UNIVERSIDADE FEDERAL DE PERNAMBUCO
CENTRO DE TECNOLOGIA E GEOCIÊNCIAS
DEPARTAMENTO DE OCEANOGRAFIA
PROGRAMA DE PÓS-GRADUAÇÃO EM OCEANOGRAFIA

GABRIELA GUERRA ARAÚJO ABRANTES DE FIGUEIREDO

ANÁLISE INTEGRADA DOS ESPECTROS DE TAMANHOS E ASSINATURAS ISOTÓPICAS DA COMUNIDADE ZOOPLANCTÔNICA AO LARGO DO NORDESTE DO BRASIL

Recife
2020

GABRIELA GUERRA ARAÚJO ABRANTES DE FIGUEIREDO

ANÁLISE INTEGRADA DOS ESPECTROS DE TAMANHOS E ASSINATURAS ISOTÓPICAS DA COMUNIDADE ZOOPLANCTÔNICA AO LARGO DO NORDESTE DO BRASIL

Tese apresentada ao Programa de Pós-graduação em Oceanografia da Universidade Federal de Pernambuco, como requisito parcial para obtenção do título de Doutora em Oceanografia.

Área de concentração: Oceanografia Biológica.

Orientador: Prof. Dr. Ralf Schwamborn.

Coorientador: Prof. Dr. François Le Loc’h.

Recife

2020

Catalogação na fonte
Bibliotecária Margareth Malta, CRB-4 / 1198

F475a Figueiredo, Gabriela Guerra Araújo Abrantes de.
Análise integrada dos espectros de tamanhos e assinaturas isotópicas da comunidade zooplanctônica ao largo do nordeste do Brasil / Gabriela Guerra Araújo Abrantes de Figueiredo. - 2020.
104 folhas, il., gráfs., tabs.

Orientador: Prof. Dr. Ralf Schwamborn.
Coorientador: Prof. Dr. François Le Loc'h.

Tese (Doutorado) – Universidade Federal de Pernambuco. CTG. Programa de Pós-Graduação em Oceanografia, 2020.
Inclui Referências.

1. Oceanografia. 2. Gradiente costa – oceano. 3. Zooplâncton. 4. Espectros de tamanho. 5. Isótopos estáveis. I. Schwamborn, Ralf (Orientador). II. Le Loc'h, François (Coorientador). III. Título

UFPE

551.46 CDD (22. ed.) BCTG/2020-261

GABRIELA GUERRA ARAÚJO ABRANTES DE FIGUEIREDO

ANÁLISE INTEGRADA DOS ESPECTROS DE TAMANHOS E ASSINATURAS ISOTÓPICAS DA COMUNIDADE ZOOPLANCTÔNICA AO LARGO DO NORDESTE DO BRASIL

Tese apresentada ao Programa de Pós-graduação em Oceanografia da Universidade Federal de Pernambuco, como requisito parcial para obtenção do título de Doutora em Oceanografia.

Aprovada em: 11 / 08 / 2020.

BANCA EXAMINADORA

Prof. Dr. Ralf Schwamborn (Orientador)
Universidade Federal de Pernambuco

Prof. Dr. Rubens Mendes Lopes (Examinador Externo)
Universidade de São Paulo

Prof^a. Dr^a. Catarina da Rocha Marcolin (Examinadora Externa)
Universidade Federal do Sul da Bahia

Prof. Dr. Rodrigo Ferreira Bastos (Examinador Interno)
Universidade Federal de Pernambuco

Prof. Dr. Pedro Augusto Mendes de Castro Melo (Examinador Interno)
Universidade Federal de Pernambuco

AGRADECIMENTOS

Agradeço a Deus por toda força, que busquei Nele, ao longo de toda essa jornada que não me fez fraquejar nos momentos de agonia, e assim chegar aonde cheguei.

A toda minha família que sempre esteve presente me apoiando em todos os momentos. Agradeço especialmente as minhas avós, Kika e Ninita, pelo apoio, por entender minha ausência e por todas as orações; a meu irmão Rafa que em toda sua quietude sempre me apoiou, a minha madrinha Fafá por todo o incentivo e conselhos e a querida irmã Rosangela por todo carinho e orações.

Agradeço especialmente a minha mãe (Adriana) pelo carinho, cuidado e preocupação. Por sempre acreditar em mim, por ser minha fonte de força, por não me deixar desistir, pelas rezas, por todo incentivo diário, por sempre estar presente (mesmo longe) e por me escutar nos momentos que mais precisava desabafar. Obrigada Mãe.

Também agradeço a meu Pai (Jorge) que foi meu forte durante toda minha vida acadêmica, dono dos melhores conselhos. Obrigado por sempre ouvir e me direcionar. Obrigada por me ajudar a passar por todas as dificuldades que tive ao longo dessa longa jornada. Além disso, se não fosse sua esperteza em programação, metade dessa tese não teria sido feita. haha Obrigada pai!

Ao meu amor Thi que chegou já com o barco andando e desde então sempre esteve ao meu lado, me apoiando, me ouvindo e me ajudando de todas as formas. Obrigada meu amor!

Ao Conselho Nacional de Pesquisa e Desenvolvimento (CNPq), pela concessão da minha bolsa de doutorado no Brasil;

À Coordenação de Aperfeiçoamento do Pessoal do Ensino Superior (CAPES), juntamente ao projeto SMAC, pela concessão a bolsa de doutorado sanduiche no exterior;

Ao grupo do projeto ABRAÇOS, e a tripulação do ANTEA pela coleta dos dados que geraram essa tese e ao IRD pelo financiamento das coletas.

Ao INCT AmbTropic (CNPq/CAPES/FAPESB) pelo suporte de material de laboratório que ajudaram no desenvolvimento da tese;

Ao meu orientador Ralf Schwamborn por ter aceitado o desafio de me orientar, pelos ensinamentos científicos que contribuíram para o meu aprendizado, pelas oportunidades e confiança.

Ao meu co-orientador François Le Loc'h por ter aceitado me orientar na França, por ter tornado essa experiência mais fácil, por todas as contribuições ao meu aprendizado e pela oportunidade de participar de diferentes atividades que fizeram parte do meu crescimento profissional.

À Arnaud Bertrand e Flávia Lucena-Frédou pela oportunidade e confiança de participar do projeto ABRAÇOS e SMAC que me proporcionou experiências incríveis no meu doutorado. Arnaud, obrigada por toda paciência e contribuições. Flávia, obrigada por todo carinho e preocupação ao longo de toda jornada aqui e no exterior!

À professora Sigrid Neumann Leitão por sempre estar disponível para tirar dúvidas e ajudar todos os alunos do Laboratório. Agradeço pelo carinho, pelos conselhos e pelos ricos ensinamentos relacionados à ciência e à vida, pelos almoços e pelas risadas que sempre estão presentes.

Aos meus amigos André, Guilherme, pelas longas conversas, pelo apoio no momento mais delicado do doutorado e por tornarem meu doutorado menos estressante.

À Gleice por toda atenção em me ajudar assim que ingressei no laboratório, por mostrar a dinâmica do laboratório, por me proporcionar as primeiras coletas de zooplâncton e por toda troca de conhecimento que foi importantíssimo no meu crescimento e aprendizado.

À minha parceira Simone, parceira do projeto ABRAÇOS além de ter se tornado uma grande amiga. Obrigada por todos os conselhos, apoio, fofocas e desabafos por toda essa jornada, principalmente quando o bicho pegou. Obrigada pela parceria e amizade que construímos ao longo desses três anos de muito trabalho.

Aos meus amigos de laboratório Nath, Dr. Reninha, Claus, Cynthiazinha, Fio, Simone Black, Gabrielinho, Caio, Morg, que me acolheram tão bem e tornaram essa caminhada mais menos estressante, mais alegre e mais fácil. Por todas as conversas, estudos, e apoio. Vocês são peças chave nessa minha conquista.

Aos demais parceiros e amigos do Laboratório de Zooplâncton que estiveram presentes ao longo de todo o doutorado, seja me ensinando sobre o mundo do zooplâncton, ou compartilhando almoços e conversas diárias tornando o laboratório um lugar agradável de trabalhar.

À Jean-Marie e Eric, pela atenção, ajuda e ensinamentos ao ingressar na França.

Às minhas companheiras de sala Clarice, Mariana e Alexandra as inúmeras canecas de chá e barras de chocolate para aguentar dias e dias de frio, vento e chuva.

Aos amigos que a França me deu, Ashley, Jie, Max, Manu, Mauricio, André, Carmem, Vera, pelo companheirismo, pelas cervejas e vinhos, por estarem sempre apoiando e aconselhando. Brest não teria sido a mesma sem vocês!

A Alex pela amizade e companheirismo durante nossa jornada na França. Obrigada por toda parceria em viver em terras francesas, toda a ajuda no R, discussões sobre o trabalho, vida, política e futuro. Seguimos na luta!

Amigos de longas datas Priscila, Brisa e Dani que me acompanham desde sempre!

Aos membros da banca por aceitarem o convite e poderem participar dessa etapa da minha vida;

Aos demais amigos e colegas que não foram citados aqui, mas que sabem que fazem parte da minha vida e sabem de todo esforço e batalha nesses 4 anos.

RESUMO

O presente trabalho analisou a estrutura e organização das comunidades zooplanctônicas dos ambientes de plataforma continental e ilhas oceânicas em função dos espectros de tamanho e da sua assinatura isotópica. Foram realizadas coletas ao longo do litoral do nordeste brasileiro, que compreende a plataforma continental, quebra de plataforma e ambientes oceânicos. As amostras foram coletadas no âmbito do projeto “ABRACOS” entre setembro e outubro de 2015. As coletas do zooplâncton foram realizadas com o auxilio de redes do tipo bongo. Para a análise dos espectros de tamanho, as amostras foram fixadas em formol e analisadas através do sistema Zooscan. As amostras para análise isotópica foram congeladas e processadas para a obtenção dos valores de δ13C e δ15N. Vinte e sete taxa de zooplâncton foram registrados. Dentre eles, relatamos o primeiro registro de *Firoloida desmarestia* Lesueur (1817), de Fernando de Noronha e plataforma continental, ampliando sua distribuição geográfica e destacando a importância de estudos detalhados sobre a biodiversidade de plâncton de grande porte em oceanos tropicais. A estrutura da comunidade do zooplâncton diferiu entre as áreas de plataforma e ilhas oceânicas. Copepoda foi o grupo mais abundante em todas as áreas estudadas, porém em termos de biovolume, larvas de peixes e gelatinosos foram os mais dominantes. A análise dos espectros de tamanhos mostrou uma maior contribuição de organismos menores na plataforma continental, e uma maior contribuição de organismos maiores nos ambientes oceânicos. Investigando a relação entre o tamanho e a composição isotópica ao longo do gradiente costa oceânica, observamos que as classes de tamanho dos zooplâncton foram dominadas por copépodos, exceto pela maior fração de tamanho (> 2000µm), que mostrou um alto biovolume de quetognatos, decápodes e larvas de peixes. A matéria orgânica particulada mostrou δ13C consistentemente mais baixo que o zooplâncton, indicando uma seletividade de fontes alimentares ricas em δ13C pelo zooplâncton. O δ15N e o nível trófico do zooplâncton apresentou um aumento conforme o aumento do tamanho corporal. O δ15N da fração de tamanho de 200 - 500µm foi usado como *baseline* para a estimativa de níveis tróficos. As áreas oceânicas apresentaram um valor de δ15N mais alta que a plataforma continental e as áreas de quebra de plataforma. Os valores de δ15N produziram um padrão consistente de aumento log-linear no nível trófico com o aumento do tamanho, em todas as áreas. A escolha dos valores do fator de enriquecimento trófico (TEF) alterou apenas ligeiramente as inclinações log10 (tamanho do corpo) versus nível trófico. Porém, essa escolha teve um efeito considerável nas estimativas da razão tamanho predador/presa e razão de massas predador/presa. Usar um TEF acima de 2.3 leva a estimativas irrealistas das razões. Esta tese forneceu resultados inéditos sobre distribuição de abundância, biovolume, espectros de tamanho e isótopos estáveis do zooplâncton ao longo da costa do nordeste brasileiro, obtendo dados para o entendimento da estrutura e organização do zooplâncton em função dos espectros de tamanho. O uso integrado das análises de isótopos com a análise de classes de tamanho contribui para o estudo da ecologia trófica nessas áreas.

Palavras-chave: Gradiente costa – oceano. Zooplâncton. Espectros de tamanho. Isótopos estáveis.

ABSTRACT

This work analyzed the structure and organization of zooplankton communities in continental shelf and oceanic island environments according to their size spectrum and isotopic signature. Samples were collected along the coast of northeastern Brazil, which includes the continental shelf, platform break and oceanic environments. The samples were collected under the "ABRACOS" project between September and October 2015. Zooplankton sampling was made with bongo nets. For the size spectra analysis, samples were fixed and analyzed using a Zooscan system. Samples for isotopic analysis were frozen and processed to obtain δ13C and δ15N. Twenty-seven zooplankton taxa were recorded. We report the first record of *Firoloida desmarestia* Lesueur (1817), from Fernando de Noronha Archipelago and the continental shelf of northeastern Brazil, considerably extending its geographical distribution and highlighting the importance of detailed studies on the biodiversity of large gelatinous plankton in tropical oceans. The zooplankton community structure was significantly different between the continental shelf and slope areas and oceanic islands in terms of abundance and biovolume. Copepoda was the most abundant group in all studied areas, but in terms of biovolume, fish larvae and gelatinous organisms were the most dominant. Size spectra analysis displayed a greater contribution of smaller organisms on the continental shelf and slope, as well as a greater contribution of larger organisms (fish larvae, gelatinous organisms, decapods) in oceanic environments. Size-based approaches are key tools for the study of marine food webs. Thus, we investigate the relationship between size and isotopic composition along the ocean-coast gradient. Zooplankton size classes were dominated by copepods, except for the largest size fraction (> 2000µm), which showed a high biovolume of chaetognaths, decapods and fish larvae. Particulate organic matter displayed δ13C consistently lower than zooplankton, indicating a selective use of primary food sources rich in δ13C by zooplankton. δ15N and the trophic level of zooplankton showed an increase as body size increased. The δ15N size fraction of 200 - 500 µm was used as baseline for the estimation of trophic levels. Oceanic areas had higher δ15N than the continental shelf and the shelf break areas. The δ15N values produced a consistent pattern of log-linear increase in trophic level with increasing size in all areas. The choice of trophic enrichment factor (TEF) values only changed log10 (body size) *versus* trophic level slopes. However, this choice had a considerable effect on the estimates of the predator size / prey (PPSR) and predator mass prey (PPMR) ratios. Using a TEF above 2.3 leads to unrealistic estimates of PPSR and PPMR. This thesis provided results on abundance distribution, biovolume, size spectra and stable isotopes of zooplankton along the continental shelf, shelf break and oceanic islands, in order to obtain data to understand the structure and organization of these communities as a function of their size spectra. The integrated use of stable isotope analysis and size class analysis contributed to trophic ecology studies in these areas which are extremely important from a socio-economic point of view.

Keywords: Coastal – oceanic gradient. Zooplankton. Size spectra. Stable isotope.

SUMÁRIO

1 INTRODUÇÃO

Nessa introdução iremos abordar sobre as comunidades zooplanctônicas, bem como os estudos envolvendo análises de classes de tamanho e isótopos estáveis. Além disto, traremos um apanhado geral dos trabalhos realizados anteriormente nos ambientes de estudo.

1.1 Comunidades planctônicas

O plâncton é definido como a comunidade de organismos que vivem em suspensão na coluna d'água, com pouca mobilidade, sendo transportados conforme as correntes oceânicas (ODUM, 1971; DECLINCE, 1992;). São organismos essenciais para a dinâmica dos oceanos, uma vez que eles possuem um papel importante na transformação de energia química assimilável para os demais organismos. No plâncton incluem os produtores primários (fitoplâncton), e consumidores (zooplâncton). Essa comunidade constitui a base da cadeia alimentar pelágica nos ecossistemas marinhos. Mudanças nessas comunidades podem ocasionar alterações estruturais em todos os níveis do ecossistema marinho (BRANDINI et al., 1997; NEUMANN-LEITAO et al., 2008; LIRA et al., 2014). Dessa forma, estudar esses organismos contribui substancialmente para a ciência e sociedade.

O zooplâncton abrange organismos desde pequenos protozoários a grandes águas vivas e possui uma grande importância, visto que eles são o elo de conexão entre os produtores primários aos demais níveis tróficos (SAIZE et al., 2007; GUIDI et al., 2016; GOVE et al., 2016). Além disto, o zooplâncton contribui para o ciclo biogeoquímico dos oceanos uma vez que ele controla a produção de carbono, através do consumo de fitoplâncton, exportando-o para grandes profundidades. Em algumas regiões oligotróficas, como ilhas oceânicas, por exemplo, o aumento da abundancia zooplactônicas é consideradas um dos principais contribuintes para o aumento da produtividade dessas regiões, estando associada a diversos parâmetros como disponibilidade de nutrientes e fatores abióticos (temperatura, salinidade, correntes) (LIRA et al. 2014; CAMPELO et al., 2018, 2019). Dessa forma, a compreensão de como as comunidades zooplanctônicas se estruturam ao longo dos ecossistemas oligotróficos como ilhas e áreas oceânicas é necessária para o entendimento do seu papel nos ambientes marinhos (YANG et al., 2017; LIRA et al., 2014; CAMPELO et al., 2019).

1.2 Estudos de comunidades através da distribuição de tamanhos e isótopos estáveis

Uma das formas de estudar o zooplâncton é através da análise do espectro de tamanho e biomassa dos organismos. Essa metodologia compreende a transferência de biomassa e energia desde os produtores primários aos níveis tróficos superiores, e tem potencial de explicar as relações ecológicas nos ecossistemas. Sendo assim, o tamanho dos organismos é um parâmetro importante para caracterização das comunidades, uma vez que ela está diretamente influenciada pelas taxas fisiológicas dos organismos (PLATT e DENMAN, 1978). Sheldon e colaboradores (1972) foram os primeiros a identificar padrões regulares na estrutura de tamanho de diferentes comunidades pelágicas. Desde então, modelos teóricos vem sendo desenvolvidos e, nas últimas décadas os trabalhos que utilizaram essa técnica forneceram informações úteis sobre a dinâmica e o funcionamento dos ecossistemas pelágico (KERR, 1974; POPE et al., 1988, DUPLISEA AND KERR, 1995; RICE AND GISLASON 1996; QUIÑONES, 1994; MARCOLIN et al., 2013; DAY et al., 2017). Além disto, essa metodologia pode revelar interações ecológicas que não são tão facilmente descritas com abordagens taxonômicas convencionais (KRUPICA et al., 2012), como por exemplo, é usada para (1) prever a eficiência trófica e a relação presa – predador na cadeia alimentar de ambientes marinhos (JENNINGS et al., 2002), (2) avaliar o impacto da pesca em ambientes de recifes de corais (GRAHAM, 2005), além de (3) examinar mudanças espaço-temporais nos espectros de tamanho de comunidades zooplanctônicas (SATO et al, 2015).

A análise de espectro de tamanho e biomassa baseia-se na teoria de que o tamanho corpóreo dos organismos determina potenciais relações presa-predador, visto que na maioria das vezes, os predadores se alimentam de presas menores que eles mesmos (COHEN et al., 1993). Assim, os espectros de tamanhos têm sido considerados como descritores sintéticos da caracterização da estrutura e funcionamento das comunidades planctônicas (GLAZIER, 2005). A mortalidade, o consumo de presas, as taxas de produção, taxas de crescimento populacional dentre outros aspectos, são exemplos de funções dos organismos que expressam relações com o tamanho. A teoria sugere uma relação inversa entre o tamanho corporal e a abundância, onde as maiores taxas de crescimento populacional estão localizadas na base da cadeia alimentar. Sendo assim, os maiores valores de abundância estão representados por pequenos organismos, em contrapartida, os valores de abundância menos representativos correspondem a organismos que apresentam tamanho corporal maior (ZHOU, 2006).

Assim, o espectro de tamanho de biomassa é um equilíbrio entre ganhos de energia através do crescimento, e perda de energia através da respiração e predação/mortalidade

(BLANCHARD et al., 2017), ou seja, é a distribuição da frequência de biomassas agrupadas por pesos individuais e normalizados pelo tamanho da classe também estimada em peso (ZHOU, 2006). O espectro de tamanho e biomassa normalizados (NBSS – Normalized Biomass Size Spectra) é assim plotado numa escala log-log, na qual a teoria (KERR e DICKIE, 2001) relaciona a inclinação de uma regressão linear ajustada ao espectro para taxa de produção de biomassa. As mudanças na inclinação da reta podem ser usadas para avaliar a eficiência da transferência de energia entre os ambientes, bem como interações entre presa/predador, uma vez que, está relacionada com a quantidade de níveis tróficos e a eficiência energética assimilada (ZHOU, 2006). Os efeitos de bottom-up e Top-down, por exemplo, podem aumentar a produtividade e mudar as formas dos espectros de tamanho em um ambiente marinho (DAI et al., 2016). Os processos de bottom-up aumentam os nutrientes com o aumento da abundância de organismos zooplanctônicos nas menores classes de tamanho, produzindo regressões lineares menos acentuadas.

Ao longo dos últimos 30 anos, sistemas de imagens e ferramentas de classificação vêm sendo desenvolvidos para fornecer medições de tamanho de qualquer objeto. Por exemplo, equipamentos como VPR, LOPC e UVP são dispositivos ópticos *in situ* que melhoram a cobertura espacial e temporal da análise dos ecossistemas pelágicos. Essas ferramentas aplicadas a estudos de abundância e distribuição de plâncton ajudam a obter parâmetros de tamanho e biomassa do zooplâncton em seus ambientes naturais. Além destes, existem dispositivos de imagem de bancada, como o ZooScan que fornecem imagens de alta qualidade, a partir de amostras preservadas, através de um sistema semi-automático, permitindo uma boa classificação de zooplâncton e partículas que foram suspensas na coluna d'agua (GROSJEAN et al., 2004; SILVA et al., 2019).

Outra forma de estudar as comunidades planctônicas é através da análise de isótopos estáveis. Nas ultimas décadas, o uso de isótopos estáveis é um exemplo de abordagem que vem sendo bastante utilizada em estudos ecológicos, porque na maioria das vezes, o meio aquático impede a observação direta do comportamento dos organismos e sua interação com o ambiente. Isótopos são átomos de um mesmo elemento que diferem no número de nêutrons, como por exemplo, ^{12}C e ^{13}C ou ^{14}N e ^{15}N (FRY, 2006). Normalmente, os estudos expressam a composição isotópica em termos de δ, que representa partes por mil (‰) de isótopo da amostra em relação ao padrão conhecido. De fato, a abundância relativa dos isótopos estáveis na natureza pode ser empregada como marcador natural de fluxo de matéria e energia entre os organismos e o ecossistema (MICHENER e LAJTHA, 2007). As razões entre isótopos podem ser utilizadas na identificação de fontes orgânicas para os produtores, como também o fluxo da matéria ao longo da teia trófica em várias categorias de consumidores (FRY, 2006).

Os isótopos estáveis mais utilizados em estudos ecológicos são os de carbono ($^{13}C/^{12}C$) e nitrogênio ($^{15}N/^{14}N$) (GREY, 2006). Devido à baixa discriminação isotópica (usualmente entre 0,5 e 1 permil), ou seja, enriquecimento ou empobrecimento de um isótopo em relação a outro, o carbono relaciona as fontes alimentares e os consumidores, enquanto que o nitrogênio, que possui uma discriminação isotópica mais acentuada a cada nível trófico, permite estimar a posição trófica dos consumidores (PETERSON e FRY, 1987; POST et al., 2000; POST, 2002; VANDERKLIFT e PONSARD, 2003). O uso integrado da análise isotópica com espectros de tamanho é de fato uma boa ferramenta para obtenção de respostas do ecossistema, tais como o aumento da posição trófica com o aumento do tamanho corpóreo do plâncton, invertebrados e peixes (FRY e QUINONES 1994; FRANCE et al., 1998, JENNINGS et al., 2002).

1.3 Justificativa e hipótese

O Nordeste brasileiro possui uma linha de costa de cerca de 2000 km de extensão. A região oceânica adjacente é caracterizada como regiões oligotróficas, apresenta baixa concentração de nutrientes, o que consequentemente diminui a produtividade primária e biomassa planctônica (BOLOTOVSKOY, 1981). Em contrapartida, existem ambientes de com maiores *inputs* de nutrientes como as ilhas oceânicas (LIRA et al., 2014; CAMPELO et al., 2019), e a região de quebra de plataforma, que devido a suas características topográficas, combinado com correntes e circulação (SANTANA et al., 2020), acabam alterando a hidrodinâmica desses ambientes (DOTY e OGURY, 1956), tornando-os "*hotspots*" de biodiversidade, aumentando assim a produtividade planctônica. Além dos sistemas oceânicos, nas áreas costeiras, devido à proximidade de regiões estuarinas e de ambientes recifais, pode existir um aumento na abundância e diversidade dos organismos zooplanctônicos.

Vários desses ecossistemas marinhos do Nordeste do Brasil vêm sendo ameaçados por inúmeros fatores como, por exemplo, acidificação dos oceanos, perda de habitat, sobrepesca e poluição (FAO, 2010). Trabalhos científicos das comunidades vêm sendo realizados ao longo da plataforma continental e zonas oceânicas do nordeste brasileiro (KOENING et al., 2009; JALES et al. 2015). Entretanto, a maioria desses estudos voltados para comunidades planctônicas, são direcionados para ambientes específicos, e poucos tratam de trabalhos que comparam as comunidades pelágicas ao largo do nordeste brasileiro, como exemplo, Marcolin *et al*. (2013) que avaliaram a diferença na composição e espectro de tamanhos do plâncton entre ambientes costeiros e oceânicos no Banco de Abrolhos e áreas adjacentes.

Neste contexto, alguns estudos têm enfatizado os espectros de tamanho das comunidades zooplanctônicas ao longo do nordeste brasileiro (MARCOLIN et al., 2013, 2015; SOUZA et al., 2020). Entretanto, esses estudos ainda são pontuais. Assim, estudar as comunidades zooplanctônicas em termos de abundância, espectros de tamanho e isótopos estáveis é crucial para entender o papel dessa comunidade no ecossistema. Assim, esta tese busca descrever como as comunidades zooplanctônicas estão organizadas e estruturadas ao longo de ambientes costeiros e oceânicos. Para responder esta pergunta, a hipótese levantada foi que as relações entre comprimento dos organismos e a posição trófica das comunidades zooplanctônicas variam em função do espaço (ambiente costeiro *vs.* ambientes oceânicos) e das comunidades (micro- meso- e macrozooplâncton).

2 OBJETIVOS

Nessa sessão abordaremos os objetivos gerais e específicos da tese.

2.1 Objetivo geral

Comparar a estrutura das comunidades zooplanctônicas dos ambientes costeiros e oceânicos em função dos espectros de tamanho e das suas razões isotópicas, bem como contribuir para o conhecimento da biodiversidade do zooplâncton nos ambientes estudados.

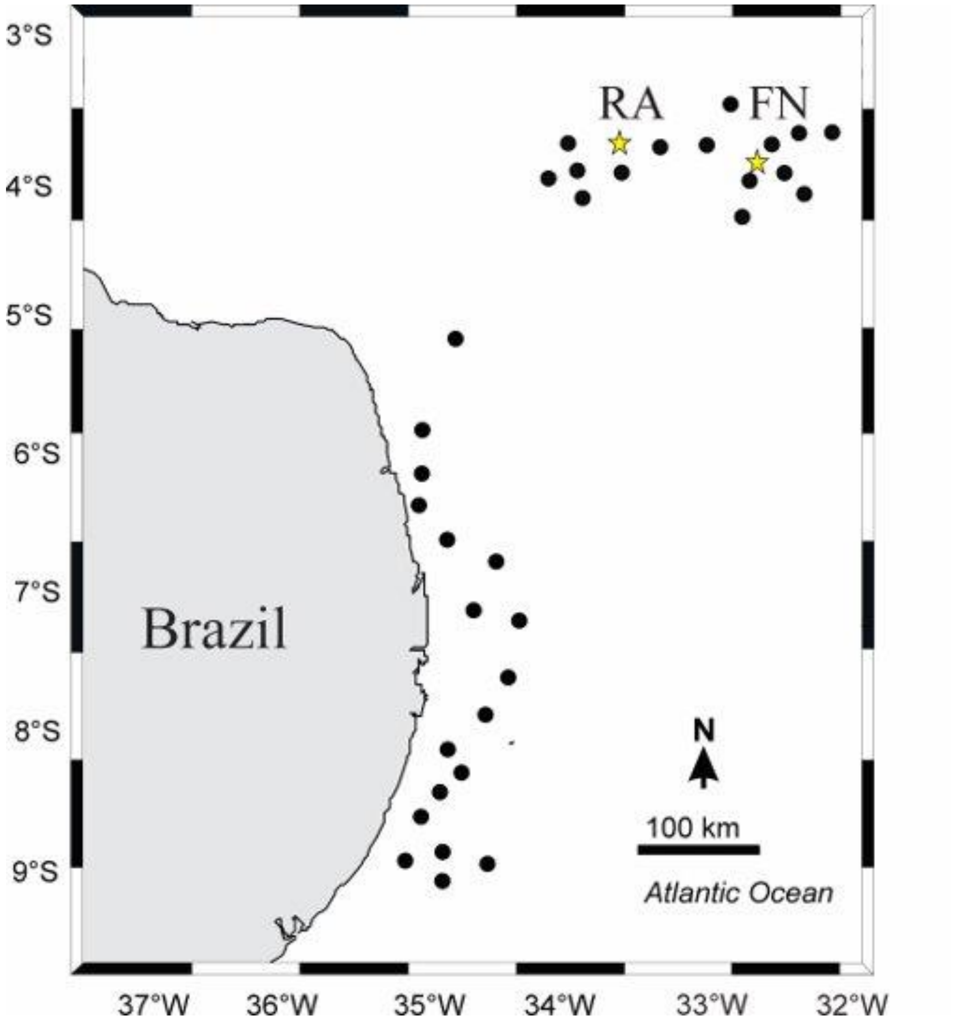
2.2 Objetivos específicos

a) Comparar os ambientes neríticos, oceânicos e ilhas oceânicas em relação aos espectros de tamanho do zooplâncton (comprimento *vs*. biovolume);
b) Comparar a razões isotópicas ($^{13}C/^{12}C$ e $^{15}N/^{14}N$) dos grupos taxonômicos e das classes de tamanho entre si;
c) Analisar a relação entre o tamanho e a razão isotópica das comunidades zooplanctônicas em uma comparação entre os ambientes nerítico e oceânico.
d) Identificar novas ocorrências de organismos zooplanctônicos nas áreas de estudo.

3 ÁREA DE ESTUDO

A área estudada compreende ambientes localizados ao longo do litoral do nordeste do Brasil, entre os estados de Pernambuco e Rio Grande do Norte (Figura 1): ambientes neríticos que compreende a costa e plataforma continentais, e ambientes oceânicos representados por duas ilhas oceânicas Fernando de Noronha e Atol das Rocas. Esses ambientes são influenciados por duas massas de água principais: água tropical e água central do Atlântico Sul (STRAMMA et al., 1999).

Figura 1 - Mapa da área de estudo. Bolinhas pretas indicam as estações de coleta, estrela amarela indica as ilhas oceânicas: Atol das Rocas (RA) e Fernando de Noronha (FN)



Fonte: A Autora (2019).

A costa do nordeste brasileiro, de maneira geral, é uma região de baixa produtividade e elevada biodiversidade. Possui um perfil regular com a presença notável de uma barreira de recifes, bem como a presença de ilhas oceânicas, como Fernando de Noronha (03°51'S, 32°25'O) e Atol das Rocas (3°51'S, 33° 49'O), (REVIZEE, 2006). Além das ilhas oceânicas, ao largo da plataforma continental, observam-se bancos rasos (pertencentes às cadeias Norte-brasileiras e Fernando de Noronha). A maior parte do domínio oceânico é formada por áreas bastante profundas, entre 4000 e 5000 metros (REVIZEE, 2006). A costa do nordeste brasileiro é banhada pelas águas trazidas pelo braço central do sistema da Corrente Sul Equatorial (CSE), que flui de leste a oeste do Oceano Atlântico, e se estende da superfície até a profundidade em torno de 100 m (PETERSON e STRAMMA, 1991). A CSE se bifurca na Corrente Norte do Brasil (CNB) e Corrente do Brasil (CB) que segue no sentido Sul (RODRIGUES et al., 2007).

O Arquipélago de Fernando de Noronha localiza-se no Atlântico Equatorial Tropical, cerca de 345 Km da costa brasileira, apresentando uma ilha principal e vinte ilhas menores que fazem parte de um complexo sistema de correntes e correntes cruzadas que fluem principalmente Leste-Oeste sob influência da Corrente Equatorial-Sul (RODRIGUES et al., 2006). Devido à disposição morfológica da ilha dois tipos de mares podem ser destacados: o mar de dentro (mais protegido) e o mar de fora (mais exposta) (ASSUNÇÃO et al., 2016). O clima do arquipélago é tropical e influenciado pelo Oceano Atlântico, com temperatura média de 27,5^{o}C. Fernando de Noronha possui duas estações bem demarcadas: Chuvosa (Março a Julho) e seca (Agosto a Janeiro) (ASSUNÇÃO et al., 2016).

O Atol das Rocas está localizado a 267 Km de Natal, RN, e 148 Km de Fernando de Noronha. É uma reserva biológica, pertencente ao estado do Rio Grande do Norte (RN), que abrange 360 km^{2} incluindo o atol e as águas circundantes, até a isóbata de 1000 m. Possui um clima equatorial com ventos alísios e temperatura média de 26^{o} C. A estação chuvosa estende-se de Março a Julho, semelhante a Fernando de Noronha (GUSMÃO, 2005).

4 ESTRUTURA DA TESE

De acordo como os objetivos e os resultados obtidos ao longo da realização do estudo, a tese de doutorado foi dividida em três capítulos. Cada capítulo refere-se a um artigo científico. Os artigos foram e serão submetidos em periódicos científicos e seguem as normas de publicação dos respectivos periódicos.

Capítulo 1: Artigo 1. Zooplankton biovolume and size spectra on the continental shelf and off oceanic islands in the western tropical Atlantic (in prep) - Manuscrito a ser submetido ao periódico Journal of Sea Research;

Capítulo 2: Artigo 2. Body size and stable isotope composition of zooplankton in the western tropical Atlantic). (Publicado) - Manuscrito aceito e publicado no periódico Journal of Marine Systems;

Capítulo 3: Artigo 3. New records of the mollusk *Firoloida desmarestia* (Gastropoda: Pterotracheidae, Lesueur, 1817) off Fernando de Noronha and the north-east Brazilian continental slope, Tropical Atlantic (Publicado) - Artigo aceito e publicado no periódico Tropical Oceanography

5 ZOOPLANKTON BIOVOLUME AND SIZE SPECTRA AT THE CONTINENTAL SHELF, SLOPE, AND OCEANIC ISLANDS IN THE WESTERN TROPICAL ATLANTIC

Manuscrito a ser submetido ao periódico Journal of Sea Research

Gabriela Guerra Araújo Abrantes de Figueiredo*[1], Simone Maria de Albuquerque Lira[1,2], Arnaud Bertrand[1,3,4], Ralf Schwamborn[1.]

[1]Departamento de Oceanografia, Universidade Federal de Pernambuco, Recife, Brazil, [2] Departamento de Biologia, Universidade Federal Rural de Pernambuco, Recife, Brazil,[3] Institut de Recherchepourle Développement (IRD), MARBEC, Université de Montpellier, CNRS, Ifremer, IRD, Sète, France, [4] Departamento de Pesca e Aquicultura, Universidade Federal Rural de Pernambuco, Recife, Brazil.

*Corresponding author: gabriela.gaaf@gmail.com

Abstract

Abundance and biovolume spectra were obtained for zooplankton in several areas of the southwestern tropical Atlantic. Sampling was carried out in September and October 2015, at 34 stations on the northeastern Brazilian continental shelf, slope and at two oceanic island systems (Fernando de Noronha and Rocas Atoll). Oblique tows with a 300-µm mesh bongo net were performed from 200 m depth to the surface, and samples were analyzed with the ZooScan system. Twenty-seven zooplankton taxa were recorded. Mean abundance and biovolume were 62.59 ind m^{-3} and 36.23 mm^3 m^{-3}, respectively. Zooplankton community structure was significantly different between continental shelf & slope and oceanic islands areas, in terms of both abundance and biovolume (PERMANOVA $p < 0.05$). The most abundant group was Copepoda (66% and 57% in coastal areas and oceanic islands, respectively). Fish larvae showed the highest total biovolume values off oceanic islands (~25%), considerably higher than Copepoda (17%), followed by Chaetognatha (15%) and Thaliacea (~12%). Steeper size spectra (NNSS and NBSS) slopes were found on the shelf and slope areas (slopes: -1.94 and -0.72 and intercept of 0.82 and 0.80 for NNSS and NBSS, respectively), due to higher contributions of small copepods and higher contribution of large copepods and other large organisms off oceanic islands (slopes: -1.74 and -0.72 and intercept: 0.56 and 0.58 for NNSS and NBSS respectively). This study shows the importance of large planktonic organisms (e.g. fish larvae, decapods and gelatinous plankton) off oceanic islands.

Key-words: NNSS, NBSS, ZooScan, northeastern Brazil, tropical oceanic islands

1. Introduction

Zooplankton play a key role in marine ecosystems, by conveying energy from the base of the food web to higher trophic levels and by contributing to the biological carbon pump (Banse, 1995; Kruse et al., 2010; Schukat et al., 2013; Dai et al., 2016; Guidi et al., 2016; Gove et al. 2016). To provide a comprehensive vision of zooplankton communities, it is important to rely not only on abundance but also on biomass, directly using proxys such as biovolume (Dai et al. 2016). In general, studies are carried out with abundance, but it is well established that metrics such as biovolume are more adequate to assess the biomass contribution of these organisms to the ecosystem. In addition, size and biomass spectra analyses are now commonly used to describe plankton communities (Sheldon et al., 1972; Zhou et al., 2008; Marcolin et al., 2013; Dai et al., 2015; Edward et al., 2017), since they provide useful information on ecosystem structure (Quinones, 1994; Shin et al. 2005; Yamaguchi, 2008; Edward et al., 2017).

The relationship between abundance and body size (i.e. the size spectrum) has been widely used to describe the productivity, energy transfer and to infer about the state of environmental degradation (Zhou, 2006). For example, the slope from a linear regression between body size and abundance can provide information on productivity and energy transfer (Platt and Denman, 1978). In general, steeper slopes show a higher contribution of smaller organisms and will present a lower efficiency in the energy transfer between the trophic levels, in comparison to flat slopes, where the community presents a better efficiency in trophic transfers and more balanced environments (Sprules and Munawar, 1986; Sheldon, 1972; Zhou, 2006).

The zooplankton community is driven by a series of environmental factors, including currents, temperature, salinity and nutrient inputs (Kodama et al., 2018). In oligotrophic tropical oceans, the abundance of the zooplankton generally decreases from coastal waters towards offshore areas. This is mostly due to nutrients inputs, which are higher in estuaries and coastal lagoon environments (Neumann-leitão et al., 1999; Schwamborn et al., 1999a,b). The same can occur off oceanic islands (island mass effect, Doty and Oguri, 1956), due to the presence of topographic upwelling (Strama at al., 1990; Gove et al., 2016). In contrast, in open oceanic waters, zooplankton abundance tends to be very low, sometimes associated to high diversity (Neumann-Leitão et al, 1999; Gusmão et al., 2015).

The western tropical Atlantic off northeastern Brazil is characterized by low productivity and high diversity (Boltovskoy et al., 1999). It encompasses oceanic islands such as Fernando de Noronha and Rocas Atoll, which are considered hotspots, since they are areas of upwelling, favoring these environments for a higher amount of organisms. Several studies focused on diversity patterns, abundance, community structure and taxonomy of zooplankton (e.g. Neumann-Leitão et al. 1999; Diaz et al., 2008; Brandão et al., 2013; Lira et al., 2014; 2017 Santana et al. 2018) have been carried out in this environments, however, little is known about the contributions of zooplankton groups in terms of biomass or biovolume, and size-spectra in neritic and oceanic areas, except studies in Bank of Abrolhos (Marcolin et al., 2013).

Here, we describe the zooplankton community in terms of abundance, biovolume and size spectra in the western tropical Atlantic. In particular, we analyze how zooplankton distribution, composition, abundance, biovolume and size spectra change between ecological domains (shelf areas *vs.* oceanic islands).

We test the hypothesis that zooplankton abundance is higher in shelf areas than in oceanic islands, but oceanic islands have a greater diversity. Also, we hypothesized that large amounts of smaller organisms occur in more productive inshore waters, and thus, the slope of the size spectrum should be steeper in coastal areas compared to oceanic islands.

2. Materials and Methods

2.1 Sampling data

The study area comprises the northeastern Brazilian shelf (from 9ºS to 5.7ºS) and two oceanic island systems (Fernando de Noronha and Rocas Atoll) (Fig. 1) which are protected areas. Fernando de Noronha Archipelago, located about 345 km from the Brazilian coast (03°51’S - 32º25’W) presents 21 islands and islets (Rodrigues et al. 2006; Assunção et al., 2016) and Rocas Atoll is located about 267 km from the Brazilian coast (3º 51’ S and 33º 49’ W) and 148 km from Fernando de Noronha (Gherardi & Bosence, 2005).

These oceanic islands are located in a complex current system, dominated by the South Equatorial Current, flowing from east to west, and by the South Equatorial Under Current, which moves from west to east (Assunção et al., 2016). These islands are considered as protected areas (UNESCO), once they are extremely important for many species such as sharks, tuna turtle and marine mammals, playing a crucial in the natural fish restocking of the region.

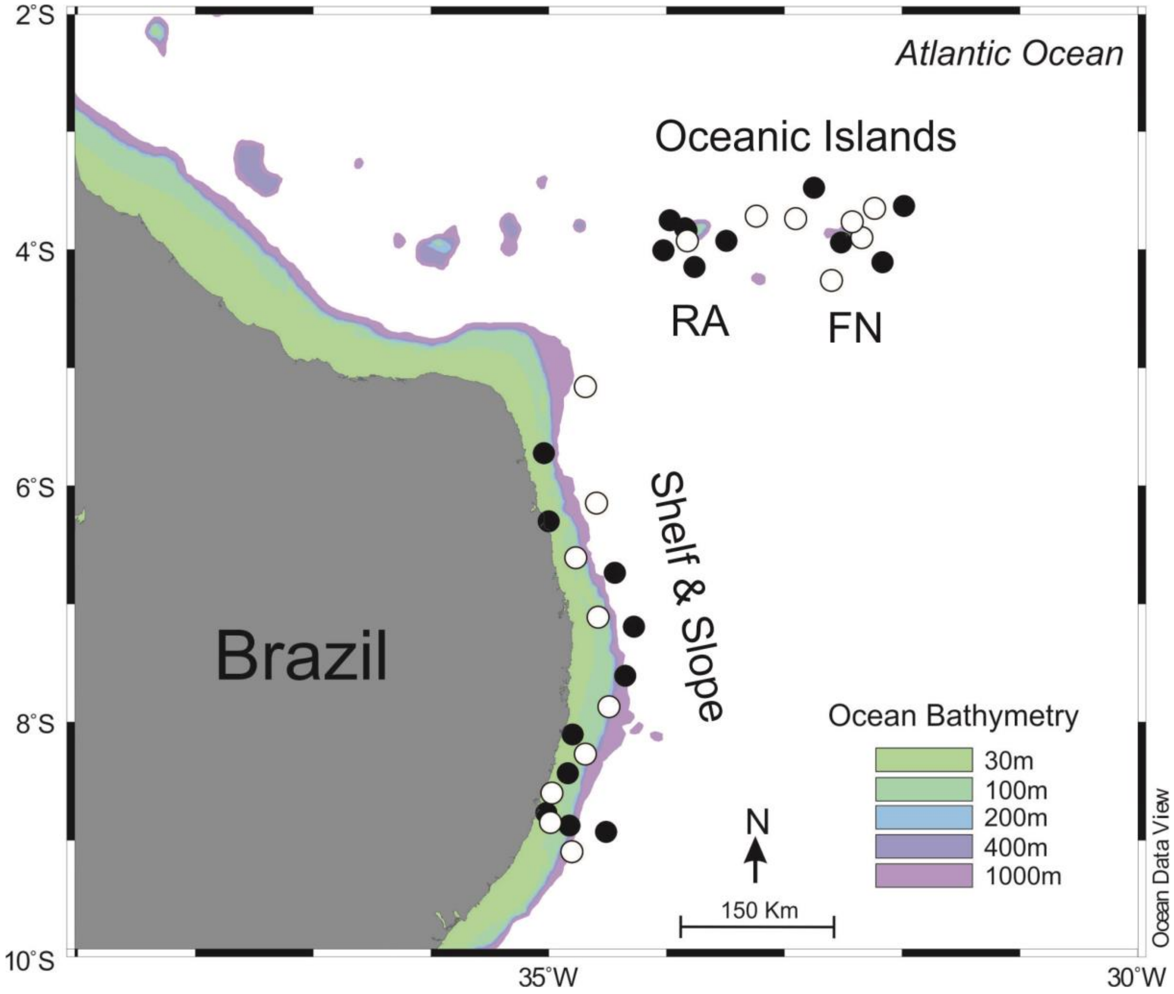


Figure 1.Location of sampling stations off northeastern Brazil during September and October of 2015. Black circles: night-time sampled stations; white circles: day-time sampled stations; FN: Fernando de Noronha, RA: Rocas Atoll.

Data were collected in the dry season from September 29 to October 21, 2015 during the ABRACOS cruise (Acoustics along the Brazilian coast: doi: http://dx.doi.org/10.17600/15005600), conducted on board the IRD R/V "ANTEA". Zooplankton sampling was carried out using a bongo net with nets fitted (300µm) covered oceanographic regions ranging from shallow nearshore waters to oligotrophic oceanic areas during day or night. In this study, only the 300µm bongo net was used. In oceanic waters, the bongo net was towed obliquely from 200 meters depth up to the surface. In shallow areas, it was towed from 10 meters above the bottom to the surface. The filtered volume was estimated using a *Hydro-B*ios flowmeter fixed to the net opening. All zooplankton samples were preserved in 4% formaldehyde buffered with sodium tetraborate (0.5 $g.l^{-1}$), in accordance with Newell and Newell (1963).

Temperature and salinity profiles were achieved with a CTD (model: SeaBird911). In addition, water samples were collected by Niskin bottles to measure nutrients (ammonia NH_{3-}, nitrite NO_{2-}, nitrate NO_{3-}, phosphorous PO_{4-} and silicate SiO_{2-}).

2.3 ZooScan analysis

Zooplankton samples were separated into two fractions using a 1000µm mesh to prevent the underestimation of large and rare organisms (Gorsky et al. 2010). Each size fraction was split into 1/2 to 1/64 subsamples with a Motoda box splitter to obtain up to 2000 objects in each scan. Subsamples were scanned and digitalized with the ZooScan system at a resolution of 2400 dpi. Scanned data were processed with the ZooProcess software, which isolates each object in images (vignettes) and generates a range of size parameter. Vignettes were classified into taxonomic groups (see Table 1) using the Random Forest algorithm of the Plankton Identifier software according to a learning set (Gorsky et al. 2010). All results were manually validated using XnView and Plankton Identifier software to correct any misclassifications.

2.4 Zooplankton abundance and biovolume

All artefacts (e.g., bubbles, shadows), multiple touching objects and detritus were excluded from the data set prior to the estimation of zooplankton abundance and biovolume. Abundance ($ind.m^{-3}$) for total zooplankton and of each taxonomic group was calculated as:

$$abundance = \frac{numberoforganisms \times splittingratio}{filteredvolume}.$$

The biovolume ($mm^3.m^{-3}$) was calculated according to the following equation:

$$biovolume = \frac{volumeoforganismswithinthesametaxonomicgroups \times splittingratio}{filteredvolume}.$$

The volumes of each individual organism were calculated based on the major and minor axes of the equivalent ellipse of each vignette, as the ellipsoidal volume (mm^3):

$$volume = \frac{4\pi}{3}\left(\frac{majoraxis}{2}\right)\left(\frac{minoraxis}{2}\right)^2$$

2.5 Size spectra

Normalized biovolume size spectra (NBSS, Platt and Denman, 1977) were calculated for each sample as

$$NB = \frac{B}{\Delta b}$$

where NBSS is the normalized biovolume ($mm^3.m^{-3}.mm^{-3} = m^{-3}$) in each biovolume class b ($mm^3.ind.^{-1}$), *B* is the total biovolume per cubic meter ($mm^3.m^{-3}$) and Δb is the width of each size class (mm^3). The NBSS plot is then a plot of $\log_{10}$ (NB) over $\log_{10}$ (b). Linear regression analyses were conducted to estimate slope and intercept of NBSS.

The same approach was used to calculate the normalized number size spectra (NNSS; Vandromme et al., 2012), where instead of using total biovolume per cubic meter, we used normalized total abundance per cubic meter ($ind.\ m^{-3}\ mm^{-3}$) within each biovolume class.

The biovolume classes (b) used for NBSS and NNSS were defined using the following equation: $b = 10^{(k^3),}$ where k is a linear, regular sequence of 81 values from -1.597 to 1.674. The biovolume and abundance data for each taxonomic group were separated into 81 geometrically increasing biovolume classes between $b = 8.5\times10^{-5}$ $mm^3\ ind^{-1}$ and $b = 4.9\times10^{4}$ $mm^3\ ind.^{-1}$. Only the central part of the spectrum was used for linear regression, between $10^{-0.8}$ and $10^{-1.39}$ mm^3 (i.e. from 0.15 to 24.5 mm^3, or from 0.67 to 3.6 mm equivalent spherical diameter - ESD).

2.6 Statistical analyses

Permutation one-way tests were performed to evaluate significant differences in mean abundance and biovolume of total zooplankton and specific taxonomic groups according to the following spatio-temporal factors: shelf areas *vs.* oceanic islands areas and day *vs.* night. PERMANOVA was also used to test for differences in mean intercepts and mean slopes of NBSS and NNSS and factors. A similarity matrix between samples was calculated by Bray-Curtis index (Bray & Curtis, 1957) and square-root transformed to create a multidimensional scaling (MDS) analysis plot. All multivariate analysis was performed based on abundance and biovolume of all taxonomic groups.

A redundancy analysis (RDA) was used to evaluate how environmental and spatio-temporal factors may impact the zooplankton community structure (abundance and biovolume). First, correlations between abiotic data were tested to decide which parameters would be used for the RDA analyzes. Biological data were Hellinger-transformed, while non-numerical spatial data were transformed into dummy (1 and 0) variables (Legendre & Legendre, 1998 and Legendre & Gallagher, 2001). Non-significant variables ($p > 0.05$) were excluded from the environmental matrix in a step by-step procedure using a Monte Carlo permutation test with 9999 permutations (TerBraak & Smilauer, 2002).

3. Results

3.1 Hydrography

Sea surface temperature varied from 22.9^{o}C to 26.6^{o}, and was nearly homogeneous (median: 26.6°C) over the whole study area. Surface salinity varied from 36.1 to 36.6, with higher values along the shelf and slope areas. Mixed layer depth ranged between 80 and 170 m in the shelf and slope areas and 90 and 130 m to the oceanic islands areas (Assunção et al. 2020). The chlorophyll a fluorescence maximum was generally located below the deep margin of the upper mixed layer.

3.2. Zooplankton abundance and biovolume composition

A total of twenty two zooplankton taxonomic groups were considered in this study (Table 1). Zooplankton abundance from shelf and slope areas ranged from 0.08 ind.m^{-3}to 798.69 ind.m^{-3}, while at oceanic islands ranged from 0.05 ind.m^{-3} to 275.96 ind.m^{-3} (Table 1). In general, abundances were higher at shelf and slope areas (1210.2 ind.m^{-3}) than offshore (479.6 ind.m^{-3}). Zooplankton biovolume ranged from 0.12 mm^{3}.m^{-3}to 365.4 mm^{3}.m^{-3} at shelf and areas and from 0.02 mm^{3}.m^{-3} to 273.7 mm^{3}.m^{-3} off oceanic islands. Biovolumes were higher off oceanic islands (1085.05 mm^{3}.m^{-3}) and total abundance was higher in shelf and slope waters than off oceanic islands (one-way PERMANOVA $p < 0.01$). However, total biovolume values did not significantly differ between areas. There was no significant day/night difference for total abundance or for total biovolume in both areas.

Copepoda was the most abundant zooplankton group along the study area, with relative abundances of ~66% and 60% for shelf and slope areas and oceanic islands respectively. Decapoda were the second most abundant group in shelf areas (~ 10%), while Chaetognatha were the second most abundant group off oceanic islands, with a relative abundance of ~15% (table 1).

Although Copepoda presented a greater contribution in biovolume at the shelf and slope areas (~37%) the difference in relation to other taxonomic groups decreased. The second most voluminous group at the shelf was Chaetognatha with ~ 18%, followed by Decapoda (13%). The biovolume contribution of copepods off oceanic islands areas did not present the same pattern as at the shelf and slope areas. Fish larvae showed the highest total biovolume values off oceanic islands (~25%), considerably higher than Copepoda (17%), followed by Chaetognatha (15%) and Thaliacea (~12%).

When analyzing the distribution of zooplankton organisms at each station, we could observe the dominance of Copepoda in all the stations (> 50%) along the study areas (figure 2A). Unlike abundance, biovolume showed a different pattern. Copepoda were more representative only in few shelf stations (figure 2B). Despite this, in some shelf stations, biovolume of copepods decreased in relation to other taxonomic groups, such as Chategonatha (figure 2B). Off oceanic islands, large organisms such as gelatinous organisms and fish larvae were more important in terms of biovolume (Figure 2B).

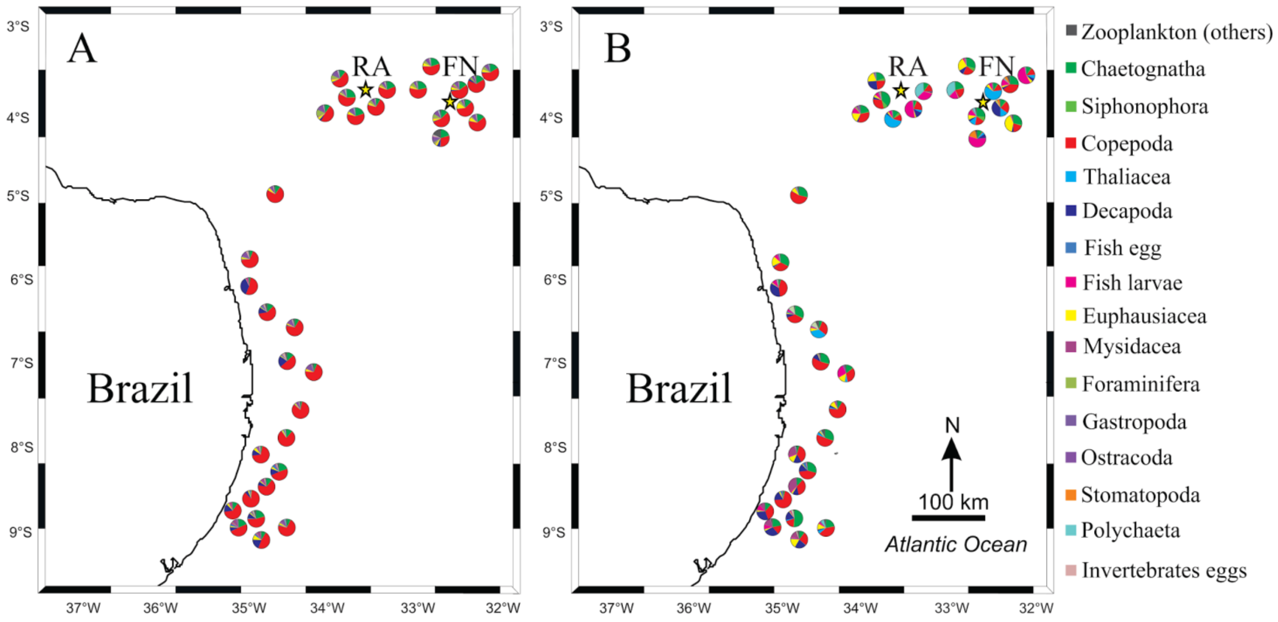


Figure 2. Distribution of Zooplankton abundance (A) and biovolume (B) along each sampling station off northeastern Brazil during September and October of 2015

The taxonomical composition varied considerably between size classes. The smallest size class (0.3 – 2.0 mm ESD) was dominated by Copepoda, representing more than 50% abundance and biovolume (figure 3). The larger size classes (> 3.0 mm ESD) were more diverse. In abundance, the most important organisms were Chaetognatha, fish larvae, Euphausiacea and Decapoda. For biovolume in shelf areas, the highest size class were composed by Chaetognatha, Thaliacea, Euphausiacea Fish Larvae and Mysidacea whereas in oceanic islands Chaetognatha, Siphonophora, Fish Larvae, and Thaliacea where the most representative (figure 3).

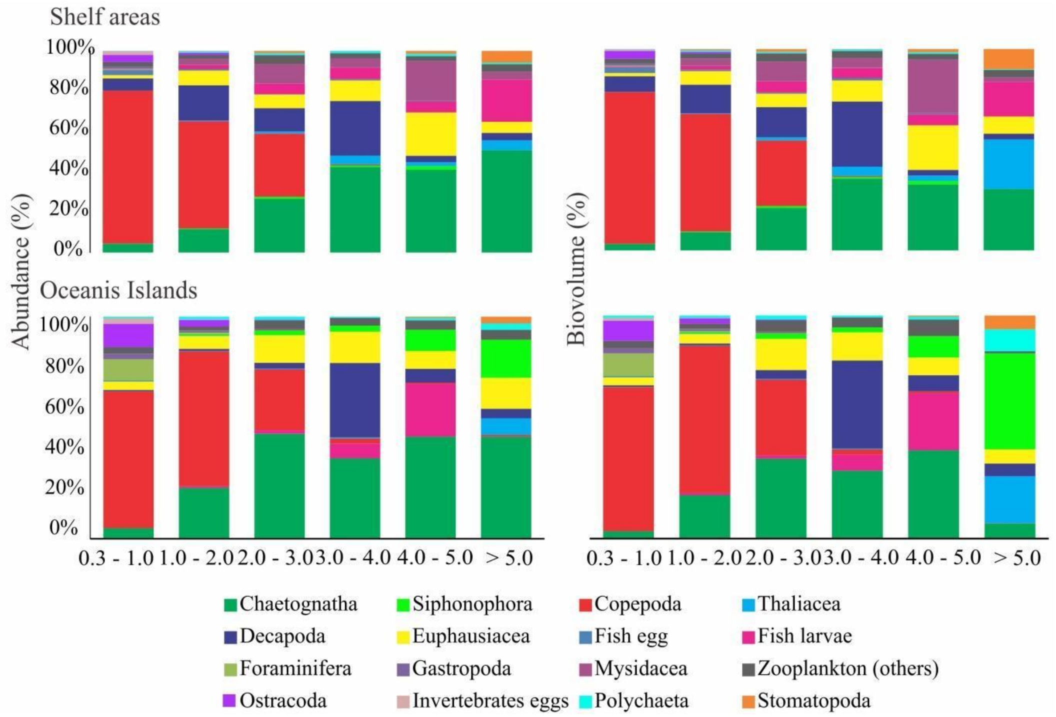


Figure 3: Relative abundance and biovolume composition of zooplankton taxonomic groups by ESD size-class

3.2 *Community structure*

The nMDS presented that shelf and oceanic areas were well separated into two groups of samples (figure 4). Shelf and oceanic areas were significantly different in their community structure for zooplankton abundance and biovolume (multivariate PERMANOVA, $p < 0.05$).

No groups or statistical differences were detected between day and night times (multivariate PERMANOVA, $p > 0.05$).

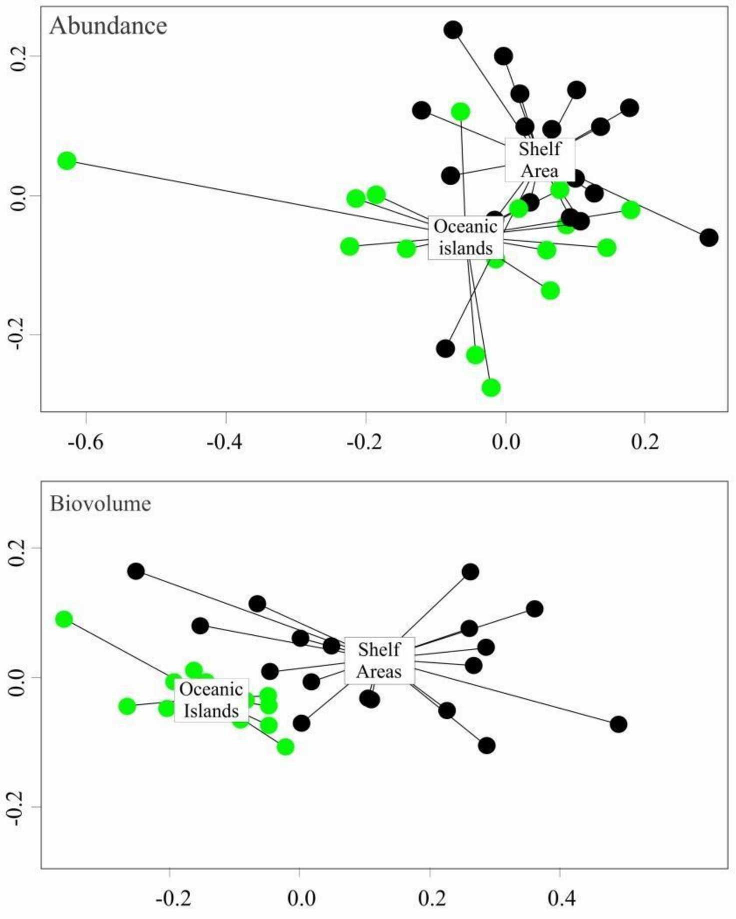


Figure 4. Non-metric multidimensional scaling (MDS) of zooplankton abundance and biovolume showing the groups formed according to areas (green circles: oceanic islands; black circles: Shelf areas).

Redundancy analysis (RDA) revealed similar patterns for zooplankton communities. The spatial-temporal variables explained 22% of the zooplankton abundance and biovolume variance (RDA; $p < 0.05$). It was possible to describe two main RDA axes for these communities, the first one separating shelf and oceanic islands areas samples (left and right regions of the RDA plots, figure. 5). Day and night-time was also relevant (upper *vs*. lower region of the RDA plots, figure. 5).

Groups such as Copepoda, Decapoda, Mysidacea, were distributed (both in abundance and in biovolume) towards the portion of the RDA plots corresponding to shelf and slope areas. On the other hand, Syphonophora, Thaliacea, Fish larvae, Ostracoda were distributed towards oceanic islands.

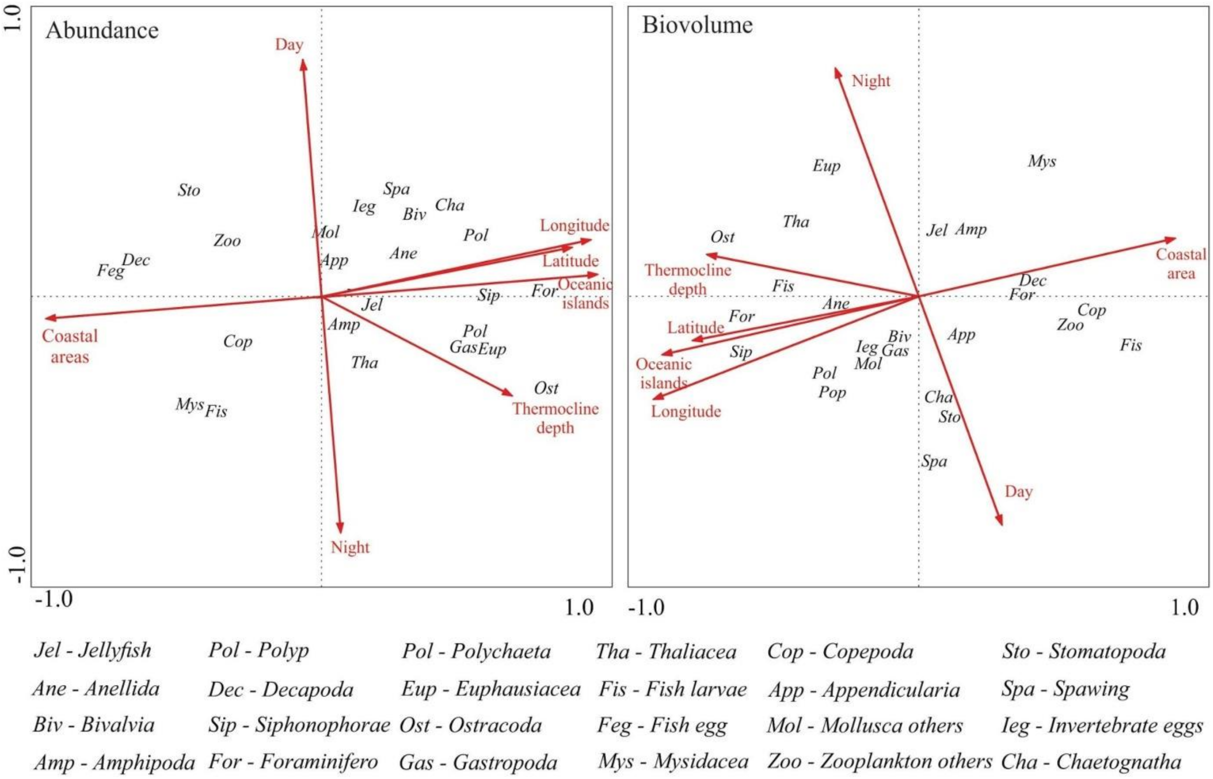


Figure 5. Ordination diagram of the Redundancy Analysis (RDA). Significant vectors of spatio-temporal vectors (in red), and zooplankton species classification according to abundance and biovolume values. Samples were taken off northeastern Brazil during September and October of 2015

3.3 Size spectra

The abundance and biovolume size distribution of the zooplankton community (NNSS and NBSS respectively) displayed marked differences between study areas (Figure 6). For both NNSS and NBSS, slopes and intercepts were significantly steeper and higher in shelf and slope waters than off oceanic islands (Fig. 6, $p < 0.05$, $n = 32$, three outliers removed). Intercepts were significantly higher ($p<0.0001$, Fig. 6) for both NNSS and NBSS, at the shelf and slope areas (0.82 and 0.80) than off oceanic islands (0.56 and 0.58), due to overall higher abundance and biovolume inshore, and due to the significant ($p < 0.05$) differences in slope (see below).

Slopes were significantly steeper ($p<0.0001$, Fig. 6) for both NNSS and NBSS, on the shelf & slopes (slopes: -1.94 and -0.72 for NNSS and NBSS respectively), than off oceanic islands ((slopes: -1.74 and -0.72 for NNSS and NBSS respectively),

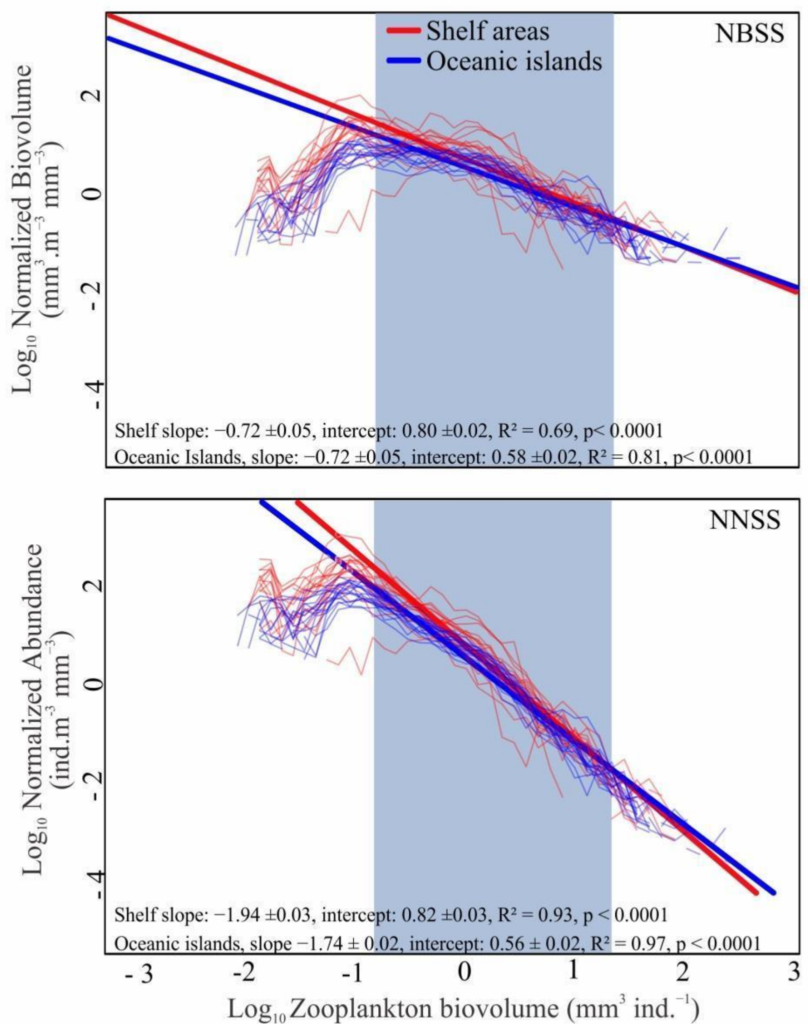


Figure 6. Zooplankton normalized abundance (NNSS) and biovolume size spectra (NBSS) in shelf and slope waters (red) and off oceanic islands (blue). Shaded area: biovolume classes used for linear regression. Samples were taken off northeastern Brazil during September and October of 2015

The contribution of small-sized zooplankton, especially copepods, was much higher in shelf and slope areas, which therefore showed steeper slopes. Conversely, large-sized organisms such as fish larvae and jellyfish were more abundant off oceanic islands, which showed flatter slopes (Figure 6).

4. Discussion

The present study provides new insights into zooplankton abundance, biovolume and size spectra distribution in the western tropical Atlantic. We detected differences in NBSS/

NNSS slopes between shelf and slope and off oceanic islands. These slopes can be used as a proxy of energy transfer efficiencies for different communities. We identified and compared the most abundant taxa and the groups that presented higher total biovolumes between oceanic islands and shelf areas. In this way, we observed a higher abundance of small organisms (copepods) in shelf areas. Although Copepoda was the most abundant group, we highlighted the contribution of gelatinous organisms for the biovolume, especially in oceanic islands areas, revealing that they may be responsible for the aggregation of other organisms in these environments. Also, the finding that fish larvae had the highest biovolume (and thus biomass) in oceanic waters indicates that these animals may be a hitherto neglected key element of pelagic food webs off tropical oceanic islands.

4.1 Shelf and Slope versus Oceanic islands

The comparison of zooplankton communities between shelf and oceanic regions revealed important spatial differences in abundance and biovolume. While abundance was higher in shelf areas, biovolume had higher values offshore, due to the presence of larger zooplankton (e.g. fish larvae and gelatinous plankton). Typically, in tropical environments, shelf areas have several smaller organisms than in oceanic areas because of a variety of processes that influence organism’s abundance. For example, input of nutrients from estuaries and rivers which stimulate the primary production growth and consequently the primary consumer. This pattern is commonly found in shelf areas (Dias et al. 2015; Neumann-Leitão et al. 2019).

The higher zooplankton abundance in shelf areas compared to oceanic islands consist with the findings in the Brazilian Abrolhos region (Marcolin et al. 2013), in the Western North Pacific (Sato et al. 2015), and in the subtropical North Pacific Ocean (Dai et al. 2016). Although abundance is widely applied in studies of zooplankton, it cannot fully reflect the importance of all the taxonomic groups (Dai et al. 2015) once it underestimates the importance of larger zooplanktons organism’s that are usually less abundant. For example, gelatinous, Chaetognatha and others was the most important groups for biovolume. Studies around the world showed that their relative contribution decreases significantly when switching from abundance to units biovolume, with an increase in the importance of gelatinous taxa (e.g., shiphonophores, hydromedusae, and chaetognaths) (e.g. Marcolin et al. 2013; Sato et al.; 2015; Dai et al. 2016; 2017, Lira et al., unpublished).

Copepoda were the most abundant group in all areas. This pattern reflects their dominant position in different marine environments, for example, most of times, they are considered as the group of organisms that dominate different marine environments (Dai et al. 2016, Champarbert et al. 2005) such as tropical Atlantic islands (Melo et al. 2012, Lira et al. 2014, Capelo et al. 2018). Although, Copepoda presented higher abundance, they weren't the taxonomic group with higher biovolume values. In oceanic islands, fish larvae (25%) had the highest biovolume followed, by Chaetognatha, Copepoda, and Thaliacea.

4.2 Spatial and temporal community structure

Organism distribution can be related to several factors, such as salinity, temperature and nutrients. In the present study, the thermocline was closer to the surface, which favored the upwelling of colder water masses that may have influenced the presence of larger organisms in oceanic environments. Recent results from acoustic studies and 3D–mapping of the pelagic realm in the study area revealed new structuring roles of gelatinous organisms, confirming the results of the present study (see preliminary results in Vargas et al., 2017). Lira et al (2014) visualized that Chaetognatha and fish eggs were the most abundant group, after copepods, in Fernando de Noronha Archipelago during July and August. This period is considered a spawning season for many fish species (Mafalda Jr. 2008), which may explain the large number of organisms in terms of biovolume in our study, since our sampling were carried out in September/ August, a period shortly after the spawning period. Although this study was not realized in the same year, it is possible that the high biovolume may be associated to the spawning period.

Many zooplankton communities perform diel migration. Therefore, we first tested for a diel effect on all our analyses (global and specific abundance and biovolume, NNSS, NBSS). Significant differences were not observed. Sato et al. (2015) also reported no significant differences between day and night samples. The lack or low difference can be due to the fact that we sampled the entire water column in the shelf area and both the mixed layer and the thermocline layer offshore. Most taxonomic groups may perform no migration or migration restricted to those upper layers. On this basis we decided to merge day and night data for all global analyses (abundance, biovolume, NNSS, NBSS) but considered the diel effect on the RDA analysis, which explicitly incorporates the different taxonomic groups.

Euphausiacea was one of the groups associated with the night period. They are known to perform huge diel vertical migrations (Mujica and Pavez 2008; Peralta and Moura, 2010) constituting one of the groups that are found mostly at night as opposed to the day time that was represented by the spawning of several invertebrate organisms, such as Stomatopoda and Chaetognatha. Zooplankton organisms migrate to deeper and darker environments to protect themselves from predation by larger organisms, and rise to the surface during the night to feed in these more productive environments (e.g., Forward Jr. 1988). These diel migrations were also described for some zooplanktonic groups off oceanic islands (Koettker et al. 2010; Brandão et al. 2012; 2013; Lira et al. 2014) and recently, this pattern was also seen in an acoustics study conducted around Fernando de Noronha (Vargas et al. 2017).

4.3 Size spectra, NNSS, NBSS

The higher abundance of small organisms in shelf and slope waters and the relatively larger amount of large-sized groups off oceanic islands determined the shape of our size spectra. NBSS slopes and intercepts have been used to evaluate the structure of numerous marine ecosystems worldwide (e.g. Matsuno et al. 2012; Sato et al. 2015; Zhou et al. 2009, Dai et al. 2016; 2017) and also as indicators of trophic transfer efficiency and productivity, respectively. Quantitative interpretations of size spectra slopes have been done under the aspects either of trophic efficiency (e.g., Sheldon, 1972 , Garcia-Comas et al., 2014) or the number of trophic levels per size class (Zhou, 20006, Thompson et al., 2013). The higher NNSS and NBSS intercepts in shelf and slope areas compared to oceanic islands, suggest a higher primary production indicating the larger contribution of smaller zooplankton. Bottom-up and top-down effects can increase productivity and shape size spectra in marine ecosystems (Dai et al, 2016). Bottom–up processes increase nutrients by the increase of zooplankton abundance in smaller size class and then produce steeper slopes (as in our shelf waters), while top – down process such as predation by zooplanktivorous species that selectively feed on zooplankton in larger size classes can also lead to steeper slopes (Moore and Suthers, 2006).

While shelf and slope areas were dominated by small-size classes such as copepods and ostracods, off oceanic islands the presence of large-sized gelatinous plankton and fish larvae had a strong influence on the NNSS and NBSS slopes, making them flatter. However, we need to be careful in using these parameters as proxies of system productivity. In this study, the differences in slope between shelf and slope areas and oceanic islands areas were mainly due to changes in the relative contributions of small copepods (more abundant in the shelf areas) and fish larvae and large gelatinous organisms (relatively more abundant in oceanic areas).

Using examples, equations and approaches presented by Zhou (2006), the overall mean NBSS slope of –0.85, observed in the present study, can be considered to be relatively flat, indicating a high level of energy recycling within each size bin. The idea of a strong energy recycling within size classes agrees well with the observation of herbivorous, omnivorous and carnivorous copepods within the same size classes (Boltovoskoy, 1999). A similar methodology, using ZooScan and biovolume NBSS, was applied by Garcia-Comas et al. (2014), for a subtropical pelagic ecosystem in the East China Sea, with a slope of –0.8, very similarly to the results of the present study. This indicates that both the subtropical system studied by Garcia-Comas et al. (2014) and the tropical plankton food webs studied in the present study may have a similar trophic structure (i.e., similar trophic efficiency and number of trophic levels per size class).

In contrast, biovolume NBSS slopes of zooplankton in the upwelling ecosystem of the California Current reported by Zhou (2006) were much steeper with –1.8 in the coastal community and –1.1 in the offshore community, indicating highly linear fluxes and less recycling within each size class in such productive waters. Other slopes reported were –1.48 for Sørfjorden, (Norway), and –1.14 to –0.92 for Marguerite Bay, Antarctic Peninsula. All these ecosystems have much less diverse copepod communities and a more linear and less complex food web, which explains less recycling per size class and steeper NBSS slopes, than in the present study. Thus, the observed relatively shallow NBSS slope in tropical ecosystems in the present study is well in agreement with the theoretical framework presented by Zhou (2006). However, care must be taken in such comparisons since the data of Zhou (2006) were mostly obtained with an OPC (optical plankton counter), which counts many non-organism particles (e.g., bubbles, aggregates and other detritus) and may thus be less precise for the study of zooplankton size and biovolume spectra that the ZooScan approach used in the present study.

Conclusion

Our results indicated a difference in zooplankton community according to spatial variations. For instance, larger planktonic organisms, such as fish larvae and gelatinous organisms contributed significantly to biovolume in oceanic environments, while abundance were dominated mainly by small copepods in all areas. These different distribution and contribution patterns reflected in zooplankton communities and size spectra between areas. The steeper slope and a higher intercept of NNSS and NBSS in shelf areas and a flatter slope in oceanic islands areas highlight the importance of specific taxonomic groups and their feeding strategies in the organization and structuring of communities in these environments.

Acknowledgements

We would like to thank the National Council for Scientific and Technological Development (CNPq, PhD fellowships awarded to the first and second authors and productivity fellowships awarded to the fourth and fifth authors), the ABRACOS project (Acoustics along the Brazilian Coast, funded by Institut de Recherche pour le Développement, IRD), the crew of R/V ANTEA, the Brazilian National Institute of Science and Technology in Tropical Marine Environments (INCT-AmbTropic, CNPQ/CAPES/FAPESB) for the logistic and financial support. RS and AB received support from the European Union’s Horizon 2020 research and innovation programme under Grant Agreement No 734271. Many thanks to Simone Maria A. Lira, Xiomara F.G. Díaz, Pedro A.M.C. Melo and Lucas Figueiredo, for the support in sampling and valuable comments.

Supplementary material

	Abundance								Biovolume							
	Coastal area				Oceanic islands				Coastal area				Oceanic islands			
	Total ind.m^{-3}	Mean	sd	RA (%)	Total ind.m^{-3}	Mean	sd	RA (%)	Total mm^{3}.m^{-3}	Mean	sd	RB (%)	Total mm^{3}.m^{-3}	Mean	sd	RB (%)
Foraminifera	3.10	0.17	0.30	0.26	25.65	1.60	1.55	5.35	0.43	0.02	0.05	0.04	4.94	0.31	0.34	0.46
Cnidaria – Jellyfish	0.08	0.00	0.01	0.01	0.11	0.01	0.03	0.02	4.35	0.24	0.63	0.44	6.35	0.40	1.59	0.59
Siphonophora	1.83	0.10	0.22	0.15	2.98	0.19	0.16	0.62	4.72	0.26	0.33	0.47	24.80	1.55	1.32	2.29
Bivalvia	0.93	0.05	0.08	0.08	0.84	0.05	0.04	0.17	0.30	0.02	0.02	0.03	0.24	0.01	0.02	0.02
Gastropoda	8.23	0.46	0.47	0.68	7.87	0.49	0.50	1.64	2.39	0.13	0.17	0.24	2.52	0.16	0.19	0.23
Mollusca (others)	0.11	0.01	0.01	0.01	0.05	0.00	0.01	0.01	2.64	0.15	0.57	0.27	2.45	0.15	0.37	0.23
Polychaeta	4.53	0.25	0.33	0.37	4.66	0.29	0.19	0.97	6.50	0.36	0.71	0.65	65.84	4.11	9.99	6.07
Copepoda	798.69	44.37	29.56	65.99	275.96	17.25	4.84	57.54	365.37	20.30	11.98	36.75	184.55	11.53	4.08	17.01
Amphipoda	7.82	0.43	0.44	0.65	3.61	0.23	0.14	0.75	14.02	0.78	0.65	1.41	10.63	0.66	0.60	0.98
Ostracoda	30.35	1.69	2.58	2.51	32.61	2.04	0.97	6.80	7.79	0.43	0.69	0.78	8.47	0.53	0.29	0.78
Mysidacea	16.96	0.94	1.80	1.40	0.47	0.03	0.10	0.10	52.60	2.92	4.87	5.29	1.10	0.07	0.24	0.10
Euphausiacea	45.42	2.52	2.63	3.75	25.54	1.60	0.74	5.32	76.26	4.24	4.88	7.67	79.27	4.95	6.65	7.31
Decapoda	122.63	6.81	8.78	10.13	6.81	0.43	0.43	1.42	133.33	7.41	8.78	13.41	79.52	4.97	6.73	7.33
Stomatopoda	1.61	0.09	0.17	0.13	0.06	0.00	0.01	0.01	21.59	1.20	2.64	2.17	37.98	2.37	8.17	3.50
Thaliacea	2.72	0.15	0.24	0.22	0.73	0.05	0.05	0.15	49.45	2.75	8.49	4.97	129.10	8.07	15.45	11.90
Chaetognatha	96.92	5.38	4.08	8.01	72.09	4.51	1.62	15.03	181.50	10.08	10.67	18.26	166.65	10.42	4.88	15.36
Appendicularia	0.86	0.05	0.18	0.07	0.21	0.01	0.03	0.04	0.12	0.01	0.03	0.01	0.02	0.00	0.00	0.00

Invertebrates eggs	14.37	0.80	0.88	1.19	6.95	0.43	0.21	1.45	0.77	0.04	0.07	0.08	0.84	0.05	0.04	0.08
Spawning	3.18	0.18	0.26	0.26	4.03	0.25	0.54	0.84	1.28	0.07	0.13	0.13	2.10	0.13	0.38	0.19
Fish egg	21.76	1.21	1.11	1.80	1.64	0.10	0.14	0.34	8.30	0.46	0.62	0.84	0.56	0.03	0.05	0.05
Fish larvae	13.20	0.73	0.66	1.09	3.01	0.19	0.16	0.63	52.52	2.92	3.28	5.28	273.70	17.11	31.07	25.22
Zooplankton (others)	15.00	0.83	0.67	1.24	3.77	0.24	0.26	0.79	8.00	0.44	0.36	0.80	3.42	0.21	0.30	0.31
TOTAL	1210.31	67.24	55.48	100.00	479.63	29.98	12.72	100.00	994.23	55.24	60.64	100.00	1085.05	67.82	92.73	100.00

REFERENCE

Ashjian, C. J. and Wishner, K. (1993) Temporal persistence of copepodspecies groups in the Gulf Stream. Deep-Sea Res.,40, 483–516
Alcaraz, M., Saiz, E.,Calbet, A., Trepat, I., Broglio, E. 2003. Estimating zooplankton biomass through image analysis. Mar. Biol. 143, 307-315.

Ashjian, C. J. and Wishner, K. 1993. Temporal persistence of copepods species groups in the Gulf Stream. Deep-Sea Res.,40, 483–516

Banse, K. 1995. Zooplankton: pivotal role in the control of ocean production. ICES J. Mar. Sci. 52, 265–277.

Bertrand, A. 2015. ABRACOS cruise, RV Antea, http://dx.doi.org/10.17600/15005600

Boltovskoy, D. 1999. South Atlantic zooplankton. Leiden: Backhuys Publishers.

Boltovskoy, D.; Gibbons, M. J.; Hutchings, L.; Binet, D. General biological features of the South Atlantic.South Atlantic Zooplankton.Backhuys Publishers, Leiden, v. 2, p. 1-41, 1999.

Boudreau, P.R. & Dickie, L.M. 1992. Biomass spectra of aquatic ecosystems in relation to fisheries yield. Canadian Journal of Fisheries and Aquatic Sciences. 49, 1528–1538.

Boyd, P.W., Sherry, N.D., Berges, J.A., Bishop, J.K.B., Calvert, S.E., Charette, M.A., Giovannoni, S.J., Goldblatt, R., Harrison, P.J., Moran, S.B., Roy, S., Soon, M., Strom, S., Thibault, D., Vergin, K.L., Whitney, F.A. & Wong, C.S. 1999. Transformations of biogenic particulates from the pelagic to the deep ocean realm. Deep Sea Research Part II: Topical Studies in Oceanography, 46, 2761-2792.

Brandão, M.C., Koettker, A.G., Freire, A.S. 2012a. Distribution of decapod larvae in the surface layer of an isolated equatorial oceanic archipelago: the capes of benthic Grapsusgrapsus(Brachyura: Grapsidae) and pelagic Sergestesedwardsi (Dendrobranchiata: Sergestidae). Helgoland Marine Research. 67, 1-11.

Brandão, M.C., Koettker, A.G., Freire, A.S. 2013a Abundance and composition of decapod larvae at Saint Paul's Rocks (equatorial Atlantic).Marine Ecology. 34, 171-185.

Campelo, R.P.S., Diaz, X.F.G., Melo-Junior, M., Figueiredo, L.G.P., Silva, A.P., Bezerra, L.E.A., Montes, M.J.F., Neumann-Leitão, S. 2018. Small-scale distribuction of the mesozooplankton in a tropical insular system. BJOCE, 66.

Chang, C.-Y., Ho, P.-C., Sastri, A.R., Lee, Y.-C., Gong, G.-C., Hsieh, C.-h., 2012. Methods of training set construction: towards improving performance for automated mesozooplankton image classification systems. Cont. Coastal areas Res. 36, 19–28.

Cowen,R.K., Hare J.A. and Fahay,M.P. 1993. Beyond hydrography, can physical processes explain larval fish assemblages within the middle Atlantic bight? BulL Mar. ScL, S3,567-587.

Dai, L., Li, C., Tao, Z., Yang, G., Wang, X., & Zhu, M. 2017. Zooplankton abundance, biovolume and size spectra down to 3000 m depth in the western tropical North Pacific during autumn 2014. Deep Sea Research Part I: Oceanographic Research Papers, 121, 1-13.

Dai, L., Li, C., Yang, G., Sun, X. 2016. Zooplankton abundance, biovolume and size spectra at western boundary currents in the subtropical North Pacific during winter 2012. J. Mar. Syst. 155, 73–83.

Diaz, X.F.G.; Gusmão, L.M.O., Neumann-Leitão, S. 2009.Biodiversidade e dinâmica espaço-temporal do zooplâcton. In: Viana, D.L.; Hazin, F.H.V.; Souza, M.A.C. 2009. O arquipélago de São Pedro e São Paulo: 10 anos de Estação Científica. Brasília: SECIRM, 128-137.

Doty, M.S.; Ogury, M. 1956.The island mass effect. Journal Du Conseil Permanent International pour le Exploration de la Mer, 22, 33-37.

Ducklow, H.W., Steinberg, D.K., 2001. Upper Ocean Carbon Export and the Biological Pump.

Edwards, A. M., Robinson, J. P., Plank, M. J., Baum, J. K., & Blanchard, J. L. 2017. Testing and recommending methods for fitting size spectra to data. Methods in Ecology and Evolution. 8, 57-67.

Folt, C.L., Burns, C.W., 1999. Biological drivers of zooplankton patchiness. Trends in Ecology and Evolution 14, 300e305

Forest, A., Stemmann, L., Picheral, M., Burdorf, L., Robert, D., Fortier, L., Babin, M., 2012. Size distribution of particles and zooplankton across the coastal areas–basin systemin southeast Beaufort Sea: combined results from an Underwater Vision Profiler and vertical net tows. Biogeosciences 9, 1301–1320.

García-Comas, C., Chang, C.-Y., Ye, L., Sastri, A.R., Lee, Y.-C., Gong, G.-C., Hsieh, C.-h., 2014.Mesozooplankton size structure in response to environmental conditions in the East China Sea: how much does size spectra theory fit empirical data of a dynamic coastal area? Prog.Oceanogr. 121, 141–157.

Gorsky, G., Ohman, M.D., Picheral, M., Gasparini, S., Stemmann, L., Romagnan, J.B., Cawood, A., Pesant, S., Garcia-Comas, C., Prejger, F., 2010. Digital zooplankton image analysis using the ZooScan integrated system. J. Plankton Res. 32, 285–303.

Gove, J. M., McManus, M. A., Neuheimer, A. B., Polovina, J. J., Drazen, J. C., Smith, C. R., Merrified, M. A., Friiedlaner, A. K., Ehses, A. S., Young, A. W., Dillon, A. K., & Williams, G. J. 2016. Near-island biological hotspots in barren ocean basins.Nature communications, 7, 1058.

Grosjean, P., Picheral, M., Warembourg, C., Gorsky, G., 2004. Enumeration, measurement, and identification of net zooplankton samples using the ZOOSCAN digital imaging system. ICES J. Mar. Sci. 61, 518–525.

Guidi, L., Chaffron, S., Bittner, L., Eveillard, D., Larhlimi, A., Roux, S., Darzi, Y., Audic, S., Berline, L., Brum, J.R., Coelho, L.P., Espinoza, J.C.I., Malviya, S., Sunagawa, S., Dimier, C., Kandels-Lewis, S., Picheral, M., Poulain, J., Searson, S., Coordinators, T.O.C., Stemmann, L., Not, F., Hingamp, P., Speich, S., Follows, M., Karp-Boss, L., Boss, E., Ogata, H., Pesant, S., Weissenbach, J., Wincker, P., Acinas, S.G., Bork, P., de Vargas, C., Iudicone, D., Sullivan, M.B., Raes, J., Karsenti, E., Bowler, C., Gorsky, G., 2016. Plankton networks driving carbon export in the oligotrophic ocean. Nature 24 (3), 165–180.

Gusmão, L. M. O., Diaz, X. F. G., de Melo Jr, M., Schwamborn, R., & Neumann-Leitão, S. 2015. Jellyfish diversity and distribution patterns in the tropical S outhwesternAtlantic. Marine Ecology, 36(1), 93-103.

Hirota, Yuichi, & Seizo Hasegawa. 1999. The zooplankton biomass in the Sea of Japan. Fisheries Oceanography 8.4.274-283.

Holthuis, L. B. 1946. The DecapodaMacrura of the Snellius Expedition, 1.The Stenopodidae, Nephropsidae, Scyllaridae and Palinuridae.Temminckia. 7, 1–178.

Koettker, A. G., Freire, A.S. & Sumida, P. Y. G. 2010.Temporal, diel and spatial variability of decapod larvae from St Paul's Rocks, an equatorial oceanic island of Brazil.Journal of the Marine Biological Association of the United Kingdom. 90, 1227-1239.

Krupica, K.L., Sprules, W.G., Herman, A.W., 2012. The utility of body size indices derived from optical plankton counter data for the characterization of marine zooplankton assemblages. Continental Coastal areas Research. 36, 29–40

Kruse, S., Brey, T., Bathmann, U., 2010.Role of midwater chaetognaths in Southern Ocean pelagic energy flow. Mar. Ecol. Prog. Ser. 413, 275–285.

Legendre P, Legendre L (1998) Numerical ecology, 2nd English edn. Elsevier, Amsterdam.

Legendre, P.; Gallagher, E. D. 2001.Ecologically meaningful transformations for ordination of species data.Oecologia. 129, 271-280.

Lira, S. M. D. A., Teixeira, I. D. Á., Lima, C. D. M. D., Santos, G. D. S., Leitão, S. N., &Schwamborn, R. 2014. Spatial and nycthemeral distribution of the zooneuston off Fernando de Noronha, Brazil.Brazilian Journal of Oceanography. 62, 35-45.

Longhurst, A.R., 1991. Role of the marine biosphere in the global carbon cycle.Limnol. Oceano. 36, 1507–1526.

Macedo-Soares, L. C. P.; Freire, A.; Muelbert, J. 2012. Small-scale spatial and temporal variability of larval fish assemblages at an isolated oceanic island.Marine Ecology Progress Series. 444, 207-222.

Marcolin, Cd.R.,Schultes, S., Jackson, G.A., Lopes, R.M., 2013. Plankton and seston size spectra estimated by the LOPC and Zoo Scan in the Abrolhos Bank ecosystem (SE Atlantic). Cont. Coastal areas Res. 70, 74–87.

Matsuno, K.,Yamaguchi, A., Imai, I., 2012. Biomass size spectra of mesozooplankton in the Chukchi Sea during the summers of 1991/1992 and 2007/2008: an analysis using optical plankton counter data. ICES J. Mar. Sci. 69, 1205–1217.

Melo Júnior, M., Marcolin, C. R., Miyashita, L. K.,& Lopes, R. M. 2016. Temporal changes in pelagic copepod assemblages off Ubatuba, Brazil. Marine ecology. 37, 877-890.

Melo, P. A. M. C.; Diaz, X. F. G.; Macedo, S. J.; Neumann-Leitão, S. 2012. Diurnal and spatial variation of the mesozooplankton community in the Saint Peter and Saint Paul Archipelago, Equatorial Atlantic. Mar. Biodiversity Rec. 5, 121-135.

Michaels, A.F., Silver, M.W., 1988. Primary production, sinking fluxes and the microbial food web.Deep-Sea Res. A 35, 473–490.

Moore, S.K., Suthers, I.M. 2006. Evaluation and correction of subresolved particles by the optical plankton counter in three Australian estuaries with pristine to highly modified catchments. Journal of Geophysical Research 111, 1–14.

Neumann-Leitão, S., Gusmão, L. M. O., Silva, T. A. et al. 1999.Mesozooplankton biomass and diversity in coastal and oceanic waters off North-Eastern Brazil.Arch. Fish. Mar. Res., 47, 153–165

Neumann-Leitão, S., Sant'anna, E. M. E., Gusmão, L. M. D. O., Do Nascimento-Vieira, D. A., Paranaguá, M. N., &Schwamborn, R. 2008. Diversity and distribution of the mesozooplankton in the tropical Southwestern Atlantic. Journal of Plankton Research, 30, 795-805.

Newell, G. E. & Newell, R. C. 1963. Marine plankton: a practical guide. London: HutchlsonEducational.

Pinto, N. C. T., Mafalda, P., & Santos, A. T. 1997. Caracterização do Zooplâncton da Reserva Biológica do Atol das Rocas, na Campanha de Março-1991 (Verão). Tropical Oceanography, 25(1).

Platt, T., Denman, K., 1977.Organisation in the pelagic ecosystem.HelgoländerWiss. Meeresunters. 30, 575–581.

Quinones, R.A. 1994. A comment on the use of allometry in the study of pelagic ecosystem processes. Scientia Marina 58, 11–16.

Santana, C. S. D., Schwamborn, R., Neumann-Leitão, S., Montes, M. D. J. F., & Lira, S. M. D. A. (2018). Spatio-temporal variation of planktonic decapods along the leeward coast of the Fernando de Noronha archipelago, Brazil. Brazilian Journal of Oceanography, 66(1), 1-14.

Schukat, Anna; Teuber, Lena; Hagen, Wilhelm; Wasmund, Norbert; Auel, Holger (2013): Respiration rates and abundances of dominant copepods of the northern Benguela Current System. MARUM - Center for Marine Environmental Sciences, University Bremen, PANGAEA, https://doi.org/10.1594/PANGAEA.823322.

Schultes, S., Sourisseau, M., Le Masson, E., Lunven, M., Marie, L.. 2013. Influence of physical forcing on mesozooplankton communities at the Ushant tidal front. J. Mar. Syst. 109, S191–S202.

SCHWAMBORN, R.; BONECKER, A. Seasonal changes in the transport and distribution of meroplankton into a Brazilian estuary with emphasis on the importance of floating mangrove leaves.Brazilian Archives of Biology and Technology, v. 39, p. 451-462, 1996.

SCHWAMBORN, R.; EKAU, W.; SILVA, A.; SILVA, T. A.; SAINT-PAUL, U.The contribution of estuarine decapod larvae to marine zooplankton communities in North-East Brazil.Archive of Fishery and Marine Research, v. 47, n. 2/3, p. 167-182, 1999b.ISSN 0944-1921.

Schwamborn, R. ; Melo Jr, Mauro de ; Leitão, Sigrid Neumann ; Ekau, Werner ; Paranaguá, Maryse Nogueira . Dynamic patterns of transport and migration of zooplankton at catuama inlet (pernambuco, brazil), with emphasis on the decapoda. Investigaciones Marinas (Valparaíso) , v. 36, p. 109-113, 2008.

Schwamborn, R., de Melo Júnior, M., Neumann Leitão, S., Ekau, W.,& Nogueira Paranaguá, M. 2017. Dynamic patterns of zooplankton transport and migration in Catuama Inlet (Pernambuco, Brazil), with emphasis on the decapod crustacean larvae.Submission article platform-Latin American Journal of Aquatic Research, 36(1).

Sheldon, R.W., Prakash, A., Sutcliffe, J., 1972. The size distribution of particles in the ocean. Limnology and Oceanography 17, 327–340.

Shin, Y.-J., Rochet, M.-J., Jennings, S., Field, J.G. &Gislason, H. 2005.Using size-based indicators to evaluate the ecosystem effects of fishing. ICES Journal of Marine Science, 62, 384–396

SnprooN, R. W., Suticliffer Jr, W.H. &Paranjape, M.A. 1977.Structure of pelagic food chain and relationship between plankton and fish production. J. Fish. Res. Board Can. 34:2344-2353

Sprules, W.G., Munawar, M., 1986. Plankton size spectra in relation to ecosystem productivity,productivity, size,size, and perturbation. Can. J. Fish.Aquat. Sci. 43, 1789–1794.

TerBraak, C. J. F.; Smilauer, P. 2002 Canoco reference manual and CanoDraw for Windows user's guide: software for canonical community ordination (version 4.5).

Thompson, G. A.; Dinofrio, E. O.; Alder, V. A. 2013. Structure, abundance and biomass size spectra of copepods and other zooplankton communities in upper waters of the Southwestern Atlantic Ocean during summer. Journal of plankton research. 35, 610-629.

Vandromme, P., Nogueira, E., Huret, M., Lopez-Urrutia, A., Gonzalez, G.G.N., Sourisseau, M., Petitgas, P., 2014.Springtime zooplankton size structure over the continental coastal areas of the Bay of Biscay. Ocean Sci. 10, 821–835.

Vandromme, Pieter, et al. 2012. Assessing biases in computing size spectra of automatically classified zooplankton from imaging systems: A case study with the ZooScan integrated system. Methods in Oceanography.1 , 3-21.

Yamaguchi, A., 2008. Comparison of Mesozooplankton Biomass Down to the Greater Depths (0–3000 m) between 165°E and 165°W in the North Pacific Ocean: The Contribution of Large Copepod Neocalamuscristatus. Nova Science Publishers.

Zhou, M., 2006. What determines the slope of a plankton biomass spectrum? J. Plankton Res. 28, 437–448.

Zhou, M., Huntley, M.E., 1997.Population dynamics theory of plankton based on biomass spectra. Marine Ecology Progress Series 159, 61–73.

Zhou, M., Tande, K.S., Zhu, Y., Basedow, S., 2009. Productivity, trophic levels and size spectra of zooplankton in northern Norwegian coastal areas regions. Deep Sea Research Part II: Topical Studies in Oceanography 56, 1934–1944.

6 BODY SIZE AND STABLE ISOTOPE COMPOSITION OF ZOOPLANKTON IN THE WESTERN TROPICAL ATLANTIC

Manuscrito aceito e publicado no periódico Journal of Marine Systems

DOI: https://doi.org/10.1016/j.jmarsys.2020.103449

Gabriela Guerra Araújo Abrantes de Figueiredo[a], Ralf Schwamborn*[a], Arnaud Bertrand[b,c], Jean-Marie Munaron[d], François Le Loc'h[d]

*Corresponding author: ralf.schwamborn@ufpe.br

[a]Department of Oceanography, Federal University of Pernambuco, Recife, Brazil,[b] Programa de pós-graduação em Ecologia, Universidade Federal Rural de Pernambuco, Recife, Brazil, [c]Institut de Recherche pour le Développement (IRD), MARBEC, Université de Montpellier, CNRS, Ifremer, IRD, Sète, France. [d]Institut de Recherche pour le Développement, Univ Brest, CNRS, IRD, Ifremer, LEMAR, IUEM, F-29280 Plouzané, France

Abstract

Size-based approaches are paramount tools for the study of marine food webs. Here, we investigated the relationship between zooplankton body size, stable isotope composition and trophic level (TL) along a large-scale onshore-offshore gradient in the western tropical Atlantic. Samples were obtained on the Brazilian continental shelf, slope and in oceanic waters (off Fernando de Noronha archipelago and Rocas Atoll) in September and October 2015. Zooplankton was sieved into five size fractions. Zooplankton was dominated by copepods, except for the largest (>2000µm) size fraction, that showed a high biovolume of chaetognaths, decapods, and fish larvae. Maximum zooplankton abundance and biovolume was found at the continental slope. POM showed consistently lower $\delta^{13}C$ than zooplankton, indicating a selective use of ^{13}C-rich primary food sources by zooplankton. Particulate organic matter (POM) was more ^{13}C-enriched in shelf areas (average: -22.8, -23.6 and -24.3‰ at the shelf, slope and oceanic islands, respectively), probably due to the higher abundance of diatoms nearshore. POM had δ^{15}N values between 2.5 and 6.9‰ (average: 4.0, 4.9 and 4.2‰ at the shelf, slope and oceanic islands, respectively). Zooplankton δ^{15}N and TL increased with body size. The δ^{15}N of the 200 – 500 µm size fraction was used as baseline for TL estimation. Oceanic areas (average baseline δ^{15}N = 5.8‰ ± 0.52, n =14) showed a higher baseline δ^{15}N than the shelf (average = 3.9‰ ± 0.69, n = 9) and the slope areas (average = 3.1‰± 0.93, n = 9). In spite of differing baselines, the δ^{15}N data produced a consistent pattern of log-linear increase in TL with increasing size, in all areas. The choice of input trophic enrichment factor (TEF) values only slightly changed the $\log_{10}$ (body size) *vs* TL slopes, but this choice had a considerable effect on the estimates of predator/prey size ratio (PPSR) and predator/prey mass ratio (PPMR). Using a TEF above 2.3 leads to unrealistic PPSR and PPMR estimates. Overall average slope was 0.59 ± 0.08 TL μm^{-1} with TEF = 2.3 and 0.42 ± 0.07 TL μm^{-1} with TEF = 3.2.

Keywords: Plankton; δ^{13}C; δ^{15}N; Size classes; Trophic level; Predator / prey mass ratio

1. Introduction

A large number of factors influence the functioning of pelagic ecosystems, including the spatio-temporal variability of physical and chemical variables, as well as dynamic interactions between species. These processes shape species distribution and trophic structure. Body size, which is easily and quickly determined, is considered one of the most important determinants of ecosystem structure (Jennings et al., 2007; Petchey et al., 2008) since metabolic requirements, food selection, growth and reproductive capacity are related to body size. Size-based analyses are therefore paramount tools for studying marine food webs (Jennings et al., 2001; Bănaru et al., 2014; Hunt et al., 2015; Yang et al., 2016). In pelagic marine food webs, predators are generally larger than their prey (Cohen et al., 1993) and trophic level (TL) is almost exclusively size-based. Thus, pelagic marine ecosystems can be well described by a log-linear size spectrum, where abundance continuously decreases with size, due to the energy loss in trophic transfers (Platt and Denman, 1977; Fry and Quinones, 1994; Jennings et al., 2002; Hunt et al., 2015). This theory was reinforced by Fry and Quinones (1994), who estimated zooplankton TLs with stable carbon and nitrogen isotopes, and determined how TLs changed with body size. Their results supported the arguments that trophic organization and metabolism are important structuring forces. Analyzes of pelagic organisms aggregating them by size, may contribute to the understanding of the functioning of pelagic ecosystems.

Stable isotope analysis (SIA) is widely used to elucidate trophic relationships in marine food webs (Post, 2002; Hunt et al., 2015). Nitrogen and carbon stable isotopes ($\delta^{15}N$ and $\delta^{13}C$) are natural tracers that incorporate information on trophic position and food source (Fry, 2006; Wang et al., 2013). For instance, $\delta^{15}N$ increases with trophic position (Post, 2002), i.e., predators are generally ^{15}N-enriched in relation to their prey (Minagawa and Wada, 1984). Conversely, carbon stable isotopes ($\delta^{13}C$) are incorporated by organisms with less modification between predators and prey (McConnaughey and McRoy, 1979). Since predator $\delta^{13}C$ values do not differ too much from their food sources (Miller et al., 2008), they can be used as tracers of food sources or feeding areas.

Lower trophic levels, such as most plankton organisms, are important for SIA in marine environments, since they are very sensitive to physical processes that result in changes in hydrographic patterns (Bode et al., 2007; Mompéan et al., 2013; Espinasse et al., 2014). Zooplankton plays a key role in pelagic ecosystems by connecting primary producers to higher trophic levels (Saiz et al., 2007; Guidi et al., 2016; Gove et al., 2016). Understanding the structure and function of zooplankton communities is necessary to understand their role in marine ecosystems (Yang et al., 2017). SIA provides a tool to analyze zooplankton food webs and to measure trophic relationships between food web components (Yang et al., 2016). Combined with size-based approaches, SIA can provide comprehensive understanding of zooplankton food webs (Jennings et al., 2002; Bănaru et al., 2014; Espinasse et al., 2014; Yang et al., 2016).

The western tropical Atlantic off northeastern Brazil is mostly dominated by the warm oligotrophic waters that are derived from the south equatorial current (SEC). This region comprehends the extension from the shelf, slope and slope, seamounts and oceanic islands, all with low levels of nutrient supply and productivity and high zooplankton diversity (Boltovskoy et al., 1999). Numerous studies have investigated zooplankton communities in this region, most of which focusing on community structure, abundance diversity (e.g., Neumann-Leitão et al., 1999; Diaz et al., 2009; Brandão et al., 2013; Lira et al., 2014; Santana et al., 2018), and size spectra (Marcolin et al., 2013). In this region, the stable isotope composition ($\delta^{13}C$ and $\delta^{15}N$) of zooplankton and particulate organic matter (POM) has been investigated in mangrove estuaries, on the shelf and at the adjacent slope, revealing that any measurable estuarine influence was limited to the line of intertidal coastal reefs, approximately 10 km from the coast (Schwamborn et al., 1999, 2002).

In this study, we investigate the relationship between body size and stable isotope composition of zooplankton communities in the western tropical Atlantic, to understand the relationship between trophic levels and body size, and to test the hypothesis that there are differences in zooplankton trophic structure among different environments along a large-scale onshore-offshore gradient.

2. Methodology

2.1 Sampling strategy

Zooplankton and particulate organic matter (POM) were sampled on the continental shelf, at the slope, and in oceanic waters off northeastern Brazil (Figure 1). Two oceanic island systems were studied: Fernando de Noronha archipelago (FN) and Rocas Atoll (RA, Figure 1). Samples were collected between September 29 and October 21, 2015, during the Acoustic along the Brazilian coast cruise (ABRACOS, Bertrand, 2015) conducted on board R/V ANTEA.

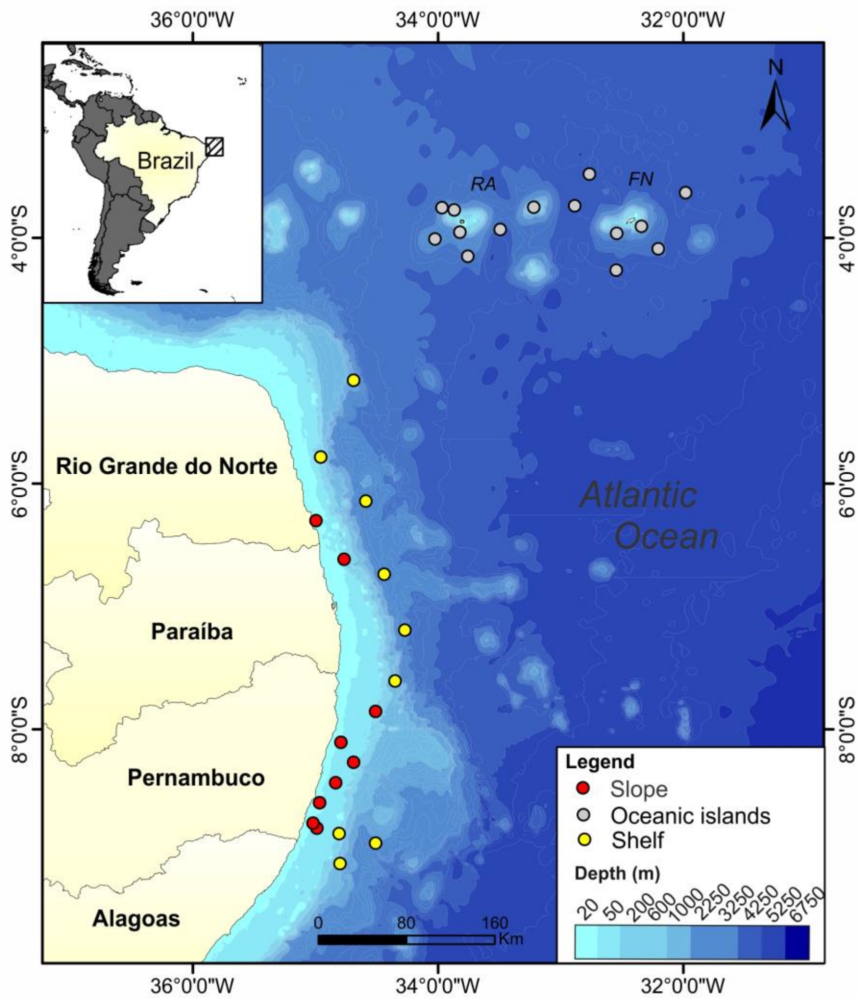


Figure 1.Sampling stations in the tropical Atlantic off northeastern Brazil, in September and October 2015.Color codes indicate sampling stations on the continental shelf, at the slope, and off two oceanic islands (FN: Fernando de Noronha Archipelago and RA: Rocas Atoll).

At each station, vertical profiles of conductivity, temperature and chlorophyll a fluorescence were acquired using a Seabird SBE911+ CTD probe. Zooplankton sampling was conducted by towing a regular bongo frame with four nets fitted with mesh sizes of 64 µm (30 cm mouth opening diameter), 120 µm (30 cm diam.), 300 µm (60 cm diam.) and 500 µm (60 cm diam.). At each station, two oblique hauls were conducted between 200 meters and the surface or between 10 meters from the bottom to the surface at locations with less than 200 m of bottom depth. A total of 14 and 18 samples were collected during day night, respectively.

A Hydro-Bios flowmeters were fixed inside the net opening of each net to estimate filtered volume. Seawater samples for particulate organic matter (POM) were collected at the surface (3 m) and at the depth of maximum fluorescence using a CTD/rosette equipped with Niskin bottles. A total of 8 liters of water were filtered on a 47 mm diameter Whatman GF/F filter. In the laboratory, all filter samples were dried at 40ºC during 36h.

2.2 *Size spectra*

Oblique bongo haul samples, taken simultaneously with 120 µm, 300 µm and 500 µm meshes, were used to estimate zooplankton size spectra. They were preserved in 4% formaldehyde buffered with sodium tetraborate (0.5 g.l^{-1}, Newell and Newell, 1963). These formaldehyde-preserved samples were used for the size spectrum analysis under a stereo microscope (120 µm) and in the ZooScan system (300 µm, 500 µm). For stereo microscope analyses (Zeiss Stemi 2000 – C), the samples were split in 1/2 to 1/256 to obtain at least 300 organisms per sample. The lengths and widths of 30 specimens for each taxonomic group were measured. If there were more than 30 individuals for each taxonomic group, they were counted for abundance analyses.

For ZooScan analyses, each zooplankton sample was separated into two fractions with a 1000 µm mesh (Gorsky et al., 2010). Each size fraction was split by a Motoda splitter into 1/2 to 1/64 subsamples to obtain up to 2,000 objects in each scan. Large, rare organisms (> 1000 µm size fraction) were scanned from 1/2 to 1/8 subsamples. For the more plentiful size fraction of small-sized organisms (< 1000 µm) a smaller subsample (1/4 to 1/64) was scanned. Subsamples were digitalized by the ZooScan system and processed with the ZooProcess software, which isolates each object into one vignette and generates a range of quantitative descriptors (size, grey level distribution and shape parameters) for each vignette. A semi-automatic approach was used to classify the vignettes into pre-established taxonomic groups, using the Plankton Identifier software (Gorsky et al., 2010). After classification, all results were manually validated to correct any misclassifications.

Equivalent spherical diameter (ESD), abundance and biovolume were calculated for each organism. Zooplankton biovolume was estimated as the ellipsoidal volume:

$$\text{Biovolume} = \frac{4\pi}{3}\left(\frac{major\ axis}{2}\right)\left(\frac{minor\ axis}{2}\right)^2$$

where the major and minor axis of each zooplankton organism were measured by the ZooScan or under the stereo microscope. Zooplankton abundance and biovolume were classified into discrete size classes, based on their equivalent spherical diameter (ESD, calculated from the 2D area). Five ESD size classes (0-IV) were defined (0 < 200 µm; I 200 – 500 µm; II 500 – 1000 µm; III 1000 – 2000 µm and IV >2000 µm).

2.3 Stable isotopes

Stable isotope analyses were conducted on particulate organic matter (POM) and on size-fractioned zooplankton samples that were obtained with a bongo net (additional subsurface hauls with 64 µm, 120 µm, 300 µm and 500 µm mesh). For each haul, all samples were pooled and sieved into five size fractions, using a multi-mesh array (0 < 200 µm; I: 200 µm – 500 µm; II: 500 µm – 1000 µm; III: 1000 µm – 2000 µm and IV > 2000 µm). Each size fraction sample was packed into previously calcined aluminum envelopes, and kept frozen at -20°C.

In the laboratory, zooplankton samples were stored in Eppendorf micro tubes, and freeze dried during at least 24 hours. Once dried, each sample was homogenized to obtain a fine powder and weighed. In order to obtain unbiased values of $\delta^{13}C$, part of the samples was separated to remove the carbonates ($CaCO_3$). These samples were acidified according to Fry (1988) by adding approximately 2 ml of 0.5 $mol.l^{-1}$ hydrochloric acid (HCl). After this procedure, samples were re-dried at 60°C for 24 hours and homogenized. Water samples collected at subsurface (~3m) and at the depth of the chlorophyll a fluorescence maximum (Fmax) were used to obtain POM samples by using pre-combusted GFF filters. POM samples were acidified for extracting the carbonates. For this, the filters were exposed to hydrochloric acid (HCl) vapor. After 4 hours, the filters were left in an aluminum covered box and dried at 40ºC during 36h.

Samples were analyzed using an elemental analyzer (Thermo Scientific Flash EA 2000) coupled to an Isotope Ratio Mass Spectrometer (Delta V+ mass) at the Pôle de Spectrométrie Océan (Plouzané, France). Results were expressed in standard δ notation based on international standards (Vienna Pee Dee Belemnite for $\delta^{13}C$ and N_2 in air for $\delta^{15}N$) following the equation: $\delta X = [(R_{sample}/R_{standard}) - 1] \times 10^3$ (in ‰), where R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$. The standard values were reproduced into a confidence limit: IAEA-600 (certified values: −27.77 ± 0.04‰ for $\delta^{13}C$ and 1.00 ± 0.20‰ for $\delta^{15}N$; measured value: −27.79 ± 0.10‰ for $\delta^{13}C$ and 1.09 ± 0.06‰ for $\delta^{15}N$), IAEACH-6 (certified values: −10.45 ± 0.08‰ for $\delta^{13}C$; measured value: −10.43 ± 0.08‰ for $\delta^{13}C$), IAEA-N-1 (certified values: 0.4 ± 0.2‰ for $\delta^{15}N$; measured value: 0.45 ± 0.10‰ for $\delta^{15}N$) and IAEA-N-2 (certified values: 20.3 ± 0.2‰ for $\delta^{15}N$;

measured value: 20.24 ± 0.12‰ for $\delta^{15}N$). One sample of a home standard (Thermo acetanilide) was analyzed for experimental precision, after every six samples.

2.4 Trophic levels

Trophic level (TL) was calculated based on $\delta^{15}N$ (Vander Zanden and Fetzer, 2007):

$$TL = \frac{(\delta_{15}Nconsumer\ -\ \delta_{15}Nbaseline)}{TEF} + \lambda$$

where TEF is the trophic enrichment factor and λ is the trophic level of the baseline. Since isotopic values of phytoplankton (TL1) are based on POM, which may be influenced by the co-occurrence of detritus (Montoya et al., 2002) and microzooplankton in the water column (Post, 2002; Hunt et al., 2015; Yang et al., 2017), primary consumers were used to estimate the trophic level, once the they are less influenced by small-scale spatial and temporal variation (Hunt et. al. 2015). Small-sized zooplankton is classically used as a baseline (TL 2; e.g., Fry and Quinones, 1994; Kline and Pauly 1998, Montoya et al., 2002; Hauss et al., 2013, Hunt el al., 2015). In this study, we assume the size-class I (200 – 500 µm), to be closest to the primary consumer with TL 2. A TEF value of 3.2‰ per TL was applied to estimate relative TLs for each zooplankton size class and sampling area (Post, 2002; Ménard et al., 2014). For comparison, TLs were also estimated using a TEF of 2.3‰ per TL, as given by Schwamborn and Giarrizzo (2015).

Differences in trophic level, stable isotopes composition, abundance and biovolume of zooplankton between areas (shelf, slope and oceanic islands) and between size classes were tested by non-parametric Kruskal-Wallis ANOVA ($p_{crit} = 0.05$), since these data displayed non-normality and heteroscedasticity. Post-hoc comparisons between pairs of samples were conducted with Dunn's test ($p_{crit} = 0.05$) (Zar, 1996).

Ordinary least squares linear regression was used to investigate the linear relationship between $\log_{10}$-transformed average body size (ESD, µm) and trophic level (TL, estimated with TEF = 3.2 and 2.3). Body size (ESD) was log10-transformed to obtain linear relationships for analysis and to improve homoscedasticity. The slope of this linear regression model was used to estimate the average predator/ prey size ratio (PPSR) and predator/ prey mass ratio (PPMR), using the following equations: $\mathrm{PPSR} = 10^{(1/\mathrm{slope})}$, if $\log_{10}$ is being used in the linear model (Hunt et al., 2015), and $\mathrm{PPMR} = \mathrm{PPSR}^3$, assuming isometry and size-invariant density (Lins et al., 2019). PPSR and PPMR estimates obtained with TEF = 3.2 and 2.3 were then compared to previously published estimates. All data are available at: https://figshare.com/articles/dataset/Body_Size_Stable_Isotope_Figueiredo_et_al_Metadata_csv/12620807.

3. Results

3.1 Hydrography

Sea surface temperature was nearly homogeneous (median: 26.6°C) over the whole study area. Surface salinity ranged from 36.1 to 36.6, with higher values along the continental slope. The thermocline ranged between ~80 and ~180 m in the slope area and ~90 and ~130 m around oceanic islands (Assunção et al., in press). The chlorophyll *a* fluorescence maximum was generally located at the upper limit of the thermocline.

3.2 Zooplankton abundance and biovolume size structure composition

A total of 15 taxonomic categories were identified: jellyfish, polychaetes, bivalves, gastropods, copepods, nauplii, euphausiids, mysids, decapods, salps, chaetognaths, appendicularians, fish eggs, fish larvae and "other zooplankton" (composed by organisms with less than 3% abundance).

No significant differences were detected between zooplankton abundance, biovolume, and stable isotope composition at both oceanic island areas, Fernando de Noronha and Rocas Atoll (K-W-ANOVA, $p > 0.05$). Therefore, data from these two areas were pooled together as “oceanic islands” for subsequent analyses. Samples obtained from the shelf and from the slope were analyzed separately, since they were different regarding several parameters, especially stable isotope composition (Fig. 5).

Abundance and biovolume differed significantly between areas (K-W ANOVA, $p < 0.05$; Table 1). Samples taken off oceanic islands had significantly lower abundances (mean: 6.0 ind.m^{-3} ± 3.1; Table 2) than those obtained from the shelf and from the slope (means: 10.3 ind.m^{-3} ± 6.5 and 14.1 ind.m^{-3} ± 16.8, respectively). The slope presented significantly higher biovolume (mean: 11.0 ± 15.4 mm^{3}.m^{-3}) than oceanic islands (mean 3.3 ± 1.5 mm^{3}.m^{-3}) and the shelf (mean: 3.7 ± 3.3 mm^{3}.m^{-3}, Figure 2).

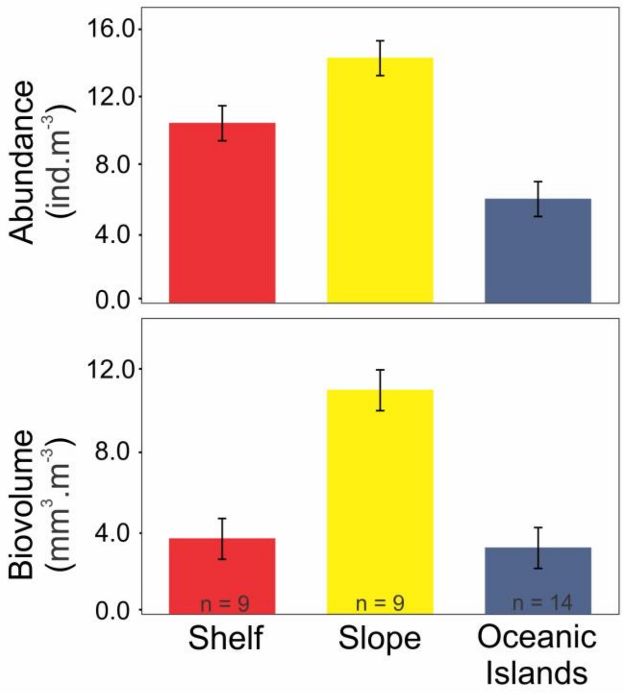


Figure 2. Mean (± standard deviations) zooplankton abundance and biovolume between continental shelf, slope and oceanic islands in the tropical Atlantic off northeastern Brazil. All values shown represent the sum of all size classes

Response variable	Factor	*P*	*Post hoc*
δ^{13}C Zooplankton	Area	< 0.001	OI > S > SB
	Size class	n.s.	n.s
δ^{15}N Zooplankton	Area	< 0.001	OI > S = SB
	Size class	< 0.001	I > 0 = III = IV; I > IV
δ^{13}C POM	Area	< 0.001	S > SB > OI
δ^{15}N POM	Area	n.s.	n.s
Abundance	Area	< 0.01	SB = S > OI
Biovolume	Area	< 0.05	S = SB; S = OI; SB > OI

Table 1. Results of Kruskal-Wallis ANOVA (p-values) and Dunn's post-hoc test on Particulate Organic Matter (POM), zooplankton δ^{13}C, δ^{15}N, abundance and biovolume according to local (S: Shelf; SB: Slope and OI: Oceanic Islands) and size classes (0: < 200 µm; I: 200 – 500 µm; II: 500 – 1000 µm; III: 1000 – 2000 µm, IV > 2000 µm). n.s: not significant (i.e., $p > 0.05$).

Zooplankton composition varied considerably among size classes (Figure 3). Copepoda was the most abundant group for the three size fractions ranging between 200 µm and 2000 µm for all environments, and presented the largest contribution to biovolume. The taxonomic composition for the > 2000 µm class showed a higher contribution of larger zooplankton organisms, such as Chaetognatha, Decapoda, and fish larvae, especially off oceanic islands (Figure 3).

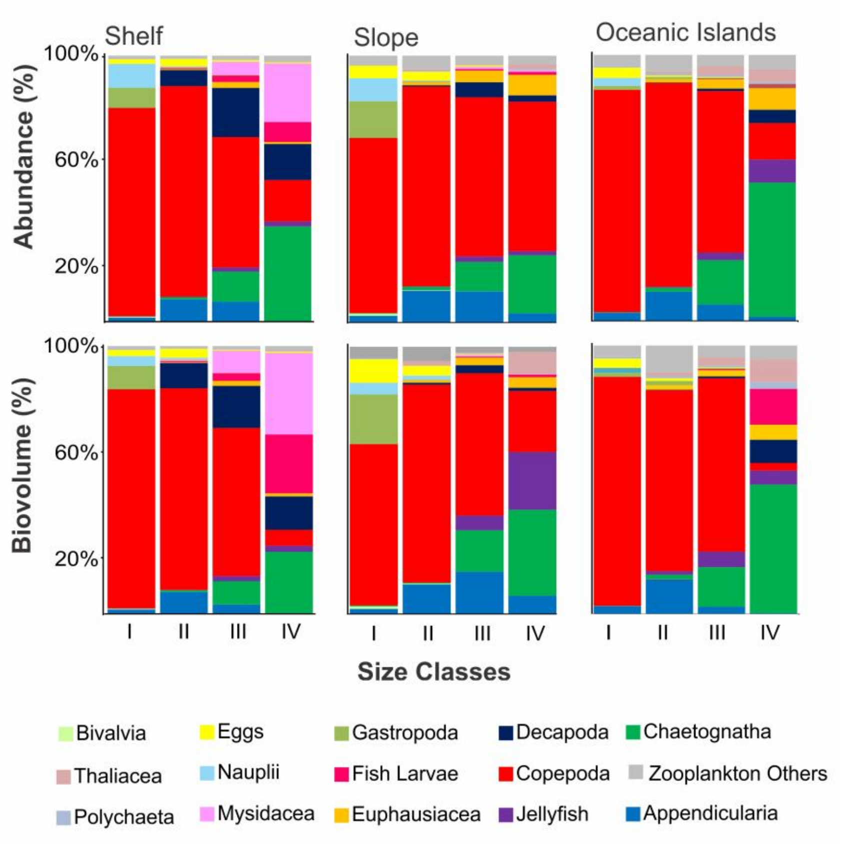


Figure 3.Relative abundance and biovolume of zooplankton classified within four size classes (0-IV). I: 200 – 500 µm; II: 500 – 1000 µm; III: 1000 – 2000 µm and IV: > 2000 µm. Samples were collected on the continental shelf, at the slope and off oceanic islands in the tropical Atlantic off northeastern Brazil.

3.3 Stable isotope composition of zooplankton and POM

Spatial patterns of stable isotope composition differed between POM and zooplankton. POM displayed consistently lower $\delta^{13}C$ than zooplankton (Figure 4). Also, $\delta^{13}C$ of POM showed a decreasing trend from the shelf towards offshore areas. $\delta^{13}C$ of POM differed significantly between areas (Figure 5, Table 1, K-W ANOVA, $p < 0.001$), with higher $\delta^{13}C$ values in shelf areas, followed by the slope and oceanic islands (Figure 5). Conversely, zooplankton displayed an opposite pattern, with increasing values towards offshore areas (Figure 5, Table 2). $\delta^{15}N$ and $\delta^{13}C$ values of all zooplankton size classes differed significantly between areas (Table 1, K-W ANOVA, $p < 0.05$), with higher values off oceanic islands (Figure 5; Table SM 1) varying from ~22 to ~19‰ for $\delta^{13}C$ and from ~5 to ~9‰ for $\delta^{15}N$.

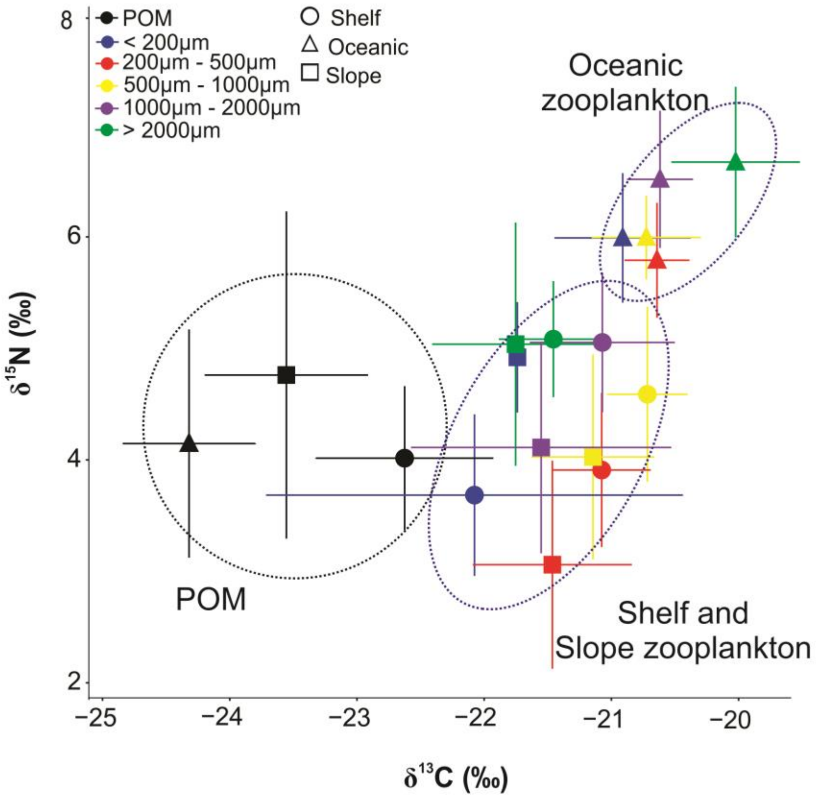


Figure 4. Mean δ^{13}C and δ^{15}N (± standard deviation) of particulate organic matter (POM) and size-fractionated zooplankton sampled on the continental shelf, at the slope and off oceanic islands in the tropical Atlantic off northeastern Brazil.

Response variable	*P*-value	*Post hoc*
	Shelf	
δ^{13}C	<0.01	II ≠ IV; II ≠ 0
δ^{15}N	<0.01	I ≠ III = IV
	Slope	
δ^{13}C	>0.05	n.s
δ^{15}N	<0.001	I ≠ 0; IV = II = III> I
	Oceanic islands	
δ^{13}C	<0.001	IV > 0 = I = II = III
δ^{15}N	>0.05	n.s

Table 2. Results of Kruskal -Wallis ANOVA and Dunns's post-hoc test with zooplankton $\delta^{13}C$ and $\delta^{15}N$, classified into five size classes (0, < 200 µm; I: 200 – 500 µm; II: 500 – 1000 µm; III: 1000 – 2000 µm; IV > 2000 µm) for each area: Continental Shelf, Slope and Oceanic islands

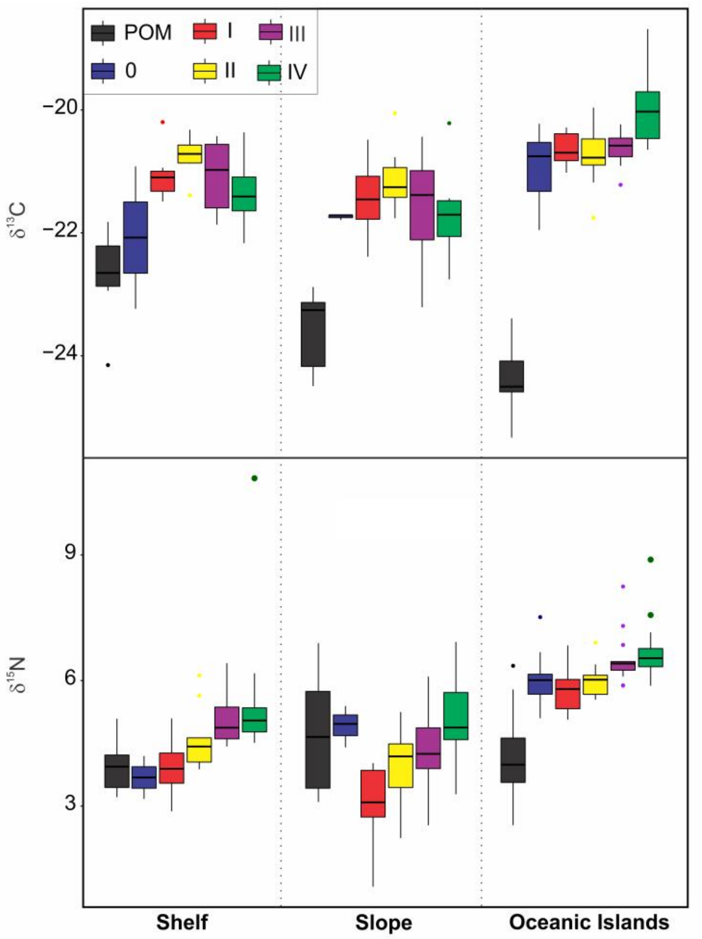


Figure 5: $\delta^{13}C$ and $\delta^{15}N$ (in ‰) of particulate organic matter (POM) and zooplankton size fractions (0, < 200 µm; I: 200 – 500 µm; II: 500 – 1000 µm; III: 1000 – 2000 µm; IV > 2000 µm) on the shelf, at the slope and off oceanic islands in the western tropical Atlantic

POM had $\delta^{15}N$ values between 2.54 and 6.89‰ (mean at oceanic islands: 4.15‰, st. dev.: 1.2‰, mean at the shelf: 4.00‰, st. dev.: 0.59‰, mean at the slope: 4.86‰, st. dev.: 1.24‰). Within the meso- and macrozooplankton, $\delta^{15}N$ generally increased with size, from the size fraction < 200 to the size fraction > 2000 µm (Figure 4). At the shelf, small-sized mesozooplankton (size fraction 200 – 500 µm) presented significantly more depleted values than the largest size (Table 2, 1000 – > 2000 µm, $p < 0.05$, K-W ANOVA). At the slope, the 200 – 500 µm size fraction showed significantly lower $\delta^{15}N$ values than the largest (> 2000µm) size fraction (Table 2, $p < 0.05$, K-W ANOVA).

3.4 Trophic levels

To estimate trophic levels (TL), according to other studies (e.g., Fry and Quinones, 1994; Kline and Pauly, 1998, Montoya et al., 2002; Hauss et al., 2013, Hunt el al., 2015) we used the mean $\delta^{15}N$ of the zooplankton sampled in the 200 – 500 µm size class, from each region, as a baseline (TL = 2), since this size fraction was consistently dominated by copepods, and the fact that this size class had the lowest $\delta^{15}N$ values. Oceanic areas (average baseline $\delta^{15}N$ = 5.8‰) had a higher baseline $\delta^{15}N$ than the shelf (average = 3.9‰) and the slope (average = 3.1‰). In spite of differing baselines, the $\delta^{15}N$ data produced a very consistent pattern of increase in trophic level with increasing size, in all regions (Figure 6). Assuming TEF = 3.2‰ TL^{-1}, the mean trophic level of the zooplankton was very similar with TL = 2.2, 2.3 and 2.1 for shelf, slope and oceanic islands, respectively. For TEF = 2.3‰ TL^{-1}, the mean were TL = 2.3, 2.5 and 2.2, in these sampling areas, respectively.

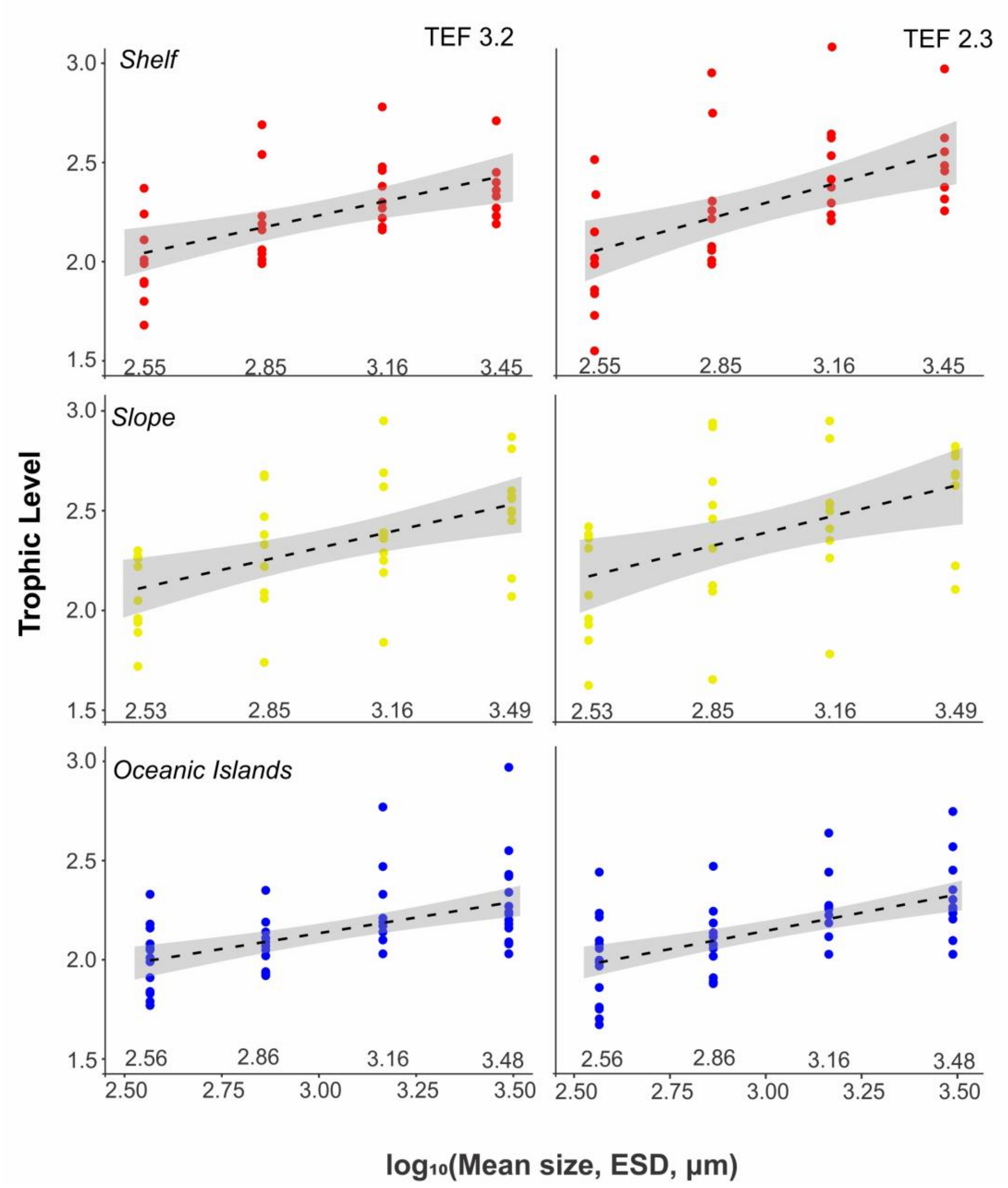


Figure 6: Trophic level (TL) and $\log_{10}$ (mean ESD size, μm) for each zooplankton size class in the western tropical Atlantic. TL was calculated from $\delta^{15}N$, assuming a trophic enrichment factor of 3.2 and 2.3‰ TL^{-1}. Grey area: 95% confidence envelope for the linear regression slope.

Linear regression analysis revealed a log-linear relationship between $\log_{10}$ (body size and TL (Figure 6). Linear models were always highly significant ($p < 0.001$), for shelf, slope and oceanic islands areas. Slopes of the log (body size) *vs* TL relationships (Table 3) were not significantly different among areas (ANCOVA, $p = 0.07$). Overall average slope was 0.59 ± 0.08 TL μm^{-1} with TEF = 2.3 and 0.42 ± 0.59 TL $\mu m^{-1}$with TEF = 3.2.

	Slope (TL $\log_{10}(\mu m)^{-1}$)	
	TEF 2.3	TEF 3.2
Shelf	0.58 ± 0.14	0.42 ± 0.10
Slope	0.85± 0.18	0.61 ± 0.12
Oceanic Islands	0.44± 0.08	0.31 ±0.06
All	0.59 ± 0.08	0.42 ±0.59

Table 3. Slope values of trophic level (TL) vs body size (ESD, µm), testing two different trophic enrichment factors (TEF = 3.2 and 2.3), for each area (± standard errors).

The choice of input TEF values only slightly changed the $\log_{10}$ (body size) *vs* TL slopes, but this choice had a considerable effect on the estimates of predator/prey size ratio (PPSR) and predator/prey mass ratio (PPMR). For example, the estimate of PPMR at Oceanic Islands was 470 times lower when using TEF = 2.3 than when using TEF = 3.2. For TEF = 2.3, PPSR was 49, and PPMR was 121,547. For TEF = 3.2, these estimated were much higher, especially for PPMR. With TEF = 3.2, PPSR was 240, and an extremely high PPMR estimate of 13,894,955.

4. Discussion

The present study revealed important variations in stable isotope ratios of zooplankton in the western tropical Atlantic that were conspicuously and significantly related to body size and geographical areas. Size-structured stable isotope analyses proved to be a useful approach to describe the structure and functioning of the systems (Fry and Quiñones, 1994; Montoya et al., 2002; Lee et al., 2013; Hunt et al., 2015). It is the first study analyzing size classes and stable isotope composition of a zooplankton community carried out in tropical shelf, slope and oceanic waters, providing several important new insights into these pelagic ecosystems.

Also, our study showed that TEF choice has a profound effect on the resulting prey-predator mass and size ratios. Lower TEF values than those widely used, clearly lead to more realistic results for this zooplankton community.

4.1 Variation of POM and zooplankton stable isotope composition

In the present study, zooplankton presented higher δ^{13}C and δ^{15}N values off oceanic islands than in shelf and slope areas. Conversely, δ^{13}C POM showed a clear coastal-offshore gradient, with ^{13}C-enriched values at shelf areas, followed by slope and oceanic islands. Stable isotope composition of primary producers typically varies with spatio-temporal and physical features as a result of differences in biogeochemical processes that occur in each environment (Graham et al., 2010). Thus, δ^{13}C values of POM followed an expected pattern, being more ^{13}C-enriched in diatom-rich shelf environments than offshore, as observed in previous studies in the study area (Schwamborn et al., 1997; Schwamborn et al., 1999) and elsewhere (Fry and Wainright, 1991).

An unexpected result was observed in relation to zooplankton δ^{13}C values, which were conspicuously and significantly different from simultaneously obtained POM δ^{13}C values. This discrepancy between POM and zooplankton carbon isotope composition could be explained by two different phenomena. First, vertically migrating zooplankton may be feeding at depths that are not represented by the sampling of POM. Second, zooplankton generally display feeding selectivity (Sailley et al., 2015; Benedetti et al., 2016), which makes their isotope composition difficult to compare directly with POM values. POM encompasses a highly variable mixture of a diversity of living organisms and non-living particles, among which only few may be selectively ingested by zooplankton (Lee et al., 2004). Our results indicate a selective use of δ^{13}C-rich food sources (e.g., diatoms) by zooplankton.

4.2 Spatial patterns of zooplankton abundance, biovolume, composition, size and stable isotope ratios

We observed higher zooplankton abundance and biovolume over the slope than the shelf and in offshore areas (Figure 2). These results contradict the typical coastal-oceanic gradient, previously found in the study area (Bueno et al., 2017; Campelo et al., 2018; Santana et al., 2018) and elsewhere (Dai et al., 2016; Giering et al., 2018). Indeed it is typically assumed that zooplankton abundance follows a continuous gradient with higher abundance nearshore (Neumann-Leitão et al., 2008; Marcolin et al., 2013; Leitão et al., 2019). This common pattern was mostly attributed to continental runoff, specifically the input of nutrients and organisms from large estuaries, and resuspension from shelf sediments (Schwamborn et al., 1999). Nutrient inputs boost the primary production and may consequently generate a coastal-ocean gradient of zooplankton density with higher abundance of organisms in coastal environments than oligotrophic oceanic waters. The lower biomass values observed at the shelf than at the slope may occur because of a series of factors. First, during the sampling period (September to October), there was a low continental influence (low river runoff during the dry season), low wind intensities (little resuspension from shelf sediments). Also, sampling was conducted off the main reproductive season for most coastal invertebrates (low larval inputs from coastal ecosystems), which is generally from January to March, in the study area. In addition, physical processes like eddies may allow a higher retention of plankton at the continental slope, leading to higher zooplankton biomass and densities (Franco et al., 2006; Katsuragawa et al., 2014). Our stations with highest abundance were located in a region close to continental slope, with mixed layer depth and upper thermocline shallower than expected for the season (Assunção et al., 2020). This leads to a shallowing of the nutricline and likely an increase in primary productivity sustaining the higher density of zooplankton.

In this oligotrophic ecosystem we demonstrated the existence of zooplankton accumulation at the continental slope. The observed pattern also agrees with the finding that any direct estuarine influence in the study area is generally limited to approximately 10 km from the coast (Schwamborn et al., 1999, 2002). The shelf break is known to play an important role in transporting and retaining zooplankton (Genin, 2004; Zhu et al., 2009). Indeed, interactions between topography and currents aggregate zooplankton seaward of the shelf-break zone (e.g. Genin, 2004; Cotté and Simard, 2005; Swartzman et al., 2005). Also, the whole slope area, up to several km off the shelf break, is characterized by strong turbulence and current shear between the base of the mixed layer and the upper thermocline that can transport nutrients from deep water masses upwards into the euphotic layer. This shear and turbulence is caused by the strong North Brazil Undercurrent (NBUC) that flows northwards along the shelf break (Stramma et al., 1995; Schott, et al., 2005). Furthermore, significantly higher abundance and biovolume at the slope, as observed in this study, may be due to small-scale mechanisms that were hitherto ignored, e.g., upwelling at submarine canyons (Kämpf, 2007; Howattand and Allen, 2013), and zooplankton accumulations at fronts and eddies (Schwamborn et al., 2001; Maps et al., 2015).

Zooplankton composition differed drastically between size-classes. Early life stages, such as invertebrate (probably mostly copepod) eggs, copepod nauplii, and gastropods dominated the smallest size class (< 200 µm), as found in many other regions, such as in the Mediterranean Sea (Bănaru et al., 2014). Similarly, in coastal areas of the Brazilian Northeast, Neumann Leitão et al. (2019) observed that nauplii and veliger larvae were the most frequent taxonomic groups in the microzooplankton (64 – 120 µm mesh net samples). Mesh size effects have already been documented in numerous zooplankton community studies (Tseng et al., 2011; Tosetto et al., 2019), which demonstrate that mesh size drastically affects the representation of the abundance, composition, and diversity of zooplankton communities.

Zooplankton composition in the size fraction from 500 to 2000 µm is generally dominated by copepods (Mauchline, 1998), as observed by Neumann–Leitão et al. (2019) and Campelo et al. (2018) in coastal and oceanic waters of the western tropical Atlantic as well as in numerous other regions, such as in the south Atlantic (Boltovskoy, 1999), the Mediterranean (Bănaru et al., 2014; Espinasse et al., 2014), the subtropical north Pacific (Dai et al., 2016), the western tropical north Pacific (Yang et al., 2016) and the eastern Atlantic (Marcolin et al., 2013).

Interestingly, in most cases, $\delta^{13}C$ values did not vary significantly with size, indicating that, in contrast to other studies (e.g., Schwamborn and Giarrizzo, 2015), the primary carbon sources of zooplankton in these size classes were similar, and carbon isotopic fractionation was negligible.

Although most zooplankton size fractions were dominated by copepods, the largest size fraction (> 2000 µm) showed the greatest richness in taxonomic groups, with many large-sized organisms such as fish larvae, euphausiids, mysids and many gelatinous organisms, such as salps and chaetognaths. The higher abundance and biovolume of large-sized predators (e.g., fish larvae and chaetognaths) in the largest size class explains well why $\delta^{15}N$ and TL increased with size, showing a good consistency within and between our data sets

Taxonomic compositions of both data sets (measured size classes and taxonomy *vs* sieving and isotope analysis) were most likely very similar, since they were obtained concomitantly at each station. Also, the measured size has an obvious relation to the retention in sieves. Furthermore, the observed distributions of taxonomic groups within size groups were as expected (e.g., copepods being dominant in the smaller size fractions). In addition, with the approach we used, the taxonomic composition does not need to be absolutely identical in both datasets (i.e., only the size distribution has to be similar). Taxonomic information is presented here for illustration and to aid in interpreting the stable isotope results. Most importantly, the increase in $\delta^{15}N$ with size in this study was expected, since it agrees well with previous studies on zooplankton food webs in the southwestern subtropical Pacific (Hunt et al., 2015) and in the western tropical north Pacific (Yang et al., 2016).

4.3 Body size as determinant of trophic level

In previous trophic ecology studies, the size classes chosen to determine the baseline differed widely between authors, e.g.: 125 – 250 µm (Fry and Quinones, 1994), 200 – 500 µm (Hauss et al., 2013) or 250 – 500 µm (Montoya et al., 2002). Assuming a size-based food web structure, in our study, we choose the 200 – 500 µm size fraction, once this size class was composed mainly by copepods, assumed to be mostly filter feeders and presented the smallest $\delta^{15}N$ values. Thus, their isotopic composition should be close to primary consumers (TL2). In addition, copepods have better integrative properties than POM, since their turnover rate is much lower than most POM.

A positive relationship between $\delta^{15}N$ and size class within the zooplankton community was also observed in the Mediterranean Sea by Koppelman et al (2009) and Bănaru et al. (2014), except for the largest size class (> 2000 µm), which had lower $\delta^{15}N$ values, probably due to the contribution of low-TL salps, in contrast to the dominance of high-TL chaetognaths in the present study. Their $\delta^{15}N$ data for size-fractioned zooplankton were generally very similar to the present study except for the largest zooplankton size class. A series of factors affect the trophic position and size of plankton. For example, variations in nutrient inputs regulate the size of primary producers (Kiørboe, 2008), thus strongly impacting species composition and size structure of herbivorous zooplankton and pelagic food webs.

4.4 TEF choice and predator – prey size ratios

The TEF is known to differ widely between groups of organisms (McCutchan et al., 2003; Vanderklift and Ponsard, 2003). Schwamborn and Giarrizzo (2015) found a lower ecosystem-wide TEF value and much lower TEFs for higher TLs, which may support criticism of the use of fixed fractionation factors. Here, we compared results for a TEF of 3.2 (Post, 2002; Ménard et al., 2014) and 2.3 (Schwamborn and Giarrizzo, 2015). A lower TEF in ecosystem-based studies, such as in Schwamborn and Giarrizzo (2015), than in laboratory feeding studies (Post, 2002), is to be expected since growing and migrating animals in real ecosystems will be constantly shifting their diets and TLs. Thus, most organisms in natural ecosystems will not attain full equilibrium with their current food source. In most laboratory feeding experiments, only the final TEF (difference in isotope composition between diet and consumer), under perfect equilibrium, is reported. TEFs that occur in natural ecosystems will not to represent this kind of situation. Thus, lower, ecosystem-based TEF values (e.g., 2.3‰ TL^{-1}) may be more realistic for the use in zooplankton food web analyses (Schwamborn and Giarrizzo, 2015) than laboratory-derived TEF estimates. Our study showed that TEF choice has a huge influence on PPMR and that the use of TEF above 3 will lead to a gross overestimation of PPMR and subsequently underestimation of ecosystem trophic efficiency (TE). Hunt et al. (2015) obtained similar results for the meso-, macrozooplankton and micronekton communities in the subtropical Pacific. They also concluded that a TEF of 3.4‰ TL^{-1}, that they used, likely overestimated PPMR and underestimated TE.

4.5 PPMR as a key parameter for food webs and size spectra analyses

Our PPMR calculations assume isometry (i.e., size-invariant shape) and size-invariant density, which are hardly fulfilled in nature. In that sense, Lins et al. (2019) showed that on average, density is not significantly different from 1 in tropical zooplankton samples, and that these relationships do not change with biomass. We are therefore confident that our basic assumptions are sufficiently well fulfilled for an assessment of PPMR. However we acknowledge that the investigation of these important aspects deserves further efforts.

The large review by Hansen et al. (1994) reported typical PPSR values of 18 to 50 for mesozooplankton. In our study, extremely high PPSR and PPMR estimates obtained with TEF = 3.2 (Table 4), may be considered unrealistic, since they were much higher than previously published estimates (except for the slope area, where the lowest PPSR was observed). Conversely, the application of TEF = 2.3 produced realistic estimates for shelf and slope data, and for the overall mean. The zooplankton communities around oceanic islands had very high PPSR, being above the Hansen et al. (1994) range, with both TEF values (TEF = 2.3 and 3.2). This high PPSR is consistent with our observation of very abundant large organisms, such as fish larvae and gelatinous predators, in the waters around oceanic islands.

When using TEF = 3.2, we would obtain an overall mean PPSR value of 240, which is far above any known estimates for mesozooplankton. Yet, when using TEF = 2.3, our study indicates an overall mean PPSR value of 49, which is within the PPSR range given by Hansen et al. (1994). Similarly to the study of Hansen et al. (1994), we also used ESD to obtain PPSR estimates, so that both PPSR assessments seem well comparable, thus further strengthening the point for ESD as a standard measure of size in plankton research.

Community-wide PPSR above 1,000 should be considered extremely unlikely, such as those obtained with TEF = 3.2. This suggests that a realistic TEF for the zooplankton community sampled in this study would rather be close to 2.3, as observed by Schwamborn and Giarrizzo (2015). Since there are still very few studies available that attempt to estimate

PPMR and PPSR based on stable isotopes and size-structured zooplankton sampling, our results may be used as a baseline for future studies

	TEF 2.3		**TEF 3.2**	
	PPMR	PPSR	PPMR	PPSR
Shelf	142,770	52	13,625,858	293
Slope	3226	14	75,932	42
Oceanic Islands	6,417,294	185	3,021,138,554	1,445
All	121,547	49	13,894,955	240

Table 4. Predator/prey mass ratio (PPMR) and predator/prey size ratio (PPSR) testing two different trophic enrichment factors (TEF = 3.2 and 2.3), for each area.

5. Acknowledgements

We would like to thank the National Council for Scientific and Technological Development (CNPq, PhD fellowships awarded to the first author), the ABRACOS project (Acoustics along the Brazilian Coast), funded by Institut de Recherche pour le Développement, IRD), the crew of R/V ANTEA, the Brazilian National Institute of Science and Technology in Tropical Marine Environments (INCT-AmbTropic, CNPQ/CAPES/FAPESB) for the logistic and financial support, the Laboratoire des sciences de l'environnement Marin (LEMAR) for the stable isotope analyses support. RS and AB received support from the European Union's Horizon 2020 research and innovation program under Grant Agreement No 734271. Many thanks to the Brazilian Navy for permit (Portaria Nº 178/EMA, 08/09/2015) and to the Brazilian Ministry of the Environment MMA / ICMBio for SISBIO permit no47270-4. This study is a contribution to the LMI TAPIOCA, the SMAC project (CAPES/COFECUB n° 88881.142689/2017–01) and to the PADDLE project, which has received funding from the European Union's Horizon 2020 research and innovation program under grant agreement No 73427. Many thanks to Simone M. A. Lira, Xiomara F.G. Díaz, Pedro A.M.C. Melo and Lucas Figueiredo, for the support in sampling during the cruise.

Supplementary material

Table MS1. Zooplankton size classes stable isotope composition between the three areas $\delta^{13}C$ and $\delta^{15}N$ minimum, maximum mean and standard deviation values.

Size Classes	$\delta^{13}C$ Min	$\delta^{13}C$ Max	$\delta^{13}C$ Mean	$\delta^{13}C$ sd	$\delta^{15}N$ Min	$\delta^{15}N$ Max	$\delta^{15}N$ Mean	$\delta^{15}N$ sd
	Coast							
< 200 µm	-23.23	-20.92	-22.08	1.63	3.17	4.20	3.69	0.73
200 – 500 µm	-21.49	-20.20	-21.08	0.38	2.87	5.09	3.91	0.69
500 – 1000 µm	-21.39	-20.32	-20.72	0.32	3.88	6.12	4.59	0.79
1000 – 2000 µm	-21.87	-20.43	-21.07	0.57	4.43	6.42	5.05	0.63
>2000 µm	-22.17	-20.79	-21.46	0.43	4.51	6.17	5.08	0.52
	Slope							
< 200 µm	-21.79	-21.71	-21.74	0.05	4.40	5.39	4.92	0.50
200 – 500 µm	-22.39	-20.48	-21.46	0.63	1.07	4.03	3.06	0.94
500 – 1000 µm	-21.76	-20.05	-21.14	0.48	2.24	5.25	4.03	0.92
1000 – 2000 µm	-23.21	-20.44	-21.58	0.86	2.54	5.26	4.13	0.79
>2000 µm	-22.76	-20.22	-21.75	0.66	3.28	6.92	5.04	1.09
	Oceanic Islands							
< 20 0µm	-21.95	-20.23	-20.94	0.55	5.10	7.52	5.99	0.60
200 – 500 µm	-21.02	-20.29	-20.64	0.26	5.07	6.84	5.79	0.52
500 – 1000 µm	-21.75	-19.96	-20.72	0.43	5.54	6.91	6.00	0.38
1000 – 2000 µm	-21.22	-20.24	-20.62	0.26	5.88	8.25	6.52	0.62
>2000 µm	-20.65	-18.69	-20.02	0.50	5.88	8.89	6.67	0.68

REFERENCE

Assunção, R.V., Silva, A.C., Roy, A., Bourlès, B., Silva, C.H., Ternon, J.-F., Bertrand, A., 2020. 3D characterisation of the thermohaline structure in the southwestern tropical Atlantic derived from functional data analysis of in situ profiles. Prog. Oceanogr., in press.

Bănaru, D., Carlotti, F., Barani, A., Grégori, G., Neffati, N., Harmelin-Vivien, M., 2014. Seasonal variation of stable isotope ratios of size-fractionated zooplankton in the Bay of Marseille (NW Mediterranean Sea). J. Plankton Res. 36, 145-156.

Benedetti, F., Gasparini, S., Ayata, S.D., 2015.Identifying copepod functional groups from species functional traits. J. Plankton Res. 38, 159-166.

Bertrand, A., 2015. ABRACOS cruise, RV Antea, https://doi.org/10.17600/15005600

Bode, A., Alvarez-Ossorio, M.T., Cunha, M. E., Garrido, S., Peleteiro, J.B., Porteiro, C., Valdes, L.,Varela, M., 2007. Stable nitrogen isotope studies of the pelagic food web on the Atlantic shelf of the Iberian Peninsula. Prog. Oceanogr. 74, 115–131.

Boltovskoy, D., 1999. South Atlantic zooplankton. Leiden: Backhuys Publishers.

Brandão, M.C., Koettker, A.G., Freire, A.S., 2013. Abundance and composition of decapod larvae at Saint Paul's Rocks (equatorial Atlantic).J. Mar. Ecol. 34, 171-185.

Boltovskoy, D. (ed.) 1999. South Atlantic Zooplankton. Backhuys Publishers, Leiden.

Bueno, M., Alberto, S.F., Carvalho, R., Costa, T.M., Ciotti, A.M., Christofoletti, R.A., 2017. Plankton in waters adjacent to the Laje de Santos state marine conservation park, Brazil: spatio-temporal distribution surveys. Braz. J. Oceanogr. 65, 564–575

Campelo, R.P.S., Diaz, X.F.G., Santos, G., Melo, P.A.M.C., Melo Junior, M., Figueiredo, L.G.P., et al., 2018. Small-scale distribution of the mesozooplankton in a tropical insular system. Braz. J. Oceanogr. 66, 15–29.

Cohen, J.E, Pimm, S.L, Yodzis P., Saldaña, J., 1993. Body sizes of animal predators and animal prey in food webs. J. Anim. Ecol. 62, 67–78.

Cotté, C., Simard, Y., 2005. Formation of dense krill patches under tidal forcing at whale feeding hot spots in the St. Lawrence Estuary. Mar. Ecol. Prog. Ser. 288, 199-210.

Dai, L., Li, C., Yang, G., Sun, X., 2016. Zooplankton abundance, biovolume and size spectra at western boundary currents in the subtropical North Pacific during winter 2012. J. Mar. Syst. 155, 73-83.

Diaz, X.F.G., Gusmão, L.M.O., Neumann-Leitão, S., 2009.Biodiversidade e dinâmica espaço-temporal do zooplâcton. In: Viana, D.L., Hazin, F.H.V., Souza, M.A.C. 2009. O arquipélago de São Pedro e São Paulo: 10 anos de Estação Científica. Brasília: SECIRM, 128-137.

Espinasse, B., Harmelin-Vivien, M., Tiano, M., Guilloux, L., Carlotti, F., 2014. Patterns of variations in C and N stable isotope ratios in size-fractionated zooplankton in the Gulf of Lion, NW Mediterranean Sea. J. Plankton Res. 36, 1204-1215.

Franco, B.C., Muelbert, J.H., Mata, M.M., 2006. Mesoscale physical processes and the distribution and composition of ichthyoplankton on the Southern Brazilian shelf break. Fish Oceanogr. 15, 37-43.

Fry, B., Wainright, S.C., 1991. Diatom sources of 13C-rich carbon in marine food webs. Mar. Ecol. Progr.Ser.76, 149 - 157.

Fry, B., 1988. Food web structure on Georges Bank from stable C, N, and S isotopic compositions. Limn. Oceanogr. 33, 1182-1190.

Fry, B., 2006. Stable isotope ecology. New York: Springer.

Fry, B., Quinones, R.B., 1994. Biomass spectra and stable isotope indicators of trophic level in zooplankton of the northwest Atlantic. Mar. Ecol. Prog. Ser. 112, 201–204.

Genin, A., 2004. Bio-physical coupling in the formation of zooplankton and fish aggregations over abrupt topographies. J. Mar. Syst. 50, 3–20.

Giering, S.L., Wells, S.R., Mayers, K.M., Schuster, H., Cornwell, L., Fileman, E.S., Atkinson, A., Cool, K.B., Preece, C., Mayor, D.J., 2018. Seasonal variation of zooplankton community structure and trophic position in the Celtic Sea: a stable isotope and biovolume spectrum approach. Prog. Oceanogr. 177, 101943.

Gorsky, G., Ohman, M.D., Picheral, M., Gasparini, S., Stemmann, L., Romagnan, J.B., Cawood, A., Pesant, S., Garcia-Comas, C., Prejger, F., 2010. Digital zooplankton image analysis using the ZooScan integrated system. J. Plankton Res. 32, 285–303.

Gove, J.M., McManus, M.A., Neuheimer, A.B., Polovina, J.J., Drazen, J.C., Smith, C.R., Merrified, M.A., Friiedlaner, A.K., Ehses, A.S., Young, A.W., Dillon, A.K., Williams, G.J., 2016.Near-island biological hotspots in barren ocean basins.Nat. Commun.7, 1058.

Graham, B.S., Koch, P.L., Newsome, S.D., Mcmahon, K.W., Aurioles, D., 2010. “Using isoscapes to trace the movements and foraging behavior of top predators in oceanic ecosystems,” in Isoscapes: Understanding Movement, Pattern, and Process on Earth Through Isotope Mapping, eds J. B. West, G. J. Bowen, T. E. Dawson, and K. P. Tu (Dordrecht: Springer), 299–318.

Guidi, L., Chaffron, S., Bittner, L., Eveillard, D., Larhlimi, A., Roux, S., Darzi, Y., Audic, S., Berline, L., Brum, J.R., Coelho, L.P., Espinoza, J.C.I., Malviya, S., Sunagawa, S., Dimier, C., Kandels-Lewis, S., Picheral, M., Poulain, J., Searson, S., Coordinators, T.O.C., Stemmann, L., Not, F., Hingamp, P., Speich, S., Follows, M., Karp-Boss, L., Boss, E., Ogata, H., Pesant, S., Weissenbach, J., Wincker, P., Acinas, S.G., Bork, P., de Vargas, C., Iudicone, D., Sullivan, M.B., Raes, J., Karsenti, E., Bowler, C., Gorsky, G., 2016. Plankton networks driving carbon export in the oligotrophic ocean. Nature. 24, 165–180.

Hansen, B., Bjornsen, P.K., Hansen, P.J., 1994. The size ratio between planktonic predators and their prey. Limn. Oceanogr. 39, 395-403.

Hauss, H., Franz, J.M., Hansen, T., Struck, U., Sommer, U., 2013. Relative inputs of upwelled and atmospheric nitrogen to the eastern tropical North Atlantic food web: Spatial distribution of δ^{15}N in mesozooplankton and relation to dissolved nutrient dynamics. Deep Sea Res. Part I: Oceanogr. Res. Papers.75, 135-145.

Howatt, T.M., & Allen, S.E., 2013. Impact of the continental shelf slope on upwelling through submarine canyons. J. Geophys. Res. Oceans. 118, 5814-5828.

Hunt, B.P., Allain, V., Menkès, C., Lorrain, A., Graham, B., Rodier, M., Pagano, M. Carlotti, F., 2015. A coupled stable isotope-size spectrum approach to understanding pelagic food-web dynamics: a case study from the southwest sub-tropical Pacific. Deep Sea Res. Part II Top. Stud. Oceanogr. 113, 208-224.

Jennings, S., Oliveira, J.A.D., Warr, K.J., 2007.Measurement of body size and abundance in tests of macroecological and food web theory. J. Anim. Eco. 76, 72–82.

Jennings, S., Warr, K.J., Mackinson, S., 2002. Use of size-based production and stable isotope analyses to predict trophic transfer efficiencies and predator-prey body mass ratios in food webs. Mar. Ecol. Prog. Ser. 240, 11–20.

Kämpf, J., 2007. On the magnitude of upwelling fluxes in shelf-break canyons. Cont. Shelf Res. 27, 2211-2223.

Katsuragawa M., Dias J.F., Harari, J., Namiki, C., Zani-Teixeira, M.L., 2014. Patterns in larval fish assemblages under the influence of the Brazil current. Cont. Shelf Res. 89, 103-117.

Kiørboe, T., 2008. Optimal swimming strategies in mate-searching pelagic copepods. Oecologia. 155, 179-192.

Kline, T.C., Pauly, D., 1998. Cross-validation of trophic level estimates from a mass-balance model of Prince William Sound using $^{15}N/^{14}N$ data. p. 693-702. In: T.J. Quinn II, F. Funk. Heifetz, J.N., Ianelli, J.E., Powers, J.F., Schweigert, P.J, Sullivan, C.-I., Zhang (eds.) Proceedings of the International Symposium on Fishery Stock Assessment Models. Alaska Sea Grant College Program Report No. 98-01.

Koppelmann, R., Böttger-Schnack, R., Möbius, J., Weikert, H., 2009. Trophic relationships of zooplankton in the eastern Mediterranean based on stable isotope measurements. J. Plankton Res. 31, 669-686.

Lee, C., Wakeham, S., Arnosti, C., 2004. Particulate organic matter in the sea: the composition conundrum. AMBIO, 33, 565-576.

Lins Silva, N., Marcolin, C. R., Schwamborn, R., 2019. Using image analysis to assess the contributions of plankton and particles to tropical coastal ecosystems. Est.Coast. Shelf Sci. 219, 252-261.

Lira, S.M.D.A., Teixeira, I.D.Á., Lima, C.D.M.D., Santos, G.D.S., Leitão, S.N., Schwamborn, R., 2014. Spatial and nycthemeral distribution of the zooneuston off Fernando de Noronha, Brazil. Braz. J. Oceanog. 62, 35-45.

Maps, F., Plourde, S., McQuinn, I.H., St-Onge-Drouin, S., Lavoie, D., Chassé, J., Lesage, V., 2015. Linking acoustics and finite-time L yapunov exponents reveals areas and mechanisms of krill aggregation within the Gulf of St. Lawrence, eastern Canada. Limn. Oceanogr. 60, 1965-1975.

Marcolin, C.R., Schultes, S., Jackson, G.A., Lopes, R.M., 2013. Plankton and seston size spectra estimated by the LOPC and ZooScan in the Abrolhos Bank ecosystem (SE Atlantic). Cont. Shelf Res. 70, 74-87.

Mauchline, J., 1998. The biology of calanoid copepods. Advances in marine biology, Academic Press. 33.

McConnaughey, T., McRoy, C.P., 1979.Food-web structure and the fractionation of carbon isotopes in the Bering Sea. Mar. Biol. 53, 257-262.

McCutchan Jr, J.H., Lewis Jr, W.M., Kendall, C., McGrath, C.C., 2003. Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. Oikos, 102, 378-390.

Ménard, F., Benivary, H.D., Bodin, N., Coffineau, N., Le Loc'h, F., Mison, T., Richard, P. Potier, M., 2014.Stable isotope patterns in micronekton from the Mozambique Channel. Deep Sea Res. Part II: Trop. Stud. Stud. Oceanogr. 100, 153-163.

Miller, T.W., Brodeur, R.D., Rau, H.G., 2008. Carbon stable isotopes reveal relative contribution of shelf-slope production to the Northern California Current pelagic community. Limnol. Oceanogr. 53, 1493–1503.

Minagawa, M., Wada, E., 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between δ^{15}N and animal age. Geochim. Cosmochim. Acta. 48, 1135–1140.

Mompeán, C., Bode, A., Benítez-Barrios, V.M., Domínguez-Yanes, J.F., Escánez, J., Fraile-Nuez, E., 2013. Spatial patterns of plankton biomass and stable isotopes reflect the influence of the nitrogen-fixer *Trichodesmium* along the subtropical North Atlantic. J. Plankton Res. 35, 513-525.

Montoya, J.P., Carpenter, E.J., Capone, D.G., 2002. Nitrogen fixation and nitrogen isotope abundances in zooplankton of the oligotrophic North Atlantic. Limnol. Oceanogr. 47, 1617–1628.

Neumann-Leitão, S., Gusmão, L.M.O., Silva, T.D.E.; Nascimento-Vieira, D.A., Silva, A.P., 1999. Mesozooplankton biomass and diversity in coastal and oceanic waters off North-Eastern Brazil. Arch. Fish. Mar. Res. 47, 153-165.

Neumann-Leitao, S., Melo Junior, M., Neto, P., Figueiredo, F., Silva, A.P., Díaz, X.F.G., et al., 2019. Connectivity between coastal and oceanic zooplankton from Rio Grande do Norte in the tropical western Atlantic. Front. Mar. Sci. 6, 287.

Neumann-Leitão, S., Sant'anna, E.M.E., Gusmão, L.M.D.O., Nascimento-Vieira, D.A., Paranaguá, M.N., Schwamborn, R., 2008. Diversity and distribution of the mesozooplankton in the tropical Southwestern Atlantic. J. Plankton Res. 30, 795-805.

Newell, G.E., Newell, R.C., 1963. Marine plankton: a practical guide. London: Hutchlson Educational

Petchey, O.L., Beckerman, A.P., Riede, J.O., Warren, P.H., 2008. Size, foraging, and food web structure. Proc. Natl Acad. Sci. USA. 105, 4191–4196.

Platt, T., Denman, K., 1977. Organization in the pelagic ecosystem. Helgolander Wiss. Meeresunters. 30, 575-581

Post, D.M., 2002.Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology, 83, 703–718.

Saiz, E., Calbet, A., Atienza, D., Alcaraz, M., 2007. Feeding and production of zooplankton in the Catalan Sea (NW Mediterranean). Prog. Oceanogr. 74, 313–328.

Sailley, S.F., Polimene, L., Mitra, A., Atkinson, A., Allen, J.I., 2015. Impact of zooplankton food selectivity on plankton dynamics and nutrient cycling. J. Plankton Res. 37, 519-529.

Santana, C.S.D., Schwamborn, R., Neumann-Leitão, S., Montes, M.D.J.F., Lira, S.M.D.A., 2018.Spatio-temporal variation of planktonic decapods along the leeward coast of the Fernando de Noronha archipelago, Brazil. Braz. J. Oceanogr. 66, 1-14.

Schott, F.A., Dengler, M., Zantopp, R., Stramma, L., Fischer, J., Brandt, P., 2005. The Shallow and Deep Western Boundary Circulation of the South Atlantic at 5°–11°S. J. Phys. Oceanogr. 35, 2031–2053.

Schwamborn, R, Neumann-Leitão, S., Silva, T.A., Silva, A.P., Saint-Paul, U., 2001. Distribution and dispersal of decapod crustacean larvae and other zooplankton in the Itamaracá estuarine system, Brazil. Trop. Oceanogr. 29, 1-18.

Schwamborn, R., Ekau, W., Voss, M., Saint-Paul, U., 1999. Stable isotope composition of particulate organic matter and zooplankton in northeast Brazilian shelf waters. Arc. Fish. Mar. Res. 47, 201–210.

Schwamborn, R., Giarrizzo, T., 2015. Stable isotope discrimination by consumers in a tropical mangrove food web: How important are variations in C/N ratio? Estuar. Coast. 38, 813-825.

Schwamborn, R., Voss, M., Ekau, W., Saint-Paul, U., 2002. How important are mangroves as carbon sources for decapod crustacean larvae in a tropical estuary? Mar. Ecol. Prog. Ser. 229, 195-205.

Stramma, L., Fischer, J., Reppin, J., 1995. The North Brazil Undercurrent. Deep Sea Res. Part I: Oceanogr. Res. Papers. 42, 773–795.

Swartzman, G., Hickey, B., Kosro, M., Wilson, C., 2005. Poleward and equatorward currents in the Pacific Eastern Boundary Current in summer 1995 and 1998 and their relationship to the distribution of euphausiids. Deep Sea Res. Part II Top. Stud. Oceanogr. 52, 73–88.

Tosetto, E.G., Neumann-Leitão, S., Júnior, M.N., 2019. Sampling planktonic cnidarians with paired nets: Implications of mesh size on community structure and abundance. Estuar., Coast. Shelf Scien. 220, 48-53.

Tseng, L.C., Dahms, H.U., Hung, J.J., Chen, Q.C., Hwang, J.S., 2011. Can different mesh sizes affect the results of copepod community studies? J. Exp. Mar. Biol. Ecol. 398, 47–55.

Vander Zanden, J.M., Fetzer,W.W., 2007. Global patterns of aquatic food chain length. Oikos.116, 1378–1388.

Vanderklift, M.A., Ponsard, S., 2003. Sources of variation in consumer - diet δ15N enrichment: a meta- analysis. Oecologia 136, 169–182.

Wang, S.W., Budge, S.M., Gradinger, R.R., Iken, K., Wooller, M.J., 2014. Fatty acid and stable isotope characteristics of sea ice and pelagic particulate organic matter in the Bering Sea: tools for estimating sea ice algal contribution to Arctic food web production. Oecologia. 174, 699-712.

Yang, G., Li, C., Guilini, K., Wang, X., Wang, Y., 2017. Regional patterns of δ^{13}C and δ^{15}N stable isotopes of size-fractionated zooplankton in the western tropical North Pacific Ocean. Deep Sea Res. Part I: Oceanogr. Res. Papers. 120, 39-47.

Yang, G., Li, C.L., Guilini, K., Peng, Q., Wang, Y., Zhang, Y., Zhang, Y., 2016. Feeding strategies of four dominant copepod species in Prydz Bay, Antarctica: insights from a combined fatty acid biomarker and stable isotopic approach. Deep Sea Res. Part I: Oceanogr. Res. Papers. 114, 55–63.

Zar, J.H. Biostatistical analysis.3.ed. Upper Saddle River: Prentice Hall International Editions, 1996. p. 662.

Zhu, Y., Tande, K., Zhou, M., 2009. Mesoscale physical processes and zooplankton transport–retention in the northern Norwegian shelf region. Deep Sea Res. Part II Top. Stud. Oceanogr. 56, 1922–1933.

7 NEW RECORDS OF THE MOLLUSK FIROLOIDA DESMARESTIA LESUEUR, 1817 (GASTROPODA: PTEROTRACHEIDAE) OFF FERNANDO DE NORONHA ARCHIPELAGO AND NORTHEASTERN BRAZILIAN CONTINENTAL SLOPE, TROPICAL ATLANTIC

Artigo aceito e publicado no periódico Tropical Oceanography

Gabriela Guerra Araújo Abrantes de FIGUEIREDO[1]*; Ralf SCHWAMBORN[1]; Arnaud BERTRAND[2]; Simone Maria Albuquerque LIRA[1,3]

[1]Department of Oceanography, Federal University of Pernambuco, Recife, Brazil. Av. Arquitetura, s/n - Cidade Universitária, 50740-550 Recife, PE, Brazil. E-mail: gabriela.gaaf@gmail.com, ralf.schwamborn@ufpe.br
*Corresponding author

[2]Institut de Recherche pour le Développement (IRD), MARBEC, Université de Montpellier, CNRS, Ifremer, IRD, Sète, France. E-mail: arnaud.bertrand@ird.fr

[3]Department of Biology, Federal Rural University of Pernambuco, Recife, Brazil. E-mail: simonealira@gmail.com

RESUMO.

O conhecimento biogeográfico e taxonômico sobre moluscos planctônicos, especificamente sobre Pterotracheoidea (também conhecidos como heterópodes ou elefantes marinhos) nos oceanos tropicais, ainda está incompleto. Neste artigo relatamos o primeiro registro da heteropoda *Firoloida desmarestia* Lesueur (1817) sobre as águas da encosta continental do Nordeste brasileiro e do Arquipélago de Fernando de Noronha e ampliamos sua distribuição geográfica no Atlântico tropical. Fornecemos nova imagem digital detalhada e descrições desta espécie gelatinosa altamente frágil e transparente. As amostras foram coletadas no contexto do projeto 'ABRACOS' (Acústica ao longo da costa brasileira) usando redes de bongo. Das 96 amostras analisadas, seis exemplares foram registrados em cinco amostras, três em Fernando de Noronha e três na costa nordeste do Brasil. O presente estudo estende a distribuição de *F. desmarestia* a 3°S-9°S no oeste do Atlântico Tropical e destaca a importância de estudos detalhados sobre a biodiversidade de plâncton gelatinoso de grande porte nos oceanos tropicais.

Palavras-Chave: Ilhas oceânicas tropicais, talude continental, zooplâncton, heterópodes, Pterotracheidae

ABSTRACT. Biogeographic and taxonomic knowledge on planktonic mollusks, specifically on Pterotracheoidea (also known as heteropods or sea elephants) in tropical oceans, is still incomplete. In this paper we report the first record of the heteropod *Firoloida desmarestia* Lesueur (1817) on waters off the Northeast Brazilian continental slope and Fernando de Noronha Archipelago and extend its geographic distribution in the tropical Atlantic. We provide new detailed digital image and descriptions of this highly fragile and transparent gelatinous species. Samples were taken in the context of the 'ABRACOS' (Acoustic along the Brazilian Coast) project using bongo nets. Out of 96 samples analyzed, six specimens were recorded in five samples, three at Fernando de Noronha, and three off the Northeast Brazilian coast. The present study extends the range of distribution of *F. desmarestia* to 3°S-9°Sin the western the Tropical Atlantic and highlights the importance of detailed studies on large-sized gelatinous plankton biodiversity in tropical oceans.

Keywords: Tropical oceanic islands, Continental slope, zooplankton, heteropods, Pterotracheidae.

INTRODUCTION

The gastropod superfamily Pterotracheoidea, also known as heteropods or 'sea elephants', comprises about 250 species of fragile holoplanktonic mollusks, with a worldwide geographic distribution in tropical and subtropical oceans (Moreno-Alcántara *et al.,* 2014). One group of heteropods with very little data on their distribution is a monotypic genus represented only by *Firoloida desmarestia* Lesueur, 1817 (Gastropoda: Pterotracheidae). It is a naked pelagic heteropod with a completely transparent soft body (Lesueur, 1817). As all heteropods, *F. desmarestia* swims by movements of a single swimming fin. Furthermore, they have well-developed eyes, an indication of a visual predator (Land, 1982), with the main food source being gelatinous zooplankton (Lalli and Gilmer, 1989). The main predators of *F. desmarestia* are other heteropod species, fish, and large zooplankton, such as siphonophores, medusae and phyllosoma larvae (Lalli and Gilmer, 1989; Wang *et al.,* 2014).

This species occurs tipically at tropical and subtropical latitudes (Seapy *et al.,* 2003). These organisms were observed, among other, in the Gulf of California (Angullo-Capillo, 2010), in the Central Pacific (Seapy, 1990), off Chile (Pagès *et al.,* 2001). In the Atlantic, this species was found by Tesch (1949), Northern, Western Atlantic, Atlanto-Mediterranean faunistic centers by Van der Spoel (1976) and Gulf of Mexico by Lemus-Santana *et al.* (2015). Moreover, Vannucci (1951) recorded *F. desmarestia* from Trindade Island, Brazil, and recently, Burridge *et al.* (2017) recorded *F. desmarestia* along a meridional transect through the Atlantic. Along the Northeastern Brazilian waters, some studies addressed the spatial distribution and taxonomic diversity of planktonic mollusks (e.g., Koblitz and Larrazábal, 2014; Larrazábal and Oliveira, 2003) and reported more than 20 species of planktonic gastropods. However, none of them recorded the presence of *F. desmarestia*. In this study, we provide new records of *F. desmarestia* off the northeast Brazilian coast (continental slope) and the oceanic archipelago of Fernando de Noronha, Brazilian Province, providing detailed diagnoses and digital image of this species.

MATERIAL AND METHODS

Zooplankton samples were collected during the 'ABRACOS 2' (Acoustic along the Brazilian Coast, Bertrand, 2017) survey conducted on board R/V ANTEA off the Northeastern Brazilian continental slope waters (open areas) and oceanic islands in April 2017 (Fig. 1). A total of 96 zooplankton samples were collected using bongo net trawls (2 x 60 cm diameter, mesh sizes of 300 and 500 µm). Oblique tows were conducted between 200 m and the surface in oceanic areas and from the bottom to the surface in neritic waters. All samples were preserved in 4% formaldehyde buffered with sodium tetraborate (0.5 gl^{-1}, Newell and Newell, 1963).

In the laboratory, subsamples (1/2 to 1/64) obtained using a zooplankton Motoda splitter (up to 2,000 organisms) were analyzed and *F. desmarestia* specimens were identified according to Lesueur (1817), Seapy (2008) and Lemus-Santana *et al.* (2015). One organism was stained with 2% acetic carmine (Silva, K. unpublished results) and was used for detailed descriptions and digital images, using a Zeiss Axio Scope A1 with Zen software and later treated in Adobe Photoshop CS6. For the visualization of these fragile and transparent organisms, multi-focal images were acquired and combined using the Zen Blue 2011 (Zeiss) software.

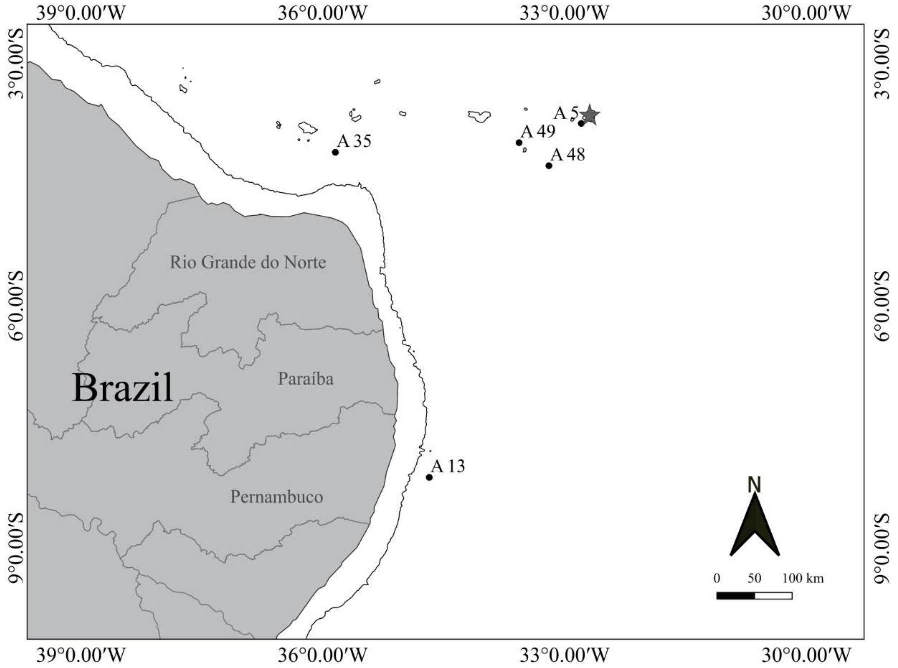


Figure 1. Map of the study area in the western tropical Atlantic showing the sampling stations with occurrence of *Firoloida desmarestia*. Continuous line: 200 m isobath. Gray star: Fernando de Noronha archipelago).

RESULTS AND DISCUSSION

Planktonic gastropods were found in all 96 samples analyzed. *Firoloida desmarestia* was represented by six specimens found at five stations (Fig. 1) i.e, 4% of samples. Over the continental slope, three specimens were recorded during nighttime (Fig 2; Tab. 1). Off Fernando de Noronha (Fig. 2; Tab. 1), three specimens were caught, during daytime and nighttime.

Figure 2. *Firoloida desmarestia* Lesuer (1817) sampled off Fernando de Noronha Archipelago, Brazil.

Table 1. Sampling station, geographic coordinates, sampling station (FN: Fernando de Noronha), abundance, gear and mesh size used to collect *Firoloida desmarestia*.

Station	Latitude (S)	Longitude (W)	Local	Date	Time	Mesh (µm)
5	-9.136	-34.753	FN	10/04/2017	23:56	300
13	-8.323	-34.402	Slope	13/04/2017	19:47	500
35	-4.297	-35.567	Slope	21/04/2017	00:29	300
48*	-4.463	-32.918	FN	30/04/2017	13:22	500
48	-4.463	-32.918	FN	30/04/2017	13:22	500
49	-4.178	-33.288	FN	01/05/2017	00:46	500

*: Photographed specimens

SYSTEMATICS

Phylum Mollusca

Class Gastropoda Cuvier, 1795

Subclass Caenogastropoda

Order Littorinimorpha

Superfamily Pterotracheoidea

Family Pterotracheidae

Genus *Firoloida* Lesueur, 1817

Species *Firoloida desmarestia* Lesueur, 1817

MATERIAL EXAMINED. Brazil, Northeast Brazilian open area waters and oceanic islands, "ABRACOS 2 survey", bongo net, 300 and 500 µm mesh sizes.

***Firoloida desmarestia* MORPHOLOGICAL CHARACTERISTICS**

A transparent elongate cylindrical body with a long trunk and short tail, a terminal visceral nucleus on the trunk, a swimming fin anterior of the middle part of the trunk (sense Lesueur, 1817). They are gonochoristic and have sexual dimorphism in which the males have a large penis, a tentacle aside each eye, a sucker on the swimming fin and a rudimentary tail. The females lack a tail, they own a permanent egg string that extends posteriorly from the base of the visceral nucleus (Lemus-Santana *et al.,* 2015). The eyes are narrowly triangular; large and oblong lens capsule with basal and distal portion slightly opaque. Little is known about the maturity of females. According to Tesch (1949) the maturity is not strictly dependent of the size of individuals once he observed egg strings in female organisms ranging from 10-40 mm in length.

REMARKS

This study provides the first record of *F. desmarestia*, a planktonic mollusk for Fernando de Noronha Archipelago and above the continental slope (open areas) off Northeast Brazil and extends its distribution between 3°S-9°S in the western Tropical Atlantic. Its absence in previous studies in the regions probably due several factors, for example the fact that these organisms are very fragile (often destroyed during plankton hauls), as well as the fact that this species was never the focus of the studies. In this study, this species showed extremely low abundance (1 to 2 ind. per sample) and frequency of occurrence (present in 4% of samples). Being several millimeters long, *F. desmarestia* was among the largest organisms in the plankton community sampled in this study. Large-sized predators are key elements of marine food webs (Gusmão *et al.,* 2014), which may have been underrepresented in many previous plankton surveys.

We mostly captured *F. desmarestia* at nighttime (four organisms at night, and two organisms during the day). These organisms, like most of gelatinous plankton, probably perform diel vertical migrations, rising from deeper depths and being captured in shallower waters at night. Although *F. desmarestia* occurs depths down to 150 meters (Seapy, 1990; Seapy, 2008), new studies with other types of nets and at greater depths are necessary to improve the knowledge on their distribution, abundance and other ecological aspects. Around Fernando de Noronha Archipelago, for example, a large biomass of gelatinous was observed by acoustic with part of the community performing consistent diel vertical migrations (Vargas *et al.,* 2017). Their study highlights the importance of large-sized gelatinous organisms (e.g., hydromedusae, salps, chaetognaths, and planktonic gastropods) that are also underestimated prey for the mesopelagic community (Eduardo *et al.,* 2020).

This study contributes to the knowledge of the planktonic fauna of the tropical Atlantic, and may provide useful information to diversity in marine protected areas off oceanic islands (Fernando de Noronha Archipelago). The plankton biodiversity in waters off these isolated insular environments should be studied more intensively, since they play invaluable biogeographic and ecological roles in the tropical Atlantic (e.g., as stepping-stones between Africa and South America) (Lira *et al.,* 2017), contributing to the dispersal and continuity of these and many other species. The other region (station 35) where *F. desmarestia* was recorded, around the Ceará seamounts, is also characterized by a lack of study.

A combined use of different sampling methods (e.g., Bongo nets, MOCNESS, opening-closing nets), will probably be necessary for an efficient capture of this species, with high potential to reveal new records of planktonic taxa in tropical oceanic waters. Lemus-Santana *et al.* (2015) used an opening-closing net and captured around 350 specimens of *F. desmarestia* in the slope region and on the narrow part of shelf of the Gulf of Mexico, evidencing their oceanic origin. They also observed that adults specimens were found in upper levels (0 – 18 m) and young specimens were mainly found between 45 and 105 m. In the future, more specific sampling campaigns may yield high numbers of these little investigated gelatinous predators in many other areas.

This study highlights the importance of detailed taxonomic studies with plankton samples, ideally to be analyzed in toto, to better quantify the rare species. Moreover, the present study extends the occurrence of *F. desmarestia* between 3°S-9°S in the western Tropical Atlantic.

ACKNOWLEDGEMENTS

We would like to thank the National Council for Scientific and Technological Development (CNPq, PhD fellowships awarded to the first author), the ABRACOS project (Acoustics along the Brazilian Coast, funded by Flotte Oceanographique Française), the crew of R/V ANTEA, the Brazilian National Institute of Science and Technology in Tropical Marine Environments (INCT-AmbTropic, CNPQ/CAPES/FAPESB) for the logistic and financial support; the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES/PORAP no 206, September, 4, 2018) This work is a contribution to the LMI TAPIOCA. RS and AB received support from the European Union’s Horizon 2020 research and innovation program under Grant Agreement No 734271. Many thanks to Kaio Farias for the photo of *Firoloida desmarestia*.

REFERENCES

Angulo-Campillo, O., Aceves-Medina, G. and Avedaño-Ibarra, R. (2011), Holoplanktonic mollusks (Mollusca: Gastropoda) from the Gulf of California, México, C*heckList: Journal of species lists and distribution*, Vol. 7, pp. 337-342. https://doi.org/10.15560/7.3.337

Bertrand, A. (2017), *ABRACOS 2 cruise*, RV Antea, https://doi.org/10.17600/17004100.

Burridge, A.K., Goetze, E., Wall-Palmer, D., Le Double, S.L., Huisman, J., and Peijnenburg, K.T. (2017), Diversity and abundance of pteropods and heteropods along a latitudinal gradient across the Atlantic Ocean, *Progress in Oceanography*, Vol. 158, pp. 213-223. https://doi.org/10.1016/j.pocean.2016.10.001.

Eduardo, L.N., Bertrand, A., Mincarone, M.M., Silva, L.V.S., Frédou, T., Assunção, R., Silva, A., Ménard, F., Schwamborn, R., Le Loch, F. and Lucena-Frédou, F. (2020), Hatchet fishes (Stomiiformes: Sternoptychidae) biodiversity, trophic ecology, vertical niche partitioning and functional roles in the western Tropical Atlantic, *Progress in Oceanography*, Vol. 185, p. 102389. DOI: 10.1016/j.pocean.2020.102389.

Gusmão, L.M.O., Diaz, X.F.G., de Melo Jr, M., Schwamborn, R. and Neumann-Leitão, S. (2014), Jellyfish diversity and distribution patterns in the tropical Southwestern Atlantic, *Marine Ecology*, Vol. 36, pp. 93-103. https://doi.org/10.1111/maec.12119

Koblitz, V., S., and Larrazábal, M., E., L. (2014), Characterization of the geographic distribution pattern of the family Limacinidae Gray, 1840 (Mollusca Gastropoda) in the waters of Northeastern of Brazil. *Biota Neotropica*, Vol. 14, pp. 1-15. DOI https://doi.org/10.1590/1676-06032014002913

Lalli C., M., Gilmer R., W. (1989), Pelagic snails: the biology of holoplanktonic gastropod mollusks. Stanford University Press, Stanford

Land M. F. (1982), Scanning eye movements in a heteropod mollusk. *J Exp Biol*, Vol. 96, pp. 427–430

Larrazábal, M.E.D., & Oliveira, V.S.D. (2003), Thecosomata e Gymnosomata (Mollusca, Gastropoda) da cadeia Fernando de Noronha, Brasil. *Revista Brasileira de Zoologia*, Vol. 20, pp. 351-360. https://doi.org/10.1590/S0101-81752003000200028

Lemus-Santana, E., Sanvicente-Añorve, L., Alatorre-Mendieta, M. and Flores-Coto, C. (2015), Population structure and mating encounter rates in a marine pelagic invertebrate *Firoloida desmarestia* (Mollusca). Sexuality and Early Development, *Aquatic Organisms*, Vol. 1, n. 2, pp. 163-173. https://doi.org/10.3354/sedao00015

Lesueur, C.A. (1817), Characters of a new genus, and descriptions of three new species upon which it is formed; discovered in the Atlantic ocean, in the months of March and April, 1816; Lat. 22°9', *Journal of the Academy of Natural Sciences*, Vol. 1, pp. 37-41.

Lira, S.M.A., Santana, C.S., Lima, C.D., Montes, M.J. and Schwamborn, R. (2017), New records of the larval forms *Cerataspis monstrosa* and *Amphionides reynaudii* (Crustacea: Decapoda) from the western tropical Atlantic, Zootaxa, Vol. 4237, pp. 335-346. https://doi.org/10.11646/zootaxa.4237.2.7

Lira, S.M.A., Santana, C.S. and Schwamborn, R. (2018), First record of *Naushonia* sp. (Decapoda: Laomediidae) larva from the Equatorial Atlantic, *Zootaxa*, Vol. 4387, pp. 183-194. https://doi.org/10.11646/zootaxa.4387.1.9

Moreno-Alcántara M., Aceves-Medina G., Angulo-Campillo O., Murad-Serrano J. (2014), Holoplanktonic molluscs (Gastropoda: Pterotracheoidea, Thecosomata and Gymnosomata) from the southern Mexican Pacific. Journal of Molluscan Studies, Vol. 80, pp. 131-138. https://doi.org/10.1093/mollus/eyu006

Newell, G., E. and Newell, R., C. (1963), Marine plankton: a practical guide. London: Hutchlson Educational

Pagès, F., González, H.E., Ramón, M., Sobarzo, M. and Gili, J.M. (2001), Gelatinous zooplankton assemblages associated with water masses in the Humboldt Current System and potential predatory impact by *Bassiabassensis* (Siphonophora: Calycophorae), *Marine Ecology Progress Series*, Vol. 210, pp. 13-24. https://doi.org/10.3354/meps210013.

Seapy, R.R. (1990), Patterns of vertical distribution in epipelagic heteropod mollusks off Hawaii, *Marine Ecology Progress Series*, Vol. 60, pp. 235-246. https://doi.org/10.3354/meps060235.

Seapy, R.R. (2008), Offshore-inshore and vertical distributional patterns of heteropod mollusks off leeward Oahu, Hawaii, *Marine Biology*, Vol. 154, pp. 985-995. https://doi.org/10.1007/s00227-008-0989-9

Seapy, R.R., Lalli, C.M. and Wells, F.E. (2003), Heteropoda from Western Australia waters, in Wells, F.E., Walker, D.I. and Jones, D.S. (Eds), *The Marine Flora and Fauna of Dampier, Western Australia*, Western Australian Museum, Perth, pp. 513-546.

Tesch, J.J. (1949), Heteropoda. *The Carlsberg Foundation's Oceanographical Expedition round the world 1928–30 and previous 'Dana' expeditions*, Dana Report No. 34, Bianco Luno A/S, Copenhagen.

Van der Spoel, S. (1976), *Pseudothecosomata, Gymnosomata and Heteropoda (Gastropoda)*, Utrecht: Bohn, Scheltema & Holkema, 484p.

Vannucci, M. (1951), Resultados científicos do cruzeiro do "Baependi" e do "Vega" à Ilha da Trindade: o gênero Firoloida, Prosobranchia Heteropoda, *Boletim do Instituto Paulista de Oceanografia*, Vol. 2, n. 2, pp. 73-93. https://doi.org/10.1590/S0100-42391951000200004.

Vargas, G., Lucena-Frédou, F., Habasque, J., Lebourges-Dhaussy, A., Roudaut, G. and Bertrand, A. (2017), *A new multi frequency acoustic method for the discrimination of biotic components in pelagic ecosystems*: Application in a high diversity tropical ecosystem off Northeast Brazil, IEEE/OES Acoustics in Underwater Geosciences Symposium (RIO Acoustics), pp. 1-8. DOI: 10.1109/RIOAcoustics.2017.8349719.

Wang, M., O'Rorke, R., Nodder, S., D., and Jeffs, A., G. (2014), Nutritional composition of potential zooplankton prey of the spiny lobster phyllosoma (Jasus edwardsii). *Marine and Freshwater Research*, Vol. 65, n. 2, pp. 337-349. https://doi.org/10.1071/MF13048

8 CONSIDERAÇÕES FINAIS

Este estudo forneceu novos conhecimentos sobre a distribuição de abundância, biovolume, espectros de tamanho e isótopos estáveis do zooplâncton ao longo da plataforma continental, quebra da plataforma e ilhas oceânicas do Nordeste do Brasil, permitindo o entendimento da estrutura e organização das comunidades zooplanctônicas em função dos espectros de tamanho.

No primeiro capítulo, a abordagem para a estimativa da distribuição, abundância e biovolume através da análise de imagens resultou na obtenção de padrões de distribuição diferente entre abundância e biovolume do zooplâncton. Os organismos maiores como os gelatinosos e larvas de peixes contribuíram significativamente para o biovolume em ilhas oceânicas, enquanto que a abundância foi representada principalmente por copépodos, em todas as áreas estudadas. Essa diferença está refletindo diretamente na comunidade zooplanctônica e nos espectros de tamanhos entre as áreas. A inclinação da reta do NNSS e NBSS na plataforma e no talude continental foi mais inclinada, indicando uma maior quantidade de organismos menores nesses ambientes. Já a inclinação mais suave em ambientes oceânicos está diretamente relacionada com a maior quantidade e biovolume dos organismos maiores nestes ambientes. Esse resultado pode ser utilizado para a inferência de produtividade e eficiência trófica dos ambientes em estudo.

No segundo capítulo, as razões isotópicas mostraram importantes variações em relação ao tamanho dos organismos e aos ambientes. Essas variações estão diretamente ligadas com os diferentes processos biogeoquímicos que ocorrem em cada ambiente, bem como a composição taxonômica e o tamanho, mostrando que a relação de tamanho e de massa entre presa/predados (PPSR e PPMS) está diretamente relacionada com o fator de enriquecimento trófico. Como ainda existem poucos estudos que estimam essa relação presa/predador com base em análises isotópicas por classes de tamanho, nossos resultados podem e devem ser usados como base para estudos futuros.

Por fim, o ultimo capítulo apresentou uma nova ocorrência de um gastrópode zooplanctônico (*Firoloida desmaresia*) para as áreas oceânicas e o Arquipélago de Fernando de Noronha, aumentando assim a distribuição dos gastrópodes na costa do Brasil.

Este trabalho demonstrou como o estudo integrado das análises de isótopos com as análises de classes de tamanho contribui para o entendimento da ecologia trófica nessas áreas (plataforma, quebra de plataforma e ilhas oceânicas) extremamente importantes do ponto de vista pesqueiro, uma vez que são áreas bastante produtivas e de ocorrência de espécies de grande valor econômico. Este entendimento é de extrema importância para as ações de gerenciamento e manejo das áreas estudadas, principalmente por serem unidades de conservação, no caso do Arquipélago de Fernando de Noronha e Atol das Rocas, bem como as áreas da plataforma e quebra da plataforma. Os resultados comprovam a importância do estudo detalhado (composição taxonômica, de tamanhos e isotópica) da comunidade zooplanctônica e suas inter-relações, principalmente em ambientes oceânicos, uma vez que pouco se sabe sobre a dinâmica desses ambientes.

REFERÊNCIAS

ALCARAZ, M. *et al*. Estimating zooplankton biomass through image analysis. **Marine Biology**, v. 143, p. 307-315, 2003.

ANGULO-CAMPILLO, O.; ACEVES-MEDINA, G.; AVEDAÑO-IBARRA, R. Holoplanktonic mollusks (Mollusca: Gastropoda) from the Gulf of California, México. **Check List**, v. 7, p. 337, 2011.

ASHJIAN, C. J.; WISHNER, K. F. Temporal persistence of copepod species groups in the Gulf Stream. **Deep Sea Research Part I: Oceanographic Research Papers,** v. 40, n. 3, p. 483-516, 1993.

ASSUNÇÃO, R.V., SILVA, A. C., ROY, A., BOURLÈS, B., SILVA, C.H., TERNON, J.-F., BERTRAND, A. 3D characterization of the thermohaline structure in the southwestern tropical Atlantic derived from functional data analysis of in situ profiles. **Prog. Oceanogr**., in press. 2020

BĂNARU, D. et al.. Seasonal variation of stable isotope ratios of size-fractionated zooplankton in the Bay of Marseille (NW Mediterranean Sea). **Journal of plankton research**, v. 36, p. 145-156, 2014.

BANSE, K. Zooplankton: pivotal role in the control of ocean production: I. Biomass and production. **ICES Journal of marine Science**, v. 52, p. 265-277, 1995.

BENEDETTI, F.; GASPARINI, S.; AYATA, S. D. Identifying copepod functional groups from species functional traits. **Journal of Plankton Research**, v. 38, p. 159-166, 2016.

BERTRAND, A. **ABRACOS 2 cruise, RV Antea**. 2017. Disponível em: https://doi.org/10.17600/17004100. Acesso em: 05/07/2019.

BERTRAND, A. **ABRACOS cruise, RV Antea**. 2015. Disponível em: http://dx.doi.org/10.17600/15005600. Acesso em: 30/03/2018.

BLANCHARD, J. L. *et al*. From bacteria to whales: using functional size spectra to model marine ecosystems. **Trends in ecology & evolution**, v. 32, n. 3, p. 174-186, 2017.

BODE, A. *et al*. Stable nitrogen isotope studies of the pelagic food web on the Atlantic shelf of the Iberian Peninsula. **Progress in Oceanography**, v. 74, n. 2-3, p. 115-131, 2007.

BOLTOVSKOY, D. (ed.) **South Atlantic Zooplankton**. Backhuys Publishers, Leiden, 1999.

BOUDREAU, P. R.; DICKIE, L. M. Biomass spectra of aquatic ecosystems in relation to fisheries yield. **Canadian Journal of Fisheries and Aquatic Sciences**, v. 49, n. 8, p. 1528-1538, 1992.

BOYD, P. W. et al. Transformations of biogenic particulates from the pelagic to the deep ocean realm. **Deep Sea Research Part II:** Topical Studies in Oceanography, v. 46, n. 11-12, p. 2761-2792, 1999.

BRANDAO, M. C.; KOETTKER, A. G.; FREIRE, A. S. Abundance and composition of decapod larvae at Saint Paul's Rocks (equatorial Atllantic). **Marine Ecology**, v. 34, n. 2, p. 171-185, 2013.

BRANDÃO, M. C.; KOETTKER, A. G.; FREIRE, A. S. Distribution of decapod larvae in the surface layer of an isolated equatorial oceanic archipelago: the cases of benthic Grapsus grapsus (Brachyura: Grapsidae) and pelagic Sergestes edwardsi (Dendrobranchiata: Sergestidae). **Helgoland Marine Research**, v. 67, n. 1, p. 155-165, 2013.

BRANDINI, F. P. *et al*. **Planctonologia na plataforma continental do Brasil -** diagnose e revisão bibliográfica. Rio de Janeiro: FEMAR, 1997. (Fundação de Estudos do MAR, 195).

BRASIL. Ministério do Meio Ambiente. **Avaliação do potencial sustentável de recursos vivos na zona econômica exclusiva.** Brasília: ReviZEE, 2006. 303p.

BUENO, M. *et al*. Plankton in waters adjacent to the Laje de Santos state marine conservation park, Brazil: spatio-temporal distribution surveys. **Brazilian Journal of Oceanography**, v. 65, n. 4, p. 564-575, 2017.

BURRIDGE, A. K. *et al*. Diversity and abundance of pteropods and heteropods along a latitudinal gradient across the Atlantic Ocean. **Progress in Oceanography**, v. 158, p. 213-223, 2017.

CAMPELO, R. P. S. *et al*. Small-scale distribution of the mesozooplankton in a tropical insular system. **Brazilian Journal of Oceanography**, v. 66, n. 1, p. 15-29, 2018.

CAMPELO, R. P. S. *et al*. Zooplankton biomass around marine protected islands in the tropical Atlantic Ocean. **Journal of Sea Research**, v. 154, p. 101810, 2019.

CHANG, C. Y. *et al*. Methods of training set construction: towards improving performance for automated mesozooplankton image classification systems. **Continental Shelf Research**, v. 36, p. 19-28, 2012.

COHEN, J. E. *et al*. Body sizes of animal predators and animal prey in food webs. **Journal of animal ecology**, p. 67-78, 1993.

COTTÉ, C.; SIMARD, Y.. Formation of dense krill patches under tidal forcing at whale feeding hot spots in the St. Lawrence Estuary. **Marine Ecology Progress Series**, v. 288, p. 199-210, 2005.

COWEN, R. K.; HARE, J. A.; FAHAY, M. P. Beyond hydrography: can physical processes explain larval fish assemblages within the Middle Atlantic Bight?. **Bulletin of Marine Science**, v. 53, n. 2, p. 567-587, 1993.

DAI, L. *et al*. Zooplankton abundance, biovolume and size spectra down to 3000 m depth in the western tropical North Pacific during autumn 2014. **Deep Sea Research Part I:** Oceanographic Research Papers, v. 121, p. 1-13, 2017.

DAI, L. *et al*. Zooplankton abundance, biovolume and size spectra at western boundary currents in the subtropical North Pacific during winter 2012. **Journal of Marine Systems**, v. 155, p. 73-83, 2016.

DELINCÉ, G. Productivity and fish production. *In*: DELINCÉ, G. **The Ecology of the Fish Pond Ecosystem**. Dordrecht: Springer, 1992. p. 127-205.

DÍAZ, X. F. G.; GUSMÃO, L. M. O.; NEUMANN-LEITÃO, S. Biodiversidade e dinâmica espaço-temporal do zooplâncton. **O Arquipélago de São Pedro e São Paulo**, v. 10, p. 139-149, 2009.

DOTY, M. S.; OGURY, M. The island mass effect. **Journal Du Conseil Permanent International pour le Exploration de la Mer**, 22, 33-37, 1956.

DUCKLOW, H. W.; STEINBERG, D. K.; BUESSELER, K. O. Upper ocean carbon export and the biological pump. **Oceanography-**washington dc-oceanography society-, v. 14, n. 4, p. 50-58, 2001.

EDUARDO, L. N. *et al*. Hatchetfishes (Stomiiformes: Sternoptychidae) biodiversity, trophic ecology, vertical niche partitioning and functional roles in the western Tropical Atlantic. **Progress in Oceanography**, p. 102389, 2020.

EDWARDS, A. M. *et al*. Testing and recommending methods for fitting size spectra to data. **Methods in Ecology and Evolution**, v. 8, n. 1, p. 57-67, 2017.

ESPINASSE, B. *et al*. Patterns of variations in C and N stable isotope ratios in size-fractionated zooplankton in the Gulf of Lion, NW Mediterranean Sea. **Journal of plankton research**, v. 36, n. 5, p. 1204-1215, 2014.

FAO species catalogue - marine lobsters of the world. Roma, FAO Fisheries Synopsis, v. 13, n. 125, 292 p., 1991.

FOLT, C. L.; BURNS, C. W. Biological drivers of zooplankton patchiness. **Trends in Ecology & Evolution**, v. 14, n. 8, p. 300-305, 1999.

FOREST, A. *et al*. Size distribution of particles and zooplankton across the shelf-basin system in southeast Beaufort Sea: combined results from an Underwater Vision Profiler and vertical net tows. **Biogeosciences**, v. 9, n. 4, p. 1301, 2012.

FRANCE, R.; CHANDLER, M.; PETERS, R. Mapping trophic continua of benthic food webs: body size δ^{15}N relationships. **Mar Ecol Prog Ser** 174:301–306, 1998.

FRANCO, B. C.; MUELBERT, J. H.; MATA, M. M. Mesoscale physical processes and the distribution and composition of ichthyoplankton on the southern Brazilian shelf break. **Fisheries Oceanography**, v. 15, n. 1, p. 37-43, 2006.

FRY, B. Food web structure on Georges Bank from stable C, N, and S isotopic compositions. **Limnology and oceanography**, v. 33, n. 5, p. 1182-1190, 1988.

FRY, B. **Stable isotope ecology**. New York: Springer, 2006.
FRY, B.; QUIÑONES, R. B. Biomass spectra and stable isotope indicators of trophic level in zooplankton of the northwest Atlantic. **Marine Ecology Progress Series**, p. 201-204, 1994.

FRY, B.; WAINRIGHT, S. C. Diatom sources of ^{13}C-rich carbon in marine food webs. **Marine Ecology Progress Series**, p. 149-157, 1991.

GARCÍA-COMAS, C. et al. Mesozooplankton size structure in response to environmental conditions in the East China Sea: How much does size spectra theory fit empirical data of a dynamic coastal area?. **Progress in Oceanography**, v. 121, p. 141-157, 2014.

GENIN, A. Bio-physical coupling in the formation of zooplankton and fish aggregations over abrupt topographies. **Journal of Marine systems**, v. 50, n. 1-2, p. 3-20, 2004.

GIERING, S. L. C. et al. Seasonal variation of zooplankton community structure and trophic position in the Celtic Sea: a stable isotope and biovolume spectrum approach. **Progress in Oceanography**, v. 177, p. 101943, 2019.

GLAZIER, D. S. Beyond the '3/4-power law': Variation in the intra- and interspecific scaling of metabolic rate in animals. **Biological Review**, v. 80, p. 611–662, 2005.

GORSKY, G. et al. Digital zooplankton image analysis using the ZooScan integrated system. **Journal of plankton research**, v. 32, n. 3, p. 285-303, 2010.

GOVE, J. M. et al. Near-island biological hotspots in barren ocean basins. **Nature communications**, v. 7, n. 1, p. 1-8, 2016.

GRAHAM, Brittany S. *et al*. Using isoscapes to trace the movements and foraging behavior of top predators in oceanic ecosystems. *In*: **Isoscapes**. Dordrecht: Springer, 2010. p. 299-318.

GREY, J. The use of stable isotope analyses in freshwater ecology: current awareness. **Polish Journal of Ecology**, v. 54, n. 4, p. 563-584, 2006.

GROSJEAN, P. *et al*. Enumeration, measurement, and identification of net zooplankton samples using the ZOOSCAN digital imaging system. **ICES Journal of Marine Science**, v. 61, n. 4, p. 518-525, 2004.

GUIDI, L. *et al*. Plankton networks driving carbon export in the oligotrophic ocean. **Nature**, v. 532, n. 7600, p. 465-470, 2016.

GUSMÃO, L. M. O. *et al*. Jellyfish diversity and distribution patterns in the tropical Southwestern Atlantic. **Marine Ecology**, v. 36, n. 1, p. 93-103, 2015.

HANSEN, B.; BJORNSEN, P. K.; HANSEN, P. J. The size ratio between planktonic predators and their prey. **Limnology and oceanography**, v. 39, n. 2, p. 395-403, 1994.

HAUSS, H. *et al*. Relative inputs of upwelled and atmospheric nitrogen to the eastern tropical North Atlantic food web: Spatial distribution of δ15N in mesozooplankton and relation to dissolved nutrient dynamics. **Deep Sea Research Part I:** Oceanographic Research Papers, v. 75, p. 135-145, 2013.

HIROTA, Y.; HASEGAWA, S. The zooplankton biomass in the Sea of Japan. **Fisheries Oceanography**, v. 8, n. 4, p. 274-283, 1999.

HOLTHUIS, L. B. The Decapoda Macrura of the Snellius Expedition. I. The Stenopodidae, Nephropsidae, Scyllaridae and Palinuridae (Biological results of the Snellius Expedition, XIV). **Temminckia**, v. 7, p. 1-178, 1946.

HOWATT, T. M.; ALLEN, S. E. Impact of the continental shelf slope on upwelling through submarine canyons. **Journal of Geophysical Research: Oceans**, v. 118, n. 10, p. 5814-5828, 2013.

HUNT, B. P. V. *et al*. A coupled stable isotope-size spectrum approach to understanding pelagic food-web dynamics: a case study from the southwest sub-tropical Pacific. **Deep Sea Research Part II:** Topical Studies in Oceanography, v. 113, p. 208-224, 2015.

IKEDA, T. Nutritional ecology of marine zooplankton. **Memoirs of the Faculty of Fisheries Hokkaido University**, v. 22, n. 1, p. 1-97, 1974.

JALES, M. C. **Influência das condições oceanográficas sobre a estrutura da comunidade fitoplanctônica no Atol das Rocas, Atlântico Sul Equatorial, Brasil**. 97f. Tese (Doutorado em Oceanografia) - Universidade Federal de Pernambuco, Recife, 2015.

JENNINGS, S.; OLIVEIRA, J. A. A; WARR, K. J. Measurement of body size and abundance in tests of macroecological and food web theory. **Journal of Animal Ecology**, v. 76, n. 1, p. 72-82, 2007.

JENNINGS, S.; WARR, K. J.; MACKINSON, S. Use of size-based production and stable isotope analyses to predict trophic transfer efficiencies and predator-prey body mass ratios in food webs. **Marine Ecology Progress Series**, v. 240, p. 11-20, 2002.

KÄMPF, J. On the magnitude of upwelling fluxes in shelf-break canyons. **Continental Shelf Research**, v. 27, n. 17, p. 2211-2223, 2007.

KATSURAGAWA, M. *et al*. Patterns in larval fish assemblages under the influence of the Brazil current. **Continental Shelf Research**, v. 89, p. 103-117, 2014.

Kerr, S. R., Dickie, L. M. **The biomass spectrum**: a predator–prey theory of aquatic production. NewYork: Columbia University Press, 2001.

KIØRBOE, T. Optimal swimming strategies in mate-searching pelagic copepods. **Oecologia**, v. 155, n. 1, p. 179-192, 2008.

KLINE, T. C.; PAULY, D. Cross-validation of trophic level estimates from a mass-balance model of Prince William Sound using $^{15}N/^{14}N$ data. *In*: **Alaska Sea Grant College**. 1998.

KOBLITZ, V. S. O.; LARRAZÁBAL, M. E. L. Characterization of the geographical distribution pattern of the family Limacinidae Gray, 1840 (Mollusca-Gastropoda) in the waters of Northeastern of Brazil. **Biota Neotropica**, v. 14, n. 2, 2014.

KOETTKER, A. G.; FREIRE, A. S.; SUMIDA, P. Y. G. Temporal, diel and spatial variability of decapod larvae from St Paul's Rocks, an equatorial oceanic island of Brazil. **Journal of the Marine Biological Association of the United Kingdom**, v. 90, n. 6, p. 1227-1239, 2010.

KOPPELMANN, R. *et al*. Trophic relationships of zooplankton in the eastern Mediterranean based on stable isotope measurements. **Journal of Plankton Research**, v. 31, n. 6, p. 669-686, 2009.

KRUPICA, K. L.; SPRULES, W. G.; HERMAN, A. W. The utility of body size indices derived from optical plankton counter data for the characterization of marine zooplankton assemblages. **Continental Shelf Research**, v. 36, p. 29-40, 2012.

KRUSE, S.; BREY, T.; BATHMANN, U. Role of midwater chaetognaths in Southern Ocean pelagic energy flow. **Marine Ecology Progress Series**, v. 416, p. 105-113, 2010.

LALLI, C. M.; GILMER, R. W. **Pelagic snails:** the biology of holoplanktonic gastropod mollusks. Redwood City, CA: Stanford University Press, 1989.

LAND, M. F. Scanning eye movements in a heteropod mollusc. **Journal of Experimental Biology**, v. 96, n. 1, p. 427-430, 1982.

LARRAZÁBAL, M. E.; OLIVEIRA, V. S. Thecosomata e Gymnosomata (Mollusca, Gastropoda) da cadeia Fernando de Noronha, Brasil. **Revista Brasileira de Zoologia**, v. 20, n. 2, p. 351-360, 2003.

LEE, C.; WAKEHAM, S.; ARNOSTI, C. Particulate organic matter in the sea: the composition conundrum. **AMBIO:** A Journal of the Human Environment, v. 33, n. 8, p. 565-575, 2004.

LEGENDRE, P.; LEGENDRE, L. **Numerical ecology**. 2 ed. The Netherlands: Elsevier, 1998.

LEGENDRE, Pierre; GALLAGHER, Eugene D. Ecologically meaningful transformations for ordination of species data. **Oecologia**, v. 129, n. 2, p. 271-280, 2001.

LEMUS-SANTANA, E. *et al*. Population structure and mating encounter rates in a marine pelagic invertebrate, Firoloida desmarestia (Mollusca). **Sexuality and Early Development in Aquatic Organisms**, v. 1, n. 2, p. 163-173, 2015.

LESUEUR, C. A. Characters of a new genus, an descriptions of three new species upon which it is formed; discovered in the Atlantic Ocean, in the months of March and April, 1816; Lat. 22 9'. **Journal of the Academy of Natural Sciences of Philadelphia**, v. 1, n. 3, p. 37-41, 1817.

LIRA, S. M. A. et al. New records of the larval forms Cerataspis monstrosa and Amphionides reynaudii (Crustacea: Decapoda) from the western tropical Atlantic. **Zootaxa**, v. 4237, n. 2, p. zootaxa. 4237.2. 7-zootaxa. 4237.2. 7, 2017.

LIRA, S. M. A. et al. Spatial and nycthemeral distribution of the zooneuston off Fernando de Noronha, Brazil. **Brazilian Journal of Oceanography**, v. 62, n. 1, p. 35-45, 2014.

LIRA, S. M. A.; SANTANA, C. S.; SCHWAMBORN, R. First record of Naushonia sp.(Decapoda: Laomediidae) larva from the Equatorial Atlantic. **Zootaxa**, v. 4387, n. 1, p. 183-194, 2018.

LONGHURST, A. R. Role of the marine biosphere in the global carbon cycle. **Limnology and Oceanography**, v. 36, n. 8, p. 1507-1526, 1991.

MACEDO-SOARES, L. C. P.; FREIRE, A. S.; MUELBERT, J. H. Small-scale spatial and temporal variability of larval fish assemblages at an isolated oceanic island. **Marine Ecology Progress Series**, v. 444, p. 207-222, 2012.

MAPS, F. *et al*. Linking acoustics and finite-time L yapunov exponents reveals areas and mechanisms of krill aggregation within the G ulf of S t. L awrence, eastern C anada. **Limnology and Oceanography**, v. 60, n. 6, p. 1965-1975, 2015.

MARCOLIN, C. R. *et al*. Plankton and seston size spectra estimated by the LOPC and ZooScan in the Abrolhos Bank ecosystem (SE Atlantic). **Continental Shelf Research**, v. 70, p. 74-87, 2013.

MATSUNO, K.; YAMAGUCHI, A.; IMAI, I. Biomass size spectra of mesozooplankton in the Chukchi Sea during the summers of 1991/1992 and 2007/2008: an analysis using optical plankton counter data. **ICES Journal of Marine Science**, v. 69, n. 7, p. 1205-1217, 2012.

MAUCHLINE, J. The biology of calanoid copepods. **Advances in marine biology**, v. 33, 1998.

MCCONNAUGHEY, T.; MCROY, C. P. Food-web structure and the fractionation of carbon isotopes in the Bering Sea. **Marine biology**, v. 53, n. 3, p. 257-262, 1979.

MCCUTCHAN J. R.; JAMES, H. *et al*. Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. **Oikos**, v. 102, n. 2, p. 378-390, 2003.

MELO JÚNIOR, M. *et al*. Temporal changes in pelagic copepod assemblages off Ubatuba, Brazil. **Marine Ecology**, v. 37, n. 4, p. 877-890, 2016.

MELO, P. A. M. C. *et al*. Diurnal and spatial variation of the mesozooplankton community in the Saint Peter and Saint Paul Archipelago, Equatorial Atlantic. **Marine Biodiversity Records**, v. 5, 2012.

MÉNARD, F. *et al*. Stable isotope patterns in micronekton from the Mozambique Channel. **Deep Sea Research Part II: Topical Studies in Oceanography**, v. 100, p. 153-163, 2014.

MICHAELS, A. F.; SILVER, M. W. Primary production, sinking fluxes and the microbial food web. **Deep Sea Research Part A.** Oceanographic Research Papers, v. 35, n. 4, p. 473-490, 1988.

MICHENER, R.; LAJTHA, K. (Ed.). **Stable isotopes in ecology and environmental science**. Hoboken, NJ: John Wiley & Sons, 2008.

MILLER, T. W.; BRODEUR, R. D.; RAU, G. H. Carbon stable isotopes reveal relative contribution of shelf-slope production to the Northern California Current pelagic community. **Limnology and Oceanography**, v. 53, n. 4, p. 1493-1503, 2008.

MINAGAWA, M.; WADA, E. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between δ^{15}N and animal age. **Geochimica et cosmochimica acta**, v. 48, n. 5, p. 1135-1140, 1984.

MOMPEÁN, C. et al. Spatial patterns of plankton biomass and stable isotopes reflect the influence of the nitrogen-fixer Trichodesmium along the subtropical North Atlantic. **Journal of plankton research**, v. 35, n. 3, p. 513-525, 2013.

MONTOYA, J. P.; CARPENTER, E. J.; CAPONE, D. G. Nitrogen fixation and nitrogen isotope abundances in zooplankton of the oligotrophic North Atlantic. **Limnology and Oceanography**, v. 47, n. 6, p. 1617-1628, 2002.

MOORE, S. K.; SUTHERS, I. M. Evaluation and correction of subresolved particles by the optical plankton counter in three Australian estuaries with pristine to highly modified catchments. **Journal of Geophysical Research:** Oceans, v. 111, n. C5, 2006.

MORENO-ALCÁNTARA, M. *et al*. Holoplanktonic molluscs (Gastropoda: Pterotracheoidea, Thecosomata and Gymnosomata) from the southern Mexican Pacific. **Journal of Molluscan Studies**, v. 80, n. 2, p. 131-138, 2014.

NEUMANN-LEITÃO, S. *et al*. Connectivity Between Coastal and Oceanic Zooplankton From Rio Grande do Norte in the Tropical Western Atlantic. **Frontiers in Marine Science**, v. 6, p. 287, 2019.

NEUMANN-LEITÃO, S. *et al*. Diversity and distribution of the mesozooplankton in the tropical Southwestern Atlantic. **Journal of Plankton Research**, v. 30, n. 7, p. 795-805, 2008.

NEUMANN-LEITÃO, S. *et al*. Mesozooplankton biomass and diversity in coastal and oceanic waters off North-Eastern Brazil. **Archive of Fishery and Marine Research**, v. 47, n. 2-3, p. 153-165, 1999.

NEWELL, G. E.; NEWELL, R. C. S. **Marine plankton:** a practical guide. 1963.

ODUM, E. P.; BARRETT, G. W. **Fundamentals of ecology**. Philadelphia: Saunders, 1971.

PAGÈS, F. et al. Gelatinous zooplankton assemblages associated with water masses in the Humboldt Current System, and potential predatory impact by Bassia bassensis (Siphonophora: Calycophorae). **Marine Ecology Progress Series**, v. 210, p. 13-24, 2001.

PETCHEY, O. L. *et al*. Size, foraging, and food web structure. **Proceedings of the National Academy of Sciences**, v. 105, n. 11, p. 4191-4196, 2008.

PETERSON B. J.; FRY, B. Stable isotopes in ecosystem studies. **Ann Rev Ecol Syst** 18:293–320, 1987

PETERSON R. G., and STRAMMA, L. Upper-level circulation in the South Atlantic Ocean. **Prog. Oceanogr**. 26(1), 1-73, 1991.

PINTO, N. C. T.; MAFALDA, P.; SANTOS, A. T. Caracterização do zooplâncton da Reserva Biológica do Atol das Rocas, na Campanha de Março-1991 (verão). **Trab. Oceanog. Univ. Fed. PE**, v. 25, p. 31-46, 1997.

PLATT, T.; DENMAN, K. Organisation in the pelagic ecosystem. **Helgoländer Wissenschaftliche Meeresuntersuchungen**, v. 30, n. 1, p. 575-581, 1977.

POST, D. M. Using stable isotopes to estimate trophic position: models, methods, and assumptions. **Ecology**, v. 83, n. 3, p. 703-718, 2002.

POST, D. M., Pace ML, Hairston NG. Ecosystem size determines food-chain length in lakes. **Nature,** 405:1047–1049, 2000.

QUIÑONES, R. A. A comment on the use of allometry in the study of pelagic ecosystem processes. **Scientia Marina(Barcelona)**, v. 58, n. 1, p. 11-16, 1994.

RICE, J.; GISLASON, H. Patterns of change in the size spectra of numbers and diversity of the North Sea fish assemblage, as reflected in surveys and models. **ICES Journal of Marine Science**, v. 53, n. 6, p. 1214-1225, 1996.

RODRIGUES, R. R.; ROTHSTEIN, L. M.; WIMBUSH, M. Seasonal variability of the South Equatorial Current bifurcation in the Atlantic Ocean: a numerical study. **Journal of Physical Oceanography,** v. 37, p. 16-30, 2007.

SAILLEY, S. F. *et al*. Impact of zooplankton food selectivity on plankton dynamics and nutrient cycling. **Journal of Plankton Research**, v. 37, n. 3, p. 519-529, 2015.

SAIZ, E. *et al*. Feeding and production of zooplankton in the Catalan Sea (NW Mediterranean). **Progress in Oceanography**, v. 74, n. 2-3, p. 313-328, 2007.

SANTANA, C. S. *et al*. Spatio-temporal variation of planktonic decapods along the leeward coast of the Fernando de Noronha archipelago, Brazil. **Brazilian Journal of Oceanography**, v. 66, n. 1, p. 1-14, 2018.

SANTANA, J. R. *et al*. Ichthyoplankton community structure on the shelf break off northeastern Brazil. **Anais da Academia Brasileira de Ciências**, v. 92, n. 2, 2020.

SATO, K. *et al.* Spatial and temporal changes in zooplankton abundance, biovolume, and size spectra in the neighboring waters of Japan: analyses using an optical plankton counter. **Zoological Studies**, v. 54, n. 1, p. 18, 2015.

SCHOTT, F. A. *et al*. The shallow and deep western boundary circulation of the South Atlantic at 5–11 S. **Journal of Physical Oceanography**, v. 35, n. 11, p. 2031-2053, 2005.

SCHUKAT, A. *et al*. Respiration rates and abundances of dominant copepods of the northern Benguela Current System. MARUM - Center for Marine Environmental Sciences, University Bremen, **PANGAEA**. 2013.

SCHULTES, S. *et al*. Influence of physical forcing on mesozooplankton communities at the Ushant tidal front. **Journal of Marine Systems**, v. 109, p. S191-S202, 2013.

SCHWAMBORN, R. *et al*. Distribution and dispersal of decapod crustacean larvae and other zooplankton in the Itamaracá estuarine system, Brazil. **Tropical Oceanography**, v. 29, n. 1, p. 1-18, 2001.

SCHWAMBORN, R. *et al*. Dynamic patterns of zooplankton transport and migration in Catuama Inlet (Pernambuco, Brazil), with emphasis on the decapod crustacean larvae. **Latin American Journal of Aquatic Research**, v. 36, n. 1, p. 109-113, 2008.

SCHWAMBORN, R. *et al*. How important are mangroves as a carbon source for decapod crustacean larvae in a tropical estuary?. **Marine Ecology Progress Series**, v. 229, p. 195-205, 2002.

SCHWAMBORN, R. *et al*. Stable isotope composition of particulate organic matter and zooplankton in North-East Brazilian shelf waters. **Archive of Fishery and Marine Research**, v. 47, n. 2/3, p. 201-210, 1999.

SCHWAMBORN, R. *et al*. The contribution of estuarine decapod larvae to marine zooplankton communities in North-East Brazil. **Archive of Fishery and Marine Research**, v. 47, n. 2/3, p. 167-182, 1999.

SCHWAMBORN, R.; BONECKER, A. C. T. Seasonal changes in the transport and distribution of meroplankton into a Brazilian estuary with emphasis on the importance of floating mangrove leaves. **Brazilian Archives of Biology and Technology**, v. 39, p. 451-462, 1996.

SCHWAMBORN, R.; GIARRIZZO, T. Stable isotope discrimination by consumers in a tropical mangrove food web: how important are variations in C/N ratio?. **Estuaries and coasts**, v. 38, n. 3, p. 813-825, 2015.

SEAPY, R. R. Offshore–inshore and vertical distributional patterns of heteropod mollusks off leeward Oahu, Hawaii. **Marine Biology**, v. 154, n. 6, p. 985-995, 2008.

SEAPY, R. R. Patterns of vertical distribution in epipelagic heteropod molluscs off Hawaii. **Marine ecology progress series. Oldendorf**, v. 60, n. 3, p. 235-246, 1990.

SEAPY, R. R.; LALLI, C. M.; WELLS, F. E. Heteropoda from western Australian waters. **The marine Flora and Fauna of Dampier, Western Australia. Western Australian Museum, Perth**, p. 513-546, 2003.

SHELDON, R. W.; PRAKASH, A_; SUTCLIFFE JR, WHr. The size distribution of particles in the Ocean 1. **Limnology and oceanography**, v. 17, n. 3, p. 327-340, 1972.

SHELDON, R. W.; SUTCLIFFE JR, W. H.; PARANJAPE, M. A. Structure of pelagic food chain and relationship between plankton and fish production. **Journal of the Fisheries Board of Canada**, v. 34, n. 12, p. 2344-2353, 1977.

SHIN, Yunne-Jai et al. Using size-based indicators to evaluate the ecosystem effects of fishing. **ICES Journal of marine Science**, v. 62, n. 3, p. 384-396, 2005.

SILVA, N. L.; MARCOLIN, C. R.; SCHWAMBORN, R. Using image analysis to assess the contributions of plankton and particles to tropical coastal ecosystems. **Estuarine, Coastal and Shelf Science**, v. 219, p. 252-261, 2019.

SOUZA, C. S. et al. Size Spectra Modeling of Mesozooplankton over a Tropical Continental Shelf. **Journal of Coastal Research**, n. 2020, p. 000-000, 2020.

SPRULES, W. G.; MUNAWAR, M. Plankton size spectra in relation to ecosystem productivity, size, and perturbation. **Canadian Journal of Fisheries and Aquatic Sciences**, v. 43, n. 9, p. 1789-1794, 1986.

STRAMMA, L.; ENGLAND, M. On the water masses and mean circulation of the South Atlantic Ocean. **J. Geophys. Res**., 104(C9), 20863-20883, 1999.

STRAMMA, L.; FISCHER, J.; REPPIN, J. The north brazil undercurrent. **Deep Sea Research Part I:** Oceanographic Research Papers, v. 42, n. 5, p. 773-795, 1995.

SWARTZMAN, G. et al. Poleward and equatorward currents in the Pacific Eastern Boundary Current in summer 1995 and 1998 and their relationship to the distribution of euphausiids. **Deep Sea Research Part II:** Topical Studies in Oceanography, v. 52, n. 1-2, p. 73-88, 2005.

TER BRAAK, C. J. F.; SMILAUER, P. **CANOCO reference manual and CanoDraw for Windows user's guide: software for canonical community ordination (version 4.5)**. 2002.

TESCH, J. J. **Heteropoda. The Carlsberg Foundation's Oceanographical Expedition round the world 1928– 30 and previous 'Dana'expeditions**. Dana Report, 1949.

THOMPSON, G. A.; DINOFRIO, E. O.; ALDER, V. A. Structure, abundance and biomass size spectra of copepods and other zooplankton communities in upper waters of the Southwestern Atlantic Ocean during summer. **Journal of plankton research**, v. 35, n. 3, p. 610-629, 2013.

TOSETTO, E.; NEUMANN-LEITÃO, S.; JÚNIOR, M. N. Sampling planktonic cnidarians with paired nets: Implications of mesh size on community structure and abundance. **Estuarine, Coastal and Shelf Science**, v. 220, p. 48-53, 2019.

TSENG, L. C. et al. Can different mesh sizes affect the results of copepod community studies?. **Journal of Experimental Marine Biology and Ecology**, v. 398, n. 1-2, p. 47-55, 2011.

VAN DER SPOEL, S. **Pseudothecosomata, Gymnosomata and Heteropoda (Gastropoda)**. Utrecht: Bohn, Scheltema & Holkema, 1976. 484p.

VANDER ZANDEN, JAKE M.; FETZER, William W. Global patterns of aquatic food chain length. **Oikos**, v. 116, n. 8, p. 1378-1388, 2007.

VANDERKLIFT, M. A.; PONSARD, S. Sources of variation in consumer-diet δ^{15}N enrichment: a meta-analysis. **Oecologia**, v. 136, n. 2, p. 169-182, 2003.

VANDROMME, P. et al. Assessing biases in computing size spectra of automatically classified zooplankton from imaging systems: A case study with the ZooScan integrated system. **Methods in Oceanography**, v. 1, p. 3-21, 2012.

VANDROMME, P. et al. Springtime zooplankton size structure over the continental shelf of the Bay of Biscay. **Ocean Science**, v. 10, n. 5, p. 821-835, 2014.

VANNUCCI, M. Resultados científicos do cruzeiro do "Baependi" e do "Vega" à Ilha da Trindade: o gênero Firoloida, Prosobranchia Heteropoda, **Boletim do Instituto Paulista de Oceanografia**, Vol. 2, n. 2, pp. 73-93. 1951.

VARGAS, G. *et al.* A new multifrequency acoustic method for the discrimination of biotic components in pelagic ecosystems: Application in a high diversity tropical ecosystem off

Northeast Brazil. *In*: **2017 IEEE/OES Acoustics in Underwater Geosciences Symposium (RIO Acoustics)**. IEEE, 2017. p. 1-8.

WANG, M. *et al*. Nutritional composition of potential zooplankton prey of the spiny lobster phyllosoma (Jasus edwardsii). **Marine and Freshwater Research**, v. 65, n. 4, p. 337-349, 2014.

WANG, S. W. *et al*. Fatty acid and stable isotope characteristics of sea ice and pelagic particulate organic matter in the Bering Sea: tools for estimating sea ice algal contribution to Arctic food web production. **Oecologia**, v. 174, n. 3, p. 699-712, 2014.

YAMAGUCHI, A. Comparison of mesozooplankton biomass down to the greater depths (0-3000 m) between 165°E and 165°W the north pacific ocean: the contribution of large copepod neocalanus cristatus. **Nova Science Publishers.** 2008.

YANG, G. *et al*. Feeding strategies of four dominant copepod species in Prydz Bay, Antarctica: insights from a combined fatty acid biomarker and stable isotopic approach. **Deep Sea Research Part I:** Oceanographic Research Papers, v. 114, p. 55-63, 2016.

YANG, G. *et al*. Regional patterns of δ13C and δ15N stable isotopes of size-fractionated zooplankton in the western tropical North Pacific Ocean. **Deep Sea Research Part I:** Oceanographic Research Papers, v. 120, p. 39-47, 2017.

ZARR, J. H. **Biostatistical analysis**. Upper Saddle River, NJ: Prentic Hall, 1999. 662p

ZHOU, M. et al. Productivity, trophic levels and size spectra of zooplankton in northern Norwegian shelf regions. **Deep Sea Research Part II:** Topical Studies in Oceanography, v. 56, n. 21-22, p. 1934-1944, 2009.

ZHOU, M. What determines the slope of a plankton biomass spectrum?. **Journal of Plankton Research**, v. 28, n. 5, p. 437-448, 2006.

ZHOU, M.; HUNTLEY, M. E. Population dynamics theory of plankton based on biomass spectra. **Marine Ecology Progress Series**, v. 159, p. 61-73, 1997.

ZHU, Y.; TANDE, K. S.; ZHOU, M. Mesoscale physical processes and zooplankton transport-retention in the northern Norwegian shelf region. **Deep Sea Research Part II:** Topical Studies in Oceanography, v. 56, n. 21-22, p. 1922-1933, 2009.