ind.m^{-3}) and biomass (ug C m^{-3}) of zooplankton was transformed (log x+1) and normality and homoscedasticity were analyzed using Kolmogorov-Smirnov and Bartlett tests, respectively. Kruskal-Wallis ANOVA was used with Mann-Whitney tests for post-hoc pairwise comparisons at $\alpha=0.05$ (Zar, 1996). The zooplankton abundance did not show statistical differences among or between campaigns. Thus, samples from different campaigns were used as replicates. Zooplankton was grouped into 3 categories: meroplankton (Cirripedia, Stomatopoda, Decapoda, Teleostei larvae and Teleostei eggs), holoplankton (Hydrozoa, Siphonophorae, Gastropoda, Copepoda, Ostracoda, Euphausiacea, Chaetognatha Appendicularia) and emergent benthic organisms (i.e., Polychaeta, Cumacea, Mysida, Isopoda, Tanaidacea and Amphipoda). The abundance of meroplankton was divided by holoplankton abundance plus emergent benthic organism abundance. These ratios were obtained to investigate if newly hatched larvae, and eggs show dominance in zooplankton assemblages. Abundance and biomass were compared between patch reefs (Ilha da Barra and Pirambu) and among sampling environments (subsurface, channel and reef edge). All analyses were performed by using Matlab R2017.b.

6.3 RESULTS

Overall, the zooplankton assemblages of the Tamandaré of reefs showed a high contribution of meroplankton groups in relation to holoplanktonic and benthic associated organisms, in all sampling days and all environments studied.

6.*3.1 Evidence of spawning and hatching events*

Large amounts of early stages of larvae and eggs were sampled. Decapod larvae were the most abundant, mainly at the reef edges, with high abundances of larvae of caridean shrimps (130.2 ± 196.6 ind.m^{-3}), zoea-stages of brachyuran crabs (46.2 ± 60.2 ind.m^{-3}), hermit crabs (12.9 ± 18.65 ind.m^{-3}), lobsters (1.54 ± 3.39 ind.m^{-3}), which included the first record of *Palinurellus gundlachi* larvae and other decapod larvae (33.64 ± 37.16 ind.m^{-3}). Cirripedian nauplii and stomatopods larvae also showed high abundances at the reef edges (41.2 ± 74.9 ind.m^{-3} and 13.7 ± 24.5 ind.m^{-3}, respectively).

Furthermore, newly hatched fish larvae were very abundant at the reef edges (108.4 ± 235.3 ind.m^{-3}). Fish eggs (42.6 ± 40.2 ind.m^{-3}) were also abundant in all campaigns, mainly at subsurface. Among fish larvae, yolk-sac and preflexion stages were dominant. Preflexion stages were identified as being mostly of the Pomacentridae family.

6.*3.2 Composition and distribution of zooplankton*

Decapod larvae was the most abundant group at reef edge (36.8%) and it was also very important at subsurface (21.2%) and channels (27.7%). Copepods were the second most important group being particular abundant at subsurface (33.5%) (Fig. 17 and Table 9).
Furthermore, fish eggs were also important at subsurface (10.7%), while stomatopods were more important at channels (16.2%) and fish larvae were more relevant at reef edge (17.8%) (Fig. 17; Table 9).

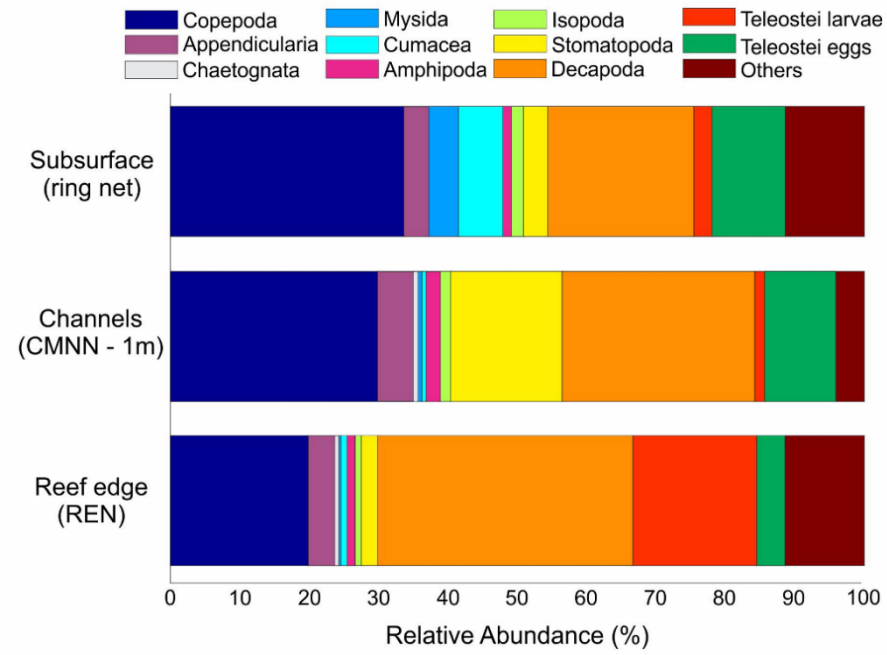
Zooplankton abundance was similar between the closed (Ilha da Barra) and the open-access (Pirambu) areas (Mann-Whitney tests, $p > 0.05$). Total abundance did not show significant differences between subsurface samples and reef edges, but both environments showed significant higher zooplankton abundance compared to the samples taken in the channels (Fig. 18; Tables 9 and 10).

Cumaceans and mysids were dominant at subsurface compared to channel and reef edge stations. Fish larvae were significantly more abundant at the reef edges and were less abundant at subsurface and channel sites (Table 9 and 11).

Holoplankton and meroplankton abundances did not show any significant difference between subsurface and reef edge environments. In opposition to that, emergent benthic organisms showed significantly higher abundance at subsurface compared to reef edges (Fig. 19; Table 10). All three categories, i.e., meroplankton, holoplankton and emergent benthic organisms, showed the lowest abundance in the channels compared to subsurface and reef edge environments (Fig. 19; Table 10).

Meroplankon / (holoplankton and emergent benthic organisms) abundance ratios showed values above 1 in all environments (Fig. 20). The difference observed in the ratios between Ilha da Barra and Pirambu reefs at channels (Mann-Whitney tests, $p = 0.02$) is mainly driven by the high contribution of stomatopod larvae at the Pirambu reef especially during campaign 1.

Figure 17 - Relative abundance (%) of zooplankton major groups sampled at reef edge, channel and subsurface environments around the reefs of Tamandaré (northeastern Brazil). The others contains: Hydrozoa, Siphonophorae, Gastropoda, Polychaeta, Cirripedia (nauplii), *Belzebub faxoni* (decapod shrimp), Euphausiacea and Ostracoda.



Fonte: o autor.

Table 9 - Relative abundance (%) and abundance (mean ± standard deviation) of the main groups sampled around the reefs of Tamandaré (northeastern Brazil). The others contains Hydrozoa, Siphonophorae, *Belzebub faxoni* (decapod shrimp), Euphausiacea and Ostracoda.

	Subsurface (ring net)		Channel (CMNN – 1m)		Reef edge (REN)	
	RA (%)	Abundance (ind.m^{-3})	RA (%)	Abundance (ind.m^{-3})	RA (%)	Abundance (ind.m^{-3})
Gastropoda	4.1	16.5 ± 17.2	1.1	0.5 ± 1.0	1.2	10.7 ± 15.5
Polychaeta	1.6	6.5 ± 4.6	0.4	0.2 ± 0.3	1.7	10.6 ± 15.8
Copepoda	33.5	133.6 ± 96.8	29.6	13.5 ± 19.4	19.8	121.1 ± 147.4
Cirripedia (nauplii)	1.7	6.9 ± 10.1	0.7	0.3 ± 0.8	6.7	41.2 ± 74.9
Stomatopoda larvae	3.3	13.2 ± 24.9	16.2	7.4 ± 16.9	2.2	13.6 ± 24.5
Cumacea	6.5	26.0 ± 42.8	0.8	0.3 ± 0.5	0.9	5.8 ± 7.6
Decapoda larvae	21.2	84.4 ± 15.0	27.7	12.6 ± 29.5	36.8	224.4 ± 278.8
Mysida	4.2	16.7 ± 11.1	0.4	0.2 ± 0.5	0.1	0.8 ± 1.4
Isopoda	1.8	7.3 ± 6.6	1.3	0.6 ± 1.2	1.1	6.6 ± 9.4
Amphipoda	1.2	4.7 ± 5.0	2.1	1.0 ± 1.7	1.0	6.4 ± 7.0
Chaetognatha	0.1	0.5 ± 0.8	0.7	0.3 ± 0.5	0.8	4.8 ± 8.9
Appendicularia	3.5	13.8 ± 10.8	5.2	2.34 ± 5.2	3.6	22.0 ± 36.9
Teleostei larvae	2.6	10.5 ± 12.5	1.6	0.7 ± 1.4	17.8	108.4 ± 235.3
Teleostei eggs	10.7	42.6 ± 40.2	10.2	4.6 ± 6.9	4.3	26.4 ± 55.1
Others	4.0	15.8 ± 15.0	2.0	0.9 ± 1.4	1.2	7.3 ± 8.0
Meroplankton	39.5	157.5 ± 116.1	56.2	25.7 ± 45.2	67.5	412.0 ± 582.5
Emergent benthic	15.4	61.5 ± 52.8	5.3	2.4 ± 3.6	5.0	30.5 ± 34.1
Holoplankton	45.1	180.1 ± 101.9	38.5	17.6 ± 23.8	27.5	165.7 ± 191.1
Total		399.0 ± 206.2		45.7 ± 61.8		610.3 ± 769.2

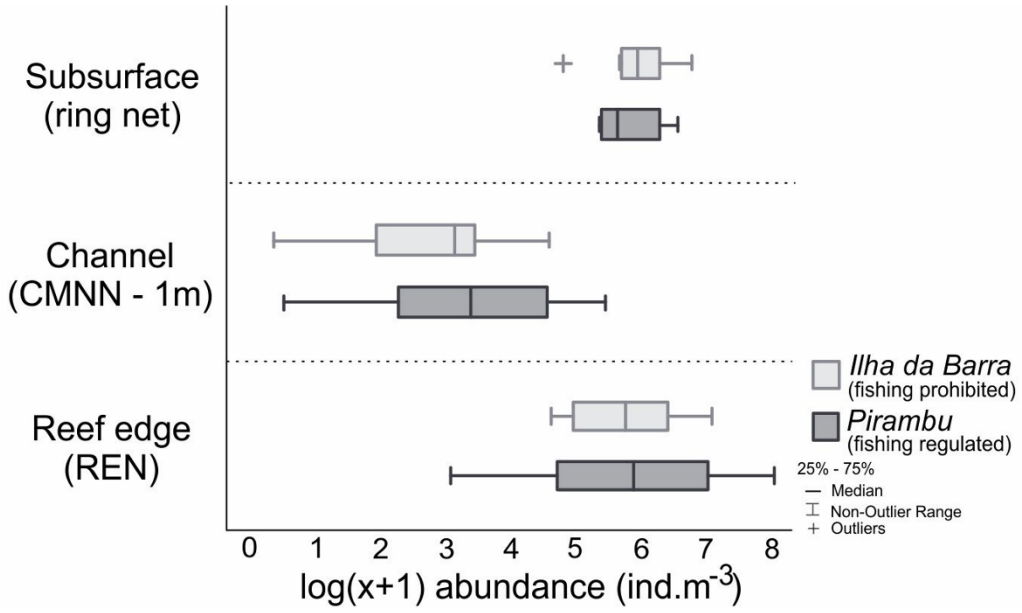
Fonte: o autor.

Table 10 – Results of Mann-Whitney tests (*p*-values) comparing the total zooplankton abundance and biomass of meroplankton, emergent benthic taxa and holoplankton in different regions around the reefs of Tamandaré (northeastern Brazil). [S] Higher values at Subsurface. [RE] Higher values at Reef edge.

	Subsurface vs Channels	Subsurface vs Reef edge	Channels vs Reef edge
		Abundance (ind.m^3)	
Meroplankton	< 0.0001 [S]	n.s.	< 0.0001 [RE]
Emergent benthic	< 0.0001 [S]	0.0167 [S]	< 0.0001 [RE]
Holoplankton	< 0.0001 [S]	n.s.	< 0.0001 [RE]
		Biomass (ug C m^{-3})	
Meroplankton	< 0.0001 [S]	n.s.	< 0.0001 [RE]
Emergent benthic	< 0.0001 [S]	0.0205 [S]	< 0.0001 [RE]
Holoplankton	< 0.0001 [S]	n.s.	< 0.0001 [RE]

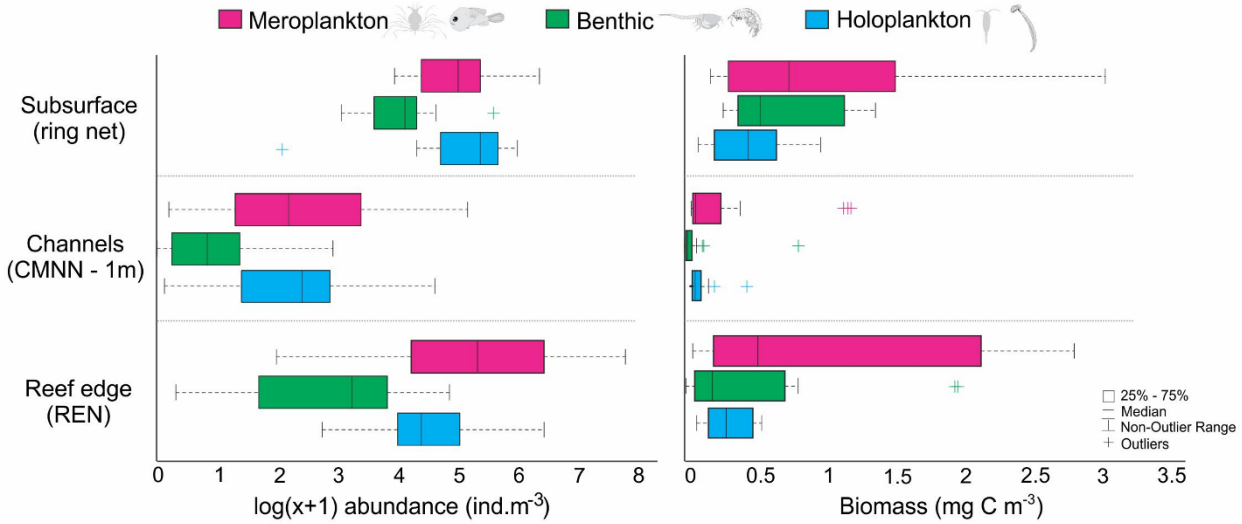
Fonte: o autor.

Figure 18 - Abundance (ind.m^{-3}) of the total zooplankton sampled at reef edge, channel and subsurface environments around the reefs of Tamandaré (northeastern Brazil).



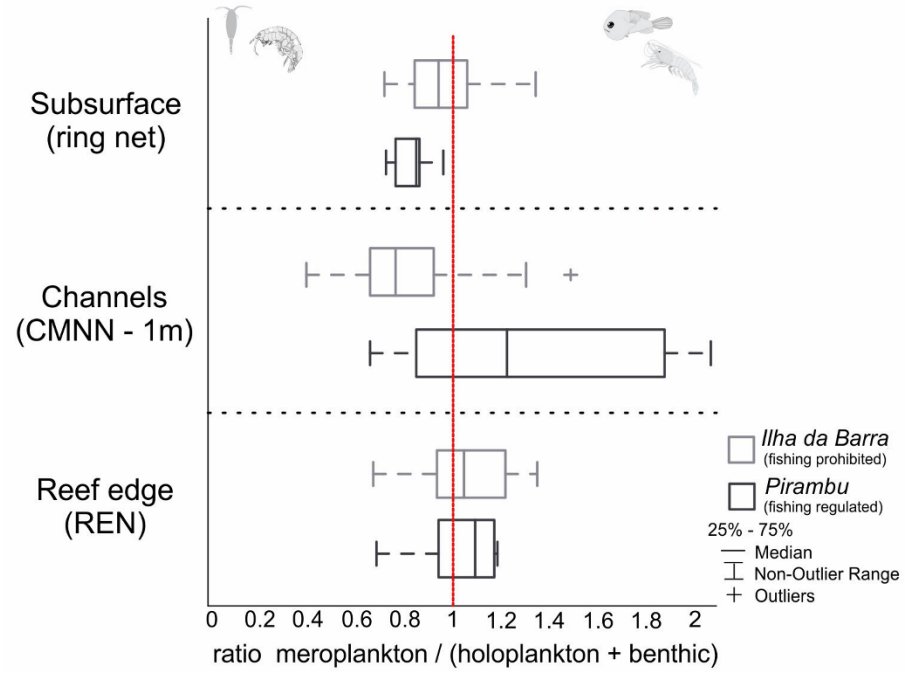
Fonte: o autor.

Figure 19 - Abundance (ind.m^{-3}) and biomass (ug C m^{-3}) of meroplankton, holoplankton and emergent benthic organisms sampled at reef edge, channel and subsurface environments around the reefs of Tamandaré (northeastern Brazil).



Fonte: o autor.

Figure 20 - Ratio of meroplankton / (holoplankton + emergent benthic organisms) abundance of zooplankton sampled at reef edge, channel and subsurface environments around the reefs of Tamandaré (northeastern Brazil).



Fonte: o autor.

Table 11 - Results of Mann-Whitney tests (p-values) comparing zooplankton abundance in different regions around the reefs of Tamandaré (northeastern Brazil). The others contains Hydrozoa, Siphonophorae, Belzebub faxoni (decapod shrimp), Euphausiacea and Ostracoda.

	Abundance (ind.m^{-3})		
	Subsurface vs Channels	Subsurface vs Reef edge	Channels vs Reef edge
Gastropoda	< 0.0001 ^{S}	n.s.	< 0.0001 ^{RE}
Polychaeta	< 0.0001 ^{S}	n.s.	< 0.0001 ^{RE}
Copepoda	< 0.0001 ^{S}	n.s.	< 0.0001 ^{RE}
Cirripedia (nauplii)	< 0.0001 ^{S}	n.s.	< 0.01 ^{RE}
Stomatopoda larvae	n.s.	n.s.	n.s.
Cumacea	< 0.0001 ^{S}	< 0.01 ^{S}	< 0.001 ^{RE}
Decapoda larvae	< 0.0001 ^{S}	n.s.	< 0.0001 ^{RE}
Mysida	< 0.0001 ^{S}	< 0.0001 ^{S}	n.s.
Isopoda	< 0.0001 ^{S}	n.s.	< 0.0001 ^{RE}
Amphipoda	< 0.0001 ^{S}	n.s.	< 0.001 ^{RE}
Chaetognatha	n.s.	n.s.	n.s.
Appendicularia	< 0.0001 ^{S}	n.s.	< 0.0001 ^{RE}
Teleostei larvae	< 0.0001 ^{S}	< 0.001 ^{RE}	< 0.0001 ^{RE}
Teleostei eggs	< 0.0001 ^{S}	n.s.	< 0.01 ^{RE}
Others	< 0.0001 ^{S}	n.s.	< 0.0001 ^{RE}

Fonte: o autor.

6.*3.3 Zooplankton biomass*

More than 50% of the total calculated zooplankton biomass in the reefs of Tamandaré was due to meroplankton taxa, mainly composed of decapod larvae, which contributed with 32.2%, 40.2% and 37.7% for total zooplankton biomass at subsurface, channels and reef edge environments, respectively (Fig. 21; Table 12). Stomatopods larvae were also very important and represented about 16.8% of total zooplankton biomass in channels sites (Fig. 21; Table 12). While copepods contributed around 20-30% for total zooplankton abundance in the Tamandaré reefs (Table 9), they accounted for only 16% of the total zooplankton biomass (Fig. 21; Table 12). Regarding emergent benthic organisms, mysids (11.8%) and cumaceans (5.5%) were the most important in biomass at subsurface (Fig. 21; Table 12).

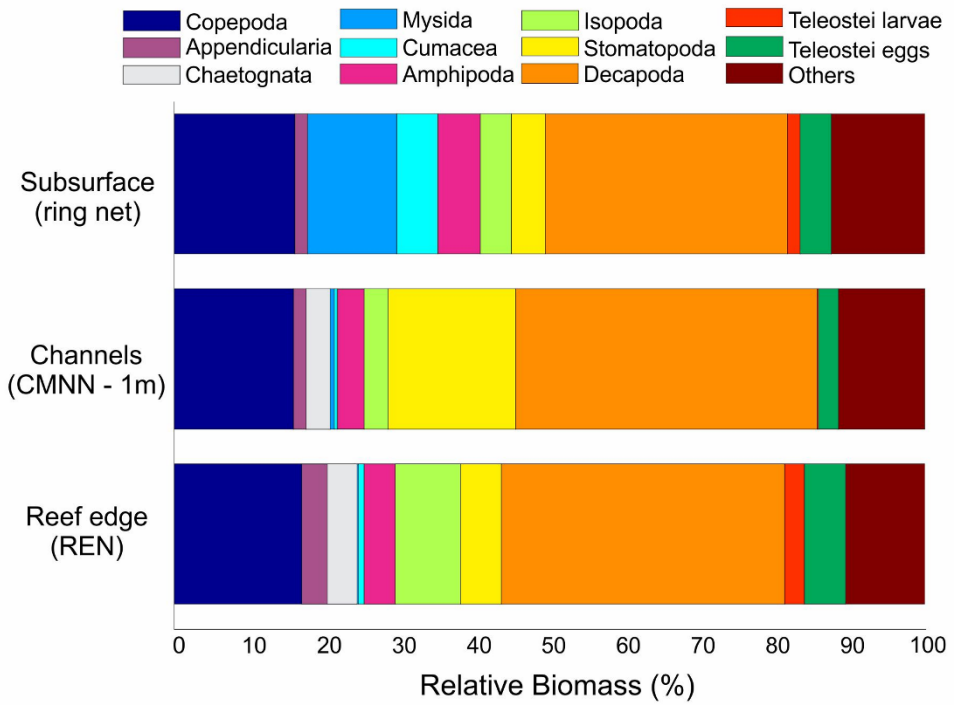
Table 12 - Relative biomass (%) and biomass (mean ± standard deviation) of the main groups sampled around the reefs of Tamandaré (northeastern Brazil). The others contains Hydrozoa, Siphonophorae, *Belzebub faxoni* (decapod shrimp), Euphausiacea and Ostracoda.

	Subsurface (ring net)		Channels (CMNN – 1m)		Reef edge (REN)	
	RB (%)	Biomass (ug C m^{-3})	RB (%)	Biomass (ug C m^{-3})	RB (%)	Biomass (ug C m^{-3})
Polychaeta	8.3	162.4 ± 149.2	5.6	8.9 ± 24.5	8.4	238.7 ± 418.8
Copepoda	16.0	306.9 ± 235.6	15.7	35.6 ± 57.8	17.0	332.6 ± 404.4
Cirripedia (nauplii)	0.1	1.5 ± 2.2	0.1	0.07 ± 0.8	0.4	9.6 ± 17.5
Stomatopoda larvae	4.6	120.9 ± 223.6	16.8	56.4 ± 125.0	5.6	126.2 ± 238.1
Cumacea	5.5	109.1 ± 132.8	0.4	1.0 ± 1.4	0.7	16.3 ± 21.0
Decapoda larvae	32.2	683.4 ± 707.5	40.2	115.0 ± 218.1	37.7	1035.9 ± 1256.9
Mysida	11.8	214.7 ± 141.2	0.5	2.5 ± 5.7	0.3	6.8 ± 14.9
Isopoda	4.1	94.5 ± 94.5	3.4	34.8 ± 132.7	8.5	133.8 ± 259.7
Amphipoda	5.7	96.5 ± 127.8	3.6	13.9 ± 25.5	4.2	78.3 ± 91.6
Chaetognatha	0.2	5.1 ± 9.5	3.4	4.94 ± 8.4	3.8	56.2 ± 110.2
Appendicularia	1.5	27.9 ± 24.3	1.6	4.1 ± 9.8	3.34	33.8 ± 60.7
Teleostei larvae	1.7	28.4 ± 35.4	0.3	0.7 ± 1.4	2.6	85.9 ± 167.6
Teleostei eggs	4.2	78.3 ± 85.0	2.7	6.2 ± 11.6	5.4	66.3 ± 208.0
Others	4.2	80.7 ± 79.5	5.9	11.6 ± 22.9	2.0	25.9 ± 26.7
Meroplankton	45.4	912.7 ± 845.7	60.3	178.4 ± 321.8	59.0	1323.9 ± 1651.5
Emergent benthic	33.7	678.6 ± 399.2	20.9	61.8 ± 162.9	21.0	475.1 ± 642.5
Holoplankton	20.9	419.5 ± 282.5	18.8	55.7 ± 85.2	20.0	447.3 ± 508.1
Total		2010.8 ± 1305.9		295.9 ± 475.8		2246.3 ± 2699.2

Fonte: o autor.

Holoplankton showed the lowest contribution to total zooplankton biomass compared to meroplankton and emergent benthic taxa in all the environments investigated (Fig. 21; Table 12). The zooplankton biomass was the lowest at channels compared to subsurface and reef edge environments, but no significant difference was found between the subsurface and the reef edge samples (Fig. 21; Table 9 and 12).

Figure 21 - Relative biomass (%) of zooplankton major groups sampled at reef edge, channel and subsurface environments around the reefs of Tamandaré (northeastern Brazil). “Others” contains: Hydrozoa, Siphonophorae, Gastropoda, Polychaeta, Cirripedia (nauplii), *Belzebub faxoni* (decapod shrimp), Euphausiacea and Ostracoda.



Fonte: o autor.

6.4 DISCUSSION

The present study revealed a notable abundance of zooplankton at near-bottom zones (sampled at the reef edges). The higher abundance and biomass of holo- and meroplankton at the reef edges, as compared to the open water (i.e., channel) samples, indicate that rather than sinks these shallow benthic ecosystems were sources of zooplankton during the study period. Conversely, previous studies on zooplankton assemblages of coral reefs have reported a strong near-reef depletion of zooplankton. Potential causes of this hitherto undescribed inverse pattern are discussed hereafter.

Our results also provide information on the relevance of newly hatched larvae and eggs of fish and invertebrates in zooplankton assemblages in shallow tropical reefs. The dominance of meroplankton in those communities suggests that the sampling carried out in the present study was performed during periods of spawning and hatching events. The high abundance of meroplankton in all environments studied in the reefs of Tamandaré (subsurface, channels and

reef edge) shows records of zooplankton released by reef resident organisms (adults of caridean shrimps, stomatopods, barnacles, lobsters and fishes) and the consequential contribution of larvae and eggs to the zooplankton biomass of coastal pelagic systems around tropical reefs.

6.4.1 *Zooplankton composition*

The numerical dominance of meroplankton organisms in relation to holoplankton groups is unusual in tropical reefs. Available information on larval variability of benthic species in the reefs of Tamandaré is limited to studies focusing on spatial distribution and community structure of zooplankton (grey literature) and few records of larvae in samplings using traps adapted to catch demersal zooplankton (Melo *et al.*, 2010). Therefore, this study is the first to elucidate the relevance of larvae and eggs within zooplankton communities in the reefs of Tamandaré.

Overall, previous studies on zooplankton ecology of shallow tropical reefs have not focused on strategies for sampling zooplankton to detect peaks of meroplankton release. Heidelberg et al. (2004) suggested that the abundance of some groups of zooplankton around tropical reefs have been underestimated, mainly because of inappropriate sampling strategies. The use of the CMNN and REN allowed the precise and intensive sampling, for hours, of zooplankton close to reefs, which increased the probability of larvae and eggs capture since the exact time and duration of larvae release and spawning events are poorly known in tropical reefs.

Although the proper period, which surveys were carried out (summer season, new moon and nocturnal ebb tides), i.e. under ideal environmental conditions for larvae and eggs release (Forward, 1987; Nanami *et al.*, 2013), the mesh size used in the present study (300 µm) may be another important factor that explains the considerable capture of larvae and fish eggs in the devices used in the reefs of Tamandaré. Previous studies in tropical reefs have mostly focused on zooplankton which was caught by towing and passive nets with much smaller mesh sizes, i.e., 40, 80, 90 and 100 µm (Alldredge e King, 1985; Heidelberg *et al.*, 2004; Holzman *et al.*, 2005; Yahel *et al.*, 2005; Nakajima *et al.*, 2008; Heidelberg *et al.*, 2010; Nakajima *et al.*, 2014; Pagano *et al.*, 2017).

Few studies have recorded peaks of meroplankton in the zooplankton communities sampled with small mesh sizes. For instance, Pagano et al. (2017) detected peaks of bivalve

larvae in the zooplankton assemblages sampled with a 80 µm towing net around a reef lagoon that harbor an oyster farming in coral reefs from French Polynesia. Nevertheless, small mesh apertures (< 200) are not suitable for capturing active swimmers such as decapods larvae. Additionally, the use of small pumps in coral reefs have demonstrated inefficiency to capture larger zooplankton groups, which can easily avoid pumps (Holzman *et al.*, 2005).

The higher abundance of meroplankton forms rather than holoplankton organisms in the zooplankton assemblages recorded in this study is in accordance with Hammer et al. (2007) work, which used a similar device to CMNN, i.e., channel nets with 305 µm mesh size which sampled during ebb tide periods. The authors reported decapods as the most important group in the zooplankton communities, sampled during ebb tides, in Palau barrier reefs (Republic of Palau) and highlighted that these reefs produce and export fish eggs to adjacent open sea.

Alldredge & King (2009) also reported an increase in decapod larvae abundance in the zooplankton assemblages sampled with 200 and 300 µm mesh-size nets in the coral reefs of Moorea (French Polynesia) during new moon periods. Thus, the use of nets equipped with 200 and 300 µm mesh sizes around tropical reefs appeared to be suitable for a reliable quantification of fish eggs and larvae with swimming abilities, such as decapods and fishes. While small mesh-size nets (< 200 µm) have focused the importance of copepods in tropical reefs, this work suggests that the sampling strategy used in the surveys carried out in the reefs of Tamandaré highlighted the numerical relevance of meroplankton in relation to copepods in tropical reef systems.

On the other hand, emergent benthic groups were also important in the zooplankton assemblages sampled in the reefs of Tamandaré. Peracarid crustaceans have been classified as "pseudoplanktonic" organisms by its high abundance in the plankton sampled mainly at night around reefs ecosystems (Echelman e Fishelson, 1990). These organisms remain close to the bottom or buried during the day, and then migrate towards the surface at night to mate and feed in the water column (Johnson *et al.*, 2012a; Johnson *et al.*, 2012b). The high abundance of cumaceans and mysids recorded at the subsurface around the reefs of Tamandaré may be related to summer reproduction periods and nocturnal feeding habits.

6.4.2 *Small-scale distribution of zooplankton*

The distribution of zooplankton around the coastal reefs of Tamandaré showed an enrichment of organisms at subsurface and at reef edge environments. These results suggest that these shallow reef tops did not function as a relevant sink of zooplankton during nocturnal ebb tides of new moon days.

The zooplankton of coral reefs avoids near-bottom areas at night, mainly due to the high predation pressure caused by corals. The moonlight also attracts them to the surface. These features increases the nocturnal abundance of zooplankton near surface (Alldredge e King, 1985; Holzman *et al.*, 2005; Yahel e Yahel, 2005; Yahel *et al.*, 2005; Alldredge e King, 2009; Heidelberg *et al.*, 2010). In any case, the zooplankton produced around coral reefs is generally quickly consumed by planktivorous species (Hamner *et al.*, 1988; Hamner *et al.*, 2007).

The organisms sampled in RENs were washed by local currents of ebb tides from near-bottom zones towards reef edge and channel stations. The high abundance of zooplankton at reef edge stations may partly be attributed to the low coverage of scleractian corals in the coastal reefs of Tamandaré, which probably implicates in a low predation pressure on zooplankton.

In contrast, the low abundance of zooplankton recorded at midwater in the channels around the reefs of Tamandaré indicates that these sites do not seem to be as important as subsurface environments for the transportation of organisms from reefs to continental shelf during ebb tide regime.

Overall, the data of this study suggest that the reefs of Tamandaré present a relevant stock of zooplankton organisms available for planktivorous predators during nocturnal ebb tides.

6.4.3 *Benthopelagic coupling*

The results of the present study show a remarkable benthopelagic coupling during the surveys carried out in the reef systems of Tamandaré. The significant abundance of fish eggs and initial stages of decapod and fish larvae in the zooplankton assemblages sampled in this work indicates that the capture of freshly hatched larvae were obtained from adult organisms that reside in patch reefs, since early-stage larvae in pelagic systems indicates presence of adult stocks (Forward, 1987; Brandão *et al.*, 2015). The values above 1 observed in the ratios of meroplankton / (holoplankton and emergent benthic organisms) abundances demonstrate that

the benthopelagic coupling in the reefs of Tamandaré during the period of this study was relevant.

Shallow tropical reefs harbor several species of sponge-inhabiting alpheids, hermit crabs, coral guard-crabs, carideans associated with sea anemones, carideans considered fish cleaners, etc. (Omori *et al.*, 1994; Gilchrist, 2003; Macdonald *et al.*, 2006; Mccammon *et al.*, 2010; Mckeon e Moore, 2014). A diverse community of epibenthic and endobenthic decapods has been described for these coastal reefs (Giraldes *et al.*, 2015), but the ecology of these organisms is still poorly studied.

The high abundance of zoea stages of caridean shrimps and crabs quantified in this work demonstrates the importance of benthic decapods for zooplankton communities in the shallow reefs of Tamandaré and opens new perspectives for research on ecology of these invertebrates on coastal tropical reefs. The large amounts of stomatopod larvae detected in the zooplankton samples also revealed that the shallow sand-gravel seafloor around the reefs of Tamandaré harbors an abundant and hitherto unknown population of mantis shrimps. Information on these organisms is limited to sporadic records of occurrence (Lucatelli *et al.*, 2012) but their ecology has not been studied in those reefs yet.

This study also recorded the first capture of the first zoea-stage of the furry lobster *Palinurellus gundlachi*. This small lobster species displays cryptic habits and is used in aquarium trade (Giraldes *et al.*, 2015). Common spiny lobsters, such as *Palinurus argus, P. echinatus* and *P. laevicauda* are fishing targets in reefs of northeast of Brazil. These species usually release their larvae far from the coastal reefs, on the continental shelf or slope (Acosta *et al.*, 1999; Jeffs *et al.*, 2005). However, there is no currently information on spawning regimes of *Palinurellus gundlachi* in coastal waters of Brazil. Our results suggest that the sampling of the first zoea-stage of *P. gundlachi* in subsurface waters and in fixed stations (channel and reef edge environments) close to reefs indicates that this species releases its larvae around reef systems, differently of the *Palinurus* species that habit the reefs of Tamandaré. Supplementary studies are necessary to assess the dynamics of *P. gundlachi* larval dispersal or retention in these coastal tropical areas.

The nocturnal ebb tide flows around the reefs of Tamandaré also revealed a remarkable abundance of fish eggs and fish larvae. It is worth noting that the morphotypes of fish larvae sampled in this study are not commonly found in ichthyoplankton samples taken on reefs or

elsewhere in northeastern Brazil. Brazilian coastal reefs harbors a dense community of reef fishes from the Pomacentridae family (Feitosa *et al.*, 2012) characterized by a territorial habitat (Jones, 2005) and parental care (Bessa e Sabino, 2012; Francini-Filho *et al.*, 2012). However, the dynamics of Pomacentridae larvae in Brazilian reefs is poorly studied. Likely, the mesh sizes of nets used in previous studies (< 300 µm) on zooplankton assemblages were not suitable to catch these small larvae.

The dominance of early hatched fish larvae (mostly of pomacentrids) at the reef edges and their hitherto total absence in earlier studies, suggests that these larvae may avoid their transport by surface currents towards the continental shelf (at subsurface and channels areas), remaining close to the reefs.

6.4.4 *Zooplankton biomass*

This study shows for the first time the relevance of meroplankton biomass for pelagic systems of tropical reefs, based on their carbon content. Our results are similar to the findings of Heidelberg et al. (2010), who reported that although copepods are considered very abundant in zooplankton assemblages of coral reefs of Jamaica (i.e., representing > 85% of total abundance) they contributed only 35% to total zooplankton biomass, while larger groups (mostly decapods) had a relevant impact on total biomass. However, the authors did not describe carbon contents of these specific larger groups of the zooplankton comunities investigated.

Regarding holoplankton organisms, our data show that in the reefs of Tamandaré, copepods composed only 16% of total biomass. On other locations (reefs of Malaysia), Nakajima et al. (2014) have been reported copepods and larvaceans as the most important groups in zooplankton biomass. Besides that, Marcolin et al. (2013) have discussed the relevance of copepods and ostracods for the zooplankton biomass in coral reef ecosystems of Brazil. However, the influence of ostracods on zooplankton biomass was negligible in the reefs of Tamandaré during the period of this study.

It is worthy noting that although the emergent benthic groups presented low abundance in the reefs of Tamandaré, they contributed much more to the total zooplankton biomass than holoplankton taxa. Nevertheless, among the all taxa sampled in the reefs of Tamandaré, decapod larvae presented the greatest contribution to biomass within the zooplankton

communities. Larger groups (i.e., > 1 mm), such as decapod larvae, stomatopod larvae, amphipods, cumaceans, isopods and polychaetes are very important prey for diurnal and nocturnal planktivorous fishes in reef systems (Holzman e Genin, 2003). Thus, the meroplankton production and the nocturnal vertical migration of emergent benthic organisms present a strong influence on transference of carbon to higher trophical levels in tropical reefs.

Overall, the present study suggests that larval production, additionally to providing new settlers for the recruitment of benthic and pelagic species around reefs, has important implications for local productivity in pelagic systems of shallow coastal reefs. Therefore, the plankton fraction investigated in the present study (including bottom-dwelling organisms found in all pelagic environments sampled) shows an important role regarding carbon transfers, representing a link between primary energy sources (nano- and microplankton, mucus producing by zoanthids and detritous in general, etc.) and planktivorous species of coastal food webs. Rather than being sinks, these highly productive coastal reefs are important sources of zooplankton to pelagic systems.

7 CONSIDERAÇÕES FINAIS

Nessa tese foram apresentados novos métodos de coleta de zooplâncton para a amostragem de organismos em recifes costeiros rasos, visando a captura de larvas e ovos recém eclodidos. Também foi realizada uma abordagem inédita para estimativas de biomassa do zooplâncton tropical, através da análise de imagens obtidas com o uso do ZooScan, o que culminou a elaboração de equações empíricas. Nossos resultados também registram novos padrões no tocante à distribuição do zooplâncton no entorno de recifes costeiros tropicais, bem como a elucidação de alguns aspectos da interação entre componentes da megafauna residente dos recifes e o sistema pelágico adjacente.

O primeiro capítulo relatou que as redes *Channel Midwater Neuston Net* (CMNN) e *Reef Edge Net* (REN) foram eficazes na coleta de zooplâncton, com ênfase na captura de ovos e larvas de peixes e invertebrados bentônicos que residem nos recifes. O uso destas redes permitiu a realização de coletas noturnas e uma quantificação confiável do meroplâncton em pontos fixos próximos aos recifes de Tamandaré (PE, Brasil). As estratégias de amostragem de zooplâncton com o uso da CMNN e REN abrem novas perspectivas para a realização de estudos de monitoramento do zooplâncton em ecossistemas recifais costeiros de águas rasas.

O segundo capítulo mostrou os erros associados às estimativas de biomassa do zooplâncton de origem tropical com o uso de fórmulas elaboradas com a análise de organismos de ambientes subtropicais e antárticos. Sugerimos que o uso dos fatores de conversão propostos no presente trabalho estimam de forma mais precisa a biomassa do zooplâncton (peso seco, massa de carbono e nitrogênio) de origem costeira tropical, baseando-se em dados de comprimento, diâmetro esférico equivalente, área e biovolume de organismos.

O último capítulo mostrou a relevância do meroplâncton na composição e biomassa do zooplâncton em um recife costeiro tropical. Estes resultados demonstram que a produção de zooplâncton por organismos bentônicos e pelágicos residentes dos recifes de Tamandaré vem sendo subestimada, bem como a influência de organismos bentônicos emergentes (misidáceos, anfípodes, isópodes e cumáceos), larvas e ovos de peixes e invertebrados bentônicos (principalmente decápodes e estomatópodes) no aporte de biomassa para os sistemas pelágicos costeiros no entorno desses recifes.

A análise detalhada da biomassa corporal individual do zooplâncton revelou que as larvas de decápodes bentônicos representam o grupo com maior contribuição na biomassa

mesozooplanctônica dos sistemas pelágicos dos recifes de Tamandaré. Os resultados do terceiro capitulo também sugerem que a baixa cobertura de corais e a alta cobertura de macroalgas dos recifes estudados causam uma pressão predatória baixa nas assembleias de zooplâncton desses ambientes, o que pode ser explicado pela abundância alta de zooplâncton nas bordas desses recifes.

Portanto, os recifes de Tamandaré representam um ecossistema produtivo e ao invés de sumidouros, podem ser considerados fontes de zooplâncton para o sistema pelágico costeiro. Provavelmente, esses recifes são potenciais exportadores de zooplâncton para a plataforma continental adjacente durante períodos de liberação de ovos e larvas de peixes e invertebrados bentônicos residentes desses recifes. Os dados apresentados nesta tese abrem novas perspectivas para a elaboração de estudos que abordam temas como relações tróficas, predação do zooplâncton, dispersão, retenção larval, etc., para uma melhor compreensão de outros aspectos ecológicos do meroplâncton desses ecossistemas tropicais costeiros.

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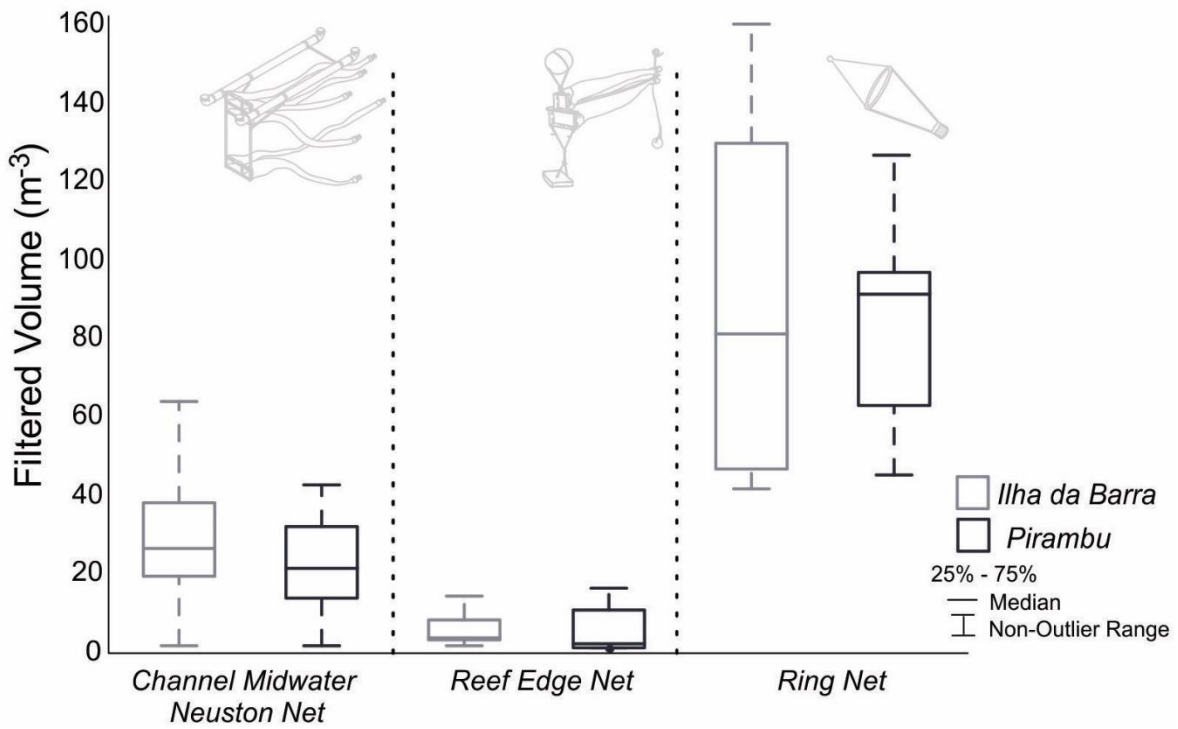
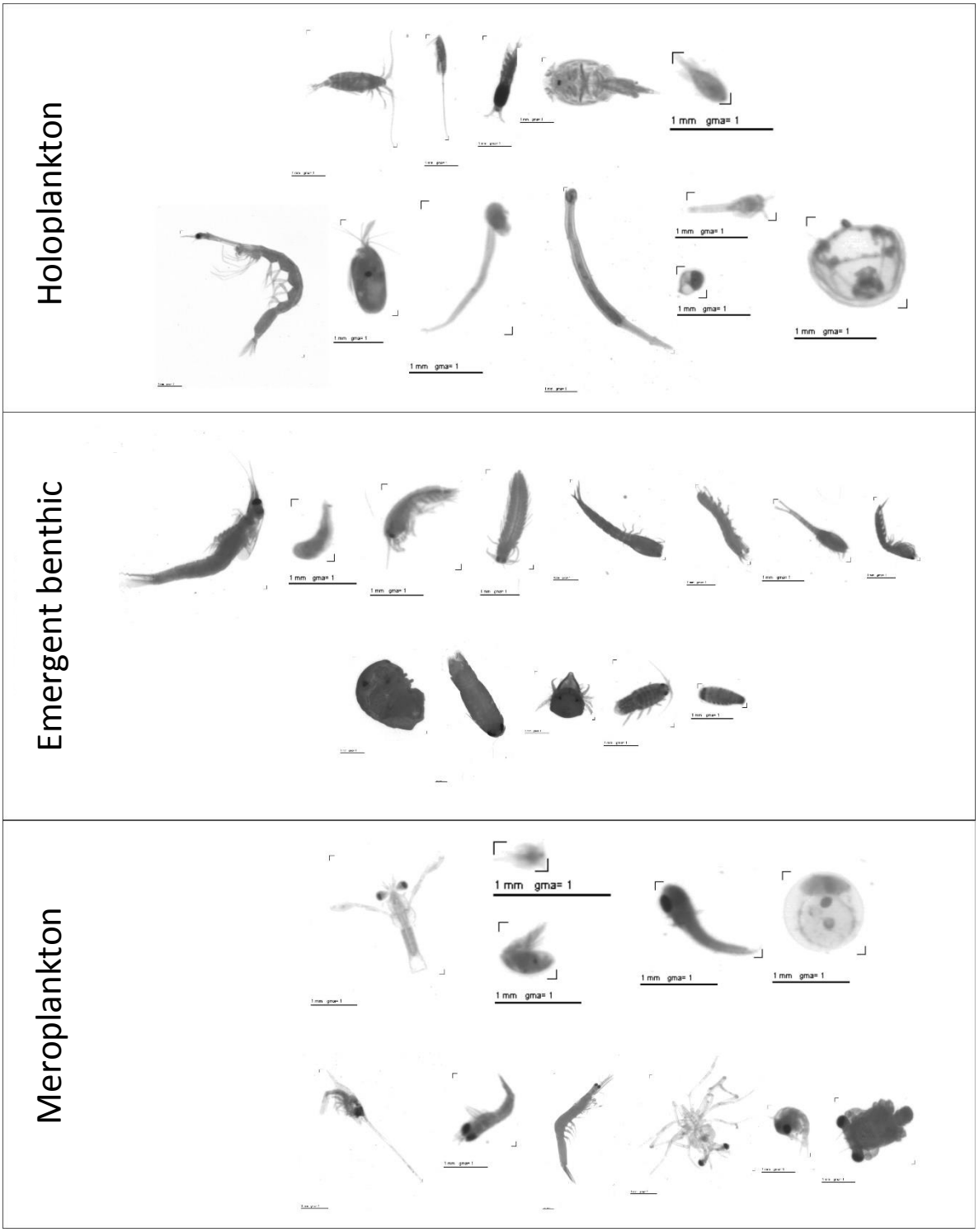
APÊNDICES

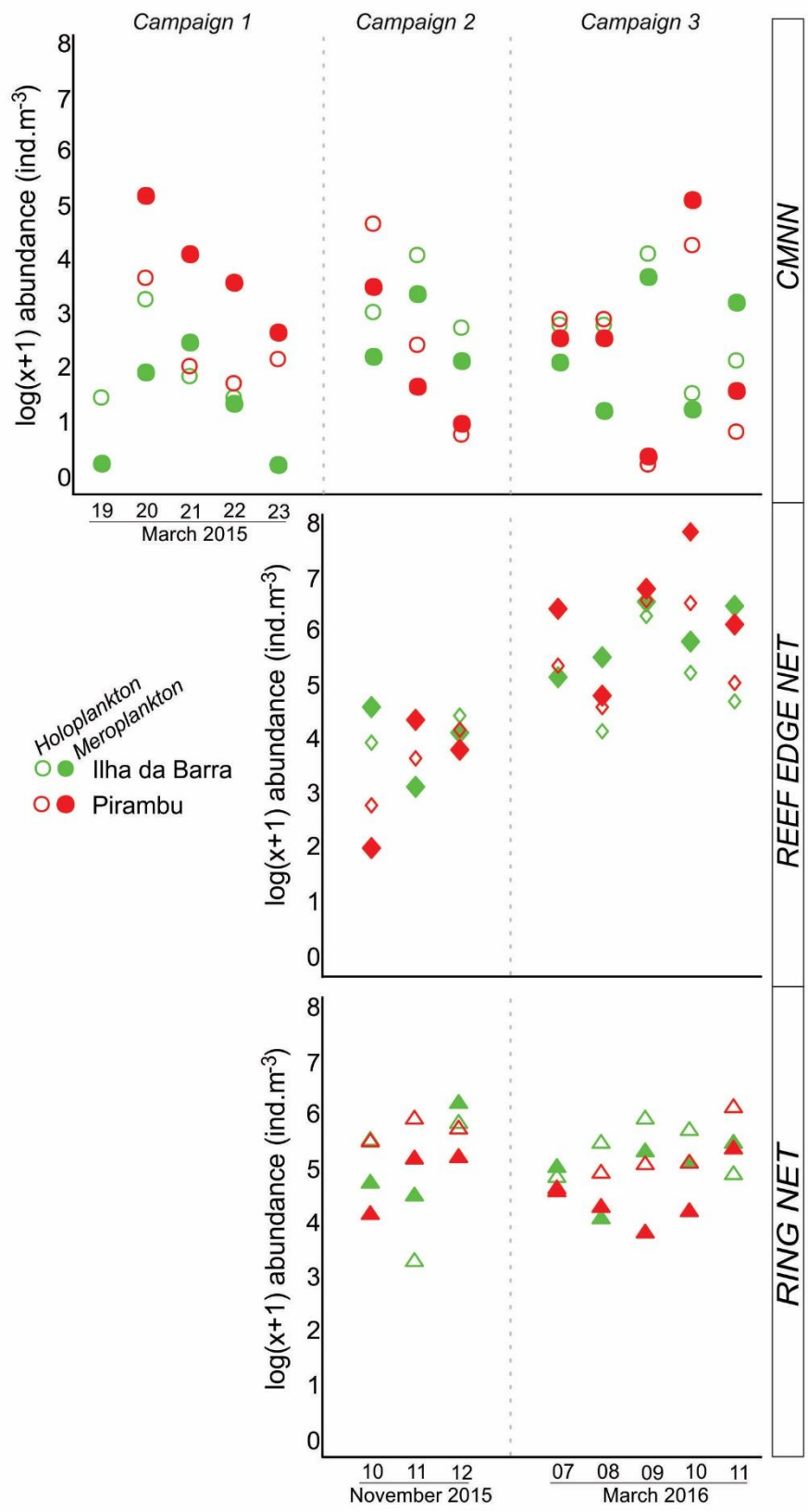
APÊNDICE A – Boxplots com os dados de volume filtrado das redes Channel Midwater Neuston Net (1 m), Reef Edge Net (REN) e rede cônica usadas na coleta de zooplâncton dos recifes de Tamandaré (PE, Brasil).



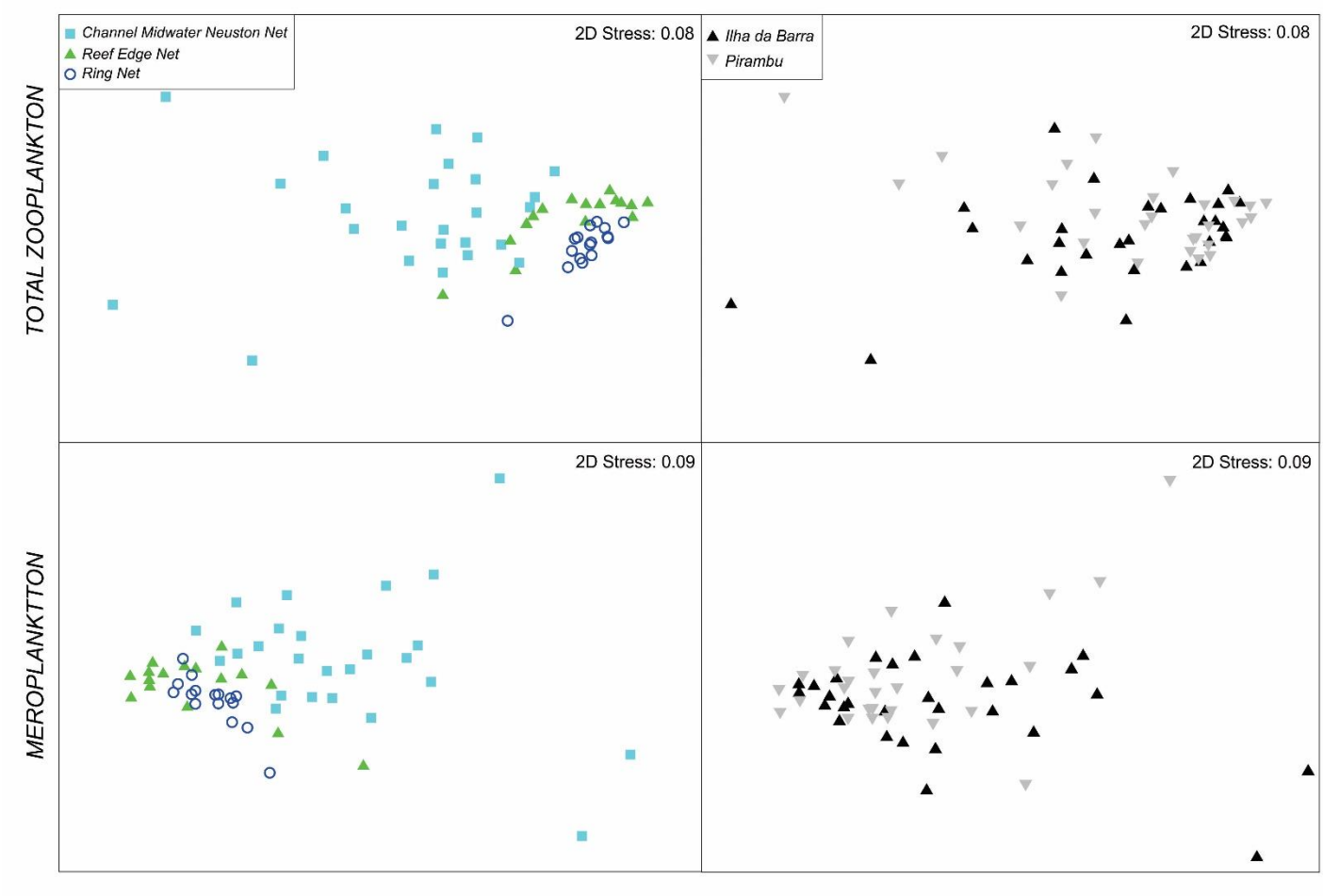
APÊNDICE B – Vinhetas obtidas com o uso do ZooScan. Organismos coletados nos recifes de Tamandaré (PE, Brasil).



APÊNDICE C – Abundâncias do meroplâncton e do holoplâncton amostrados nos recifes de Tamandaré (PE, Brasil).



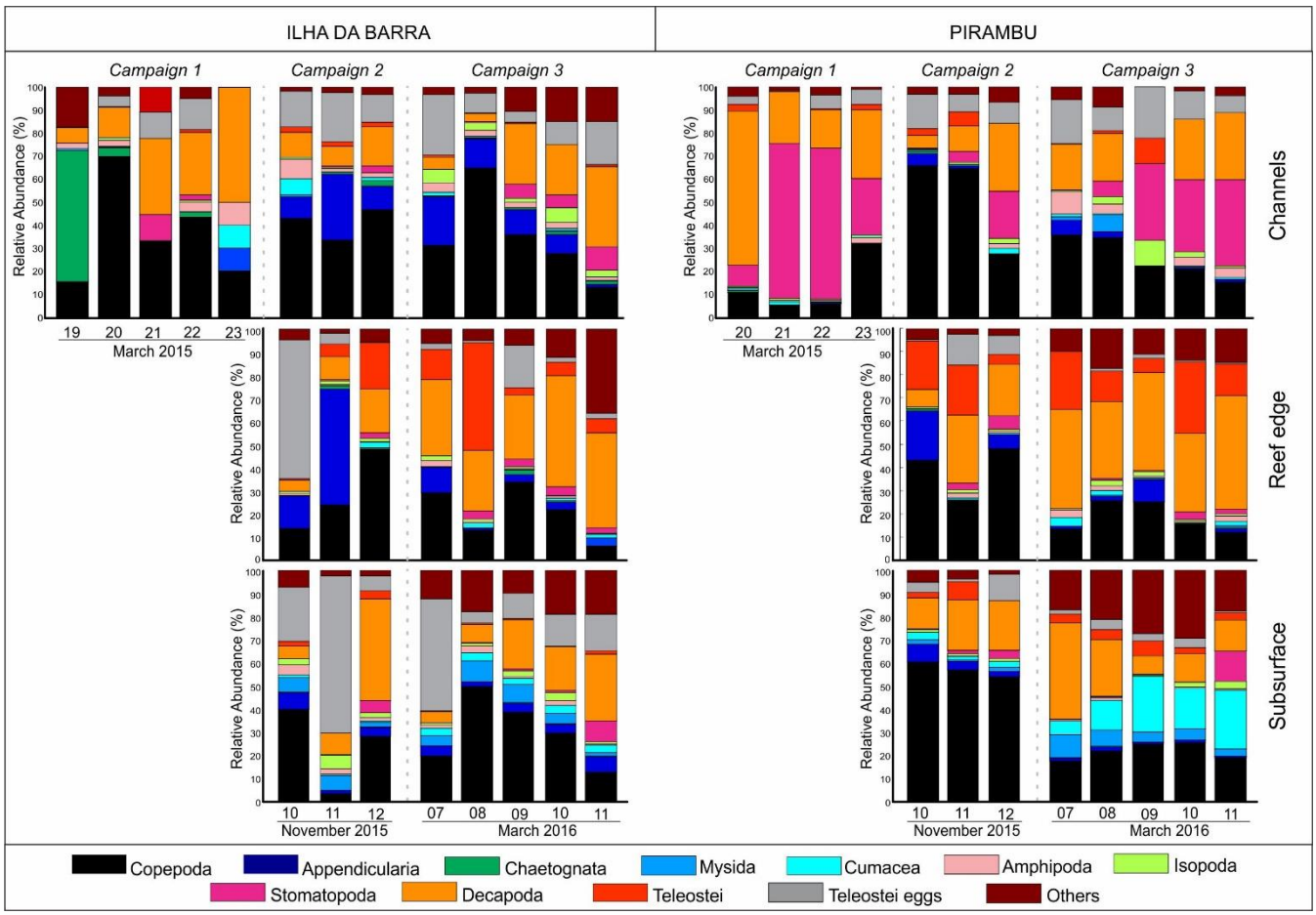
APÊNDICE D – Escalonamento multidimensional não métrico (nMDS) do zooplâncton amostrado nos recifes de Tamandaré (PE, Brasil).



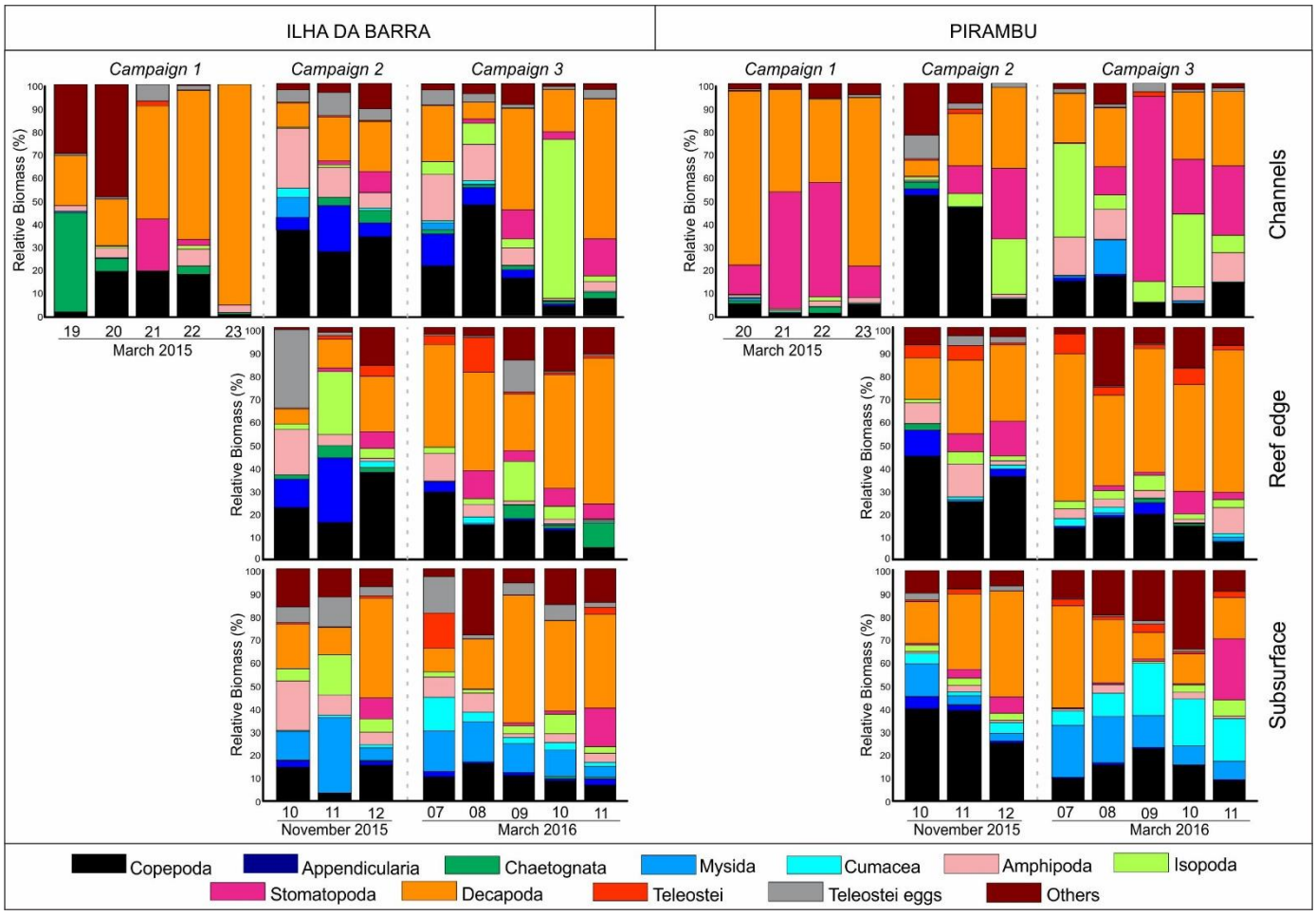
APÊNDICE E – Porcentagem de carbono e nitrogênio (em relação ao peso seco) usada para o cálculo da biomassa do zooplâncton dos recifes de Tamandaré (PE, Brasil).

Grandes grupos do zooplancton	C (%)	N (%)	referências
Amphipoda	33.15	9.3	Ikeda & Mckinnon (2012)
Appendicularia	46.3	12.7	Uye (1982)
Chaetognatha	51.5	14.52	Presente estudo
Cirripedia	36.9	7.83	Beers (1966)
Copepoda	41.43	10.63	Presente estudo
Cumacea	36.9	7.83	Beers (1966)
Decapoda	39.1	10	Presente estudo
Euphausiacea	50.39	8.74	Ikeda & Mckinnon (2012)
Hydrozoa	7.2	2.89	Beers (1966)
Isopoda	36.9	7.83	Beers (1966)
Mysida	46.08	8.38	Presente estudo
Ostracoda	18	2.4	Ikeda & Mckinnon (2012)
Polychaeta	41.6	15.27	Presente estudo
Siphonophorae	10.9	2.97	Beers (1966)
Stomatopoda	45.1	9.6	Ikeda & Mckinnon (2012)
Tanaidacea	36.9	7.83	Beers (1966)
Teleostei larvae and eggs	47.58	11.95	Presente estudo

APÊNDICE F – Abundância relativa (%) do zooplâncton amostrado na borda recifal, nos canais entre os recifes e em águas subsuperfíciais ao entorno do complexo recifal de Tamandaré (PE, Brasil). A categoria “outros” contém: Hydrozoa, Siphonophorae, Gastropoda, Polychaeta, Cirripedia (náuplios), *Belzebub faxoni* (camarão), Euphausiacea e Ostracoda



APÊNDICE G – Biomassa relativa (%) do zooplâncton amostrado na borda recifal, nos canais entre os recifes e em águas subsuperfíciais ao entorno do complexo recifal de Tamandaré (PE, Brasil). A categoria “outros” contém: Hydrozoa, Siphonophorae, Gastropoda, Polychaeta, Cirripedia (náuplios), *Belzebub faxoni* (camarão), Euphausiacea e Ostracoda



APÊNDICE H – Biomassa (ug C m^{-3}) dos principais grupos do zooplâncton amostrado na borda recifal, nos canais entre os recifes e em águas subsuperfíciais ao entorno do complexo recifal de Tamandaré (PE, Brasil). A categoria "Gelatinous" contém: Hydrozoa e Siphonophorae.