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**ESTRUTURA, PRODUTIVIDADE E FLUXO DE BIOMASSA DA
COMUNIDADE ZOOPLANCTÔNICA PELÁGICA E DEMERSAL DO BANCO
DE ABROLHOS**

**RECIFE
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RESUMO

A Tese foi dividida em 6 capítulos sendo o primeiro, introdutório e o último, composto pelas considerações finais. Para o segundo capítulo, o zooplâncton foi coletado durante o verão, em três áreas distintas. Duas estações em cada área foram estabelecidas para coletar durante o ciclo diurno. Aproximadamente 110 taxa foram identificados, e as comunidades das duas redes utilizadas foram significativamente diferentes. As abundâncias de zooplâncton foram três ordens de grandeza mais altas nas amostras da rede de 64 μm com uma abundância média de $217.000 \pm 93.418 \text{ ind m}^{-3}$ (64- μm) e $189 \pm 122 \text{ ind m}^{-3}$ (200- μm). A estrutura da comunidade do zooplâncton revelou diferenças significativas entre as três regiões. As formas holoplanctônicas dominaram as duas comunidades. A mudança diurna foi devida a um aumento na abundância apenas dos organismos maiores ($> 200 \mu\text{m}$), principalmente pelágicos, ao anoitecer. Assim, os resultados sugerem que os componentes pelágicos dessa comunidade zooplanctônica recifal podem ser tão importantes como os organismos demersais para o acoplamento bentônico-pelágico. Para o terceiro capítulo, o zooplâncton demersal no Banco Abrolhos foi estudado em resposta a diferentes formações de recifes e a substratos distintos. As coletas foram realizadas em dois locais de acordo com as formações locais do recife. Foram implantados dois tipos de armadilhas de emergência que revelaram uma comunidade diversificada com 53 taxa. A composição da fauna emergente dos diferentes locais diferiu estatisticamente, bem como a comunidade emergente dos substratos distintos (PERMANOVA). A abundância do zooplâncton demersal foi de $6.050 \pm 6.419 \text{ ind. m}^{-2}$, enquanto a biomassa total foi de $6.918,93 \pm 5,029,41 \mu\text{gC. m}^{-2}$. “Enxames” notáveis de *Dioithona oculata* foram registrados na estação do pináculo, enquanto os harpacticóides, compostos por 14 famílias, dominavam os recifes de franja. Esses resultados indicam que a morfologia da formação de recifes pode ter grande influência na distribuição do zooplâncton demersal, mas os substratos parecem ser o principal fator de influência. Para o quarto capítulo dois novos registros de *Paraspadella nana* (Owre, 1963) são relatados. Os indivíduos foram encontrados em dois locais distintos separados a mais de 1.000 km um do outro (o Banco Abrolhos e a baía de Tamandaré, no Nordeste do Brasil). Foram utilizadas armadilhas emergentes para o zooplâncton demersal para a coleta da amostra. Esta metodologia é proposta como a mais eficiente para capturar espécies de Spadellidae e possivelmente alterando a perspectiva sobre a distribuição desse grupo. Para o quinto capítulo, a mortalidade dos copepodes e sua consequência para as características ecológicas da comunidade foram avaliadas, considerando as variações espaciais e diurnas. O estudo foi realizado em 2 áreas (área recifal costeira; e área recifal afastada da costa). O maior percentual de indivíduos mortos foi de 83% (malha de 64 μm). Limitação de alimento e predação são indicadas como as prováveis causas da alta percentagem de indivíduos mortos encontrada. Muitas conclusões equivocadas podem ser feitas quando se considera que todos os indivíduos coletados estão vivos, principalmente quando se usa parâmetros relacionados com a densidade de organismos como a taxa de grazing, biomassa e produção.

Palavras-chave: Pelágico. Zooplâncton demersal. Armadilhas. Biomassa.

ABSTRACT

For the second chapter, the zooplankton samples were collected in summer and in three distinct Neotropical areas (the coastal reef arc, the outer reef arc and the Abrolhos Archipelago). Two stations in each sampling area were established to collect samples during a diel cycle. 110 taxa were identified, and the assemblages from the two nets used were significantly different. Zooplankton abundances were three orders of magnitude higher in the 64- μm net samples with an average abundance of $217,000 \pm 93,418 \text{ ind m}^{-3}$ (64- μm net) and $189 \pm 122 \text{ ind m}^{-3}$ (200- μm net). Total zooplankton abundances were approximately twice as high at the inshore reefs when compared with the offshore reefs. The PERMANOVA revealed significant differences between all three regions. Holoplanktonic forms dominated both net communities. The diel change was due to an increase in the abundance of only large and mostly pelagic zooplankters around dusk. Thus, our results suggest that the pelagic components of these reef zooplankton assemblages may be as important as demersal zooplankters to benthic-pelagic coupling. For the third chapter, the demersal zooplankton was studied in terms of composition, abundance and biomass, and their distributions patterns were assessed in response to different reef formations and to distinct substrates. Emergence trap were deployed and revealed a diverse community with 53 taxa. The composition of the emergent fauna differed between different sites and distinct substrates (PERMANOVA). The overall abundance of the demersal zooplankton was $6,050 \pm 6,419 \text{ ind. m}^{-2}$, whereas the overall biomass was $6,918.93 \pm 5.029.41 \mu\text{gC. m}^{-2}$. Remarkable swarms of *Dioithona oculata* were recorded in the pinnacle reef site whereas the harpacticoids, composed by 14 families, dominated the fringing reefs. These results indicate that the morphology of the reef formation may have great influence on the distribution of demersal zooplankton. For the fourth chapter, two new records of *Paraspadella nana* (Owre, 1963) are reported. The individuals were found in two distinct locations apart more than 1,000 km from each other (the Abrolhos Bank and the Tamandaré bay, Northeastern Brazil). Emergent traps for demersal zooplankton were used for the sample collection. This methodology is proposed as the most efficient to catch Spadellidae species and possibly changing the perspective on the distribution of this group. For the fifth chapter, the copepod mortality and its consequences to the ecological features of the community were assessed, considering the spatial and diel variations. The study was conducted in 2 areas. The vital status of the copepods was achieved with the use of the Neutral Red method. At the coastal reef area, *P. quasimodo* (200- μm net) and the Oithonids (mainly *O. nana*, 64- μm net) dominated the community, comprising 33% and 74% respectively. At the offshore reef area, *L. acutifrons* dominated both net catches in terms of biomass. The maximum percent dead copepods was recorded in the offshore reef area (83%, 64- μm net), although there was no significant differences between the areas. Food limitation and predation are addressed as the probable causes of the high mortality observed.

Keywords: Pelagic zooplankton. Demersal zooplankton. Emergence trap. Biomass.

SUMÁRIO

1	INTRODUÇÃO GERAL	9
1.1	Estrutura E Objetivos Da Tese	12
2	SUMMER MICRO- AND MESOZOOPLANKTON FROM THE LARGEST REEF SYSTEM OF THE SOUTH ATLANTIC OCEAN (ABROLHOS, BRAZIL): RESPONSES TO COAST PROXIMITY AND DIEL CYCLE	14
2.1	Introduction	14
2.2	Material And Methods	16
2.2.1	Study area	16
2.2.2	Field collection	18
2.2.3	Sample analyses	19
2.2.4	Data analyses	19
2.3	Results.....	20
2.3.1	Zooplankton communities	20
2.3.2	64- μ m mesh net	21
2.3.3	200- μ m mesh net	28
2.4	Discussion.....	36
2.5	Conclusions	42
2.6	Acknowledgements.....	43
3	INFLUENCE OF DIFFERENT HABITATS ON THE STRUCTURE PATTERNS OF CORAL REEF DEMERSAL ZOOPLANKTON AT ABROLHOS BANK.....	44
3.1	Introduction	44
3.2	Materials And Methods	45
3.2.1	Study area	45
3.2.2	Sampling strategy	45
3.2.3	Laboratory Procedures.....	47
3.2.4	Statistical analysis	48
3.3	Results.....	49
3.3.1	General results	49
3.3.2	Sites influence	53
3.3.3	Substrates effect	56
3.3.4	Traps efficacy	57
3.4	Discussion.....	58
3.5	Conclusions	62
4	A NEW PERSPECTIVE ON THE DISTRIBUTION OF CHAETOGNATHA, SPADELLIDAE, PARASPADELLA NANA OWRE, 1963: TWO NEW OCCURRENCES FROM THE WESTERN TROPICAL ATLANTIC OCEAN.....	63
4.1	Introduction	63
4.2	Material And Methods.....	64
4.3	Results And Discussion	65
4.4	Acknowledgements.....	67

5	SPATIAL AND DIEL VARIATIONS OF LIVE/DEAD COMPOSITIONS OF A REEF COPEPOD COMMUNITY: IMPLICATIONS FOR ECOLOGICAL STUDIES	68
5.1	Introduction	68
5.2	Materials And Methods	69
5.2.1	Study area.....	69
5.2.2	Field collection.....	70
5.2.3	Laboratory procedures.....	71
5.2.4	Statistical analysis	72
5.3	Results.....	74
5.3.1	Environmental parameters.....	74
5.3.2	Copepod community composition and abundance.....	74
5.3.3	Copepod biomass and vital status.....	75
5.4	Discussion	78
5.4.1	Copepod abundance and biomass.....	78
5.4.2	Live/dead composition of copepods	78
5.4.3	Vital Status implications for ecological studies	80
6	CONSIDERAÇÕES FINAIS	82
	REFERÊNCIAS	85

1 INTRODUÇÃO GERAL

Recifes de coral estão entre os ecossistemas mais diversos do planeta (Andradi-Brown *et al.*, 2017). Nesses ambientes altamente diversos a importância do Zooplâncton é reconhecida por seu papel ecológico no transporte de energia (Alldredge e King, 1977) e nos processos de acoplamento bento-pelágico (Schnack-Schiel e Isla, 2005) atuando de forma fundamental sobre outras comunidades coabitantes dos recifes, como organismos sésseis planctívoros (Sebens, 1977) e peixes planctívoros noturnos (Robertson e Howard, 1978). Estudos relatam ainda, efeitos das variações de concentração do zooplâncton sobre a taxa de assimilação de corais (Palardy *et al.*, 2006). Embora os corais possam obter 100% de sua demanda energética através da fotossíntese das zooxantelas endossimbióticas, nutrientes como nitrogênio e fosforo são apenas assimilados através do zooplâncton (Titlyanov *et al.*, 2001).

O zooplâncton apresenta-se, portanto, como um dos grupos mais importantes na teia trófica, agindo como eficiente elo na transferência de energia fitoplâncton-bacterioplâncton e/ou material orgânico particulado para os demais níveis tróficos, participando também na regeneração e transporte de nutrientes (Elser *et al.*, 1988). Emery (1968) descreveu pela primeira vez a existência de uma comunidade zooplancônica residente dos recifes de coral. Posteriormente, Porter (1974) usou o termo “zooplâncton demersal” para descrever uma comunidade que apresenta uma migração vertical ativa, permanecendo próxima ao substrato durante o dia e ascendendo a coluna d’água durante a noite. Apesar do termo zooplâncton demersal ser comumente usado, é difícil determinar nas comunidades zooplancônicas recifais quais organismos são de fato demersais, uma vez que muitas espécies, inclusive de copepodes, são conhecidamente pelágicas holoplancônicas, porém são observadas com comportamento demersal quando estão em ambientes recifais (Alldredge e King, 1977).

A comunidade zooplancônica demersal se distingue do zooplâncton que permanece continuamente na coluna d’água (zooplâncton pelágico ou holozoplâncton) por suas associações periódicas com o substrato bentônico (Cahoon e Tronzo, 1992). Embora tenha uma distribuição ampla de habitats, nos recifes de coral o zooplâncton demersal é particularmente abundante e diverso (Alldredge e King, 1977). Devido à dificuldade de classificação desses organismos que migram entre os domínios bênticos e

pelágicos, vários termos têm sido utilizados ao longo do tempo, na tentativa de melhor descrever esse grupo. Porter *et al.* (1977), como mencionado anteriormente, se referiu a esses organismos como “plâncton demersal”. Assim como Porter, outros autores fazem referência a essa comunidade utilizando termos relacionados ao comportamento migratório, como “fauna emergente” ou “zooplâncton emergente” (Jacoby e Greenwood, 1989; Pitt *et al.*, 2008; Kramer *et al.*, 2013), e há ainda menções ao termo ecológico “plâncton bento-pelágico” (Vereshchaka e Anokhina, 2014).

Independente do termo usado para se referir ao zooplâncton demersal, o fato dessa comunidade realizar as migrações que a caracterizam, a torna um importante componente do acoplamento bento-pelágico, realizando a transferência de carbono entre os domínios bênticos e pelágicos, tanto em ambientes recifais como em outros ambientes costeiros (Pitt *et al.*, 2008). O zooplâncton demersal é um importante componente da dieta de animais tanto pelágicos (Couturier *et al.*, 2013) como bentônicos (Heidelberg *et al.*, 2004).

O zooplâncton tem um papel fundamental nos ecossistemas, atuando na ciclagem biogeoquímica (Longhurst e Harrison, 1988), exportação de matéria orgânica através de pelotas fecais (Haney e Trout, 1990) e atuando ainda como link trófico. Nos ecossistemas recifais, os copepodes tem sido reportados como o principal link trófico, sendo o principal componente da dieta de larvas de peixe (Mckinnon e Duggan, 2003). Entretanto, a mortalidade dos copepodes reduz a abundância total e o número de indivíduos ativos, reduzindo assim o impacto dessa população quanto ao “*grazing*”, a biomassa e sua produção.

A mortalidade é um processo inerente a vida que afeta a dinâmica das populações. Apesar da sua importância, a mortalidade é ainda pouco estudada em recifes de coral (Genin *et al.*, 1995). Apesar da principal causa ser atribuída a predação, muitos estudos tem relatado a importância da mortalidade não predatória sobre as comunidades de copepodes (Di Capua e Mazzocchi, 2017). Essa mortalidade está relacionada a doenças, poluição, estresse ambiental, parasitas, senescência e falta de recursos alimentares (Tang *et al.*, 2014; Di Capua e Mazzocchi, 2017).

De fato, o conhecimento da taxa de mortalidade é um dos componentes mais cruciais para o entendimento da dinâmica natural das populações de copepodes (Tang e

Elliott, 2014). Além de potencialmente reduzir impactos dessa população em determinados ambientes, uma grande quantidade de carcaças pode representar o principal componente do fluxo de sedimentação de matéria orgânica (Tang e Elliott, 2014), além de servir como recurso para organismos que vivem perto ou diretamente relacionados com o bentos. Ignorar a ocorrência de carcaças, mesmo que nas menores concentrações pode levar a erros significantes no entendimento da dinâmica populacional dos copepodes e dos processos ecológicos associados a isso (Elliott e Tang, 2011).

O Banco de Abrolhos é bem conhecido por ser ter o sistema recifal mais importante do atlântico sul, com alto grau de endemismo, e uma agregação única de corais (Leão e Kikuchi, 2005), rodolitos (Amado-Filho, G.M. *et al.*, 2012), prados de fanerógamas e algas (Creed e Amado-Filho, 1999), mangue (Moura *et al.*, 2011) e substrato inconsolidado (Marchioro *et al.*, 2005). Apesar de todo o conhecimento dessa região, a comunidade zooplanctônica ainda representa uma lacuna nos estudos em Abrolhos. Os principais estudos do zooplâncton em Abrolhos abordam a comunidade de tintínídeos (Costa *et al.*, 2015), a estrutura espacial do meroplâncton (Koettker e Lopes, 2013), e o espectro de tamanho das comunidades zooplanctônicas (Schultes e Lopes, 2009; Marcolin *et al.*, 2013; Marcolin *et al.*, 2015).

1.1 Estrutura E Objetivos Da Tese

Esta tese é composta por um estudo dividido em 4 partes, escritos em formato de manuscrito com a intenção de responder aos seguintes questionamentos:

O capítulo 2 avalia o zooplâncton recifal do Banco de Abrolhos em termos de abundância e diversidade, com o objetivo de compreender a distribuição das espécies em relação a proximidade da costa, levando-se em conta as variações diurnas, além de avaliar a influência dos recifes sobre a composição da comunidade e as diferentes resultados obtidos com redes de plâncton com malhas diferentes (64 μm e 200 μm). Os questionamentos específicos foram:

- Como ocorre a distribuição das espécies (densidade e diversidade) nos recifes costeiros e nos afastados da costa?
- O recife de coral influencia a composição da comunidade zooplânctônica pelágica?
- Ocorrem flutuações na densidade e ocorrência de espécies ao longo de um ciclo diurno?
- Que influência o uso de diferentes malhas pode exercer sobre o resultado obtido?

O capítulo 3 teve como objetivo examinar o comportamento e distribuição do zooplâncton demersal, procurando avaliar as respostas da comunidade com relação a diferentes habitats. Os questionamentos específicos foram:

- A formação de recifes de franja tem uma fauna emergente diferente da encontrada em recifes de chapeirões?
- O quão forte é a influência do tipo de formação recifal sobre a diversidade, densidade, abundância e distribuição do zooplâncton demersal?
- A influência das formações recifais é superior a exercida pelos diferentes tipos de substratos?

O capítulo 4 reporta a ocorrência de uma espécie rara de Chaetognatha bentônico (*Paraspadella nana*) e procura estabelecer uma nova perspectiva para a distribuição de espécies da família Spadellidae fazendo referência a metodologia de coleta utilizada para

a captura dos espécimes reportados, que não é comumente utilizada para a coleta de Chaetognatha com comportamento demersal.

O capítulo 5 teve como objetivo avaliar a ocorrência de carcaças de Copepoda (porcentagem de indivíduos mortos) no sistema recifal do Banco de Abrolhos, buscando relacionar os valores encontrados com as consequências ecológicas atribuídas a essa mortalidade, além de fazer uma avaliação das possíveis consequências para os estudos ecológicos que são realizados sem que se leve em conta a incidência de indivíduos mortos. Para isso foram utilizados parâmetros como a composição, abundância e biomassa. Os questionamentos específicos foram:

- Qual a porcentagem de indivíduos mortos na comunidade dos Copepoda no Banco de Abrolhos?
- Diferentes áreas recifais próximas e afastadas da costa e o ciclo diurno tem influência sobre a incidência de indivíduos mortos?
- Os parâmetros ambientais no Banco de Abrolhos influenciam a mortalidade dos Copepoda?
- Quais as consequências ecológicas para a comunidade dos Copepoda?
- Quais as consequências que a falta de informação quanto a mortalidade tem para os estudos ecológicos em áreas recifais?

2 SUMMER MICRO- AND MESOZOOPLANKTON FROM THE LARGEST REEF SYSTEM OF THE SOUTH ATLANTIC OCEAN (ABROLHOS, BRAZIL): RESPONSES TO COAST PROXIMITY AND DIEL CYCLE

2.1 Introduction

Coral reefs are limited to tropical oceans and cover only 0.1% of the surface of the earth, yet they have major consequences for global marine biodiversity. Reefs provides habitat for remarkably diverse animal phyla with characteristic distribution patterns and composition (Kohn, 1997). These patterns reflect the effect of several processes, which are largely characterized as niche-based (Armstrong e Mcgehee, 1980; Leibold, 1995) or determined by dispersal limitation (Hubbell, 2001).

In assessing any group of species in reef areas, it is central to specify the scale (type of diversity) that is being studied, particularly when dealing with patterns of diversity. Whittaker (1972) classified the types of diversity as alpha diversity, which refers to the diversity inside a specific area or ecosystem, where all species are supposed to interact and compete with each other for similar limiting resources, and this is frequently expressed by the species number (i.e., richness). However, beta diversity measures the modification in diversity of species from one ecosystem to another; and gamma diversity is the amount of the total diversity for the different ecosystems inside a region, and the operated processes are much more evolutionary than ecological.

Besides scale type, Walker (1992) mentions the importance of concentrating on the groups that are important to maintaining environmental resilience. Among these, zooplankton play major roles in most ecosystem processes and are essential links in food webs. In addition, they also exhibit a tremendous diversity of traits, ecological strategies and consequently impact other trophic levels in the cycling of materials and energy (Litchman *et al.*, 2013).

Zooplankton are probably the best studied component of planktonic communities of reef ecosystems because they have been studied since the 1930s (Sorokin, 1990a). In most of these pioneer studies (Russel, 1934; Edmondson, 1937; Farran, 1949), zooplankton were collected only during the daytime and the migratory behavior of this community was unknown, which led to a misunderstanding that reef zooplankton consist

mostly of planktonic organisms of adjacent waters passing over the reef (Emery, 1968; Johannes *et al.*, 1970). However, according to Sorokin (1990a), a feature of reef zooplankton is the domination of the population by species connected to the benthos to which they migrate during the daytime. At night some species go up into the water column causing reef zooplankton to differ from that of the surrounding pelagic areas in its species composition, behavior, and abundance. Among these species are holoplanktonic forms (copepods, mysids and amphipods) as well as demersal species and meroplanktonic larvae (Emery, 1968; Alldredge e King, 1980; Melo, P. A. M. C. *et al.*, 2010).

Recent studies have created a better understanding of the dynamics of reef zooplankton based on their diversity, vertical distribution, biomass and production. Many studies have used finer mesh (i.e. 64 μm) aiming to collect the smaller zooplankton fractions missed when passing through coarser meshes (i.e. 200-300 μm) (Hopcroft *et al.*, 1998). Small-size classes play an essential role in marine food webs by feeding on autotrophic and heterotrophic protists, marine snow and bacteria (Roff *et al.*, 1995; Green e Dagg, 1997; Turner, 2004) and may represent the greater portion of local zooplankton production (Hopcroft *et al.*, 1998). Therefore, Hopcroft *et al.* (1998) stressed the importance of using two standard nets in field work (64 and 200 μm) to better assess the community and reduce possible biases due to the selectivity of the nets. Nevertheless, reef zooplankton studies simultaneously using two different mesh nets are rare around the world (Chisholm e Roff, 1990a; b; Webber, M. K. e Roff, J. C., 1995; Webber, M.K. e Roff, J.C., 1995; Hopcroft *et al.*, 1998) and absent in the Abrolhos Bank.

A great deal is known about reef zooplankton communities from the Pacific Ocean (the Great Barrier Reef in Australia) (Alldredge e King, 1977; Hamner *et al.*, 1988; Roman *et al.*, 1990; Mckinnon e Thorrold, 1993; Mckinnon *et al.*, 2005) and the North Atlantic Ocean (Caribbean Sea reefs) (Moore e Sander, 1976; Yoshioka *et al.*, 1985; Heidelberg *et al.*, 2004; Álvarez-Cadena *et al.*, 2009; Heidelberg *et al.*, 2010). However, even though the Abrolhos Bank in the South Atlantic is comparable in size to the Caribbean Sea in the North Atlantic Ocean (Amado-Filho, G. M. *et al.*, 2012; Moura *et al.*, 2013), fewer studies have been conducted in this area.

The Abrolhos Bank comprises the most important coralline reefs in the South Atlantic with high levels of endemism and unique mushroom-shaped coralline pinnacles (Leão e Kikuchi, 2005). The continental shelf in the Abrolhos Region encompasses a complex benthic habitat mosaic in which the world's largest rhodolith bed covers $\approx 20,900$ km², whereas coralline reefs cover ≈ 8800 km² (Moura *et al.*, 2013). However, despite the ecological importance of the Abrolhos Bank, other smaller reef sites of Brazil have been better studied. In the Abrolhos, studies have detailed the tintinnids community (Costa *et al.*, 2015), phytoplankton biomass and production (Gaeta *et al.*, 1999), meroplankton spatial structure (Koettker e Lopes, 2013), zooplankton communities size spectra (Schultes e Lopes, 2009; Marcolin *et al.*, 2013; Marcolin *et al.*, 2015), pico-, nano-, and microplankton (Ribeiro, 1999), and microphytoplankton structure (Susini-Ribeiro *et al.*, 2013).

The present study was conducted to evaluate the reef zooplankton biodiversity and abundance in the Abrolhos Region using two different mesh nets encompassing the alpha and beta diversities. Our goal was to assess the community in terms of species composition, diel cycle, the community changes related to the coast proximity, and the influence of the reefs over the pelagic zooplankton community. Until we have a better knowledge of the zooplankton diversity of coral reefs and the processes that control it, we have little confidence in conserving the reef ecosystems.

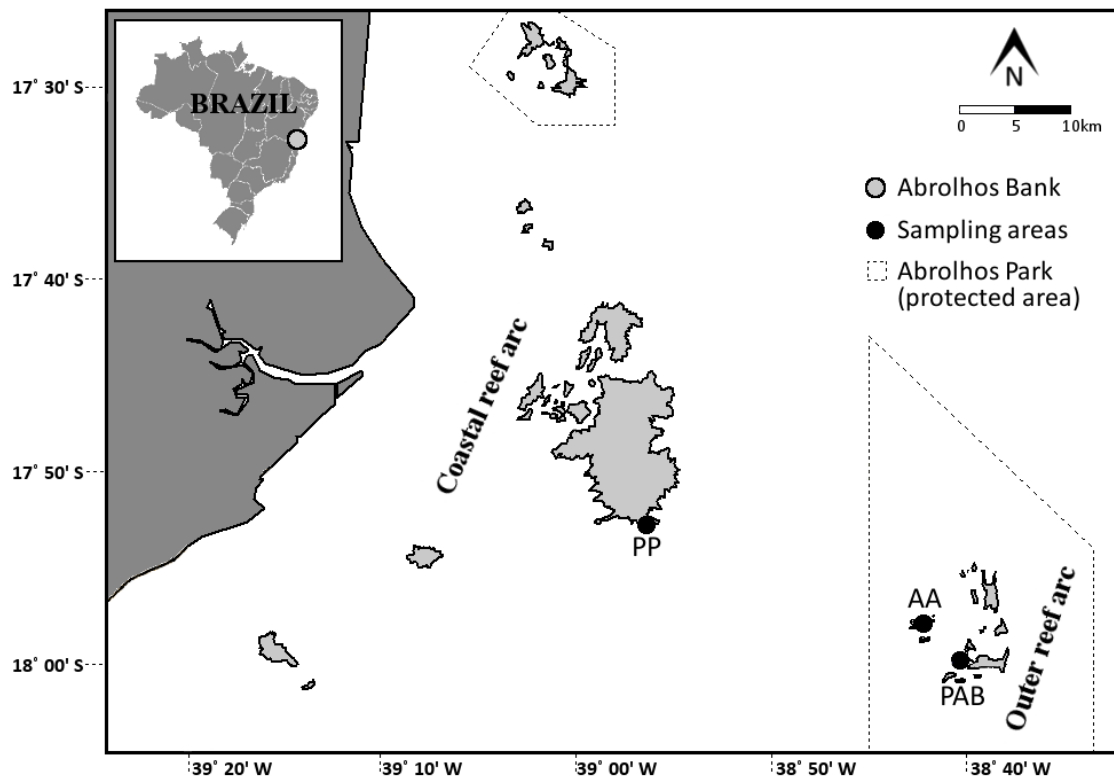
2.2 Material And Methods

2.2.1 Study area

The Abrolhos Bank is located between 17°S and 20°S on the Eastern Brazilian Continental Shelf (EBCS) (Fig 1). The EBCS is generally narrow from 5°S up to 15°S and at some point reaches less than 10 km offshore, which results in a strong influence by oceanic oligotrophic waters of the South Equatorial Current (Lopes e Castro, 2013). The Abrolhos Bank represents an enlargement of the EBCS, reaches 245 km offshore (Knoppers *et al.*, 1999), and covers an amazing set of megahabitats hosting rhodolith beds (Amado-Filho, G. M. *et al.*, 2012) and unique coralline reef cover (Leão e Kikuchi, 2001a; Moura *et al.*, 2013), seagrass, and algae bottoms (Creed e Amado-Filho, 1999)

with a great extent of soft bottom (Marchioro *et al.*, 2005). Despite this enlargement, the topographic gradient of the continental shelf of the Abrolhos Bank facilitates a high shoreward intrusion of Tropical Water coming from the Brazil Current, which is warm ($T > 20^{\circ}\text{C}$), saline ($S > 36.4$) and nutrient-poor (Castro e Miranda, 1998; Koettker e Lopes, 2013). Wind stress is the primary agent forcing water motion southward on the inner and middle shelf, whereas the Brazil current is a major influence on the outer shelf.

Fig 1. Study area. Sampling locations across the Abrolhos Bank. The sampling areas according to the proximity to the continent (i.e., Parcel das Paredes - PP; Abrolhos Archipelago - AA; Parcel dos Abrolhos - PAB). Dotted lines correspond to Abrolhos Park (protected area).



Fonte: Lucas Figueirêdo

The Abrolhos Bank's coralline reefs are unique in terms of structure. Coralline mushroom-shaped pinnacles, known locally as "Chapeirões", grows towards the surface (Leão, 1999). The combined influences of oligotrophic oceanic waters and muddy sediment deposition on the Abrolhos coastal reefs originating from river discharge (Doce

River) also contribute to the unique features of this reef ecosystem, since carbonate sedimentation predominates in other tropical reefs (Lopes e Castro, 2013). The major coralline formations include an inner arc and an outer arc in relation to the proximity of the coast.

The coastal arc is located at 5–30 km from the coastline in which “Parcel das Paredes” (PP) is the main coralline formation. Here, the reef developed to form coalesced reef tops reaching up to 17 km wide at “Pedra Grande” (Leão, 1999). Depths from the unconsolidated bottom to the surface are typically 15 m, though the reef top can emerge in places during low tide periods. The outer arc is located at 60–65 km offshore and borders the east side of the Abrolhos Archipelago at depths of up to 25 m (Moura *et al.*, 2013). Extending for 15 km in the north-south direction, the outer arc consists of multiple and sparse pinnacles that sometimes reach the surface. This arc is known as “Parcel dos Abrolhos” (PAB) (Leão, 1999). The Abrolhos Archipelago (AA) presents fringing reefs extending up to 50-60 m from the coast. These reef formations developed over volcanic or sedimentary hard substrates with little growth upward at depths up to 5 m (Leão, 1999).

2.2.2 Field collection

Intensive samplings were conducted during the summer (February) of 2012. Three areas were sampled: Parcel das Paredes (PP) located ≈ 30 km from the coastline ($17^{\circ}52'48.1''\text{S}$, $38^{\circ}56'19.2''\text{W}$); Abrolhos Archipelago (AA) located ≈ 52 km from the coastline ($17^{\circ}57'57.4''\text{S}$, $38^{\circ}42'09.2''\text{W}$); and Parcel dos Abrolhos (PAB) located ≈ 62 km from the coastline ($17^{\circ}59'55.2''\text{S}$, $38^{\circ}40'15.9''\text{W}$). In each area, one station was established directly over the reef top (reef station; RS) and another was located nearly 1 km away from the reef (outer station; OS). Sub-surface plankton tows were conducted simultaneously with two cylindrical-conical nets (mesh sizes: 64 and 200 μm) equipped with a flowmeter for 5 minutes. The hauls were conducted every 6 h over a 24-h period (0 h, 6 h, 12 h, 18 h) in subsequent days for each station. The samples were fixed with 4% formaldehyde and buffered with 4 g L⁻¹ sodium tetraborate for laboratory analyses.

2.2.3 Sample analyses

The 64- μm samples were subsampled (1 mL) and examined using Sedgewick-Rafter chambers and an optical microscope. For each sample, three subsamples with at least 300 individuals were analyzed, and their mean was calculated for later estimation of abundance. For the 200- μm samples, aliquots were taken with a Motoda splitter and analyzed using Bogorov counting chambers under a stereomicroscope. Considering a minimum of 300 individuals per subsample, the aliquots ranged up to 1/64 of the original sample (Omori e Ikeda, 1984). The identification was performed at the lowest taxonomic level possible. The abundance for all of the species throughout the paper is expressed as the number of individuals per cubic meter (ind m^{-3}).

2.2.4 Data analyses

The structure of the community was described by commonly used diversity parameters including species richness, total abundance of all taxa, Pielou's evenness (Pielou, 1977) and the Shannon-Wiener diversity index (Shannon, 1948). A normality test was performed with the abundance and ecological indices data (Kolmogorov-Smirnov test). Diversity and density metrics between communities were tested for statistical significance by using T-test and one-way ANOVA (parametric) or *Mann-Whitney* and *Kruskal-Wallis* (non-parametric) to compare the different periods (0 h, 6 h, 12 h, 18 h), stations (RS and OS), and areas (PP, AA, PAB). When the differences were significant ($P < 0.05$), Dunn's method of pairwise comparisons among groups was performed.

Additionally, a permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001) was used to test for significant differences between zooplankton community groupings on the three studied sites. To achieve this, a Bray-Curtis similarity matrix was previously obtained where the raw data for species abundance were transformed into $\log(x+1)$. For all of the analyses, 999 random permutations were tested. Based on this index, non-metric multidimensional scaling (MDS) was used to graphically

visualize differences in the zooplankton community structure. To assess the distribution pattern of zooplankton assemblages at the intra-specific level, the similarity of zooplankton assemblages among the sampling sites was compared by similarity percentage analysis (SIMPER). Also, to identify species assemblages that characterize each area, the Indicator Value index (IndVal, Dufrene and Legendre et al., 1997) was calculated for each species based on the fidelity and specificity of the species in relation to groups of sites. The indicator value of species i for class j is obtained with the equation $\text{IndVal}_{ij} = A_{ij} \times B_{ij} \times 100$, where A_{ij} is specificity, i.e., the proportion of the individuals of species i that are in class j ; and B_{ij} is fidelity, i.e. the proportion of sites in class j that contain species i (Chew *et al.*, 2015)

2.3 Results

2.3.1 Zooplankton communities

A total of 110 taxa were detected across all of the sampling areas and belonging to the Amoebozoa, Foraminifera, Ciliophora, Cnidaria, Bryozoa, Mollusca, Annelida, Arthropoda (Crustacea), Echinodermata, Chaetognatha and Chordata.

In the 64- μm net, Foraminifera and Ciliophora were the more diverse groups with 11 and 5 species respectively. Tintinnids, Foraminifera, nauplii and juveniles of Copepoda, veligers of Gastropoda and Bivalvia and young appendicularians of the genus *Oikopleura* represented the community captured with the 64 μm net. However, the 200- μm net were comprised mostly of copepods, other crustacean larvae (mainly Caridea), and adult appendicularians, with Copepoda as the most diverse group with 32 species divided into the families Calanidae, Paracalanidae, Clausocalanidae, Temoridae, Pontellidae, Acartidae, Oithonidae, Miraciidae, Harpacticidae, Metidae, Tegastidae, Oncaeidae and Corycaeidae. Holoplankton dominated both net samples and represented $85 \pm 11\%$ of the 64 μm net and $74 \pm 12\%$ of the 200 μm net community.

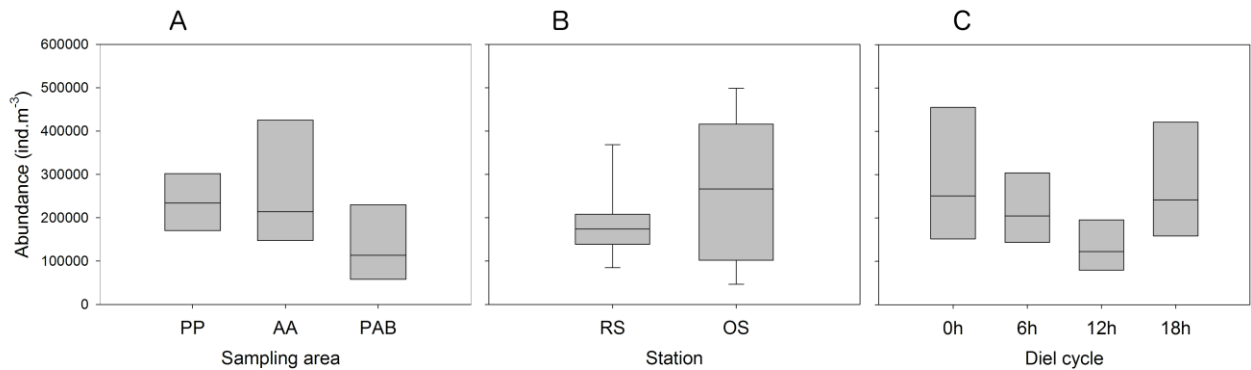
With reference to the holoplankton, Copepoda was the most important group both in the 64- μm and the 200- μm net with $67 \pm 18\%$ and $41 \pm 24\%$ of total abundance, respectively. However, in the 64- μm net, mainly copepodids of *Oithona* spp. and copepod nauplii were responsible for the holoplankton dominance (Table 1), whereas in

the 200- μm net, Paracalanidae and Pontellidae species had the greatest contributions (Table 2). Zooplankton densities in the 200- μm net samples were significantly lower, being only 9% of that in the 64- μm net samples (Mann-Whitney test, $P > 0.05$).

2.3.2 64- μm mesh net

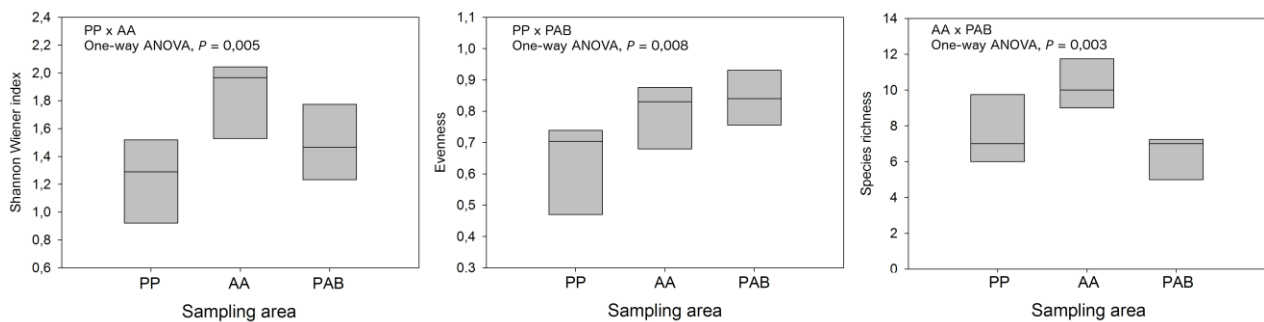
Total density in the 64 μm net samples averaged $239,729 \pm 99,270$ ind. m^{-3} (PP), $261,347 \pm 151,058$ ind. m^{-3} (AA) and $151,166 \pm 132,265$ ind. m^{-3} (PAB) (Fig 2). Although the highest values occurred in AA, no significant differences were observed between the sampling areas (one-way ANOVA, $P > 0.05$). Regarding the diel cycle, the abundance averaged $286,056 \pm 162,104$ ind. m^{-3} (0 h), $226,355 \pm 114,035$ ind. m^{-3} (6 h), $135,590 \pm 75,863$ ind. m^{-3} (12 h) and $269,717 \pm 150,781$ ind. m^{-3} (18 h) (Fig 3). There was no significant variation during the diel cycle (Mann-Whitney test, $P > 0.05$), even though a slight elevation of the abundance values was observed during the night period (0 h and 18 h) driven by *Oithona* spp. (juvenile), Copepod nauplii and *Codonellopsis schabi*. The estimates of abundance from the 64 μm net catches had no significant differences between stations (Mann-Whitney test, $P > 0.05$), which presented an average of $183,950 \pm 85,865$ ind. m^{-3} (RS) and $262,922 \pm 159,095$ ind. m^{-3} (OS) (Fig 2). Regarding the diversity indices, differences were only found between the sampling areas (Fig 3). The Shannon diversity index was significantly lower in PP, which was induced by the dominance of a few species.

Fig 2. Abundance from the 64 μm net catches (ind. m^{-3}) in Summer 2012. (A) Sampling area (Parcel das Paredes - PP; Abrolhos Archipelago - AA; and Parcel dos Abrolhos - PAB), (B) stations (reef station – RS; outer station – OS), and (C) diel cycle- Abrolhos Bank in February 2012.



Fonte: Lucas Figueirêdo

Fig 3. Diversity indices from the 64 μm net catches in Summer 2012. Parcel das Paredes - PP; Abrolhos Archipelago – AA, and Parcel dos Abrolhos - PAB. Pair-wise test results for significant differences between the sampling areas at the top of each plot. Abrolhos Bank in February 2012.



Fonte: Lucas Figueirêdo

Table 1: Mean abundances (ind. m^{-3}) for the principal zooplankton taxonomical groups for the 64- μm net in Summer 2012.

Species/Taxa	PP		AA		PAB	
	RS	OS	RS	OS	RS	OS
Zooplankton	163623	315833	185038	337657	209603	92729
Holoplankton (85 ± 11%)	152756	285334	128517	269311	192030	79926
Meroplankton (15 ± 11%)	10867	30499	56521	68346	17573	12803
Foraminifera						
<i>Amphistegina</i> sp.	239	986				1834
<i>Globorotalia</i> sp.				2468	309	589

Species/Taxa	PP		AA		PAB	
	RS	OS	RS	OS	RS	OS
<i>Quinqueloculina</i> sp.		449	3116		4659	
<i>Spirillina</i> sp.			662	737	3499	1834
<i>Spiroloculina</i> sp.				581	3191	2052
<i>Textularia</i> sp.		1435	369	823	8235	
<i>Tretomphalus bulloides</i>	362	449	565	1083		917
<i>Codonellopsis schabi</i>	8909	24634	13160	43526		917
<i>Epiplocylys</i> sp.	239		3107	1083		
<i>Leprotintinnus nordqvistii</i>	4340	4317		542	1595	
Gastropoda (veliger)	7767	15842	24599	55512	10012	6800
Bivalvia (veliger)	943	9613	10576	4327	4981	4902
Polychaeta (larvae)	1793	2612	2845	4782	1474	
<i>Nereis</i> sp.			511	581		
Ostracoda	218	1709	2494	1559	3558	294
Copepoda (67 ± 18%)	133224	240642	89552	189316	159862	70681
<i>Paracalanus aculeatus</i>	1091	1446		1645		
<i>Paracalanus</i> spp.	1207	7178	1946	4704	1165	2204
<i>Labidocera acutifrons</i>		723	881		17470	2061
<i>Oithona</i> spp. (juvenile)	33111	74076	20605	62751	16094	12029
<i>Tigriopus</i> sp.	3226	5867	4166	10469	1904	2936
<i>Metis</i> sp.		449	3779	4961	2329	
<i>Agetus typicus</i>		536	588	823		
<i>Farranula gracilis</i>		542	1692			
Copepoda (nauplii)	94589	149376	55678	102802	120899	51452
Cumacea		362	294			294
Gammaridae		362	588			294
Isopoda (manca larvae)	122	1971		581		
Brachyura (zoëa)		362	805		309	
Brachyura (megalopa)			294	581		294
Decapoda (other larvae)			15066		798	
<i>Oikopleura</i> spp.	2099	7658	9061	17914	2947	
<i>Fritillaria</i> sp.	1196		4899	8519		
Others	102	144	135	215	209	51

Percentage contribution of mero- and holoplankton and Copepoda to the total zooplankton density (average ± SD) and the main taxa identified in the Abrolhos Bank (February 2012) for each sampling area (Parcel das Paredes - PP, Abrolhos Archipelago – AA, and Parcel dos Abrolhos - PAB) and station (Reef station – RS and outer station - OS). *Others include Amoebozoa (*Arcella* sp.), Foraminifera (*Cornuspira* sp. and *Notophthalmidium* sp.), Nematoda, Copepoda (*Paracalanus quasimodo*, *Temora stylifera* and *Oncaea venusta*), Mysidacea, Amphipoda, Bryozoa, Chaetognatha and Teleostei. Fonte: Lucas Figueirêdo

Table 2. Mean abundances (ind. m⁻³) for the principal zooplankton taxonomical groups for the 200- μ m net in Summer 2012.

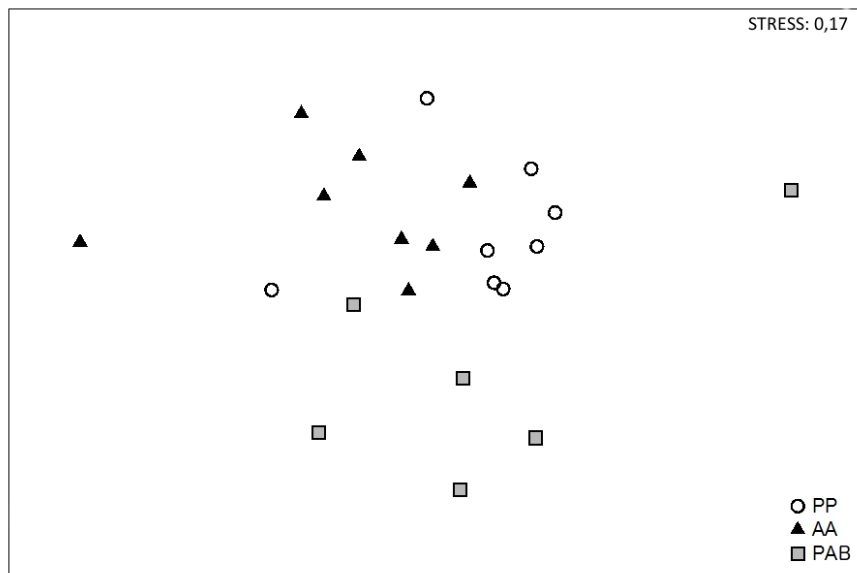
Species/Taxa	PP		AA		PAB	
	RS	OS	RS	OS	RS	OS
Zooplankton	102	295	246	345	90	56
Holoplankton (74 \pm 12%)	64	189	147	217	77	43
Meroplankton (26 \pm 12%)	18	47	99	128	13	13
Foraminifera						
<i>Tretomphalus bulloides</i>	9	15	14	12	11	15
Bryozoa (larvae)	1	1				
Gastropoda	3	8	15	14	1	1
Veliger stages	3	7	12	11	1	1
<i>Lamellaria</i> sp.		1	3	3		
Mollusca						
Bivalvia (veliger)	1					
Polychaeta (larva)	1	4	2	3		1
Ostracoda			1		1	2
Copepoda (41 \pm 24%)	62	196	88	114	64	23
<i>Undinula vulgaris</i>			1	1		
Calanidae (unidentified)				1		
<i>Paracalanus aculeatus</i>			1			
<i>Paracalanus quasimodo</i>	17	71	26	21		1
<i>Paracalanus</i> spp.	30	100	11	15	2	2
<i>Clausocalanus furcatus</i>			3	4		
<i>Centropages velificatus</i>		1				
<i>Centropages</i> sp.						1
<i>Temora stylifera</i>		1	11	19		
<i>Calanopia americana</i>		2				
<i>Labidocera acutifrons</i>		1	2	4	61	17
<i>Labidocera</i> sp.			1			
<i>Acartia danae</i>			1	2		
<i>Oithona nana</i>	2	7	6	3		
<i>Oithona oculata</i>	1					
<i>Oithona plumifera</i>		1	1			
<i>Oithona setigera</i>		1	1	9		
<i>Oithona simplex</i>		1				
<i>Oithona</i> spp.			1	4		
<i>Macrosetela gracilis</i>					1	
<i>Tigriopus</i> sp.	3	1	3	10		
<i>Metis</i> sp.		1	1			
Tegastidae			1			
Harpacticoida (others)	3	2	1	2		1
<i>Oncaea mediterranea</i>		1	1	2		
<i>Oncaea scottodicarloi</i>		2				
<i>Oncaea venusta</i>			1			

Species/Taxa	PP		AA		PAB	
	RS	OS	RS	OS	RS	OS
<i>Agetus typicus</i>					1	
<i>Onychocorycaeus agilis</i>			2	2		
<i>Onychocorycaeus giesbrechti</i>	3	4	11	7		
<i>Farranula gracilis</i>	1		1			
<i>Farranula</i> spp.			3	6		
Copepoda (nauplii)	3	3	6	4		
Cirripedia (nauplii)	1	4	5	6		1
Euphausiacea (larvae)	1	4		1		
Decapoda	5	28	39	53	6	6
<i>Lucifer faxoni</i>			1			
<i>Lucifer faxoni</i> (mysis)			1			
Sergestidae (protozoa)			1	1		
Brachyura (zoea)	2	11	15	21	1	2
Porcellanidae (zoea)					1	
Caridea	2	17	21	25	3	4
Calianassidae			1	2		
Anomura				2		
Decapoda (other larvae)				2		
Amphipoda	1		15	20	1	1
Cumacea		1	2	4		1
Echinodermata (larvae)			2	7		
Chaetognatha	4	7	3	12		
Chordata	3	5	12	19	1	1
<i>Oikopleura</i> spp.	4	16	35	62		
Teleostei (egg)	4	4	11	9		2
Teleostei (larvae)	1	1	2	5	2	1
Others		1	1	1	1	

(Parcel das Paredes - PP, Abrolhos Archipelago - AA, and Parcel dos Abrolhos - PAB) and station (Reef station - RS and outer station - OS). *Others include Hydromedusae, Gastropoda, Mysidacea and Isopoda groups. Fonte: Lucas Figueirêdo.

The results of multivariate analyses demonstrated that there were significant differences in the community structure relative only to the sampling areas, which showed three distinct zooplankton assemblages (PERMANOVA, Pseudo- $F = 3,173$, $P = 0,001$) (Table 3, pairwise comparisons). The groupings of the zooplankton assemblages from each sampling area can be visualized in the MDS plot (Fig 4).

Fig 4. Multidimensional scaling (MDS) plot for the 64 μm net catches in Summer 2012. Parcel das Paredes - PP; Abrolhos Archipelago - AA; and Parcel dos Abrolhos – PAB. Abrolhos Bank in February 2012.



Fonte: Lucas Figueirêdo.

Table 3: Results of the PERMANOVA analyses (pairwise test) for the 64 μm net catches among the sampling areas in Summer 2012. Parcel das Paredes (PP), Abrolhos Archipelago (AA), and Parcel dos Abrolhos (PAB). Abrolhos Bank in February 2012.

Groups	<i>t</i>	<i>P</i>
PP, AA	1,61	0,001
PP, PAB	1,81	0,005
AA, PAB	1,87	0,002

Fonte: Lucas Figueirêdo.

SIMPER analyses revealed that nearly the same group of taxa (i.e., copepod nauplii, *Oithona* spp., and the veligers of Gastropoda) had a higher percentage of contributions for the average similarity within all of the sampling areas (Table 4). In addition, *Codonellopsis schabi*, *Oikopleura* spp. and the veligers of Bivalvia contributed to PP, AA and PAB, respectively (Table 4). Dissimilarities were relatively low (Table 5) with the highest value occurring between AA and PAB (54.56%), which was mostly directed by the low abundance of *Codonellopsis schabi* in PAB. *Fritillaria* sp., in the same way as *C. schabi*, occurred predominantly in AA and contributed to the

dissimilarities among the other sampling areas. Since most of the taxa occurred in all of the sampling areas, the general results lead to an understanding that the composition of the individuals within the range of the microzooplankton is similar throughout the Abrolhos Bank, with the dissimilarities between sampling areas driven mostly by variations in species abundance rather than its presence/absence. However, the nonspecific identification of those early stages of Copepoda (nauplii) and *Oithona* spp. (juvenile) may have influenced this absence of the coastal-oceanic gradient. Despite the microzooplankton looking similar in each area, IndVal results showed singular species as indicators of each area, with *L. nordqvistii* as indicator of PP (IndVal = 0.708, $p = 0.045$), *Fritillaria* sp. as indicator of AA (IndVal = 0.83, $p = 0.01$) and *Spirillina* sp. as indicator of PAB (IndVal = 0.727, $p = 0.05$).

Table 4: SIMPER analysis (4 taxa contributing most to the similarity) for the 64 μm net catches. Assemblages densities per group/sampling area (average group similarity) in Summer 2012. C, contribution and Cum., cumulative contribution; Abrolhos Bank in February 2012

Group and characteristic species	C (%)	Cum. (%)
PP group (62.33%)		
Copepoda (Nauplii)	38.84	38.84
<i>Oithona</i> spp. (juvenile)	23.41	62.25
<i>Codonellopsis schabi</i>	9.28	71.53
Gastropoda (<i>veliger</i>)	7.06	78.58
AA group (54.41%)		
Copepoda (Nauplii)	23.47	23.47
<i>Oithona</i> spp. (juvenile)	14.71	38.18
Gastropoda (<i>veliger</i>)	13.98	52.16
<i>Oikopleura</i> spp.	9.35	61.51
PAB group (47.41%)		
Copepoda (Nauplii)	44.63	44.63
Gastropoda (<i>veliger</i>)	16.43	61.06
Bivalvia (<i>veliger</i>)	11.73	72.79
<i>Oithona</i> spp. (juvenile)	11.47	84.26

Fonte: Lucas Figueirêdo.

Table 5: SIMPER analysis (6 taxa contributing most to dissimilarity) for the 64 μm net catches. Assemblages among the sampling areas (average dissimilarity) in Summer 2012. Abrolhos Bank in February 2012

PP versus AA (average dissimilarity = 43.23)			
Taxa	Average abundance		Contribution (%)
	PP	AA	
Copepoda (nauplii)	343	265	9.66
Gastropoda (veliger)	92	179	9.62
<i>Oithona</i> spp. (Juvenile)	221	183	8.10
<i>Codonellopsis schabi</i>	112	141	7.90
<i>Oikopleura</i> spp.	61	108	5.08
<i>Fritillaria</i> sp.	8	63	5.04

PP versus PAB (average dissimilarity = 49.86)			
Taxa	Average abundance		Contribution (%)
	PP	PAB	
Copepoda (nauplii)	343	270	12.63
<i>Oithona</i> spp. (Juvenile)	221	101	12.32
<i>Codonellopsis schabi</i>	112	9	9.72
<i>Oikopleura</i> spp.	61	21	4.87
Gastropoda (veliger)	92	89	4.84
<i>Leprotintinnus nordqvisti</i>	48	12	4.59

AA versus PAB (average dissimilarity = 54.56)			
Taxa	Average abundance		Contribution (%)
	AA	PAB	
<i>Codonellopsis schabi</i>	141	9	9.60
Copepoda (nauplii)	265	271	8.91
Gastropoda (veliger)	179	89	8.50
<i>Oithona</i> spp. (Juvenile)	183	101	7.91
<i>Oikopleura</i> spp.	108	21	6.96
<i>Fritillaria</i> sp.	63	0	4.63

Fonte: Lucas Figueirêdo.

2.3.3 200- μm mesh net

The 200 μm net catches had much lower abundances, with total density averaging 198 ± 174 ind. m^{-3} (PP), 295 ± 197 ind. m^{-3} (AA) and 73 ± 88 ind. m^{-3} (PAB) (Fig 5). The abundance in PAB was significantly lower than in AA (*Kruskal-Wallis*, $P = 0,021$), whereas other pairwise comparisons between sampling areas had no significant differences (Fig 5). Regarding the diel cycle, pairwise comparisons showed significant

fluctuations in abundance with the highest values occurring during the night period (326 ± 243 ind. m^{-3} (18 h) and 313 ± 149 ind. m^{-3} (0 h)), and the abundances at the 0 h were significantly higher than at 6 h and 12 h (Fig 5), driven by the abundance elevation of a group of taxa at 0 h (i.e., *Paracalanus quasimodo*, *Paracalanus* spp. (juvenile), Caridea, Amphipoda and Brachyuran larvae). Conversely, *Oikopleura* spp. had lower densities at night with an elevation at 6 h and decreasing again towards 12 h. Even though the Outer Station presented an average abundance that was higher than the Reef Station (248 ± 220 ind. m^{-3} and 151 ± 125 ind. m^{-3} , respectively) (Fig 5) and those higher values had no statistical significance (Mann-Whitney test, $P > 0.05$). With respect to the diversity indices, the community captured by the 200 μm net had higher values but followed the same pattern as the 64 μm net catches with significant differences only found between the sampling areas (Fig 6). The dominance of *Labidocera acutifrons* drove the Shannon diversity index to the lowest value in the PAB.

Fig 5. Abundance from the 200- μm net catches (ind. m^{-3}) in Summer 2012. (A) Sampling area (Parcel das Paredes - PP; Abrolhos Archipelago - AA; and Parcel dos Abrolhos – PAB), (B) stations, and (C) diel cycle. Pair-wise test result for significant differences between the sampling areas. Abrolhos Bank in February 2012.

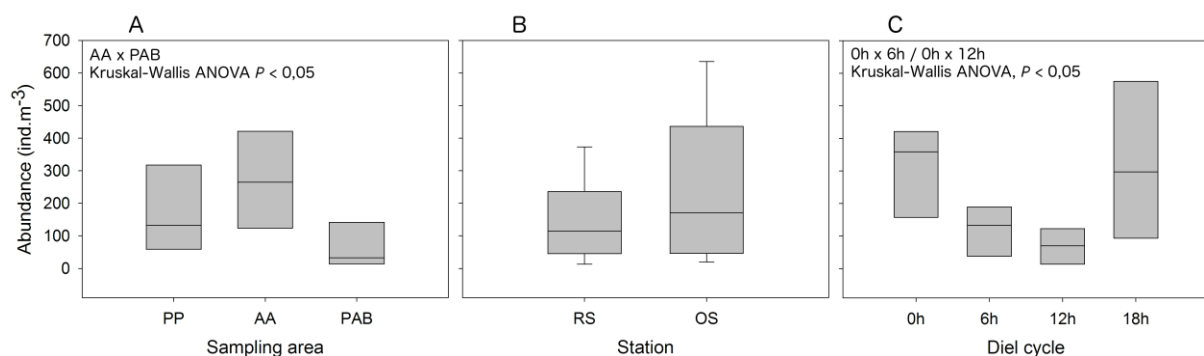
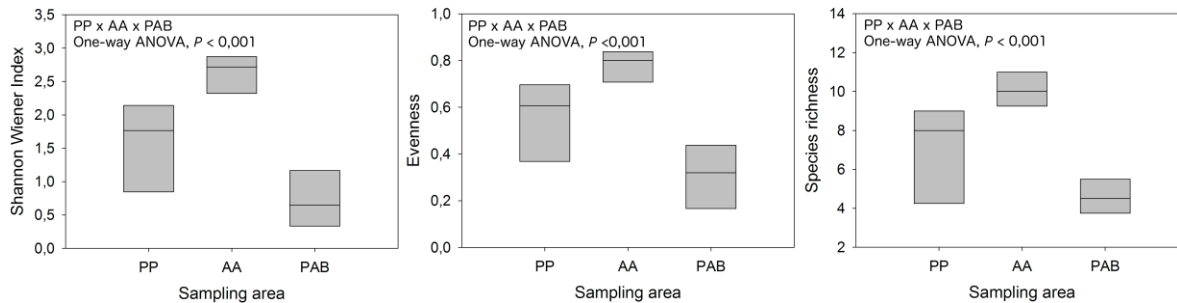
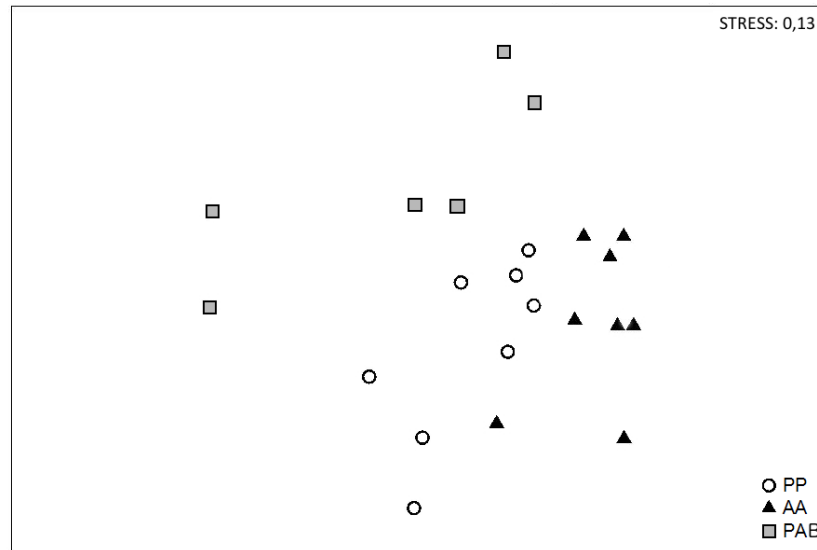


Fig 6. Diversity indices from the 200 μm net catches in Summer 2012. Parcel das Paredes - PP; Abrolhos Archipelago - AA; and Parcel dos Abrolhos - PAB. Pair-wise tests results for significant differences between the sampling areas at the top of each plot. Abrolhos Bank in February 2012.



The results of the multivariate analyses revealed significant differences in the community structure defining distinct assemblages for each sampling area (PERMANOVA, pseudo-F = 5,72; P = 0,001) (Table 6, pairwise comparisons) that can be visualized in the MDS plot (Fig 7). SIMPER analyses allowed the identification of the taxa that were contributing most to the average similarity within each sampling area (Table 7). PP had the greatest contribution that was dependent on individuals of the *Paracalanus* genus (i.e., *P. quasimodo* and unidentified juveniles of *Paracalanus* spp.), whereas in AA, *Oikopleura* spp. had the highest contribution, and in PAB, *Tretomphalus bulloides*, *Labidocera acutifrons* and Caridea contributed the most.

Fig 7. Multidimensional scaling (MDS) plot for the 200 μm net catches in Summer 2012. Parcel das Paredes - PP; Abrolhos Archipelago - AA; and Parcel dos Abrolhos – PAB. Abrolhos Bank in February 2012



Fonte: Lucas Figueirêdo.

Some taxa had a significant contribution (5 taxa contributing most to the similarity, Table 7) within all of the sampling areas or at least two of them (i.e., *Tretomphalus bulloides*, Teleostei (egg) and the veligers of Gastropoda). Table 8 shows the taxa contributing most to the dissimilarity between the sampling areas. The contribution of taxa to the dissimilarity was relatively low (i.e., SIMPER values 7.80 (PP \times AA) and 9.47 (AA \times PAB); Table 8), which suggests that the dissimilarity found between those sampling areas is driven mostly by the change in abundance of a group of species rather than the presence/absence of a particular species. In contrast, the dissimilarity between PP and PAB (the sampling area closest to and farthest from the coast) shows that the highest contributions were induced by the presence/absence of a particular species (i.e., *P. quasimodo*, *Paracalanus* spp. and *L. acutifrons*) rather than a change in the abundance of a group species, which highlighted the coastal-oceanic gradient.

Table 6: Results of the PERMANOVA analyses (pairwise test) for the 200- μ m net catches among the sampling areas in Summer 2012. Parcel das Paredes (PP), Abrolhos Archipelago (AA), and Parcel dos Abrolhos (PAB). Abrolhos Bank in February 2012.

Groups	<i>t</i>	<i>P</i>
PP, AA	2.06	0.002
PP, PAB	2.29	0.002
AA, PAB	2.77	0.001

Fonte: Lucas Figueirêdo

Significant variations were also found when analyzing the community structure in terms of its fluctuation during the diel cycle (PERMANOVA, pseudo-F = 1.98, P = 0.009). Pairwise comparisons suggest a gradual change in the community structure with two distinct assemblages (night (0 h) and day (12 h)) and two periods of transition between those assemblages (dawn (6 h) and dusk (18 h)), with the dusk period showing a more rapid rate of change toward the night assemblage (Table 9). SIMPER analyses results showed higher average dissimilarity between 12 h and 18 h (67.88%), which was followed by the dissimilarity between 0 h and 12 h (66.23%) according to the significant differences found with PERMANOVA pairwise comparisons (Table 10). The contribution of each taxon was low and needed 10 and 11 dominant taxa to reach 50% of the cumulative contribution to the dissimilarities between the periods previously mentioned. The contributions are induced by the lower abundances of all of the taxa at 12 h in comparison with that of 0 h and 18 h. Table 10 shows the faunal groups responsible for 50% of the dissimilarities between period 0 h and 12 h and 12 h and 18 h with a predominance of Copepoda.

Each of the three areas had good indicators as showed by the IndVal values. PP had the maximum IndVals for Euphausiacea larvae (IndVal = 0.810, p = 0.01) and Bryozoa larvae (IndVal 0.707, p = 0.03). In AA IndVal values were highest for Echinodermata larvae (IndVal = 1.000, p = 0.005), *Temora stylifera* (IndVal = 0.982, p = 0.005), *Farranula* spp. (IndVal = 0.924, p = 0.005), *Clausocalanus furcatus* (IndVal = 0.911, p = 0,005), and *Undinula vulgaris* (IndVal = 0.707, p = 0,035). PAB had the maximum IndVals for *Labidocera acutifrons* (IndVal = 0.961, p = 0,005), Ostracoda (IndVal = 0.754, p = 0,01), *Centropages* sp. (IndVal = 0.713, p = 0,025), and zoea of Porcellanidae (IndVal = 0.707, p = 0,01). In PP and AA the indicator species are much

more important for their relative frequency than for their relative abundance, since they showed no significant density on those areas. In contrast, the IndVal value obtained for *L. acutifrons* in PAB are more related with its relative abundance, since this species was present in all the areas but dominated the community in PAB.

Table 7: SIMPER analysis (5 taxa contributing most to similarity) for the 200 µm net catches. Assemblages densities per group/sampling area (average group similarity) in Summer 2012. C, Contribution and Cum., cumulative contribution. Abrolhos Bank in February 2012.

Group and characteristic species	C (%)	Cum. (%)
PP group (53.07%)		
<i>Paracalanus quasimodo</i>	15.41	15.41
<i>Paracalanus</i> spp. (juvenile)	15.23	30.63
<i>Tretomphalus bulloides</i>	10.23	40.86
Teleostei (egg)	8.12	48.99
Chaetognatha	6.43	55.42
AA group (67.72%)		
<i>Oikopleura</i> spp.	11.24	11.24
<i>Paracalanus quasimodo</i>	9.02	20.26
<i>Tretomphalus bulloides</i>	8.95	29.21
Gastropoda (veliger)	7.55	36.76
Teleostei (egg)	5.99	42.75
PAB group (70.15%)		
<i>Tretomphalus bulloides</i>	26.35	26.35
<i>Labidocera acutifrons</i>	10.82	37.17
Caridea	8.12	45.29
Teleostei (egg)	5.72	51.01
Gastropoda (veliger)	5.17	56.18

Fonte: Lucas Figueirêdo.

Table 8: SIMPER analysis (6 taxa contributing most to dissimilarity) for the 200 μm net catches among the sampling areas (average dissimilarity) in Summer 2012. Abrolhos Bank in February 2012

PP versus AA (average dissimilarity= 55.84%)			
Taxa	Average abundance		Contribution (%)
	PP	AA	
<i>Paracalanus</i> spp. (juvenile)	64.86	13.05	7.80
<i>Oikopleura</i> spp.	10.33	48.51	7.18
<i>Paracalanus quasimodo</i>	43.93	23.91	5.02
<i>Temora stylifera</i>	0.46	14.78	4.81
Caridea	9.59	23.27	4.76
Brachyura (zoea)	6.35	18.12	4.25
PP versus PAB (average dissimilarity= 62.22%)			
Taxa	Average abundance		Contribution (%)
	PP	PAB	
<i>Paracalanus</i> spp. (juvenile)	64.86	1.76	13.26
<i>Paracalanus quasimodo</i>	43.93	0.81	11.83
<i>Labidocera acutifrons</i>	0.42	39.01	7.41
<i>Oikopleura</i> spp.	10.33	0.24	4.91
Caridea	9.59	3.40	3.98
Chaetognatha	5.42	0.32	3.40
AA versus PAB (average dissimilarity = 67.74%)			
Taxa	Average abundance		Contribution (%)
	AA	PAB	
<i>Oikopleura</i> spp.	48.51	0.24	9.47
<i>Paracalanus quasimodo</i>	23.91	0.81	6.12
<i>Labidocera acutifrons</i>	2.78	39.01	5.52
<i>Temora stylifera</i>	14.78	0.08	4.71
Caridea	23.27	3.40	4.01
Gastropoda (veliger)	11.21	1.12	3.88

Fonte: Lucas Figueirêdo.

Table 9: Results of the PERMANOVA analyses (pairwise test) for the 200- μm net catches during the diel cycle in Summer 2012. Significant F-values ($P < 0.05$) are in bold numbers. Abrolhos Bank in February 2012.

Groups	<i>t</i>	<i>P</i>
0h, 6h	1.30	0.136
0h, 12h	1.91	0.008
0h, 18h	0.92	0.420
6h, 12h	1.18	0.208
6h, 18h	1.15	0.240
12h, 18h	1.70	0.026

Fonte: Lucas Figueirêdo.

Table 10: SIMPER analysis (50% cut-off) for the 200 µm net catches among the diel cycle (average dissimilarity) in Summer 2012.

0 h versus 12 h (average dissimilarity = 66.23%)				
Taxa	Average abundance		Contribution (%)	Faunal group
	0 h	12 h		
Caridea	5.13	0.09	7.36	Decapoda
<i>Paracalanus</i> spp.	5.28	2.54	6.34	Copepoda
Brachyura (zoea)	4.18	0.24	5.75	Decapoda
<i>Paracalanus quasimodo</i>	5.87	2.86	5.67	Copepoda
Amphipoda	3.77	0.09	5.16	Amphipoda
<i>Oikopleura</i> spp.	3.46	1.3	4.45	Appendicularia
<i>Corycaeus (Onychocorycaeus) giesbrechti</i>	2.85	0.3	3.82	Copepoda
<i>Tigriopus</i> sp.	2.62	0.49	3.62	Copepoda
<i>Temora stylifera</i>	2.77	0.55	3.4	Copepoda
Harpacticoida (outros)	1.93	0.22	3.28	Copepoda
Teleostei (larva)	2.03	0.26	2.9	Teleostei
12 h versus 18 h (average dissimilarity = 67.88%)				
Taxa	Average abundance		Contribution (%)	Faunal group
	12 h	18 h		
<i>Labidocera acutifrons</i>	0.31	4.29	9.39	Copepoda
<i>Paracalanus</i> spp.	2.54	4.92	7.26	Copepoda
<i>Oikopleura</i> spp.	1.3	4.71	6.49	Appendicularia
Caridea	0.09	4.18	6.34	Decapoda
<i>Paracalanus quasimodo</i>	2.86	4.18	6.11	Copepoda
Brachyura (zoea)	0.24	3.75	5.57	Decapoda
Amphipoda	0.09	1.83	3.06	Amphipoda
<i>Tretomphalus bulloides</i>	3.42	3.68	3.05	Foraminifera
<i>Oithona nana</i>	0.45	1.61	2.7	Copepoda
<i>Corycaeus (Onychocorycaeus) giesbrechti</i>	0.3	2	2.68	Copepoda

Fonte: Lucas Figueirêdo.

2.4 Discussion

The analyses of the zooplankton revealed a community composed mostly of species with a wide distribution in the tropical realms of the Atlantic Ocean (Boltovskoy, 1999; Neumann-Leitão *et al.*, 2008). We found a total of 110 taxa among all of the samples from both nets, which was slightly higher than the number reported for other Brazilian reefs (Porto Neto *et al.*, 2000; Neumann-Leitão *et al.*, 2009). Diversity among the reef zooplankton of the Brazilian coast is generally lower than other reefs around the world considering the high diversity typical of these environments. With a simple comparison of copepod species richness from different reefs, this feature becomes even more evident. For example, in the present study, we found 32 copepod taxa (64- and 200- μm nets), which was much less than the 87 copepod species encountered by Alvarez-Cadena *et al.* (1998) at the Caribbean Sea reefs and the 74 copepod taxa found at the Great Barrier Reefs by Mckinnon e Thorrold (1993). Most of the copepod species found in the present study are common to other reef-related environments all over the world (Yoshioka *et al.*, 1985; Alvarez-Cadena *et al.*, 1998; Suárez-Morales e Gasca, 2000; Heidelberg *et al.*, 2010) (Table XI).

The higher diversity in the Caribbean and Pacific reefs can be explained by Connell's **Intermediate Disturbance Hypothesis** (IDH) (Connell, 1978; Wilkinson, 1999) (1), which proposes that native species diversity is maximized when environmental disturbance is neither too sporadic nor too common (the optimal quantity of disorder inside a system). At intermediate levels of disturbance, diversity takes full advantage of the ecosystem because species that boom at both the initial and late successional stages can co-occur and exist, and at elevated levels of disturbance, species richness is reduced due to a rise in species displacement. At the Abrolhos reef and in all Brazilian Tropical reefs, ecological disturbances are too rare, which results from one species driving a competitor to extinction and becoming dominant in the ecosystem (2,3). "Gause's Law" (4) is also known as competitive exclusion and explains how species that compete for the same resources cannot coexist in the same niche.

The families Paracalanidae and Othonidae were the dominant taxa at the sampling areas closest to the shoreline in the Abrolhos Bank (i.e., PP and AA). Actually, the *Paracalanus* genus is known to greatly contribute to copepod assemblages in the tropical

shelf waters (Mckinnon e Duggan, 2001) and *Oithona* has been described as the most ubiquitous and abundant copepod in the world's oceans (Gallienne e Robins, 2001). Both genera are subsampled in many studies by the coarse nets used. In Abrolhos Bank, the greatest contributions of these two families were from *Paracalanus quasimodo* and *Oithona nana*, which are both species that are associated with coastal waters, and *P. quasimodo* was cited as one of the most abundant species in the coastal waters of Brazil (Brandini *et al.*, 1997) and considered the top-controller of primary production on the Brazilian coast (Eskinazi-Sant'anna, 2013). Similarly, these two families were also found to greatly contribute to other reef systems (Table 11).

Regarding Paracalanidae occurrence, it is worth noting the differences recorded by the finer mesh net (64 μm) and the coarser one (200 μm). The 200- μm net lost a considerable amount of juveniles captured by the 64- μm net, and in contrast, the finer net lost (probably by avoidance) the adults captured efficiently by the coarser net. This methodology bias may clearly lead to misjudgments of the community when using just one net for fieldwork sampling and not only in reef environments (Hopcroft *et al.*, 1998; Paffenhöfer e Mazzocchi, 2003). Accordingly, the 64- μm net captured an elevated abundance of copepod nauplii that were almost absent from the 200- μm net samples. Relative to the high nauplii abundance, our results are comparable to what was found by Heidelberg *et al.* (2010) using a 40- μm mesh net, whereas other studies using coarser nets have likely underestimated smaller species, juveniles and especially naupliar stages. This information is essential for a population analysis (Miller, 1995), and the use of mesh sizes $\leq 124 \mu\text{m}$ and $61 \mu\text{m}$ for sampling juveniles and nauplii is recommended, respectively (Nichols e Thompson, 1991; Chen *et al.*, 2016). Along with the elevated abundance of nauplii and juveniles of Paracalanids and Oithonids, the finer net captured great densities of the tintinnid species *Codonellopsis schabi*, which, according to Costa *et al.* (2015), is one of the most conspicuous species in the Abrolhos Bank as an agglutinated tintinnid, being favored by the particle-rich water.

Table 11: Copepod species common to the Abrolhos Bank and other reef systems worldwide. Global reef areas where researchers collected similar species as found in the present study. The methods of collection used in each study. ◆ - species occurrence. Source - ¹Alvarez-Cadena *et al.* (1998); ²Fukuoka *et al.* (2015); ³Mckinnon e Thorrold (1993); Mckinnon *et al.* (2005); ⁴Cornils *et al.* (2010).

Location	Net mesh (µm)	Tow direction
¹ Caribbean Sea (North Atlantic)	330	Sub-surface Horizontal
² Japan (Northwestern Pacific)	100	Vertical
³ Great Barrier Reef (Southwestern Pacific)	150	Vertical
⁴ Indonesia (Indo-Pacific)	200	Vertical

Species	¹ Caribbean Sea	² Japan	³ Great Barrier Reef	⁴ Indonesia
<i>Undinula vulgaris</i>	◆	◆	◆	
<i>Clausocalanus furcatus</i>	◆	◆	◆	◆
<i>Paracalanus aculeatus</i>	◆		◆	◆
<i>Paracalanus quasimodo</i>	◆			
<i>Centropages velificatus</i>		◆		◆
<i>Temora stylifera</i>	◆			◆
<i>Temora turbinata</i>	◆	◆		◆
<i>Calanopia americana</i>	◆			◆
<i>Acartia danae</i>		◆		
<i>Oithona</i> spp.				◆
<i>Oithona nana</i>	◆	◆	◆	
<i>Oithona plumifera</i>	◆	◆	◆	
<i>Oithona setigera</i>		◆		
<i>Oithona simplex</i>		◆	◆	
<i>Macrosetella gracilis</i>	◆	◆		◆
<i>Oncaea venusta</i>	◆			
<i>Farranula gracilis</i>	◆			

Fonte: Lucas Figueirêdo

In PAB, the abundance of *Labidocera acutifrons* increased in the samples from the 200-µm net, which indicated the influence of oceanic warm waters in this sampling area (Björnberg, 1981). The influence of oceanic waters is evident in Abrolhos Bank as shown by Castro *et al.* (2013) through current pattern studies. The zooplankton community as shown by our results reflects this influence, as they present a coastal-oceanic gradient with the transition of dominance/occurrence from coastal to oceanic species, e.g., *Undinula vulgaris*, which, according to Renon (1993), is an indicator of oceanic influence in reef environments. However, the enlargement of the shelf seems to spread the coastal-oceanic gradient as well, which leads to a slower transition of species and therefore promotes lower inputs of oceanic species toward the Abrolhos reef system.

In the present study, the outermost sampling area (PAB) recorded the lowest diversity indexes in contrast with the known increasing diversity pattern toward the oceanic regions (Miyashita *et al.*, 2009). Bruce *et al.* (2012) found that nutrient levels were ten-fold higher in the Abrolhos area (and even in the PAB area) in comparison to that observed in GBR. These high levels could affect the capability of oceanic species to establish themselves and justify the slower transition in zooplankton communities. For instance, researchers have found stronger oceanic influences, in terms of copepod species distributions, over reef systems from the Caribbean Sea that permit the occurrence of several oceanic species belonging to at least 6 genera (Suárez-Morales e Gasca, 2000; Álvarez-Cadena *et al.*, 2009). The occurrence of few oceanic species recorded in the present study may still be related to the relative ability of species to survive in different water conditions. The distribution of species is often related to temperature or salinity gradients (Cornils *et al.*, 2005); however, since water masses in the Abrolhos Bank maintain the temperature and salinity of the Tropical Water, this pattern might also be related to the fact that oceanic species are adapted to relatively particle-free oligotrophic water and may be incapable of feeding in the particle-rich waters (Morgan *et al.*, 2003) of Abrolhos Bank (Leipe *et al.*, 1999; Marcolin *et al.*, 2013).

Although not harboring an elevated diversity compared to other reef systems, Abrolhos reefs support similar amounts of density as reported by other researchers using the same sampling methodology. For example, the high density values recorded in the 64- μm net samples were close to those found by Carassou *et al.* (2010) in New Caledonia reefs (Southwestern Pacific). According to these authors, the high zooplankton density recorded in New Caledonia was promoted by the input of nutrients from continental runoff. However, since terrigenous inputs are not transported far off-shore of Abrolhos Bank, due to hydrodynamic and topographic barriers (Leipe *et al.*, 1999; Koettker e Lopes, 2013), the elevated abundance estimated for the 64- μm net community is boosted by the resuspended nutrients that promote high chlorophyll-*a* biomass and a significant contribution of benthic-dwelling diatoms and other large-sized cells found to occur all over the Abrolhos shelf extension (Susini-Ribeiro *et al.*, 2013).

Zooplankton have a key role in directly supporting a wide variety of suspension-

feeding organisms and planktivorous fish on coral reefs (Mckinnon *et al.*, 2007). In this way, the predation modulates the zooplankton community in these environments (Sorokin, 1990a). According to Robertson e Howard (1978), the high level of daylight predation on planktonic crustaceans demonstrates the importance of body size in prey selectivity by midwater-feeding fish, which makes some taxa (e.g., calanoid copepods and brachyuran larvae) exhibit behavioral and morphological adaptations to withstand high visual predation. Researchers also state that prey taken by fish will vary according to a complex interaction of factors such as the density of plankton, size of prey, ability of zooplankters to escape, intensity of light, and perception of the fish (Kingsford e Macdiarmid, 1988). In this way, the great abundance of copepod nauplii and oithonids may as well be explained by the fact that nauplii are too small, and oithonids suffer limited predation because of their escape response and their reduced motion, which produces much less signal to potential predators (Paffenhoefer, 1993).

In contrast with the 64- μ m net results, the 200- μ m net recorded relatively low densities (9% of that estimated by the 64- μ m net). The density recorded by the 200- μ m net catches was similar to what was reported by Alldredge e King (1977) in the GBR but lower than the findings of several other studies (Cornils *et al.*, 2010; Carrillo-Baltodano e Morales-Ramírez, 2016). This characteristic of the mesozooplankton assemblage in Abrolhos Bank may also be related to intense visual predation suffered by this community. In the present study, the lowest abundance levels were registered at the sampling area farthest from the shoreline (PAB) where the densities of planktivorous fish are highest (Moura e Francini-Filho, 2005).

With respect to the diel cycle, no consistent differences between the periods sampled were observed among the 64- μ m net community, which was an unexpected result given the common knowledge of the night emergence of zooplankters (Emery, 1968). Nevertheless, similar patterns were observed by Mckinnon (1991), who studied copepod communities (64- μ m net) in a reef lagoon (GBR), and Heidelberg *et al.* (2010), who studied the zooplankton community of the Conch Reef (Florida) using a zooplankton pump. However, Heidelberg observed that the great abundance of nauplii in his samples affected the patterns seen in the total zooplankton assemblage, and therefore, by

removing the nauplii from the analyses, the total zooplankton assemblages were significantly higher during the night. Since the sampling methodology applied by Heidelberg *et al.* (2010) did not make a size class selection of the sampled zooplankton community, the patterns found may have been caused by the larger fractions of the collected assemblage. In the present study, the 64- μm net zooplankton assemblages had no significant differences even with the nauplii abundance removed from the analyses, whereas the 200- μm net assemblages significantly differed. This feature may be caused by the lower capability of smaller zooplankters to emerge higher in the water column (Alldredge e King, 1985; Holzman *et al.*, 2004; Kramer *et al.*, 2013), as they are dependent on local turbulence to reach the surface waters of deeper reefs and may be missed by surface hauls.

Samples collected with the 200- μm net at 0 h had a higher average abundance boosted by the copepods, Amphipoda and decapod larvae. With the exception of some truly demersal Amphipoda (i.e., Gammaridea) (Carleton *et al.*, 2001), the other taxa contributing most to the higher nocturnal abundance are all pelagic (holoplanktonic or meroplanktonic). This is an important feature since it indicates that with their daily vertical migration, the pelagic zooplankton assemblages may play a more relevant role in benthopelagic coupling in the Abrolhos Bank reefs along with the demersal community. According to Emery (1968) and Alldredge e King (1977), some species traditionally characterized as pelagic change behaviors and act like typical reef zooplankton (i.e., migrating vertically) when residing on reefs to prevent being swept off the reef by surface currents or to avoid intense predation by abundant visual predators. Appendicularians (*Oikopleura* spp.), despite showing no distinct day/night abundances in open ocean communities (Steinberg, 2008), presented density fluctuations in the Abrolhos reefs with higher averages at 6 h and decreasing again toward mid-day sampling. However, those fluctuations might be controlled by heavy diurnal planktivorous fish predation suffered by this group rather than active migrations (Hamner *et al.*, 1988; Heidelberg *et al.*, 2010).

Differences between the Reef Stations and the Outer Stations were expected to be higher. In fact, the average abundances were more elevated at the Outer Stations for both nets but with no statistical significance. Predation may play a central role in the decline of zooplankton abundance directly over the reefs. The community composition did not

differ, which was probably due to the homogeneous nature of the enlarged shelf of the Abrolhos Bank (Marcolin *et al.*, 2013) that mitigates small-scale spatial (i.e., ≈ 1 km) differences in the zooplankton community.

2.5 Conclusions

This paper provides a general vision into the micro- and mesozooplankton taxa of the Abrolhos Bank and is a contribution to reef zooplankton studies in coastal-oceanic gradients. This short-term study revealed a difference in taxa composition between the three chosen areas, which was attributed to the change in abundance of a group of species that showed wide distributions in the Abrolhos Bank. Holoplankton dominated both nets and may contribute in a remarkable way to the benthic-pelagic coupling in this reef environment. Diel cycle variations were exclusive to the mesozooplankton, which suggests that the vertical migration of microzooplankton is limited with smaller individuals migrating just a few centimeters into the water column or even permanently remaining there (Alldredge e King, 1985; Kramer *et al.*, 2013).

Diversity was considered low because a low diversity tropical coastal community typical of the Brazilian shelf dominated the zooplankton assemblage, and this was different from the Caribbean reef assemblages where the intrusion of oceanic species was reduced. In addition, the absence of endemic species in the Abrolhos reefs, which is found in reef systems from the Indo-Pacific (Cornils *et al.*, 2010), limits local diversity.

The results clearly indicate the need for sampling with at least a set of two nets with different mesh sizes to have a better look into the zooplankton community structure and distribution. Following this thought and because the much higher density of the microzooplankton assemblages compared to the mesozooplankton is a common feature of reef communities (Sammarco e Crenshaw, 2004), the majority of studies that use only coarse nets (e.g., 200 or 300 μm) miss assessing the contribution of a large and important portion of the reef zooplankton assemblage and therefore misinterpret the community as a whole.

2.6 Acknowledgements

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3 INFLUENCE OF DIFFERENT HABITATS ON THE STRUCTURE PATTERNS OF CORAL REEF DEMERSAL ZOOPLANKTON AT ABROLHOS BANK

3.1 Introduction

It is undoubtedly known that coral reef zooplankton have a resident fauna that makes daily emergence migrations from benthic habitats to an overlying water mass (Madhupratap *et al.*, 1991). The first reference to patchiness in reef zooplankton communities was made by Emery (1968), who described swarms of copepods on reef environments. It gave rise to considerable interest over the emergent plankton, resulting in several studies from coral reefs and coastal waters. The demersal community is composed of active assemblages, which exhibit particular preferences of a great variety of substrates (Alldredge e King, 1977; Jacoby e Greenwood, 1989; Melo, Pedro A. M. C. *et al.*, 2010; Smith *et al.*, 2016), as well as preferences of different reef sites (Alldredge e King, 1977; Madhupratap *et al.*, 1991; Cahoon e Tronzo, 1992; Yahel, Yahel, Berman, *et al.*, 2005).

These emergent assemblages become an important benthic-pelagic coupling agent, as they take resources to the water column when they ascend and bring back resources to the benthic domain when they migrate back to the bottom (Pacheco *et al.*, 2014). On coral reef environments these communities may be even more important given the great amount of zooplankton consumers either attached to the bottom or foraging close to the bottom and on the water column aloft (Alldredge e King, 2009).

The great majority of studies regarding the demersal zooplankton focused on the community emerging from soft substrates (Kramer *et al.*, 2013). In addition to studies being fewer in reef substrates, these environments typically exhibit high diversity of forms and shapes, which leaves room for further studies on zooplankton emerging from distinct reef formations. The Abrolhos Bank comprises the most important coralline reefs in the South Atlantic Ocean (8844 km² of reef cover) (Moura *et al.*, 2013) and most of the reef structures are composed of unique mushroom-shape pinnacles formations (Leão e Kikuchi, 2005) that attain 5 to 25 m in height and 20 to 300 m across their tops (Francini-Filho e Moura, 2008). These unique reef formations provide a good study area for the demersal communities. Besides that, very little is known about demersal

zooplankton from tropical waters of the South Atlantic Ocean, since very few studies have been performed (Silva, 2003; Melo, Pedro A. M. C. *et al.*, 2010).

The present study intends to examine the behavior and distribution of demersal zooplankton aiming to assess the responses of the community to different habitats. Some guiding questions are, therefore addressed: (1) does the fringing reef have a distinct emergent fauna in contrast with the pinnacles reefs; (2) how strong the reefs formation influences the diversity, density and biomass of the emergent fauna; and (3) Does that influence overcome that of the different substrates?

3.2 Materials And Methods

3.2.1 Study area

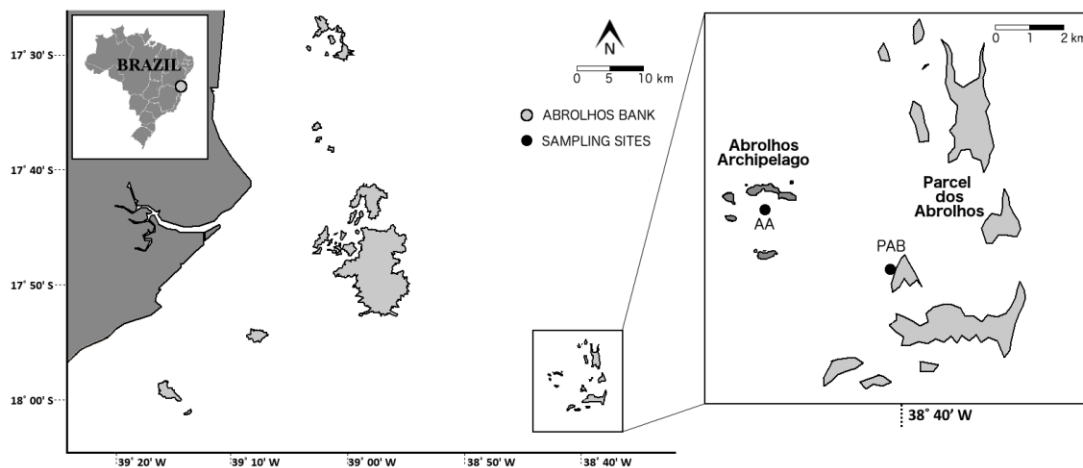
Hosting a mosaic of benthic megahabitats, the Abrolhos Bank is a wide portion of the continental shelf (46 000 km²) that reaches 245 km offshore (Knoppers *et al.*, 1999). Reefs and rhodolith beds are the more pronounced benthic features, along with a great extent of soft bottom (Marchioro *et al.*, 2005; Francini-Filho *et al.*, 2013). Most coralline formations across the continental shelf display unique mushroom-shape pinnacles, with tops extending from 20 to 300 m (Francini-Filho *et al.*, 2013). However, in the middle portion of the shelf is located the Abrolhos Archipelago where the reef formations are very distinct. At the edges of the Archipelago, a fringing rocky reef extending up to 50-60 m from the coast developed over volcanic or sedimentary hard substrates with little growth upward (Leão, 1999). The water temperature in Abrolhos Bank ranges from 24.5 °C during the winter and 27.5 °C during the summer. The summer is a period of low precipitation.

3.2.2 Sampling strategy

Samplings were carried out during the summer (February) of 2014. Demersal zooplankton was collected at 2 sites (Fig. 1). The Abrolhos Archipelago (AA) site is within a shallow rocky reef that has developed into a fringing reef. The bottom at this site (\approx 6 m depth at the reef front) consists of a reef formation dominated by turf algae, scleractinian corals, articulated calcareous algae, and fleshy algae, with a relief of up to 1

m leading to an adjacent coarse sandy bottom (Francini-Filho *et al.*, 2013). The Parcel dos Abrolhos (PAB) site comprises a series of unique mushroom-shaped pinnacles. The pinnacles tops (≈ 7 m depth) have the same coverage as the fringing reefs with the exception of the turf algae that is more abundant at the edges of the Archipelago. However, the pinnacles have a much more rugged relief, attaining up to 17 m in height, and the adjacent sandy bottom reaches approximately 25 to 30 m depth.

Figure 1: Sampling locations across the Abrolhos Bank. The sampling sites according to reef formations (AA, fringing reef; and PAB, Pinnacle reef).



Fonte: Lucas Figueirêdo.

In order to assess the influence of the substrates over the demersal community, in each site the traps were placed randomly across a hard bottom surface (fringing reef at AA and pinnacle top at PAB) and a soft bottom surface (sandy bottom adjacent to the reef formations). The placement of the traps was made during the sunset, and the retrieve occurred in the following morning at the sunrise. Two different trap designs were employed to collect the demersal zooplankton. Both traps samplers have a conical shape net that conducts vertical migrants into a catch chamber, but with different mesh sizes and dimensions. The bigger trap used is a modification of Porter *et al.* (1977) with 200 μm mesh size, 1 m mouth diameter and 1 m between the substrate and the catch chamber (P-trap herein), and the smaller is a modification of Kramer *et al.* (2013) with 64 μm mesh size, 30 cm mouth and 30 cm between the substrate and the catch chamber (K-trap herein). Surrounding the base of the traps there was a 15-cm wide, 64 μm mesh “skirt” to

seal the entrance and prevent escape and contamination by pelagic organisms. Three replicates of each type of trap were deployed simultaneously over each substrate during the full moon. After retrieving the traps, the contents were placed into sample flasks of 4% buffered formalin for further analysis.

3.2.3. Laboratory Procedures

In the laboratory the samples were transferred to a Motoda splitter. Depending on the density of a particular sample, aliquots up to 1/16 of the original sample were taken and analyzed using Sedgwick-Rafter chamber or Bogorov counting chamber under the microscope for identification and measure. An average of 350 individuals per sample were identified to the lowest practical taxonomical level. As the dominant group, the copepods were often identified to species or families (i.e. harpacticoid families) while the other taxa were identified to general groups. Previously determined length-weight regressions were applied to estimate the individual carbon weight. To achieve that, an average length was determined accordingly to the appropriate body portion of each taxonomic group and the length measurements were then converted to carbon weight of zooplankton individuals (see table 1). For the copepod equations the CW was assumed to be 40% of the dry weight (DW) (Postel *et al.*, 2000) and for the appendicularians the CW was assumed to be 44.2% of the dry weight (DW) (Uye, 1982). Biomass ($\mu\text{gC} \cdot \text{m}^{-2}$) was calculated for each taxonomic group based on its abundance (ind. m^{-2}) and individual carbon weight (CW, μgC).

Table 1: Length–weight regressions applied for biomass calculation of different taxa.

Taxa	Regression	Reference
Gastropoda	$\log CW (\mu\text{g}) = - 5.85 + 2.46 \times \log TL (\mu\text{m})$	Hirota (1986)
Bivalvia	$\log CW (\mu\text{g}) = - 3.45 + 1.47 \times \log L (\mu\text{m})$	Hirota (1986)
Polychaeta	$\log CW (\mu\text{g}) = - 5.97 + 2.10 \times \log TL (\mu\text{m})$	Hirota (1986)
Ostracoda	$\ln CW (\mu\text{g}) = 1.03 + 1.46 \times \ln TL (\text{mm})$	Heidelberg (2010)
Copepoda		
Calanoida	$\ln DW (\mu\text{g}) = 2.73 \ln PL (\mu\text{m}) - 15.93$	Webber & Roff, (1995a)
Cyclopoida	$\ln DW (\mu\text{g}) = 1.53 \ln PL (\mu\text{m}) - 8.7$	Webber & Roff, (1995a)
Harpacticoida	$\text{Log } DW (\mu\text{g}) = - 8.51 + 3.26 \times \log TL (\mu\text{m})$	Hirota, (1986)
Nauplii	$\ln CW (\mu\text{g}) = 2.48 \ln L (\mu\text{m}) - 15.70$	Hopcroft et al. (1998)
Decapoda	$\ln CW (\mu\text{g}) = 1.03 + 1.46 \times \ln BL (\text{mm})$	Hirota (1986)
Amphipoda	$\ln CW (\mu\text{g}) = 1.03 + 1.46 \times \ln TL (\text{mm})$	Heidelberg (2010)
Isopoda	$\ln CW (\mu\text{g}) = 1.03 + 1.46 \times \ln BL (\text{mm})$	Heidelberg (2010)
Mysidacea	$\log CW (\mu\text{g}) = - 0.167 + 3.10 \times \text{Log } L (\text{mm})$	Uye (1982)
Chaetognatha	$\text{Log } CW (\mu\text{g}) = 0.93 + 2.79 \times \text{Log } BL (\text{mm})$	Hirota (1986)
Appendicularia	$\log DW (\mu\text{g}) = - 6.10 + 2.47 \times \log TL (\mu\text{m})$	Hopcroft et al. (1998)

TL – total length; L – length; BL – body length; P – prosome length. CW – carbon weight; DW – dry weight. Fonte: Lucas Figueirêdo.

3.2.4 Statistical analysis

The patchiness in distribution of taxa among replicate samples of each substrate, site and trap were examined using a similarity percentage analysis (SIMPER). Abundance and biomass data were averaged across the substrates, sites and traps to test for significant variations (Mann-Whitney test; $P < 0.05$).

Zooplankton data were further analyzed by cluster analysis to compare taxa composition between each site, substrate and trap. The cluster analysis was based on the Manhattan distance matrix with standardized data to adjust for differences in magnitude of raw data.

To test for statistical significance between demersal community groupings, the data were analyzed using a permutational multivariate analysis of variance (PERMANOVA). Pair-wise tests were used for the sites and substrates, aiming to test differences between sites independently of the substrates influences and inversely to test differences between substrates apart from hydrological characteristics of distinct sites. The tests were performed with both abundance and biomass data. The same data treatment was used to achieve the MDS groupings. To determine substrate and site preferences, the Indicator Value index (Dufrêne e Legendre, 1997) was calculated. Additionally, the distinct trap designs were tested to determine if the assemblages collected were statistically different (PERMANOVA).

3.3 Results

3.3.1 General results

A total of 53 taxa were considered. Of all the taxa, 35 were copepods, divided among calanoids, cyclopoids, harpacticoids and, in rare appearances, monstrolids (Table 2). The overall abundance of the demersal zooplankton was $6,050 \pm 6,419$ ind. m^{-2} with maximum abundance reaching 25,661 ind. m^{-2} (attributed to the occurrence of a swarm of *Dioithona oculata*). Copepods swarms are large aggregation found in coastal areas such as reefs and estuaries. Copepods were the dominant component of the demersal community, followed by the amphipods (Fig. 2). However, typical demersal forms, such as gastropods, polychaetes, decapods, ostracods, mysids, and cumaceans were also frequent.

The high variability observed is due to the presence of large swarms of *D. oculata* found especially in PAB site where the similarity among samples were very low (19.10%, SIMPER). This fact suggests a strong spatially patchy distribution. The harpacticoids were the most representative taxon at AA site with their abundance distributed between 14 families. The similarity among the samples from AA site was higher (i.e. 36.94%, SIMPER) suggesting that the demersal community is more evenly distributed at AA than it is at PAB site. Similar distribution behavior was observed among the sandy bottom samples (21.4%, SIMPER) and the coral reef samples (22.31%, SIMPER), and among each trap (29.83% for the 64 μm trap; and 24.12% for the 200 μm trap).

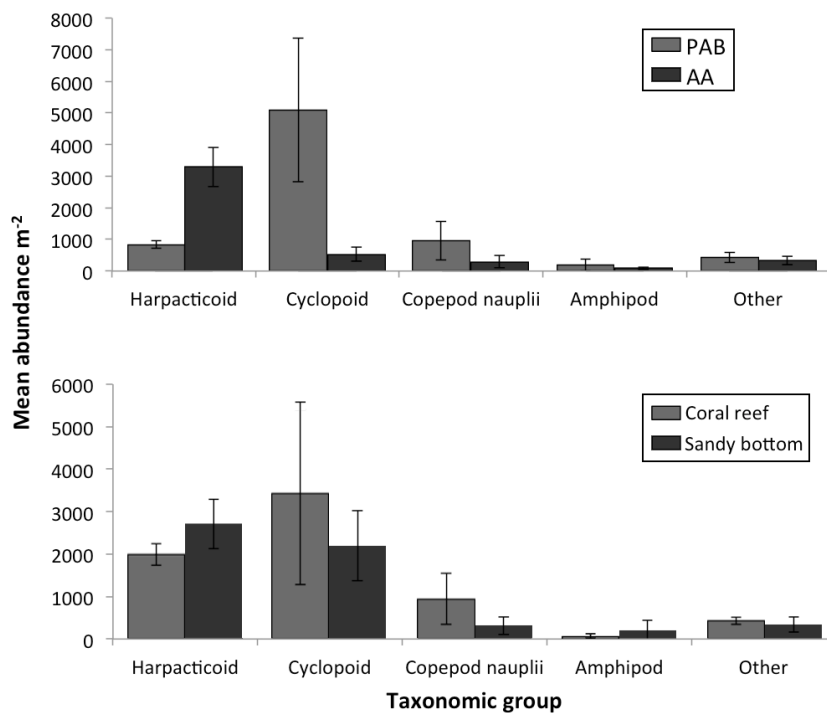
Table 2: Mean abundance (ind. m⁻²) for the demersal zooplankton collected with both traps in each site and substrates.

Taxa	Site		Substrate	
	AA	PAB	Sandy bottom	Coral reef
Foraminifera	6	5	5	6
Gastropoda (veliger)	12	67	5	73
Bivalvia (veliger)	0	2	0	2
Polychaeta (larvae)	67	31	34	64
Calanoida				
<i>Paracalanus quasimodo</i>	1	2	2	1
<i>Paracalanus</i> spp.	3	0	0	3
<i>Temora stylifera</i>	1	1	0	2
<i>Temora turbinata</i>	0	0.4	0	0.4
<i>Calanopia americana</i>	2	31	31	2
<i>Pseudocyclops</i> sp.	13	70	38	45
Calanoida (unidentified)	2	17	12	7
Cyclopoida				
<i>Oithona nana</i>	14	51	39	26
<i>Oithona plumifera</i>	0	5	1	4
<i>Oithona simplex</i>	367	12	312	67
<i>Oithona</i> spp.	162	44	123	83
<i>Dioithona oculata</i>	4	4981	1719	3265
<i>Oncaea venusta</i>	0.4	0	0	0.4
<i>Onychocorycaeus giesbrechti</i>	0.4	0	0	0.4
<i>Farranula</i> spp.	0	5	5	0
Corycaeidae	1	0	0	1
Harpacticoida				
Diosaccidae	0	26	14	12
Ectinosomatidae	122	87	65	144
Hamondiidae	52	7	30	28
Harpacticidae	393	75	143	325
Laophontidae	79	52	23	109
Longipediidae	21	8	15	14
Metidae	56	109	47	119
Novocriniidae	1	0	0	1
Peltidiidae	29	3	7	25
Rotundiclipeidae	7	1	2	6
Tegastidae	72	30	19	82
Tetragonicipitidae	2	0	2	0
Thalestridae	1845	315	1535	625
Tisbidae	328	62	41	349
Harpacticoida (unidentified)	286	65	189	161
Monstrilloida	1	4	0	5
Copepoda nauplii				
Calanoida	17	98	2	112
Cyclopoida	50	309	143	216
Harpacticoida	243	544	168	619
Ostracoda	30	23	25	28
Cirripedia (nauplii)	0	4	0	4
Decapoda	89	25	17	97
Euphausiacea	0	0.4	0.4	0
Mysidacea	26	51	45	32
Cumacea	37	73	65	44
Isopoda	19	1	18	3

Taxa	Site		Substrate	
	AA	PAB	Sandy bottom	Coral reef
Amphipoda	100	184	205	79
Echinodermata (larva)	1	0	0	1
<i>Paraspadella nana</i>	18	4	20	2
Chaetognatha (unidentified)	1	2	1	2
Larvacea	2	2	0	4
Teleostei (larvae)	2	0	0	2
Diptera larvae	23	4	22	5

Fonte: Lucas Figueirêdo.

Figure 2. Mean abundance (ind m⁻²) of demersal zooplankton. Main taxonomic groups displayed at each site and substrate.

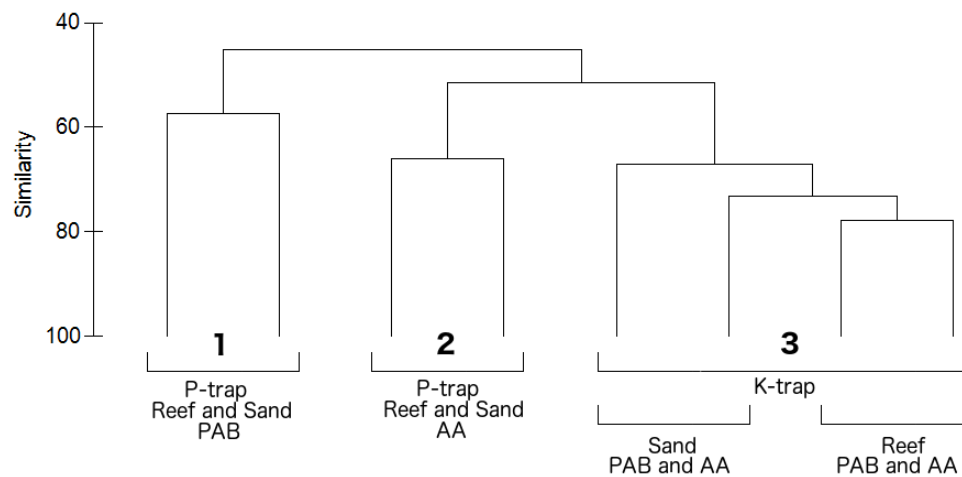


Fonte: Lucas Figueirêdo.

The Cluster analysis grouped the demersal zooplankton in three main groups (Fig. 3). The group 1 and 2 encompasses the samples collected with the P-trap, and the group 3 is formed by the samples collected with the K-trap. The trap factor seems to be the main contributor to the Cluster groupings. However, among P-trap samples, the influence of the sites formed separate subgroups while among the K-trap samples, the substrates appear to have more influence.

The overall biomass of the demersal zooplankton was $6,918.93 \pm 5,029.41 \mu\text{gC} \cdot \text{m}^{-2}$ with a maximum of $20,190.20 \mu\text{gC} \cdot \text{m}^{-2}$ (Fig. 4). Some taxonomic groups that have large body length/weight showed increased percentage contributions to total biomass in contrast with their contribution to total abundance (Table 3). This is the case of the polychaetes, amphipods and mysids. Despite the lower abundances, these groups had a percentage contribution to total biomass up to 9, 7 and 10 times higher than their contributions to total abundance, respectively. The copepods showed an inverse pattern, with higher percentage contributions to abundance than to biomass.

Figure 3: Cluster analysis of the demersal zooplankton for each site, substrate, and trap.



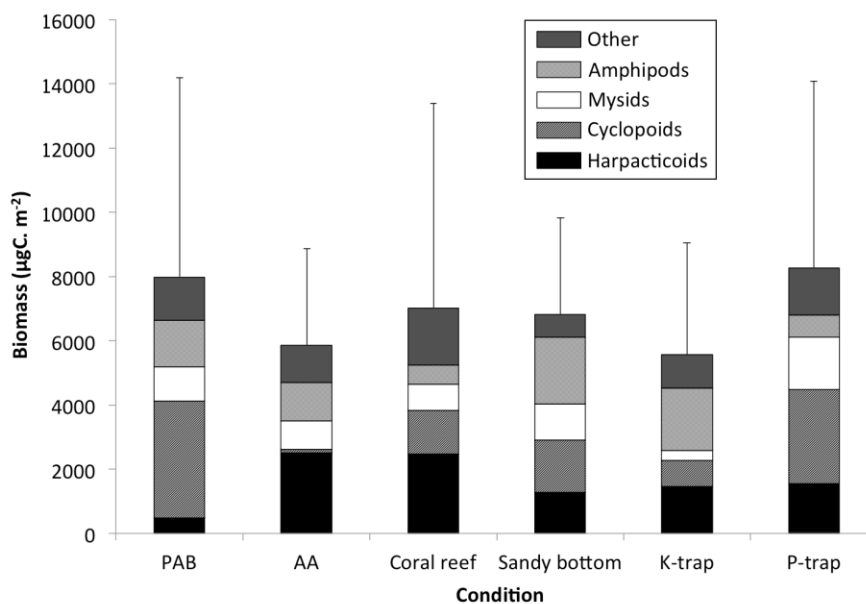
Fonte: Lucas Figueirêdo.

3.3.2 Sites influence

A total of 46 taxa were observed in each site. The demersal zooplankton composition varied greatly among sites, although the abundance and biomass were equivalent (Mann-Whitney, $P > 0.05$). Remarkably, in terms of composition, the samples collected over the coral reef substrate had significant differences between AA and PAB sites. Similarly the emergent fauna collected at the adjacent sandy bottom also differed between distinct sites (PERMANOVA, see Table 4; Cluster see Fig. 3).

Of all the taxa observed in AA, 7 were exclusive (*Novocriniidae*, *Tetragonicipitidae*, *Oncaea venusta*, *Onychocorycaeus giesbrechti*, larvae of Echinodermata and fish larvae). Individuals of Thalestridae dominated the demersal zooplankton, followed in some cases by copepods of the families Harpacticidae and Tisbidae, and amphipods. Among the calanoids, the *Pseudocyclops* sp., known to be epibenthic, were almost exclusive, considering the rare occurrences of *Paracalanus quasimodo*, *Temora stylifera* and *Calanopia americana*. Among chaetognaths, the benthic *Paraspadella nana* was the most abundant at both sites, even though other pelagic forms were also found. The IndVal analysis showed five indicators of AA site. Among them, four belonged to harpacticoid families commonly encountered associated with algae (Table 5).

Figure 4. Mean biomass ($\mu\text{g C m}^{-2}$) of demersal zooplankton at each site, substrate, and trap. Percent composition is shown for the main taxonomic groups.



In PAB, of all the taxa (i.e. 46), 6 were exclusive as well (*Temora turbinata*, *Oithona plumifera*, *Diosaccidae*, *Farranula* sp., Bivalve veligers, nauplii of Cirripedia and *Euphausiacea*). A surprisingly large number of *D. oculata* dominated the PAB samples. Swarms reached a peak abundance of 25,192 ind m^{-2} . The IndVal analysis showed three indicators of PAB site with *D. oculata* as the stronger indicator (Table. 5).

In terms of biomass, the cyclopoids were dominant in PAB, mostly due to the contributions of *D. oculata*, and at AA the harpacticoids dominated. The other major contributors to biomass (i.e. amphipods and mysids) showed similar average biomass in both sites (Fig. 4).

Table 3. Abundance (mean \pm SD, ind m⁻²) and biomass (mean \pm SD, μ g C m⁻²), and percent contribution to total abundance and biomass of main taxonomic groups. bold numbers highlights the taxonomic groups that showed an increase in biomass contribution in relation to its abundance contribution.

Taxonomic group	AA							
	Coral reef				Sandy bottom			
	Abundance	%	Biomass	%	Abundance	%	Biomass	%
Gastropoda	23.6 \pm 22.5	1.1	21.6 \pm 27.7	0.4	0.0	0.0	0.0	0.0
Polychaeta	76.0 \pm 67.9	2.1	662.9 \pm 924.8	10.1	57.1 \pm 95.6	1.3	215.9 \pm 241.7	5.6
Calanoida	34.2 \pm 24.0	1.6	38.3 \pm 37.6	1.1	10.5 \pm 10.6	0.3	18.4 \pm 22.4	0.4
Cyclopoida	245.7 \pm 291.7	6.0	57.7 \pm 59.8	2.1	849.7 \pm 1598.6	7.6	158.8 \pm 348.3	2.1
Harpacticoida	2701.4 \pm 3583.8	61.2	1990.3 \pm 1876.4	33.4	3886.7 \pm 4198.1	75.3	3014.6 \pm 1621.3	50.9
Copepod nauplii	295.2 \pm 340.9	8.8	2.4 \pm 2.9	0.1	323.8 \pm 375.4	5.1	2.5 \pm 2.9	0.1
Decapoda	171.0 \pm 199.3	5.6	534.8 \pm 797.0	7.0	6.8 \pm 10.5	0.4	77.9 \pm 130.1	1.6
Ostracoda	27.2 \pm 18.2	1.2	228.2 \pm 396.8	5.1	33.3 \pm 27.9	1.3	67.3 \pm 74.0	1.2
Mysidacea	37.9 \pm 44.1	1.7	1484.1 \pm 2964.0	17.8	14.3 \pm 15.3	0.7	294.5 \pm 490.4	5.6
Amphipoda	88.9 \pm 51.6	5.9	805.0 \pm 584.2	19.9	111.8 \pm 105.9	3.8	1587.5 \pm 857.8	28.7
Isopoda	5.1 \pm 12.5	0.3	6.8 \pm 16.5	0.1	33.0 \pm 20.1	1.2	129.3 \pm 92.3	2.5
Chaetognatha	5.1 \pm 6.5	0.4	203.2 \pm 461.7	2.8	33.3 \pm 52.4	0.4	112.5 \pm 176.7	1.6
Larvacea	4.2 \pm 8.2	0.2	3.1 \pm 6.9	0.0	0.0	0.0	0.0	0.0
Taxonomic group	PAB							
	Coral reef				Sandy bottom			
	Abundance	%	Biomass	%	Abundance	%	Biomass	%
Gastropoda	123.0 \pm 241.4	1.3	1235.6 \pm 2797.7	7.7	10.4 \pm 23.0	0.2	29.0 \pm 69.9	0.3
Bivalvia	4.8 \pm 11.7	0.1	3.4 \pm 8.3	0.1	0.0	0.0	0.0	0.0
Polychaeta	51.5 \pm 37.1	1.3	407.3 \pm 394.1	12.2	10.4 \pm 23.0	0.3	6.3 \pm 13.7	0.1
Calanoida	89.2 \pm 63.0	2.3	78.6 \pm 70.9	3.2	154.7 \pm 95.9	8.6	368.1 \pm 304.7	4.8
Cyclopoida	6648.8 \pm 10475.2	41.5	4872.0 \pm 7866.8	30.1	3547.0 \pm 5457.8	39.7	2408.0 \pm 3656.6	25.9
Harpacticoida	1302.0 \pm 1312.2	23.1	725.2 \pm 829.3	23.3	375.6 \pm 420.4	16.9	237.8 \pm 96.2	5.3
Copepod nauplii	1598.6 \pm 1769.9	25.5	14.7 \pm 13.5	0.7	303.2 \pm 692.0	2.6	2.4 \pm 5.1	0.0
Decapoda	23.6 \pm 33.5	0.7	54.6 \pm 60.5	1.7	27.2 \pm 35.7	1.0	156.7 \pm 250.5	1.5
Ostracoda	29.6 \pm 36.9	0.5	26.9 \pm 23.0	1.1	16.1 \pm 27.8	1.4	48.8 \pm 64.0	0.8
Mysidacea	26.0 \pm 24.6	0.8	170.1 \pm 226.2	4.2	75.6 \pm 87.5	5.4	1959.5 \pm 3107.9	20.0
Amphipoda	69.7 \pm 62.7	1.5	368.7 \pm 375.7	13.8	298.4 \pm 423.9	16.7	2549.5 \pm 3395.4	38.3
Isopoda	0.0	0.0	0.0	0.0	2.4 \pm 5.8	0.1	0.0	0.0
Chaetognatha	3.2 \pm 5.8	0.1	30.5 \pm 48.8	2.0	9.0 \pm 11.5	1.3	203.9 \pm 251.1	3.0
Larvacea	3.4 \pm 8.3	0.0	1.0 \pm 2.4	0.0	0.0	0.0	0.0	0.0

Table 4 – PERMANOVA analysis based on abundance and biomass from the sites, substrates, and traps. Significant values of P are in bold.

Groupings (Abundance)	PERMANOVA analysis	
	t	P
AA x PAB		
Sandy bottom samples	2.16	0.005
Coral reef samples	1.89	0.004
Sandy bottom x Coral reef		
AA samples	2.21	0.005
PAB samples	1.63	0.026
K-trap x P-trap	4.09	0.001
Groupings (Biomass)	PERMANOVA analysis	
	t	P
AA x PAB		
Sandy bottom samples	2.53	0.005
Coral reef samples	1.49	0.049
Sandy bottom x Coral reef		
AA samples	2.17	0.008
PAB samples	1.87	0.020
K-trap x P-trap	2.51	0.002

Fonte: Lucas Figueirêdo.

3.3.3 Substrates effect

The comparisons between the substrates showed the same patterns as the sites. The abundance and biomass of the zooplankton emerging from the distinct substrates did not differ significantly (Mann-whitney, $P > 0.05$), although variations in composition were noted (PERMANOVA, Table 4). A total of 50 taxa occurred in Coral reef substrate and 40 taxa occurred in the sandy bottom. The swarms of *D. oculata* were more frequent on the coral reef than on the sandy bottom surface. Moreover, the average abundance of the swarms observed on sandy bottom was only 35% of that found on the coral reef substrate. The largest swarm found on sandy bottom samples reached an abundance of 11,886 ind. m⁻². The IndVal analysis revealed only two indicator taxa for sandy bottom substrate and three for coral reef (Table 5). All the calanoids (with the exception of *Calanopia americana*), the monstrilloids and the larvaceans were more frequent in coral reef samples. Inversely, *Farranula* sp. and chaetognaths were more frequent in sandy bottom samples.

In terms of biomass, the harpacticoids dominated the coral reef substrate followed

by the cyclopoids, while in the sandy bottom substrate the biomass was more evenly distributed across the amphipods, cyclopoids, harpacticoids and mysids (Fig. 4). The polychaets, decapods, isopods, and chaetognaths were more representative in the coral reef substrate.

3.3.4 Traps efficacy

The type of trap has a major impact over the results obtained by emergent fauna studies. In the present study, the mean abundance of the K-trap ($6,883 \pm 5,153$ ind. m^{-2}) was significantly higher than the mean abundance collected by the P-trap ($5,216 \pm 7,621$ ind. m^{-2}) (Mann-whitney, $P < 0.05$). Most of the difference in abundance is driven by the great occurrence of copepod nauplii in the K-trap samples, whereas in the P-trap samples nauplii were almost absent, as an effect of mesh selection. The emergent fauna composition also differed significantly (PERMANOVA, see Table 3). The IndVal results showed twelve indicator taxa of the K-trap (Table 4). All of those are copepod taxa that have small sized bodies. P-trap had only two taxa with significant indicator values. True demersal forms as *Pseudocyclops* sp. and the majority of individuals of harpacticoid families were most frequently caught in the K-trap.

However, the biomass estimations showed similar values for both traps (Mann-Whitney, $P = 0.192$), indicating that in terms of biomass the small taxa may not play a significant role on the community as expected if looking solely to their abundance values. The cyclopoid *D. oculata* was the exception to that pattern. Due to its extraordinary abundance found mainly in the P-trap samples the biomass was estimated to be high as well.

Table 5 – IndVal analysis. Zooplankton taxa that characterize each site, substrate, and trap. Taxa are sorted by decreasing IndVal values within each group.

Group	Indicator value analysis	
	Taxa	IndVal
AA	Tisbidae**	0.918
	Hamondiidae**	0.856
	Harpacticidae*	0.794
	Peltidiidae*	0.730
	Isopoda*	0.687
PAB	<i>Dioithona oculata</i> **	0.913
	Diosaccidae**	0.700
	<i>Calanopia Americana</i> *	0.690
Sandy bottom	<i>Calanopia Americana</i> *	0.690
	Isopoda*	0.661
Coral reef	Gastropoda (veliger)*	0.837
	Calanoida (nauplii)**	0.700
	Laophontidae*	0.695
K-trap	Harpacticoida (nauplii)**	1
	Cyclopoida (nauplii)**	0.995
	Harpacticidae**	0.952
	Ectinosomatidae**	0.952
	<i>Oithona</i> spp.**	0.949
	Metidae**	0.923
	<i>Oithona simplex</i> **	0.912
	Tisbidae*	0.911
	Laophontidae**	0.861
	Calanoida (nauplii)**	0.764
	<i>Pseudocyclops</i> sp.*	0.752
	Longipediidae*	0.641
	P-trap	Diptera larvae**
Mysidacea*		0.831

** $P < 0.01$; * $P < 0.05$. Fonte: Lucas Figueirêdo.

3.4 Discussion

In Abrolhos Bank the night abundance of the zooplankton collected from net tows (200 μ m net; ≈ 300 ind. m^{-3}) were reported to be in average 3 times higher than the day abundances (Figueiredo, 2018). If a calculation is made to transform the abundance of the demersal community emerging from the substrate (m^{-2}) into the water column (m^{-3}), in AA (water column of 6 m) the emergent fauna would contribute to the pelagic zooplankton abundance in ≈ 768 ind. m^{-3} while in PAB (water column of 7 m) that contribution would be ≈ 1249 ind. m^{-3} . This is an evidence of the important role that demersal zooplankton

play in benthic-pelagic coupling in reef environments, as well as it indicates that night tows do not sample this population properly since the emergent fauna had an abundance ≈ 2.5 (AA) and ≈ 4 (PAB) times higher than the reported for the night tows.

One of the main factors that make abundances of net zooplankton lower than those of traps is the difference in migration capability of particular demersal forms. Alldredge e King (1985) reported that small-bodied forms, including copepods, remained in 30 cm of the bottom, while the larger animals swam freely throughout the water column. Holzman *et al.* (2004) reported that taxa with faster swimming speeds (large-bodied animals) showed stronger near bottom depletion due to rapid avoidance of the bottom. The emergent fauna clearly induces a pattern on the night zooplankton assemblages. That is, larger animals reach higher in the water column, becoming suitable food source for the fish foraging aloft (Holzman e Genin, 2003; Holzman *et al.*, 2004), and smaller animals remains near the bottom becoming suitable for the benthic foragers (Palardy *et al.*, 2006). This behavioral pattern makes the demersal zooplankton an important trophic resource for both benthic and pelagic communities residing on coral reef environments.

This study shows a clean distinction between the demersal communities resident of the reef formations assessed here, since the PERMANOVA showed differences between the same types of substrate from distinct sites. It is clear that demersal zooplankton exhibit an active behavior meaning that different taxonomic groups may have preferences for a particular substrate and even for a particular portion of a reef area (Alldredge e King, 1977). On a larger scale, the manuscript of Alldredge e King (1980), reporting differences in abundance of emergent zooplankton of two Pacific Ocean Atolls and the Great Barrier Reef in Australia was one of the first mentions of differences in demersal zooplankton communities from distinct types of reef formations. In the present study the differences in composition found between the sites (AA – fringing reef, and PAB – pinnacles reefs) is an evidence of active preference of some taxa for a particular reef formation. Since the sampling sites in this study are close to each other (4.8 km apart), salinity and temperatures are similar, and the reef substrates have similar coverage and lies at similar depths in both sites, other factors seems to be influencing the community distribution pattern.

In PAB site, the pinnacles reefs provide much more shelter because of its rugged relief with caves and crevices and large coral heads that reach heights of up to 2 m with living colonies of approximately 1 m in diameter (*Mussismilia braziliensis*) (Leão e Kikuchi, 2001b; Francini-Filho *et al.*, 2013). The best indicator of PAB site was *Dioithona oculata*, which is a swarm-forming copepod commonly found near coral reefs (Ambler *et al.*, 1991). According to Omori e Hammer (1982) the swarms of *D. oculata* are formed during the daytime when they seek for shelter from the strong currents behind coral boulders and other structures like caves and crevices. This behavior makes the swarms able to maintain their positions or slowly shift according to currents (Madhupratap *et al.*, 1991). Therefore, the pinnacles reefs are a more suitable formation for the settlement of those swarms than the fringing reefs found in AA.

Differently, in AA site the cyclopoids (mainly *D. oculata*) gave place to the harpacticoids. In agreement with the results presented here, other studies have reported the harpacticoid copepods to dominate demersal assemblages (Madhupratap *et al.*, 1991; Cahoon e Tronzo, 1992; Pacheco *et al.*, 2014) and to be the only taxa consistently captured in significantly greater numbers (Jacoby e Greenwood, 1989). In this site, 4 harpacticoid families considered phytal (Bell *et al.*, 1987) were the main indicators (see table 5). According to their habits, these families may be associated with the abundant turf algae in this fringing reef, though their occurrence were not exclusive to AA site. Moreover, the samples from PAB site, which had an abundance of *D. oculata* less than 400 ind m⁻² presented up to 9 harpacticoid families, but when *D. oculata* reached abundances higher than 400 ind m⁻² only one sample presented the maximum of 4 harpacticoid families. This fact may be an evidence of negative interaction between individual taxa, which affect the populations (Haury *et al.*, 1978; Lewis e Boers, 1991).

The high biomass of the demersal community in PAB site, driven mostly by the swarms of *D. oculata*, is an important feature of the pinnacles reefs. According to Allredge e King (1977), fish, rather than corals, are the major predators of demersal assemblages. Therefore, the demersal zooplankton is clearly a suitable food source for planktivorous fish, and the high abundance of this group of fish in PAB area in comparison to AA (Moura e Francini-Filho, 2005) may be supported by the high biomass of the demersal community found in this location.

Although species diversity was not investigated in this study the highest number of taxa emerged from coral reef substrates. Sandy bottom samples contained a more balanced contribution of taxa whereas the coral reef samples were dominated by the copepods in a similar pattern as reported by Alldredge e King (1977). According to Alldredge e King (1977), the abundance of demersal plankton harbored by each substrate is correlated with the substrate heterogeneity. Hence, progressively more plankton emerges from rock, fine sand, medium and coarse sand, rubble, and coral substrates. However, the heterogeneity that is reflected in more microhabitats as the interstices of the rubble and sand under the coral and the intricate matrix of the coral itself may provide shelter not only to a greater number of individuals, but to a greater diversity as well. In the same manner as in this study, Alldredge e King (1977), Jacoby e Greenwood (1989) and Melo, Pedro A. M. C. *et al.* (2010) found a more diverse demersal community emerging from coral substrates, Gheerardyn *et al.* (2008) and Gheerardyn *et al.* (2009) found a more diverse harpacticoid community living on coral microhabitats than on sand.

If the number of taxa found in each site and substrate is used to compare their influence, the substrates would have higher influence over the distribution of the demersal community than the sites (reef formation herein), since the same amount of taxa were found in both sites while the coral reef substrate had 10 more taxa than the sandy bottom. Likewise, the same conclusion can be drawn if the similarity among samples is used to compare the influence of sites and substrates. The groupings formed by the cluster analysis (Fig. 3) indicate that for the P-trap the substrate samples were more similar to each other than the site samples, which would lead to the conclusion that the sites induced higher diversity among samples (greater influence). However, even though the two types of trap showed similar biomass, in terms of composition, the P-trap missed many taxa probably due to its coarse mesh (see table 5) and became not the best parameter. The K-trap samples, otherwise, formed groupings where the site samples were more similar, and the substrate induced higher diversity among samples (greater influence).

The methodologies used to sample demersal zooplankton have been the subject of discussion by many authors (Alldredge e King, 1980; Youngbluth, 1982; Stretch, 1985; Jacoby e Greenwood, 1989; Cahoon e Tronzo, 1992; Kramer *et al.*, 2013) and there is

still space for more discussion since the demersal zooplankton has not been extensively sampled and studied by world's plankton researchers.

Some authors raised concerns about the efficiency of emergence traps, regarding factors like contaminations (Hobson e Chess, 1979), mesh size selection (Alldredge e King, 1980), and the height of the entrance into the catch chamber (Youngbluth, 1982). The K-trap used in this study was design based on what was proposed by Youngbluth (1982), Alldredge e King (1985), and Kramer *et al.* (2013) to enhance the efficiency of the trap reducing the influence of the concerning factors previously mentioned. In order to achieve that, it was used a 64 μm mesh net to maximize the catch, and the catch chamber was placed 30 cm from the substrate to catch the “weak migrants”.

The K-trap had abundance 25% higher than the P-trap as a probable result of the finer mesh and the shorter height of the catch chamber. However, the biomass did not differ statistically. This feature suggests that large-bodied organisms that migrate far from the substrate still get trapped on the P-trap as expected. Moreover, the indicators of P-trap were large-bodied animals, e.g. mysids that contributed up to 20 % of total biomass. Apparently, mysids and diptera larvae managed to avoid being trapped by the smaller K-trap. Despite the effort to design a more efficient trap, in Abrolhos Bank the results of both traps were complementary to each other, and the exclusion of one type of trap would impair the general results.

3.5 Conclusions

The results addressed here still corroborates with what Alldredge e King (1980) stated that emergence traps may accurately reflect the densities and biomass of true demersal zooplankton available to planktivorous predators in the water column and in addition highlights that comparable biomass is available for predators foraging close and far from the substrate. More attention should be directed toward understanding the importance of environmental factors shaping this highly diverse community, not only in terms of species but also in terms of behavior, that play an important role as trophic resources for many organisms (Robertson e Howard, 1978; Motro *et al.*, 2005; Couturier *et al.*, 2013).

4 A NEW PERSPECTIVE ON THE DISTRIBUTION OF CHAETOGNATHA, SPADELLIDAE, PARASPADELLA NANA OWRE, 1963: TWO NEW OCCURRENCES FROM THE WESTERN TROPICAL ATLANTIC OCEAN.

4.1 Introduction

Chaetognaths play an important role in marine food webs, due to their active predatory behavior. In their diet are several pelagic organisms, consisting mainly of copepods, but they may also prey on other crustaceans and even fish larvae thus impacting the zooplankton and ictioplankton communities (Casanova, 1999). Studies on chaetognaths in Brazil have concentrated on the abundant pelagic forms (Liang e Vega-Pérez, 2001; 2002), which some times are surpassed in number only by copepods (Gusmão, 1986). Not only in Brazil, but worldwide the pelagic communities of chaetognaths are better studied, and the distribution of the benthic forms such as the genus *Paraspadella* is poorly documented (Owre, 1963).

The family Spadellidae consists of 31 described species, all benthic and grouped in 5 genera. The genus *Paraspadella* was initially described by Salvini-Plawen (1986) and then combined with the genus *Gephyrospadella* by Bowman e Bieri (1989), grouping all the species that presented adhesive organs (main taxonomic feature of the genus *Paraspadella*). Currently, a total of 10 species compose the genus *Paraspadella* (*Paraspadella anops* Bowman and Bieri, 1989; *P. caecafea* (Salvini-Plawen, 1986); *P. gotoi* Casanova, 1990; *P. johnstoni* (Mawson, 1944); *P. legazpichessi* (Alvariño, 1981); *P. nana* (Owre, 1963); *P. pimukatharos* (Alvariño, 1987); *P. pulchella* (Owre, 1963); *Paraspadella schizoptera* (Conant, 1895); *P. sheardi* (Mawson, 1944).

The species *P. nana* has very few occurrences reported. Owre made the first report in 1963 at the time he describe this species. A total of 15 specimens were collected from sediment samples associated with algae at Soldier Key, Florida. A new occurrence was reported by Arruda *et al.* (2010) at the Eastern Brazilian Continental Shelf (EBCS). In that occasion, a total of 3 specimens were collected by horizontal hauls (200 µm mesh net). This study reports two new occurrences of *P. nana* in Northeastern Brazil and gives a new perspective on its distribution in the Atlantic Ocean.

4.2 Material And Methods

The specimens were collected in two sampling areas apart more than 1,000 km from each other: (1) the Abrolhos Bank (17° 57' S; 38° 42' W); and (2) the Tamandaré bay (8° 45'' S; 35° 05'' W). The samples were collected using emergence traps according to the methodology proposed by Porter *et al.* (1977) to catch demersal zooplankton. The trap consists of a conical net (200 µm mesh) placed with the mouth directed to the substrate. This type of trap conducts vertically migrating animals through a conical-shaped region into a catch chamber. The traps were placed across hard substrate (coral reef) and soft substrate (sandy bottom). In Tamandaré Bay, the traps were placed only on reef substrate. A total of 24 samples were collected in the Abrolhos Bank and 30 samples were collected in Tamandaré Bay. After collection, the samples were fixed in 4% formalin/seawater solution. In the laboratory the samples were analyzed under stereoscopic microscope and the chaetognaths were sorted and identified based on descriptions of Owre (1963).

Because of the sampling methodology (no stress by turbulence) the specimens of *P. nana* were in perfect condition (Fig. 1). The specimens are in accordance with the diagnosis proposed by Owre (1963), with the main characteristic features: (1) body relatively slender and rigid with a broader head; (2) there is 5 to 9 hooks and 1 to 3 anterior teeth depending on its maturity; (3) corona ciliata is variable in shape and situated on the anterior trunk; (4) A long collarete is present, being thickest at the neck and extending along the base of the lateral fin to the seminal vesicle; (5) There is one pair of lateral fins that originate anterior to the apertures of the seminal receptacles and terminate just anterior to the seminal vesicles. The caudal fin is broad and originates on the posterior face of the seminal vesicles; (6) A pair of adhesive organs is formed ventrally, from the posterior end of the lateral fins.

Figure 1. *Paraspadella nana* (Owre, 1963). Dorsal view of two specimens from Northeastern Brazil. The pairs of adhesive appendices can be seen on both sides at the tail region.



Fonte: Lucas Figueirêdo.

4.3 Results And Discussion

In the Abrolhos bank 12 specimens were collected, presenting a mean density of 17,8 ind. m⁻². Of the total specimens found in the Abrolhos Bank, 8 were collected on the coral reefs and 4 on the sandy bottom. In the Tamandaré bay, an overwhelming amount of 156 specimens were collected, presenting a mean density of 17 ind. m⁻².

Since the family Spadellidae is typically benthic, the occurrence of individuals of this family is scarce on studies of zooplankton. The methodology of collection in studies of zooplankton is generally based on pelagic hauls that may catch Spadellidae individuals

only in case of occasional resuspension of sediments due to local currents (Arruda *et al.*, 2010). Species of this genus have one reported occurrence in usual plankton collections (Arruda *et al.*, 2010). Benthic collections may also fail to report the occurrence of these species, because they usually overlook these animals due to their small size (Alvariño, 1981). Among the Spadellidae members, the individuals of *Paraspadella* genus have even more limited distribution because of their restricted habitat and movements (Alvariño, 1981). However, with proper sampling, new perspectives on the distributional range of species of *Paraspadella* may be obtained.

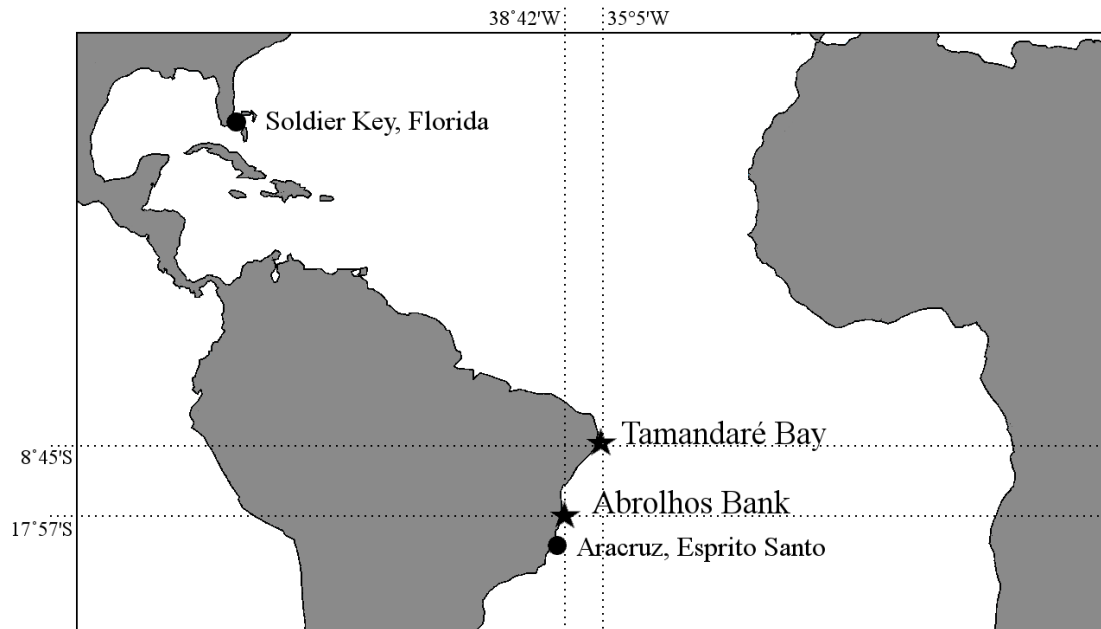
Studies of demersal zooplankton (i.e. fauna that live in close association with the benthic domain during the day and migrate into the overlying water column at night) report more frequent occurrences of Spadellidae individuals. Several authors describe these animals as demersal zooplankters (Alldredge e King, 1977; Jacoby e Greenwood, 1989; Madhupratap *et al.*, 1991). Alldredge e King (1977) collected individuals of *Paraspadella* in large numbers from several substrate types using emergent traps at the Great Barrier Reef as well as Jacoby e Greenwood (1989) which reported the occurrence of a species of the genus *Spadella* in Queensland, Australia. Madhupratap *et al.* (1991) using emergent traps in the archipelagos off the western coast of India reported the occurrence of *Spadella angulata* in densities similar to that reported here for *P. nana*.

The distribution of *P. nana* and other Spadellidae species might not be as restricted as expected. The methodology commonly used for sampling and analysis of samples in studies of zooplankton and benthic communities may not be the most efficient to catch demersal chaetognaths. According to the findings of Kramer *et al.* (2013), the benthic and the demersal communities may be significant distinct. Kramer's work compared the benthic fauna and the emergent assemblages of the same substrate and showed that 32% of the taxa captured by the emergent traps were absent from the benthic community. This is probably because these demersal taxa arise from a rich variety of structural features found in the reef matrix that are not properly sampled by benthic and zooplankton collections. Moreover, *Paraspadella* emerge primarily from coral, rubble and rock in reef areas (Alldredge e King, 1977).

This communication furnishes the report of the occurrence of the rare *P. nana* in two distinct areas and in numbers never caught before, with the use of emergent traps.

This new report expands the distribution of *P. nana*, which now has a wider range of occurrence reported for the western tropical Atlantic (Fig. 2).

Figure 2. Geographic distribution of *Paraspadella nana* (Owre, 1963). Circles – previous records; stars – New records.



Fonte: Lucas Figueirêdo.

4.4 Acknowledgements

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5 SPATIAL AND DIEL VARIATIONS OF LIVE/DEAD COMPOSITIONS OF A REEF COPEPOD COMMUNITY: IMPLICATIONS FOR ECOLOGICAL STUDIES

5.1 Introduction

Zooplankton plays a key role in the food webs of coral reefs and are the focus of intense predation by reef consumers, including fish, corals and other sessile invertebrates (Hamner *et al.*, 1988; Kappner *et al.*, 2000; Palardy *et al.*, 2006). Copepods are one of the most abundant and diverse groups in reef-associated zooplankton (Suárez-Morales e Gasca, 2000), and because of that, their biomass and production have been the subjects of many studies (Mckinnon e Thorrold, 1993; Mckinnon e Ayukai, 1996; Nakajima *et al.*, 2017). However, improper ecological conclusions can result when the live/dead compositions of copepods are not accounted (Elliott e Tang, 2011). Visual predators may less successfully encounter passive and dead organisms compared with moving and living ones. Moreover the risk of parasites may also be the cause of avoidance of dead organisms by predators (Daase *et al.*, 2014).

Evidence shows that zooplankton carcasses are ubiquitous in marine environments and in some cases exceeds the abundance of living forms, which is result of several factors, including predation, grazing, parasitism, disease and infection, starvation, maturity (resilience/size) and senescence (Genin *et al.*, 1995; Hirst e Kiørboe, 2002; Elliott e Tang, 2011; Daase *et al.*, 2014; Tang e Elliott, 2014). Methods applied for field sampling and analysis of zooplankton often assume that all collected and preserved animals were alive *in situ*. The exclusion of dead copepods can lead to significant misjudgment of population dynamics (Elliott e Tang, 2011) and caution is needed when assessing population estimates based on density, such as biomass, production and grazing.

Accurate assessment of the population abundances is fundamental in zooplankton ecological research (Elliott e Tang, 2009) and for that, quantifying the carcasses may be fundamental as well. Estimating live and dead proportions on copepod populations *in situ* is difficult. Similarly, to distinguish live and dead copepods in fixed samples at the

laboratory is often challenging, because they may have similar appearances. However, Neutral Red vital staining method requires minimal handling of the animals on board, and the stained samples can be preserved for later analysis at the laboratory (Elliott e Tang, 2009). This method consists of a vital stain that is incorporated into the lysosomes of live cells. Therefore, the individuals not stained correspond to dead organisms, since dead cells shows no uptake of stain.

The study of the abundance of dead copepods is important not only to understand population dynamics. Copepod carcasses contribute to the downward flux of carbon and nitrogen, supplying the benthic system (Sampei *et al.*, 2012), and may even be part of the dietary intake of deep-sea fauna (Haury *et al.*, 1995). This matter become even more significant in environments that contain high proportions of dead copepods, which appears to be the case of coral reefs ($\approx 65\%$ of dead copepods, see Genin *et al.* (1995)). In the present study, composition, abundance, biomass and live/dead copepod compositions in both coastal reefs and offshore reefs were analyzed, aiming to assess the copepod mortality and its consequences to the ecological features of the community, considering the spatial and diel variations.

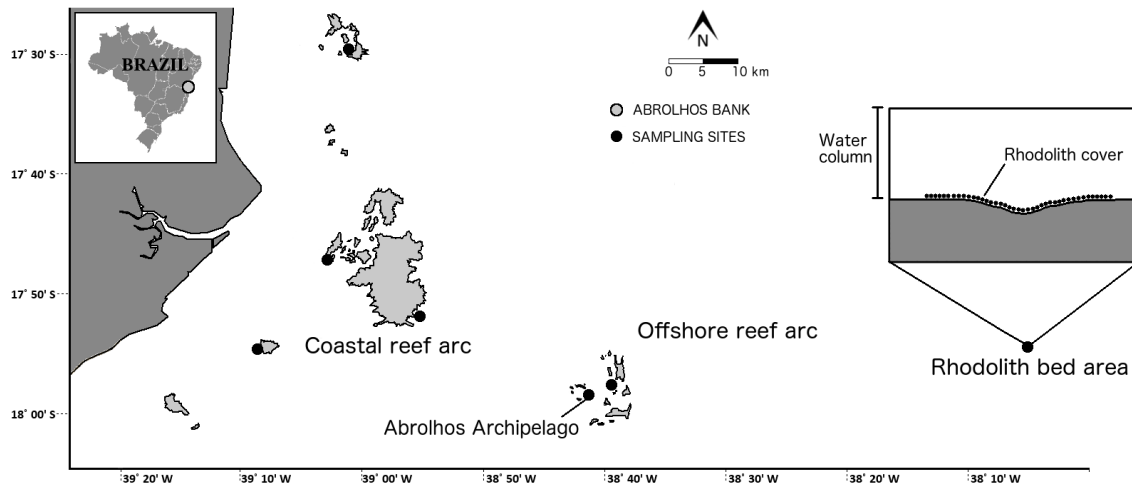
5.2 Materials And Methods

5.2.1 Study area

The study was carried out in the Abrolhos bank reefs. The Abrolhos Bank is located between 17°S and 20°S on the large (245 km) Eastern Brazilian Continental Shelf (Knoppers *et al.*, 1999). The major reef formations include a coastal reef arc, an offshore reef arc, and at the farther parts of the shelf, rhodolith beds developed in great extension (Amado-Filho, G. M. *et al.*, 2012) (Fig. 1). The coastal reef arc is located at an area 5-30 km far from the coastline with the reefs growing upward from a depth of 15 m and at some points presenting emerging tops. The offshore reef arc is located and area far 60-65 km from the coastline and borders the east side of the Abrolhos Archipelago. The reefs at the offshore reef arc grows from a depth of up to 25 m, extending for 15 km (Moura *et al.*, 2013). The rhodolith beds occupy the farthest portion of the shelf, being estimated to

cover 20,902 km² in depths of 20 m up to 110 m (Amado-Filho, G. M. *et al.*, 2012; Cavalcanti *et al.*, 2013).

Figure 1. Study area with the sampling sites as circles. The structure of the Rhodolith beds is highlighted.



Fonte: Lucas Figueirêdo.

The presence of a low relief at the Continental shelf of the Abrolhos Bank promote the shoreward intrusion of the Tropical Water from the Brazil Current (Castro e Miranda, 1998). Terrigenous inputs are not transported far offshore of Abrolhos Bank, due to hydrodynamic and topographic barriers (Leipe *et al.*, 1999). Water motion on the inner and middle shelf is primarily forced southward by wind stress, whereas the Brazil current is a major influence on the outer shelf (Lessa e Cirano, 2006; Teixeira *et al.*, 2013).

5.2.2 Field collection

Sampling was carried out during summer (February) 2016. Seven sites were sampled across the Abrolhos Bank reefs, i.e. coastal reefs (coastal arc), and offshore reefs (Abrolhos Archipelago, offshore reef arc and rhodolith beds) (Fig.1). Profiles of temperature and salinity were made with a mini CTD CastAway. Niskin bottles were

used to collect water samples for estimate the chlorophyll *a* concentration. Depending on suspended particle concentration, 0.3 up to 1.5 L of water were filtered through 47 mm GF/F (Whatman) and frozen for further analysis. At the laboratory, acetone (90%) was used for the pigment extraction and the measurements were made using a spectrophotometer (Strickland e Parsons, 1965).

Plankton tows were conducted around noon and midnight in consecutive days in each site. Two cylindrical-conical nets (mesh sizes: 64 and $200 \mu\text{m}$) equipped with a flowmeter were simultaneously towed for 5 minutes in horizontal hauls. The samples were fixed with 4% formaldehyde and buffered with 4 g L^{-1} sodium tetraborate. For mortality estimates, additional plankton samples were collected by horizontal tows with the same mesh sizes, fitted with a non-filtering cod end. The tows were conducted slowly (0.5 m s^{-1}) and during short periods (1 min). To achieve substantial density of copepods, several tows were performed. Collection was performed in order to avoid damaging the organisms, and the cod end contents were immediately transferred to a vessel, and incubated with neutral red (1:1000 stock solution) for 15 minutes, guarded from light at *in situ* temperature. After the 15 minutes staining period, the organisms were filtered through a $20\text{-}\mu\text{m}$ sieve and stored at -20°C for posterior analysis at the laboratory (Elliott e Tang, 2009).

5.2.3 Laboratory procedures

For the analysis of samples (abundance and biomass estimates), aliquots were taken with a Motoda splitter and analyzed using Sedgewick-Rafter chamber ($64 \mu\text{m}$ net samples) or Bogorov counting chamber ($200 \mu\text{m}$ net samples) under stereomicroscopes. A minimum of 300 individuals were considered per samples (Omori e Ikeda, 1984). The identification of the copepods was performed at the lowest taxonomic level possible.

The biomass was estimated using previously determined length-weight regressions to estimate the individual carbon weight. To achieve that, an average prossome length was determined for each copepod taxa in each sample and then converted to carbon weight (CW) (see table 1). The CW was assumed to be 40% of the dry weight (DW) (Postel *et al.*, 2000). Biomass ($\mu\text{gC. m}^{-3}$) was calculated for each

copepod taxa based on its abundance (ind. m⁻²) and individual carbon weight (CW, µgC). Because the juveniles of the genus *Corycaeus*, *Oithona*, and *Oncaea* were not easily separable, these genera were combined together and one generic regression was used. Because of morphological similarities, the individuals within each of the families Clausocalanidae, Paracalanidae and Temoridae were combined as well.

For vital staining analysis, samples were thawed using cold filtered seawater. To enhance the stain's color, the samples were acidified with 1M HCl (1:10 final concentration) and then observed under a stereomicroscope (dark field with low light) to determine the state of the organisms (stained copepods, live; weakly stained or not stained, dead) (Fig. 2). Only the most abundant taxa were accounted, since the rare species often showed no suitable amount of individuals to determine a reliable live/dead proportion for the entire population.

5.2.4 Statistical analysis

The abundance, biomass and percentage of dead copepods data were tested for normality (Kolmogorov-Smirnov test). Data were then tested for statistical significance by using T-test or *Mann-Whitney* analysis to compare the two reef areas (coastal reefs and the offshore reefs), the diel cycle (day and night) and the mesh sizes (64 µm and 200 µm).

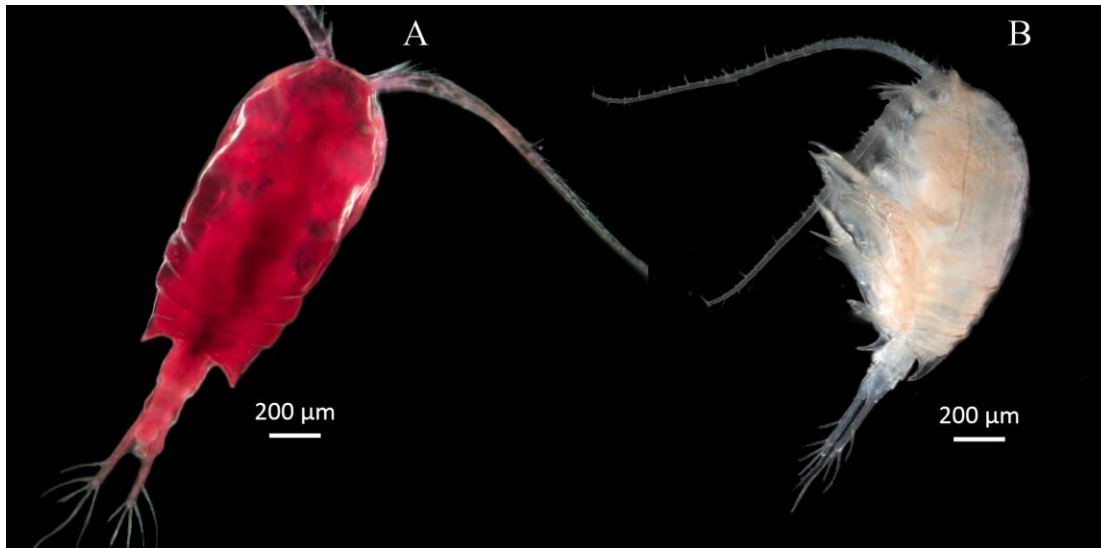
Calanoid and Cyclopoid species, i.e. *Acrocalanus longicornis*, *Calocalanus pavo*, *paracalanus aculeatus*, *Paracalanus nanus*, *Pontellina plumata*, *Oithona plumifera*, *Oithona setigera*, *Corycaeus speciosus*, *Farranula gracilis*, and some harpacticoid families, i.e. Diosaccidae, Longipedidae, Metidae, Miracidae, Peltidiidae and Tisbidae were rare or absent in many samples and the vital status and biomass of these taxa were not analyzed.

Table 1: Length–weight regressions applied for biomass calculation of different taxa.

Taxa	Regression	Reference
<i>Nannocalanus minor</i>	$\text{Ln PS} = 3.65 \ln \text{PL} - 22.89$	Chisholm & Roff, 1990
<i>Undinula vulgaris</i>	$\text{Ln PS} = 3.99 \ln \text{PL} - 25.02$	Webber & Roff, 1995a
<i>Mecynocera sp.</i>	$\text{Ln PS} = 3.65 \ln \text{PL} - 22.89$	Chisholm & Roff, 1990
<i>Subeucalanus pileatus</i>	$\text{Ln PS} = 3.65 \ln \text{PL} - 22.89$	Chisholm & Roff, 1990
Paracalanidae	$\text{Ln PS} = 2.78 \ln \text{PL} - 16.52$	Webber & Roff, 1995a
Clausocalanidae	$\text{Ln PS} = 2.78 \ln \text{PL} - 16.52$	Webber & Roff, 1995a
<i>Scolecithrix danae</i>	$\text{Ln PS} = 3.57 \ln \text{PL} - 21.36$	Webber & Roff, 1995a
<i>Centropages velificatus</i>	$\text{Ln PS} = 3.68 \ln \text{PL} - 22.86$	Chisholm & Roff, 1990
<i>Temora</i>	$\text{Ln PS} = 3.34 \ln \text{PL} - 19.59$	Chisholm & Roff, 1990
<i>Calanopia americana</i>	$\text{Ln PS} = 2.67 \ln \text{PL} - 15.47$	Chisholm & Roff, 1990
<i>Labidocera acutifrons</i>	$\text{Ln PS} = 3.65 \ln \text{PL} - 22.89$	Chisholm & Roff, 1990
<i>Oithona spp.</i>	$\text{Ln PS} = 1.10 \ln \text{PL} - 7.07$	Chisholm & Roff, 1990
Harpacticoida	$\log \text{PS} (\mu\text{g}) = - 8.51 + 3.26 \times \log \text{TL} (\mu\text{m})$	Hirota, 1986
<i>Oncaea spp.</i>	$\text{Ln PS} = 2.10 \ln \text{PL} - 11.63$	Webber & Roff, 1995a
<i>Corycaeus spp.</i>	$\text{Ln PS} = 3 \ln \text{PL} - 17.82$	Chisholm & Roff, 1990
<i>Clausocalanus furcatus</i>	$\text{Ln PS} = 2.78 \ln \text{PL} - 16.52$	Webber & Roff, 1995a

PL, Prossome length; TL total length.

Figure 2. Appearance of Neutral Red-stained copepod (*Temora styliifera*) under optical microscope with dark-field. A – individual that was alive at the time of collection appeared stained red; B – individual that was dead at the time of collection appeared unstained.



5.3 Results

5.3.1 Environmental parameters

The mean Chlorophyll *a*, temperature and salinity observed in the Abrolhos Bank was 0.67 $\mu\text{gChl m}^{-3}$, 27.42°C and 36.82 ppm, respectively. Neither Chlorophyll *a* nor temperature or salinity varied significantly between coastal reefs and offshore reefs sites and between day and night (Chl *a*, Mann-whitney $P = 0.896$; Temperature, t-test $P = 0.540$; Salinity, Mann-whitney $P = 0.151$).

5.3.2 Copepod community composition and abundance

A total of 44 taxa were identified among the 64 μm net catches, and 40 taxa among the 200 μm net catches. The Calanoids were the most diverse group with 20 species identified in from both net samples, followed by the Cyclopoids with 13 species. The harpacticoids were represented by 8 families. Some species were more abundant and frequent among the coastal reefs samples, i.e. *Paracalanus quasimodo*, *Parvocalanus crassirostris*, *Centropages velificatus*, *Calanopia americana*, *Temora stylifera*, *Temora turbinata* and *Oithona nana*, while other species were more abundant and frequent among the offshore reefs samples, i.e. *Nannocalanus minor*, *Undinula vulgaris*, *Acrocalanus longicornis*, *Calocalanus pavo*, *Mecynocera clausi*, *Subeucalanus pileatus*, *Clausocalanus furcatus* and *Labidocera acutifrons* (Table 2).

Excluding the copepods nauplii, at the coastal reef area, *P. quasimodo* was the most abundant taxa in the 200 μm net samples, comprising in average 33%, while the Oithonids (mainly *O. nana*) dominated the 64 μm net catches, comprising 74% of all copepods. Copepods nauplii occurred only in the 64 μm net samples and accounted for 22% of all taxa from both areas. At the offshore reef area, *L. acutifrons* was the most dominant species in the 200 μm net catches, comprising in average 39% of all taxa, while the 64 μm net samples were dominated by the Oithonids (66%). The mean abundance recorded for the coastal reef area was $210.2 \pm 236.0 \text{ ind m}^{-3}$ (200 μm) and $87,473.2 \pm 126,988.8 \text{ ind m}^{-3}$ (64 μm), and for the offshore reef area was $114.8 \pm 88.3 \text{ ind m}^{-3}$ (200 μm) and $11,299.0 \pm 7,585.3 \text{ ind m}^{-3}$ (64 μm). Therefore, significant variations between the two areas were observed only for the 64 μm net catches (64 μm net, Mann-Whitney P

= 0.043; 200 μm net, Mann-Whitney $P = 0.662$). No significant differences were observed between the day and night samples for both net catches (64 μm net, Mann-Whitney $P = 0.456$; 200 μm net, Mann-Whitney $P = 0.165$). The abundance recorded for the 64 μm net catches were significantly higher than the recorded for the 200 μm net (Mann-whitney, $P = 0.001$).

5.3.3 Copepod biomass and vital status

The mean biomass (live and dead individuals) recorded for the coastal reefs area was $452.4 \pm 597.5 \mu\text{gC m}^{-3}$ (200 μm) and $4932.3 \pm 7353.8 \mu\text{gC m}^{-3}$ (64 μm), and for the offshore reef area was $11,557.9 \pm 18,003.6 \mu\text{gC m}^{-3}$ (200 μm) and $30,711.4 \pm 36,210.6 \mu\text{gC m}^{-3}$ (64 μm). No significant variations of biomass were observed between the areas (64 μm net, Mann-Whitney $P = 0.181$; 200 μm net, Mann-Whitney $P = 0.081$). Similarly, no significant differences were observed between the day and night samples for both net catches (64 μm net, Mann-Whitney $P = 0.165$; 200 μm net, Mann-Whitney $P = 0.073$). The biomass recorded for the 64 μm net catches were approximately 3 times higher than the recorded for the 200 μm net (Mann-Whitney, $P = 0.016$) (Fig. 3). This difference was highest at the coastal reefs, since in that area the 200 μm net catches had approximately 0.3% of the abundance recorded for the 64 μm net and were dominated by the small bodied *P. quasimodo*. At the offshore reefs the occurrence in great numbers of the large bodied oceanic species, i.e. *N. minor*, *U. vulgaris*, *M. clausi*, *S. pileatus* and mainly *L. acutifrons* elevated the biomass of both net catches.

The percentage of dead copepods in the present study was considered high (maximum of 83%). Percent dead copepod was similar between the reef areas (64 μm net, Mann-Whitney $P = 0.865$; 200 μm net, Mann-Whitney $P = 0.762$), and between day and night (64 μm net, Mann-Whitney $P = 0.477$; 200 μm net, Mann-Whitney $P = 0.283$). However the percent dead of the 64 μm net catches (average among taxa, $63.2\% \pm 17.5\%$) was significantly higher than the 200 μm net catches (average among taxa, $45.1\% \pm 17.5\%$) (t-test, $P = 0.01$). The percent dead among small-bodied species and the large ones drove the differences found between the nets. Species with the prosome shorter than 500 μm , i.e. species of Paracalanidae, Oithonidae, Oncaeiidae and Corycaeiidae, occurred in average percent dead of 63.2% (64 μm net) and 45.7% (200 μm net), while

the species with the prosome longer than 500 μm , i.e. *N. minor*, *U. vulgaris*, *M. clausi*, *S. pileatus*, *C. americana*, *L. acutifrons*, and species of Clausocalanidae, Temoridae and Harpacticoida, occurred in average percent dead of 54% (64 μm net) and 37.7% (200 μm net) (Table 2). Most of these larger species showed higher percent dead on the 64 μm net samples in comparison with the 200 μm net, which suggests that the abundance of large copepods recorded from finer meshes may be the result of dead individuals that obviously do not avoid being caught (Table 2). Since the estimates of biomass is based on the abundance, if the dead individuals were cut out of the calculations, the biomass of the overall copepod community in the Abrolhos Bank would be reduced almost by 60% (Fig. 3).

Figure 3. Biomass and the calculated biomass (i.e. excluding the carcasses contributions) of the main taxa. Changing in contribution of taxa with the exclusion of the carcasses can be observed. Attention to different scales in coastal reef plots.

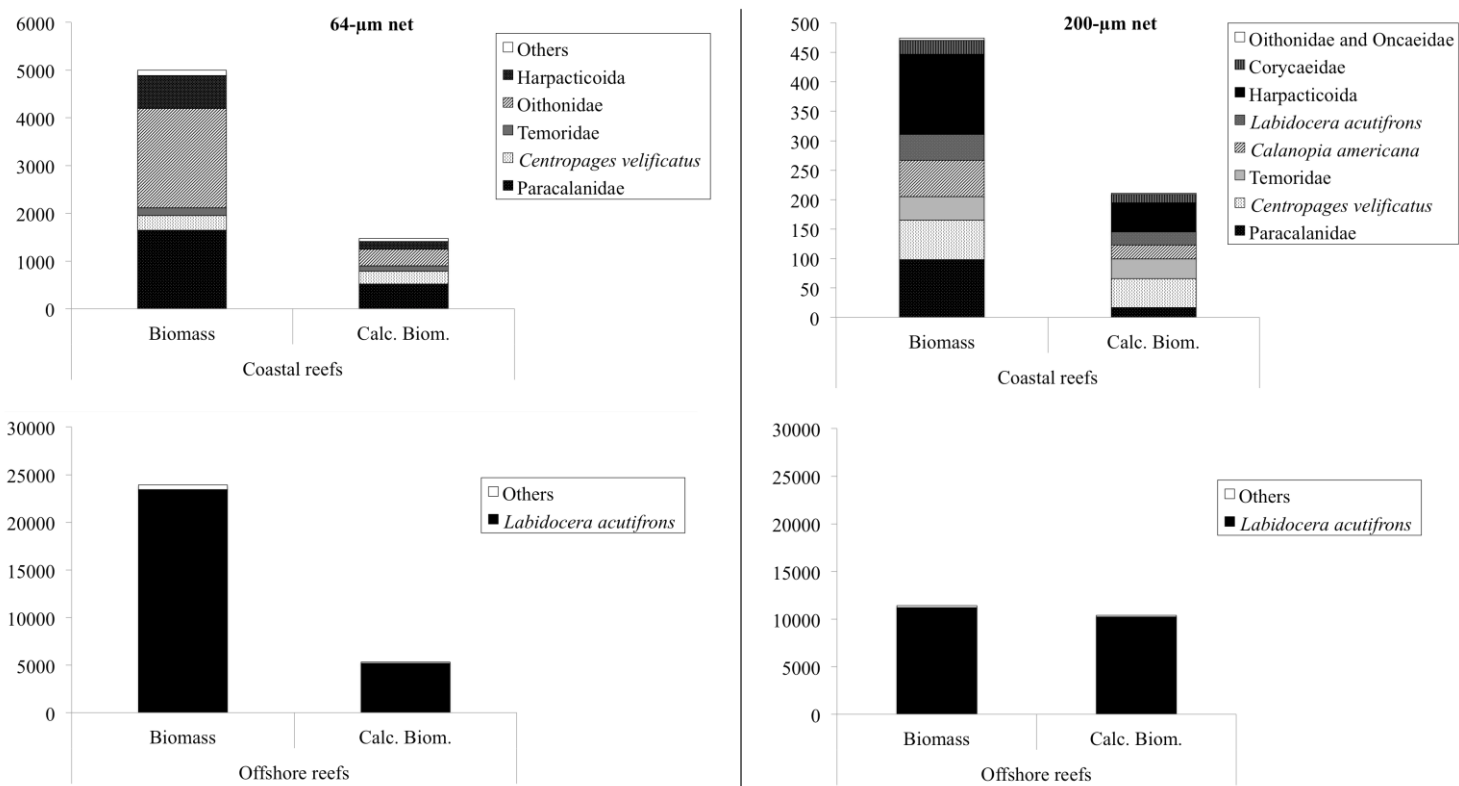


Table 2. Common copepod taxa percent dead, abundance and biomass. The calculated abundance (Calc. Abund.) and biomass (Calc. Biom.) values as a result of the exclusion of the dead individuals are addresses for each taxa and the total copepod community.

Taxa (64 μm)	Coastal reefs					Offshore reefs				
	% dead	Abundance	Calc. Abund.	Biomass	Calc. Biom.	% dead	Abundance	Calc. Abund.	Biomass	Calc. Biom.
<i>Nannocalanus minor</i>						57.5	1.6	0.7	9.6	4.1
<i>Undinula vulgaris</i>						75.7	3.2	0.8	0.8	0.2
<i>Mecynocera clausi</i>						81.4	3.2	0.6	1.5	0.3
<i>Subeucalanus pileatus</i>						68.9	12.8	4.0	2.1	0.6
Paracalanidae	68.7	8353.9	2616.8	1643.9	514.9	100.0	75.7	75.7	18.9	0.0
Clausocalanidae						86.7	49.5	42.9	44.6	5.9
<i>Centropages velificatus</i>	10.0	369.6	332.6	304.9	274.4	0.0	4.8	0.0	0.9	0.9
Temoridae	34.8	530.8	346.0	164.7	107.4	37.5	3.2	1.2	17.7	11.1
<i>Calanopia americana</i>	25.0	154.7	116.0	33.2	24.9	50.0	3.2	1.6	0.7	0.3
<i>Labidocera acutifrons</i>						77.8	105.7	82.2	23436.2	5208.0
Oithonidae	83.0	15855.2	2687.5	2084.4	353.3	86.6	1812.5	1569.3	263.9	35.4
Harpacticoida	76.8	569.7	132.2	687.0	159.4	73.7	142.8	105.2	75.8	20.0
Oncaeidae	50.0	2.6	1.3	4.4	2.2	46.1	62.1	28.6	32.9	17.7
Corycaeidae	53.0	402.7	189.3	76.4	35.9	17.9	47.6	39.1	25.7	21.1
Total copepods	75.5	26239.3	6421.7	4998.8	1472.4	83.0	2307.1	391.8	23917.2	5320.5

Taxa (200 μm)	Coastal reefs					Offshore reefs				
	% dead	Abundance	Calc. Abund.	Biomass	Calc. Biom.	% dead	Abundance	Calc. Abund.	Biomass	Calc. Biom.
<i>Nannocalanus minor</i>						44.0	1.2	0.7	11.9	6.7
<i>Undinula vulgaris</i>						52.6	0.8	0.4	4.5	2.2
<i>Mecynocera clausi</i>						23.2	2.4	1.8	6.3	4.8
Paracalanidae	82.9	65.8	11.2	98.0	16.7	65.4	3.6	1.2	5.6	1.9
Clausocalanidae						70.0	9.1	2.7	5.3	1.6
<i>Scolecithrix danae</i>						0.0	1.2	1.2	62.3	62.3
<i>Centropages velificatus</i>	26.0	23.3	17.3	66.8	49.4					
Temoridae	17.7	25.4	20.9	40.4	33.3	47.9	1.4	0.7	1.8	0.9
<i>Calanopia americana</i>	61.2	15.8	6.1	61.7	24.0	33.3	1.5	1.0	9.1	6.1
<i>Labidocera acutifrons</i>	50.0	0.5	0.2	43.6	21.8	8.7	50.9	46.5	11208.3	10233.3
Oithonidae	59.3	12.4	5.0	3.6	1.5	50.2	2.6	1.3	0.9	0.4
Harpacticoida	63.6	43.7	15.9	136.6	49.7	29.4	3.7	2.6	30.0	21.2
Oncaeidae	16.7	0.4	0.3	0.8	0.6	23.8	2.4	1.8	5.5	4.2
Corycaeidae	39.9	22.9	13.8	23.1	13.9	27.7	25.5	18.4	53.2	38.4
Total copepods	56.8	210.2	90.8	474.7	210.9	23.9	101.8	77.5	11382.1	10370.5.0

Fonte: Lucas Figueirêdo.

5.4 Discussion

5.4.1 Copepod abundance and biomass

The observed spatial patterns in copepod abundance were comparable with previous reports for the same area (first chapter in this issue). Species of the families Paracalanidae and Oithonidae are the dominant taxa at the reef areas closest to the shoreline in the Abrolhos Bank. The two dominant species, i.e. *Paracalanus quasimodo* and *Oithona nana* are abundant in Brazilian coastal waters (Brandini *et al.*, 1997) and are common in other reef systems around the world (Mckinnon e Thorrold, 1993; Alvarez-Cadena *et al.*, 1998; Mckinnon e Duggan, 2003; Fukuoka *et al.*, 2015).

Stronger spatial and diurnal fluctuations were expected to be observed in the abundance and biomass of the copepod community. However, the results showed differences only for the abundances recorded from the two reef areas by the 64 μm net. The absence of diurnal fluctuations in the zooplankton assemblage collected with the 64 μm net in the Abrolhos Bank was observed by previous study (first chapter in this issue) and may be related to the limited swimming capability of small bodied zooplankters (Alldredge e King, 1985; Holzman *et al.*, 2004). Moreover, the absence of fluctuations in the assemblage collected by the 200 μm net could be related to the low number of samples analyzed.

Similarly to previous report, the abundance of the assemblages collected by the 200 μm net was significantly lower, being on average 0.3% of the abundance reported for the 64 μm net catches. According to Hopcroft *et al.* (1998), the small species, usually despised in assessments of copepods production, may play a critical role in communities trophodynamics. On their study, the average copepods captured by the 200- μm net was only 7.5% of the total copepods, and only 55% of the biomass estimated by the 64- μm net. On the present study, in terms of biomass, the 200- μm net captured only 32.6% of the estimated by the 64- μm net.

5.4.2 Live/dead composition of copepods

It was expected that the amount of dead copepods should be highest at the coastal reefs, since coastal regions are frequently subjected to environmental gradients, e.g.

salinity and temperature gradients, and continental inputs which act as environmental stressors (Cervetto *et al.*, 1999). However, the environmental parameters in the present study did not varied along all the study area. Temperature and salinity were virtually the same in both areas. This fact may be associated with the hydrodynamics of this portion of the continental shelf, which do not allow continental inputs to reach far into the shelf, because of along-shore currents and topographical barriers (Leipe *et al.*, 1999; Lessa e Cirano, 2006; Teixeira *et al.*, 2013).

Similarly, Chlorophyll *a* estimates showed the same patterns as the other parameters studied, and this might be the reason it was not found differences between the amounts of carcasses found in the reef areas. The influence of environmental parameters over the occurrence of dead copepods is frequently addressed as a secondary factor, often showing no correlations with live/dead composition patterns (Tang *et al.*, 2006; Martínez *et al.*, 2014; Di Capua e Mazzocchi, 2017). However, the low concentration of Chlorophyll *a* in the present study is probably one of the main causes of the high incidence of dead copepods in both areas, since food availability and quality affects both initial developmental stages and adult copepods (Calbet e Alcaraz, 1997; Martínez *et al.*, 2014). The ability of copepod populations to survive in food-limited environments is reduced and evidence of non-predatory mortality caused by starvation is reported by various authors (Tang *et al.*, 2014).

Other than environmental stress may also contribute to the percent dead found in Abrolhos Bank. For instance, senescence has been reported to influence seasonal patterns of copepod mortality. Elliott e Tang (2011) reported the occurrence of the highest concentrations of carcasses during and shortly after seasonal peaks in abundance, when the community started to decline as mortality balanced or even exceeded population growth. Since the seasonal fluctuation was not evaluated in the present study, the aging affect over the copepod mortality could not be assessed.

Reef zooplankton communities are never free of predation pressure because of the various zooplanktivorous animals typical of this environments (Yahel, Yahel e Genin, 2005). Because of that, the predation may be, together with the food limitation, one of the main factors driving the carcasses incidence in Abrolhos Bank. Many dead copepods found in the samples were damaged (laboratory observations), which may

indicate predatory mortality (Daase *et al.*, 2014). Studies conducted in other environments than reefs, reported carcasses most likely resulting from non-predatory mortality. Elliott e Tang (2011) studying copepods community in Chesapeake Bay (estuary environment) reported only 1.7% of the dead copepods to be accounted for predatory mortality. The same results were found by Di Capua e Mazzocchi (2017) and Besiktepe *et al.* (2015) in the Mediterranean sea.

Differently, Genin *et al.* (1995), studying copepod carcasses near coral reefs reported the predatory mortality to be the most likely cause of dead copepods incidence. Several fish and other zooplanktivorous animals, reef residents, have been observed to egest incomplete digested copepods (Genin *et al.*, 1995), indicating that damaged copepods in fixed samples may not result mainly due to net damage (sampling artefacts) (Daase *et al.*, 2014). Moreover, the difference in carcasses incidence among distinct species in coral reef environments may have influence of species swimming ability (ability to evade predators) and body-size (vulnerability to visual predators) (Genin *et al.*, 1995). Independently of the probable causes, high percent dead copepods similar to the estimates herein were also found in marine environments by several other studies (Tang *et al.*, 2014).

5.4.3 Vital Status implications for ecological studies

Our results shows that a high percentage of the large bodied copepods caught by finer nets may be carcasses. Observing the data from the offshore reefs, which apparently is under stronger oceanic influences (given the presence of oceanic species), live copepods with large body length such as *Labidocera acutifrons* may be able to avoid finer nets by swimming, whereas carcasses would be captured leading to elevated proportion of dead individuals of these large species in the sample, as observed herein. Several studies foster the importance of the use of finer mesh nets in field sampling in order to properly catch the small species (Hopcroft *et al.*, 1998; Porri *et al.*, 2007), however, caution is needed to evaluate the abundance recorded for the larger species in samples obtained with these nets.

The separation of the live and dead individuals is necessary to rightly understand the ecology and the roles played by zooplankton communities in different environments

(Besiktepe *et al.*, 2015). When analyzing the data presented herein, the taxa that dominated the coastal reefs were the Oithonids (64- μm net), comprising 74% of all copepods, with an average abundance of 15,855.2 ind. m^{-3} , while the second most abundant taxa were the Paracalanids, with an average abundance of 8,353.9 ind. m^{-3} (20% of all copepods). However, the Oithonids showed the highest percent dead among all the taxa as well. Taking into account only the living individuals, the Paracalanids became the major taxa with the highest biomass (see Fig. 3 and Table 2). The same occurred with the assemblages collected with the 200- μm net, which showed the dominance of the Paracalanids (37% of all copepods), but when the dead individuals were excluded, the Temoridae (12%), *Centropages velificatus* (7%) and the Harpacticoids (12%) became more dominant in terms of both abundance and biomass. Therefore, studies performed with conventional field sampling may overestimate the zooplankton recruitment, biomass and production, as well as grazing impact.

In coral reef environments the zooplankton community serves as food source for both pelagic and benthic animals. In fact, increased zooplankton availability has been reported to significantly enhance coral growth (Heidelberg *et al.*, 2004), while other studies have highlighted the importance of the demersal zooplankton to the benthic-pelagic coupling through their biomass flux between reef environment realms (Ohlhorst, 1982; Bishop e Greenwood, 1994). Moreover, copepods were found to contribute 63% of the diet of corals (Lewis, 1992), being that fact attributed to the high nocturnal abundance of copepods near the reef surfaces (Heidelberg *et al.*, 2004). However, even though holoplanktonic copepods (living ones) have the ability to avoid and escape benthic suspension feeders, the dead copepods, which may exceed the abundance of living ones, may have similar or greater contributions to the nutrition of corals and other benthic suspension feeders and scavengers, than the “living” demersal forms.

Obviously, in the complexity of the coral reef systems, the ecological roles of the zooplankton communities (pelagic and demersal) are more difficult to be assessed, however the great biomass of carcasses estimated herein cannot be neglected, since the downward flux of carcasses are in fact an important source of food and nutrients for the benthic realm (Sampei *et al.*, 2012).

6 CONSIDERAÇÕES FINAIS

Os resultados apresentados nessa tese demonstram a complexidade do ecossistema de recifes de coral. O zooplâncton recifal apresenta uma relação muito íntima com o domínio bentônico, seja devido a comunidade demersal, ou via fluxo de carcaças aparentemente abundantes nesse tipo de ambiente. Os resultados obtidos através das armadilhas permitiu ainda destacar que diferentes populações zooplanctônicas podem estar disponíveis como fonte alimentar para distintos predadores, sejam eles habitantes das camadas superiores da coluna d'água ou até das regiões mais próximas a superfície recifal. Desta forma, o zooplâncton alcança um nível de importância altíssimo nesse ecossistema.

Pode-se destacar ainda que apesar de inicialmente parecer pouco diverso, o zooplâncton recifal apresenta comunidades que não são coletadas apropriadamente com a metodologia comum de coleta (arrasto). Se for levado em consideração a diversidade do zooplâncton tanto pelágico como demersal pode-se observar uma grande diversidade. O registro de nova ocorrência ainda contribui para essa conclusão, uma vez que como o zooplâncton demersal nunca havia sido estudado em Abrolhos, estudos futuros podem contribuir para o descobrimento de uma diversidade ainda maior.

De forma geral os resultados obtidos permitiram conhecer melhor o zooplâncton desse importante ambiente da costa brasileira que ainda é pouco estudado em termos de planctonologia, como também permitiu chegar a algumas conclusões importantes:

1. A comunidade zooplanctônica pelágica apresenta uma composição diferente entre os recifes do arco costeiro e os recifes do Arquipélago e do arco externo.
2. A flutuações durante o ciclo diurno foram exclusivas do mesozooplâncton, o que sugere a limitação migratória dos menores componentes da comunidade, que migram apenas alguns centímetros na coluna d'água.
3. Apesar de se achar que amostras derivadas de arrastos horizontais noturnos capturarem com eficiência a comunidade migrante, as amostras derivadas das armadilhas comprovam que muito da diversidade, densidade e biomassa da comunidade que emerge a noite não é capturada pelos arrastos noturnos

4. A diversidade da comunidade pelágica foi considerada baixa, devido a grande influência da comunidade costeira tropical, típica da costa brasileira, que dominou a região do Banco de Abrolhos.
5. As comunidades zooplanctônicas tanto demersal como pelágica exercem um importante papel no acoplamento bento-pelágico, seja através de sua migração vertical, ou através da contribuição do fluxo vertical de carcaças.
6. A comunidade demersal apresenta uma distinção clara tanto entre os diferentes substratos, como entre as diferentes formações recifais. Desta forma, fica claramente estabelecido que a topografia, e a disposição das formações recifais exercem influência no comportamento migratório de determinados organismos zooplanctônicos demersais, os quais podem apresentar preferência por determinadas porções do recife ou até diferentes formações.
7. Os substratos recifais apresentam, devido a sua diversidade de microhabitats, uma grande densidade e diversidade de organismos zooplanctônicos demersais em comparação com o substrato arenoso adjacente.
8. O uso de dois equipamentos de coleta diferentes (redes de plâncton com malhas diferentes; e armadilhas com disposições e malhas diferentes) foi fundamental para a observação mais ampla da comunidade zooplanctônica. Desta forma, os dados obtidos pelos diferente equipamentos foram complementares no sentido de se compreender melhor os padrões e comportamentos do zooplâncton tanto pelágico como demersal.
9. A maior parte da densidade de copépodes encontrados eram carcaças e este fato altera consideravelmente aspectos ecológicos dessa comunidade.
10. No Banco de Abrolhos a predação e a baixa disponibilidade de alimento foram consideradas as principais causas dessa alta mortalidade.
11. Conclusões que poderiam ser tiradas a partir dos dados brutos de densidade podem estar significativamente erradas, uma vez que se extraídos os valores relativos aos indivíduos mortos, muda-se a dominância das espécies, altera-se a contribuição de biomassa de determinados taxa, e principalmente altera-se o destino dessa biomassa.
12. O uso de duas malhas permitiu a observação de que os taxa de grande porte capturados pela malha de 64 μm na verdade estavam em sua maioria mortos, o que

leva a concluir que de fato eles só foram capturados devido a impossibilidade lógica de fuga da rede. Arrastos simultâneos com a rede de 200 μm mostraram porcentagens mais altas de indivíduos vivos desses mesmos taxa.

Os estudos apresentados nessa tese tiveram como objetivo fundamental expandir o conhecimento da comunidade zooplancônica desse que é o maior sistema recifal do Atlântico Sul. Desta forma, os resultados apresentados aqui permitiram concluir que o ecossistema recifal do Banco de Abrolhos é bastante complexo, sob o ponto de vista de todas as interações tróficas, do acoplamento bento-pelágico, e de todas as influencias oceanográficas que atuam nessa proção da plataforma continental brasileira. Todos esses fatores atuam sobre o zooplâncton formando associações ainda não bem compreendidas. Portanto, muito ainda precisa ser estudado com mais profundidade, espécies precisam ser melhor identificadas, e para isso, novas formas de coleta e pesquisas podem ser aplicadas para melhor compreender esse sistema recifal único ao Atlântico Sul.

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