UNIVERSIDADE FEDERAL DE PERNAMBUCO
CENTRO DE BIOCIÊNCIAS
PROGRAMA DE PÓS-GRADUAÇÃO EM BIOLOGIA ANIMAL

MORGANA BRITO LOLAIA

DIVERSIDADE FUNCIONAL E ISOTÓPICA DO MICROZOOPLÂNCTON DE UMA REGIÃO COSTEIRA TROPICAL (BAÍA DE TAMANDARÉ, PERNAMBUCO, BRASIL), DE 2013 A 2019

RECIFE
2023

MORGANA BRITO LOLAIA

DIVERSIDADE FUNCIONAL E ISOTÓPICA DO MICROZOOPLÂNCTON DE UMA REGIÃO COSTEIRA TROPICAL (BAÍA DE TAMANDARÉ, PERNAMBUCO, BRASIL), DE 2013 A 2019

Tese apresentada ao Programa de Pós-Graduação em Biologia Animal da Universidade Federal de Pernambuco, como requisito parcial para obtenção do título de doutor em Biologia Animal. Área de concentração: Biologia Animal

Orientador: Ralf Schwamborn

RECIFE
2023

Catalogação na Fonte:
Bibliotecária Natália Nascimento, CRB4/1743

Lolaia, Morgana Brito.
Diversidade funcional e isotópica do microzooplâncton de uma região costeira tropical (Baía de Tamandaré, Pernambuco,Brasil), de 2013 a 2019. / Morgana Brito Lolaia. – 2023.

122 f. : il., fig.

Orientador: Ralf Schwamborn.

Tese (doutorado) – Universidade Federal de Pernambuco. Centro de Biociências. Programa de Pós-graduação em Biologia animal, 2023.
Inclui referências.

1. Zooplâncton. 2. Diversidade funcional. 3. Isótopos estáveis. 4. Série temporal. 5. Atlântico Sudoeste Tropical. I. Schwamborn, Ralf.(Orient.). II. Título.

587 CDD (22.ed.) UFPE/CB – 2023-218

MORGANA BRITO LOLAIA

DIVERSIDADE FUNCIONAL E ISOTÓPICA DO MICROZOOPLÂNCTON DE UMA REGIÃO COSTEIRA TROPICAL (BAÍA DE TAMANDARÉ, PERNAMBUCO, BRASIL), DE 2013 A 2019

Tese apresentada ao Programa de Pós-Graduação em Biologia Animal da Universidade Federal de Pernambuco, como requisito parcial para a obtenção do título de Doutor em Biologia Animal. Área de concentração: Biologia Animal

Aprovada em: 28 / 07 / 2023

COMISSÃO EXAMINADORA:

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

Prof. Dr. Alexandre Oliveira de Almeida – Titular Interno
Universidade Federal de Pernambuco – UFPE

Prof. Dr. Ralf Tarciso Silva Cordeiro – Titular Interno
Universidade Federal de Pernambuco – UFPE

Profa. Dra. Sigrid Neumann Leitão – Titular Externo
Universidade Federal de Pernambuco – UFPE

Prof. Dr. Mauro de Melo Júnior – Titular Externo
Universidade Federal Rural de Pernambuco – UFRPE

Prof. Dr. André Morgado Esteves – Suplente Interno
Universidade Federal Rural de Pernambuco – UFPE

Prof. Dr. Pedro Augusto Mendes de Castro Melo – Suplente Externo
Universidade Federal Rural de Pernambuco – UFPE

Dedico este trabalho a Deus, por me carregar todo esse período.
Aos meus mestres da vida inteira, meus pais, Maria José e Oliveira.
Ao meu marido, companheiro e amigo, Felipe Lolaia.
Aos meus maiores projetos de amor, meus filhos, Felipe e Lucas.

AGRADECIMENTOS

Como é de concordância de todos, ninguém faz nada sozinho e eu nunca estive sozinha nessa caminhada.

Quero agradecer a Deus por ter me dado essa oportunidade de entrar no Doutorado e por estar ao meu lado em todos os momentos dessa jornada.

Ao meu orientador prof. Dr. Ralf Schwamborn por ter aceitado me orientar em mais um desafio, pela paciência, por me incentivar e ensinar a usar as ferramentas de análises e imagem, o que me permitiu ter mais autonomia no meu trabalho, isso fez toda a diferença! E por ser solícito todas as vezes que precisei dele. Muito obrigada!

Aos colaboradores dos meus artigos, Dr.ª. Gabriela Figueiredo, Dr.ª Gleice Santos, Dr.ª Simone Lira, Dr. Humberto Varona, Profa. Dr.ª Sigrid Neumann-Leitão, Prof. Dr. Gilvan Yogui e Prof. Dr. Ralf Schwamborn. Eu só consegui chegar até aqui porque tive a ajuda e ensinamentos de vocês!

À Universidade Federal de Pernambuco – UFPE e ao Programa de Pós-Graduação em Biologia Animal – PPGBA.

Ao Museu de Oceanografia e ao Laboratório de Compostos Orgânicos em Ecossistemas Costeiros e Marinhos (OrganoMAR) pela infraestrutura, equipamentos e todo suporte para o desenvolvimento desta pesquisa.

À Fundação de Amparo à Ciência e a Tecnologia do Estado de Pernambuco – FACEPE pela concessão da bolsa de Doutorado (Código do Processo: IBPG-1246-2.05/18).

Ao Projeto ESPLAN (CNPq nº 471038/2012-1) e ao projeto INCT AmbTropic (CNPq/FAPESB/CAPES) pelo financiamento do trabalho de campo. Ao Programa de Pesquisa Ecológica de Longa Duração - PELD-TAMS (MCTI / CNPq) e ao Instituto Recifes Costeiros (IRCOS, apoiado pelo ICMBio, SOS Mata Atlântica e Fundação Toyota do Brasil) pelo apoio logístico com as coletas e ao Projeto TRIATLAS (nº 817578).

Ao Centro de Pesquisa e Conservação da Biodiversidade Marinha do Nordeste - CEPENE, pelo suporte na logística, com a disponibilização das lanchas e laboratório em Tamandaré.

À Agência Pernambucana de Águas e Climas – APAC pelos dados de precipitação.

Aos meus queridos coorientandos, Richard Wonder Ramos Mesquita Silva e Mikaelle Helena Santos da Silva, vocês foram uma parte importante dessa etapa da minha vida. As coletas e as ajudas no laboratório foram essenciais para que esta pesquisa acontecesse. Eu aprendi mais do que ensinei!

A todos os barqueiros e ajudantes, tão gentis e trabalhadores, conhecedores das águas de Tamandaré. Vocês fizeram essa pesquisa acontecer.

Aos professores da banca que aceitaram examinar meu trabalho, Prof. Dr. Mauro de Melo Jr, Prof. Dr. Alexandre Oliveira de Almeida, Prof. Dr. Ralf Tarciso Silva Cordeiro, Profa. Dr.ª Sigrid Neumann Leitão, Prof. Dr. André Morgado Esteves e Prof. Dr. Pedro Augusto Mendes de Castro Melo.

A todos os professores e colegas do PPGBA que fizeram parte da minha formação.

Aos coordenadores anteriores Prof. Dr. Ulisses Pinheiros e Prof.ª Dr.ª Bruna Bezerra e aos novos Prof. Dr. Pedro Nunes e Prof. Dr. Leandro Vieira por toda ajuda, principalmente com os relatórios FACEPE.

Ao secretário Manoel Guimarães Jr por ser um profissional competentíssimo e um ser humano incrível! Obrigada por toda ajuda acadêmica e pelas palavras de incentivo!

Aos meus amigos do Labzoo, Denise, Simone Lira, Gabriela, Anne (juntas no sufoco com as análises de isótopos), Nathalia, Gleice, Renata, Claudeilton (Claus), Cynthia, Simone Jorge, Richard, Mikaelle, Ralf (Tarciso), Glenda, Kaio, Gabriel, Ítala, Ályssa, Laís. Vocês são uma grande família! Obrigada pelas trocas de conhecimento, boas conversas, companheirismo e ajuda nessa etapa tão importante da minha vida. “Vai dá tudo certo!”

Aos meus pais, José de Oliveira Brito e Maria José Brito, que tanto se esforçaram em me educar e me ensinar os valores que hoje carrego comigo e por ter me apoiado e ajudado com meus filhos sempre que precisei. Amo vocês eternamente!

Aos meus sogros, Félix Lolaia e Maria da Conceição, que me apoiaram sempre que precisei cuidando dos meus filhos. Amo vocês!

Ao meu marido, Felipe Lolaia, que me apoiou 100% quando decidi fazer o Doutorado e entendeu minha ausência em muitos momentos e me ajudou com nossos filhos sempre que precisei. Amo-te eternamente.

Aos meus filhos, Felipe Filho e Lucas, a razão de eu querer sempre ser melhor, meus maiores tesouros, que entendiam que mamãe tinha que trabalhar mesmo estando em casa, dividindo o tempinho que tinha com eles com o computador. Amo vocês eternamente!

Aos meus irmãos, Jônatas e Monayra, que são meus amigos, e aos meus sobrinhos, Júlio Cesar e Melyna, que são minha alegria.

E a todos que embora não mencionei aqui fizeram parte dessa jornada e contribuíram para a realização desse trabalho.

RESUMO

Análises de diversidade funcional e isótopos estáveis vêm sendo muito utilizadas como ferramentas adicionais ao estudo tradicional da ecologia do zooplâncton. A diversidade funcional é a medida dos valores das espécies, de acordo com seus atributos ou características, que influenciam o funcionamento do ecossistema. Os isótopos estáveis são indicativos de dieta (Carbono) e posição trófica (Nitrogênio) presentes no tecido dos organismos. Estudos de longo prazo são importantes na observação das variações sazonais, interanuais e os efeitos de anomalias climáticas na comunidade microzooplanctônica. Esta tese teve como objetivo principal avaliar relações ecológicas do microzooplâncton através de análises de diversidade funcional e isótopos estáveis e a sua variabilidade influenciada pela sazonalidade, interanualidade e condições ambientais ao longo de uma série temporal. As amostras foram coletadas bimestralmente (junho de 2013 a agosto de 2019) em três estações na Baía de Tamandaré (Pernambuco, Brasil), através de arrastos subsuperficiais com redes cônicas de malha de 64 μm. As amostras foram acondicionadas em potes plásticos contendo formalina a 4%, tamponadas com tetraborato de sódio (5 g L−1). Foram selecionadas quatro amostragens por ano (duas no período seco, duas no período chuvoso). As amostras foram quarteadas, uma parte foi separada para a contagem, medição e identificação do zooplâncton e a outra parte para as análises de isótopos estáveis no espectômetro de massas. Para o cálculo de diversidade funcional, a assembleia de copépodes foi analisada quanto aos seus atributos funcionais e dividida em grupos funcionais. A análise de diversidade funcional mostrou que uma mínima variação das condições ambientais (temperatura e salinidade) afetaram significativamente os grupos funcionais de copépodes (91% da variação explicada) e que o grupo mais abundante apresenta atributos funcionais (características morfológicas e estratégia reprodutiva) que permitiram sua permanência em um ambiente em constantes variações. A análise de isótopos estáveis permitiu detectar o nível trófico de espécies-chave através de uma nova abordagem, “mistura-de-espécies-biomassas-e-isótopos” (em inglês, SBIM) que analisa toda a comunidade. O copépode *Pseudodiaptomus acutus* apresentou o maior nível trófico dentro da comunidade zooplanctônica, enquanto organismos de pequeno porte, como náuplios de copépodes e larvas de poliquetos, apresentaram o menor nível trófico. Esse resultado não seria possível em estudos que analisam apenas algumas espécies pré-selecionadas. Também foram analisados os efeitos da sazonalidade e forçantes climáticas externas (por exemplo, El Niño Oscilação Sul) sobre as condições ambientais e a comunidade. O copépode *Euterpina acutifrons*, o ciliado *Favella ehrenbergii* e “outros ciliados” foram indicadores de variação sazonal, com alta abundância no período chuvoso. Diante deste estudo conclui-se que uma pequena variação dos fatores abióticos, causados pela precipitação na Baía de Tamandaré, é a principal responsável pela variação sazonal e interanual do microzooplâncton, sobretudo nos grupos funcionais de copépodes. O método SBIM é uma nova e importante metodologia para descobrir quais espécies-chave estão ocupando os níveis tróficos a partir de análise de isótopos de toda a comunidade. Os estudos desenvolvidos nesta tese ofereceram um vislumbre dos fatores ecológicos que regem a variabilidade e as relações tróficas do microzooplâncton em um ecossistema costeiro tropical.

Palavras-chave: Zooplâncton; Diversidade funcional; Isótopos estáveis; Série temporal; Atlântico Sudoeste Tropical.

ABSTRACT

Functional diversity and stable isotope analysis have been widely used additionally to the traditional study of zooplankton ecology. Functional diversity is the measure of the values of species, according to their attributes or characteristics, which influence the functioning of the ecosystem. Stable isotopes are indicative of diet (Carbon) and trophic position (Nitrogen) present in the tissue of organisms. Long-term studies are important in observing seasonal and interannual variations and the effects of climate anomalies on the microzooplankton community. This thesis aimed to evaluate the ecological relationships of microzooplankton through analyses of functional diversity and stable isotopes and their variability influenced by seasonality, interannual and environmental conditions along a time series (2013 to 2019). Samples were collected bimonthly between June 2013 and August 2019 at three stations in Tamandaré Bay (Pernambuco, Brazil), through subsurface tows with 64 µm mesh conical nets. The samples were placed in plastic jars containing 4% formalin, buffered with sodium tetraborate (5 g L−1). Four samples were selected per year (two in the dry season, two in the rainy season), except when there were no samples due to bad weather. The samples were divided, one part was separated for counting, measuring and identifying zooplankton and the other part for stable isotope analysis in the mass spectrometer. For the calculation of functional diversity, the copepod assembly was analyzed regarding their functional attributes and divided into functional groups. The functional diversity analysis showed that a minimal variation in environmental conditions (temperature and salinity) significantly affected the functional groups of copepods (91% of the explained variation) and that the most abundant group presents functional attributes (morphological characteristics and reproductive strategy) that allowed its permanence in an environment in constant variations. The analysis of stable isotopes made it possible to detect the trophic level of key species through a new approach, “species-biomass-isotopes-mixture” (SBIM) that analyzes the entire community. The copepod *Pseudodiaptomus acutus* showed the highest trophic level within the zooplankton community, while small organisms, such as copepod nauplii and polychaete larvae, showed the lowest trophic level. This result would not be possible in studies that analyze only a few pre-selected species. The effects of seasonality and external climate forcing (e.g., El Niño Southern Oscillation) on environmental conditions and the community were also analyzed. The copepod *Euterpina acutifrons*, the ciliate *Favella ehrenbergii* and “other ciliates” were indicators of seasonal variation, with high abundance in the rainy season. In view of this study, it is concluded that a small variation in abiotic factors, caused by precipitation in Tamandaré Bay, is the main responsible for the seasonal and interannual variation of microzooplankton, especially in the functional groups of copepods. The SBIM method is an important new approach for discovering which key species are occupying trophic levels based on isotope analysis of the entire community. The studies developed in this thesis offered a glimpse into the ecological factors that drive the variability and trophic relationships of microzooplankton in a tropical coastal ecosystem.

Keywords: Zooplankton; Functional diversity; Stable isotopes; Time series; Southwestern Tropical Atlantic.

LISTA DE ILUSTRAÇÕES

ARTIGO 1 – SEASONAL AND INTERANNUAL DRIVERS SHAPING COASTAL ZOOPLANKTON IN THE SOUTHWESTERN TROPICAL ATLANTIC

ARTIGO 2 – CAN THE STABLE ISOTOPE VARIABILITY IN A ZOOPLANKTON TIME SERIES BE EXPLAINED BY ITS KEY SPECIES?

ARTIGO 3 – THE FUNCTIONAL RESPONSE OF TROPICAL COASTAL COPEPODS TO ENVIRONMENTAL FORCINGS

LISTA DE TABELAS

ARTIGO 1 – SEASONAL AND INTERANNUAL DRIVERS SHAPING COASTAL ZOOPLANKTON IN THE SOUTHWESTERN TROPICAL ATLANTIC

ARTIGO 2 – CAN THE STABLE ISOTOPE VARIABILITY IN A ZOOPLANKTON TIME SERIES BE EXPLAINED BY ITS KEY SPECIES?

ARTIGO 3 – THE FUNCTIONAL RESPONSE OF TROPICAL COASTAL COPEPODS TO ENVIRONMENTAL FORCINGS

SUMÁRIO

1 INTRODUÇÃO

O microzooplâncton é composto por organismos pelágicos microscópicos que, embora possuam certa capacidade de locomoção, são incapazes de se mover independentemente das correntes oceânicas. Esta é uma comunidade-chave nas relações tróficas do ambiente marinho, uma vez que constitui o principal elo entre os organismos autotróficos, como o fitoplâncton e o bacterioplâncton, e os níveis tróficos superiores como larvas de peixes e crustáceos decápodos, muitos deles de grande importância comercial (HAMNER et al., 1988; HAYS; RICHARDSON; ROBINSON, 2005; IKEDA, 1974; TURNER; TESTER, 1992) A comunidade microzooplanctônica tem sido utilizada como indicadora de mudanças climáticas devido ao seu curto ciclo de vida e, por ser livre natante, responde rapidamente às variações ambientais no ecossistema (BEAUGRAND, 2005; HAYS; RICHARDSON; ROBINSON, 2005).

A partir das definições “clássicas” (HARRIS et al., 2000; UNESCO, 1968) de microzooplâncton (20 a 200 µm) e mesozooplâncton (0.2 a 20 mm), diversas abordagens e terminologias têm sido usadas na literatura, geralmente baseando-se nas aberturas das malhas das redes de captura de fato disponíveis. Diversas malhas de redes de plâncton são tipicamente utilizadas para coletar micro- (20, 50, 64, 100, 120 µm), meso- (100, 120, 200, 250, 300, 333 µm), macrozooplâncton (300, 333, 500 µm) e ictioplâncton (300, 333, 500, 800, 1000 µm) (CALAZANS; MUELBERT; MUXAGATA, 2011; NYBAKKEN, 1993). Coletas com garrafas de Niskin ou com garrafas de Von Dhorn também são usadas para amostrar protistas (HARRIS et al., 2000; UNESCO, 1968). Neste trabalho, usaremos o termo “microzooplâncton” (ou simplesmente “zooplâncton”) para nos referir aos organismos coletados com uma rede de plâncton com abertura de malha de 64 µm.

Dentre o zooplâncton marinho, a assembleia de copépodes se destaca pela sua abundância e biomassa, sobretudo em frações < 2000 um e, portanto, é uma importante fonte de carbono na cadeia trófica marinha (BRITO-LOLAIA et al., 2020; DA ROCHA MARCOLIN et al., 2013; DA SILVA et al., 2020; DIAS; BONECKER, 2008). Além disso, seus restos mortais e as pelotas fecais são utilizados como alimento pela alça microbiana e por organismos bentônicos através da neve marinha (ELLIOTT; HARRIS; TANG, 2010; FRANGOULIS et al., 2011). Os copépodes são importantes indicadores ecológicos do funcionamento do ecossistema (CAMPOS et al., 2017) e são um grupo chave na teia trófica marinha, também como predadores de outros consumidores, como os ciliados (GISMERVIK, 2006).

Os ciliados são importantes componentes do microzooplâncton como consumidores de da fração microbiana e fitoplanctônica em ambientes oligotróficos tropicais (LANDRY; HASSETT, 1982). Por serem altamente palatáveis, as espécies de tintinídeos são as presas preferenciais para os táxons do meso e macrozooplâncton (SCHWAMBORN et al., 2006). Ciliados loricados, como os tintinídeos, são importantes indicadores de eutrofização no ecossistema pelágico de águas estuarinas e costeiras (SIVASANKAR et al., 2018), como no ecossistema urbano extremamente poluído da Baía de Guanabara, no Sudeste do Brasil (SCHWAMBORN et al., 2006). As águas costeiras contribuem para o desenvolvimento de grande variação nas espécies de tintinídeos, devido às fortes flutuações físicas e químicas que ocorrem nesse ambiente e pela presença de gradiente estuarino (BAKKER; PHAFF, 1976). Além disso, eles apresentam variações sazonais na sua composição e abundância a depender dos fatores abióticos e disponibilidade de alimento no seu ambiente (ESKINAZI-SANT'ANNA; BJÖRNBERG, 2006; JYOTHIBABU et al., 2008; MONTI et al., 2012).

Alguns descritores ambientais são muito utilizados para avaliar a ecologia do zooplâncton nos sistemas aquáticos, como morfologia, densidade, diversidade, equitabilidade e outros. Embora essas classificações taxonômicas sejam importantes, podem não ser adequadas para muitas avaliações ecológicas (BARNETT; FINLAY; BEISNER, 2007; POMERLEAU; SASTRI; BEISNER, 2015). Contudo, atualmente existem ferramentas adicionais muito úteis para a avaliação do ecossistema. Uma das abordagens amplamente utilizadas para compreender a biodiversidade é o cálculo da diversidade funcional (MASON; MOUILLOT, 2013). Essa diversidade tem um ponto de vista mais ecológico/ecossistêmico que o estudo da taxonomia da espécie e representa uma ferramenta ecológica muito útil para o estudo das comunidades de um ecossistema (BARNETT; FINLAY; BEISNER, 2007; POMERLEAU; SASTRI; BEISNER, 2015).

A diversidade funcional foi definida por Tilman (2001) como a medida dos valores das espécies presentes em um ecossistema, de acordo com seus atributos ou características, que influenciam um ou mais aspectos do funcionamento desse ecossistema. Atributos como morfologia, história de vida, comportamento e características fisiológicas são os traços mais comuns utilizados nas análises de biodiversidade funcional (LITCHMAN; OHMAN; KIØRBOE, 2013; SODRÉ; BOZELLI, 2019).

Outra importante ferramenta no estudo da ecologia da comunidade zooplanctônica é a análise de isótopos estáveis, sendo os isótopos de Carbono (^{13}C) e o de Nitrogênio (^{15}N) alguns dos mais utilizados em pesquisas do zooplâncton. Os isótopos são átomos de um mesmo elemento, que se diferenciam apenas pela quantidade de nêutrons no seu núcleo. A composição isotópica de um elemento é expressa pela relação entre o isótopo raro, por exemplo, ^{13}C e ^{15}N e o isótopo mais abundante, ^{12}C e ^{14}N (FRY, 2006).

Os isótopos estáveis são indicativos de acúmulo de nutrientes, fracionamento metabólico e dieta presentes nos tecidos dos indivíduos no momento da captura (OHMAN; RAU; HULL, 2012; RAU; OHMAN; PIERROT-BULTS, 2003). Para melhor avaliar os efeitos climáticos sobre a comunidade do zooplâncton em escala temporal, seriam necessários dados de taxas de mortalidade e crescimento em longo prazo. Como esse tipo de estudo em amostras conservadas é inviável, o uso de isótopos estáveis como índice em escala temporal da resposta do zooplâncton às variações climáticas é uma eficiente indicação (OHMAN; RAU; HULL, 2012).

As análises de isótopos estáveis vêm sendo muito utilizadas para uma variedade de propósitos nas pesquisas do zooplâncton marinho nas últimas décadas (FRY, 2006; SCHWAMBORN; GIARRIZZO, 2015). O isótopo de carbono ($\delta^{13}C$) é muito utilizado para identificar fontes orgânicas de alimento (dieta), uma vez que as mudanças isotópicas entre presa e predador são mínimas (MCCONNAUGHEY; MCROY, 1979), por outro lado, o isótopo de nitrogênio ($\delta^{15}N$) é utilizado como indicador de posição trófica, pois há enriquecimento do nitrogênio no predador em relação a sua presa (MINAGAWA; WADA, 1984; POST, 2002). Alguns estudos demonstraram um aumento significativo do ^{15}N em copépodes e quetognatos durante mudanças climáticas, como El Niño, em estudos de longo prazo, como consequência do aumento da demanda por nitrato: suplemento na base da cadeia alimentar (OHMAN; RAU; HULL, 2012; RAU; OHMAN; PIERROT-BULTS, 2003).

Atualmente, no Brasil, há poucos estudos de séries temporais do zooplâncton que abordem mais de 3 anos. Estudos de longo prazo desempenham um papel essencial na observação das alterações na comunidade microzooplanctônica, possibilitando analisar variações sazonais ou cíclicas naturais e sucessões anuais do plâncton. Também permite observar os efeitos de anomalias climáticas como El Niño e La Niña, bem como os efeitos de fatores hidrológicos e atmosféricos (DI LORENZO; OHMAN, 2013; MACKAS; BEAUGRAND, 2010; OHMAN; RAU; HULL, 2012; OUBA; ABBOUD-ABI SAAB; STEMMANN, 2016; POMERLEAU; SASTRI; BEISNER, 2015; RAU; OHMAN; PIERROT-BULTS, 2003; ROMAGNAN et al., 2015).

Alguns fatores ambientais como salinidade, temperatura, transparência da água e disponibilidade de alimentos são importantes, pois influenciam a sazonalidade e interanualidade das espécies do microzooplâncton (COYLE; PINCHUK, 2003; D'ALCALÀ et al., 2004; SIOKOU-FRANGOU, 1996), e a precipitação é o principal fator atuando sobre a variabilidade dos fatores ambientais na região costeira do Brasil (BRITO-LOLAIA et al., 2022). Fatores externos podem atuar sobre a sazonalidade ambiental da área costeira do Nordeste. O fenômeno de oscilação sul do El Niño (ENSO) apresenta secas durante eventos de El Niño e chuvas prolongadas durante eventos de La Niña nessa região (HOUNSOU-GBO et al., 2016; HOUNSOU-GBO et al., 2019; SARAVANAN; CHANG, 2000), o que pode levar a importantes mudanças na variação natural da composição do zooplâncton nas áreas costeiras do Brasil.

Áreas marinhas costeiras são regiões de grande perturbações, quando comparadas com áreas oceânicas, devido ao seu regime de marés, ventos que podem causar ressurgências, influência dos estuários formados pelos rios em muitas áreas da costa brasileira, com aportes de água doce, sedimentos, nutrientes e organismos e também pelas ações humanas (turismo desenfreado e descargas de efluentes domésticos e industriais) (DA SILVA et al., 2020; DE SANTANA et al., 2020; HOLT et al., 2010; JUSTIC; RABALAIS; TURNER, 1997; NITTROUER et al., 1995).

A Baía de Tamandaré é caracterizada como uma baía semifechada com recifes de arenito que abrigam uma grande diversidade de espécies, pelágicas e bentônicas, algumas delas endêmicas dessa região (FEITOSA; FERREIRA, 2015; MELO et al., 2010; SANTOS et al., 2015, 2016). A baía recebe influência de estuários formados pelos riachos Mamucabas e Ilhetas que desembocam ao sul, e do Rio Una em eventos de grandes enxurradas. Esses aportes inserem partículas, nutrientes e organismos na baía (BRITO-LOLAIA et al., 2020; DA SILVA et al., 2020; SILVA; MARCOLIN; SCHWAMBORN, 2019). A baía de Tamandaré é parte de uma Área Marinha Protegida "Costa dos Corais" que foi criada em 1997 por decreto Federal. A área tem um recife totalmente fechado para atividades de turismo e pesca (FERREIRA; MAIDA, 2006; FERREIRA; MAIDA; CAVA, 2001) e presta suporte a pescadores que vivem da pesca regulada em seu entorno (PINTO; MOURÃO; ALVES, 2016). Muitos estudos que foram conduzidos na área demonstraram que os recifes de Tamandaré fornecem uma quantidade significativa de larvas meroplanctônicas e outros tipos de organismos para o sistema pelágico da baía (BRITO-LOLAIA et al., 2020; DA SILVA et al., 2020; MELO et al., 2010; SANTOS et al., 2019; SANTOS; BRITO-LOLAIA; SCHWAMBORN, 2017), que suportam a população de peixes pelágicos da região.

Portanto, a presente tese teve como hipóteses que (1) fatores ambientais regulam a variabilidade sazonal na comunidade do zooplâncton e que importantes eventos climáticos, como El Niño (no oceano Pacífico) e maior aquecimento nas águas do Atlântico (EL Niño do Atlântico), têm influência nos regimes de chuvas nas águas costeiras do nordeste do Brasil; (2)

a variação temporal da biomassa relativa de uma ou mais espécies do zooplâncton tem um significativo efeito sobre a variabilidade dos isótopos estáveis ($\delta^{13}C$ e $\delta^{15}N$) e da razão elementar (C/N) de toda a comunidade zooplanctônica, a fim de inferir quais as espécies-chave que comandam essa variabilidade; (3) os traços funcionais, grupos funcionais, indices de diversidade funcional e a abundância da assembleia de copépodes exibem variações sazonais e interanuais e que as variações ambientais e hidrológicas influenciam significantemente esses fatores. Os estudos de longo prazo do microzooplâncton podem contribuir para o entendimento das variações cíclicas naturais e os efeitos de anomalias climáticas sobre esse grupo. O microzooplâncton é um grupo muito importante no ecossistema marinho e, até o momento, pouco se sabia dos efeitos em escala temporal, analisando a diversidade funcional e isótopos estáveis, na comunidade microzooplanctônica marinha costeira do nordeste do Brasil.

1.1 OBJETIVOS

1.1.1 Objetivo geral

Avaliar o microzooplâncton de uma área costeira tropical, Baía de Tamandaré, quanto à abundância, diversidade funcional e isotópica ao longo de uma série temporal (2013 – 2019).

1.1.2 Objetivos específicos

- Analisar os efeitos climáticos na abundância e composição sazonal e interanual do zooplâncton e nas condições ambientais (salinidade, temperatura e transparência da água) em uma série temporal de 7 anos.
- Investigar quais espécies, a partir das variações temporais da biomassa relativa, têm efeito significativo nos isótopos estáveis e na razão elementar de toda a comunidade zooplanctônica.
- Avaliar as variações sazonais, interanuais, hidrológicas e ambientais sobre os traços funcionais, grupos funcionais, índices de diversidade funcional e abundância da assembleia de copépodes.

2 ESTRUTURA DA TESE

Ferramentas de análises, como diversidade funcional e isótopos estáveis, podem fornecer uma avaliação mais ecológica do zooplâncton marinho que as tradicionais. A diversidade funcional avalia as relações ecológicas através da análise dos atributos semelhantes de cada espécie e os isótopos estáveis visa avaliar fontes alimentares e posição trófica das espécies. Esta tese está dividida em 3 capítulos. Cada capítulo apresenta uma ferramenta distinta e, portanto, uma metodologia diferente de análise. O primeiro capítulo apresenta a variação sazonal e interanual do zooplâncton e as relações com descritores ambientais através de análises de variâncias e correlogramas, o segundo capítulo apresenta espécies-chave que contribuem para a variação dos isótopos estáveis do zooplâncton através de uma nova abordagem, a "mistura-de-espécies-biomassas-e-isótopos", e o terceiro capítulo apresenta as análises de diversidade funcional da assembleia de copépodes e sua relação com os descritores ambientais através de análise de redundância (RDA).

Artigo 1 - Seasonal and interannual drivers shaping coastal zooplankton in the Southwestern Tropical Atlantic

Estado: A ser submetido – Progress in Oceanography

Hipótese:

Fatores ambientais regulam a variabilidade sazonal na comunidade do zooplâncton e que importantes eventos climáticos, como El Niño (no oceano Pacífico) e maior aquecimento nas águas do Atlântico (EL Niño do Atlântico), têm influência nos regimes de chuvas nas águas costeiras do nordeste do Brasil

Objetivo geral:

Analisar os efeitos climáticos na abundância e composição sazonal e interanual do zooplâncton e nas condições ambientais (salinidade, temperatura e transparência da água) em uma série temporal de 7 anos.

Artigo 2 - Can the stable isotope variability in a zooplankton time series be explained by its key species?

Estado: publicado - Marine Environmental Research

DOI: https://doi.org/10.1016/j.marenvres.2022.105737.

Hipótese:

A variação temporal da biomassa relativa de uma ou mais espécies do zooplâncton tem um significativo efeito sobre a variabilidade dos isótopos estáveis ($\delta^{13}C$ e $\delta^{15}N$) e da razão elementar (C/N) de toda a comunidade zooplanctônica.

Objetivo geral:

Investigar quais espécies, a partir das variações temporais da biomassa relativa, têm efeito significativo nos isótopos estáveis e na razão elementar de toda a comunidade zooplanctônica.

Artigo 3 - The functional response of tropical coastal copepods to environmental forcings

Estado: a ser submetido – Environmental Research

Hipótese:

Os traços funcionais, grupos funcionais, indices de diversidade funcional e a abundância da assembleia de copépodes exibem variações sazonais e interanuais e que as variações ambientais e hidrológicas influenciam significantemente esses fatores.

Objetivo geral:

Avaliar as variações sazonais, interanuais, hidrológicas e ambientais sobre os traços funcionais, grupos funcionais, índices de diversidade funcional e abundância da assembleia de copépodes.

3 ARTIGO 1 – SEASONAL AND INTERANNUAL DRIVERS SHAPING COASTAL ZOOPLANKTON IN THE SOUTHWESTERN TROPICAL ATLANTIC

INTRODUCTION

Tropical coastal areas sustain numerous vital ecosystem services, such as artisanal fisheries, tourism, carbon fixation, biodiversity, and nursery functions for offshore fish stocks (BALASURIYA, 2018; COLLOCA et al., 2004; LUGOMELA et al., 2002; SHEAVES et al., 2015; ZAHEDI, 2008). These coastal ecosystems are extremely vulnerable to the disturbance caused by daily hydrological and atmospheric factors, such as tidal regimes, winds and freshwater runoff by the discharge of rivers (SILVA et al., 2020; SANTANA et al., 2020; HOLT et al., 2010; JUSTIC; RABALAIS; TURNER, 1997; NITTROUER et al., 1995). The Northeast Brazilian (NEB) coast also receives influences of the Atlantic Niño (i.e., the peak of sea surface temperature cooling in the Atlantic equatorial mode, HOUNSOU-GBO et al., 2020), which regulates rainfall patterns in the region (RUIZ-BARRADAS; CARTON; NIGAM, 2000). Therefore, droughts or intense rainfall events can be significant to this environment, mainly those related to additional external forcing e.g., the global El Niño Southern Oscillation (ENSO). Within the context of ENSO, drought during strong and prolonged canonical El Niño events and intense and prolonged rainfalls in La Niña events have been reported in the southern Tropical Atlantic (HOUNSOU-GBO et al., 2016; SARAVANAN; CHANG, 2000).

Time series allow the study of natural climatic oscillations or anomalies and their effects on marine zooplankton (e.g., BEAUGRAND; REID, 2003; MOLINERO et al., 2008; PLANQUE; TAYLOR, 1998; SOMMER et al., 2012). The zooplankton abundance and community structure often exhibit seasonal variations in response to environmental conditions (e.g., salinity, temperature and food source) (CALBET; LANDRY; SCHEINBERG, 2000; COYLE; PINCHUK, 2003; D'ALCALÀ et al., 2004; PITOIS; YEBRA, 2022; ROMAGNAN et al., 2015; SIOKOU-FRANGOU, 1996; SOMMER et al., 2012). In general, copepods are numerically dominant within coastal marine zooplankton (SILVA et al., 2020; DIAS; BONECKER, 2008) and their biomass is an important food source for a wide range of animals, including fish larvae, macroinvertebrates, corals and some microbial organisms that feed on carcasses and faecal pellets of copepods (CASTONGUAY et al., 2008; ELLIOTT; HARRIS; TANG, 2010; FRANGOULIS et al., 2011; HEIDELBERG et al., 2010). They are a key group in marine food webs, also as predators of other consumers, e.g., ciliates (GISMERVIK, 2006).

Zooplankton abundance and community differences were observed between the dry and rainy seasons in the tropical coastal region (SILVA et al., 2020; NASCIMENTO-VIEIRA; DE FIGUEIREDO; NETO, 2010; LINS SILVA; MARCOLIN; SCHWAMBORN, 2019). However, these studies were carried out in short periods of time (1 or 2 years only), not considering possible climatic anomalies. Brito-Lolaia et al. (2022) observed a seasonal succession of zooplankton relative biomass in a time series of seven years. However, explaining the key drivers for these changes was not the focus of their study.

Recently, a record-strength El Niño event, named "Godzilla El Niño" occurred in 2015-2016 (CORIA-MONTER et al., 2019; SCHIERMEIER, 2015). Such strong canonical El Niño events are the sum of the natural variability of local systems plus global climatic variations (SARAVANAN; CHANG, 2000). However, although the less strong El Niños in 2010 and 2019 did affect specific key areas in the tropical and subtropical Atlantic (FERREIRA et al., 2013; GASPAR et al., 2021), there are yet no studies that evaluated whether the strong 2015/16 El Niño modified hydrological and biological conditions in coastal waters of the NEB.

One of the meteorological variables with a strong impact on coastal areas is rainfall. Strong variations in rainfall are characteristic of most tropical regions, oscillating between dry and rainy seasons and years. In NEB coastal regions, rainfall is strongly influenced by variations in the Sea Surface Temperature (SST) of the Tropical Pacific and Atlantic Oceans (MARENGO et al., 2011; SILVA; MANDÚ, 2020). Intense rainfall events were recorded in NEB coastal regions for the years 2017 and 2019 (SILVA; MANDÚ, 2020), which may interfere with hydrological conditions and the transport of nutrients and sediments, with potentially relevant consequences for the structure of the pelagic community in the region. However, to date, the 2017 and 2019 extreme rainfall events and their consequences for NEB coastal ecosystems were not yet investigated in detail.

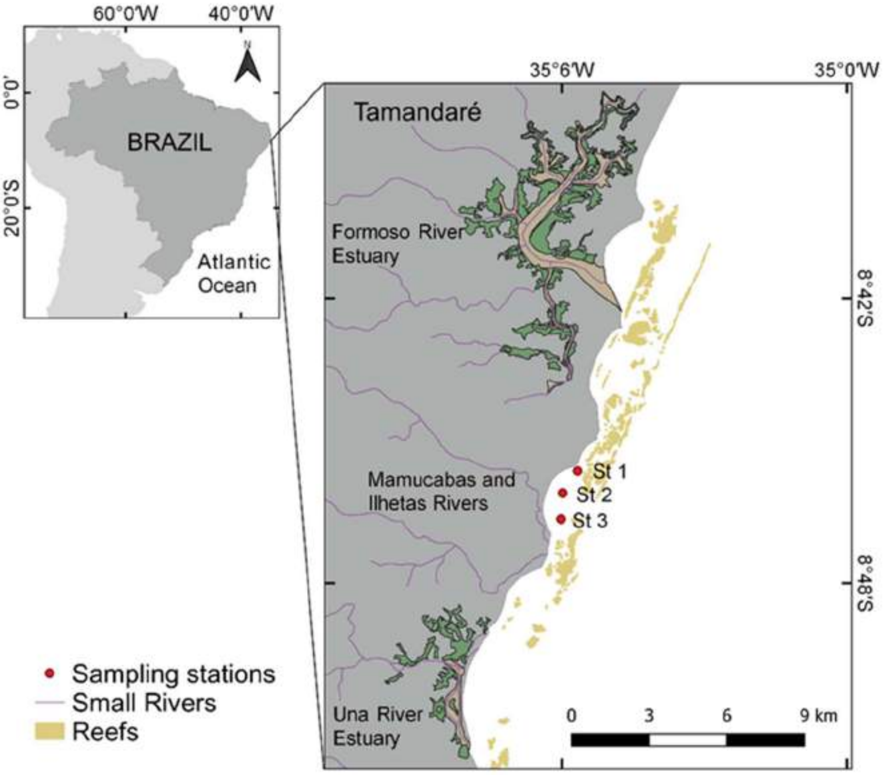
We hypothesized that (i) environmental factors drive seasonal variability in zooplankton communities and (ii) important climate events (i.e., the strong 2015-2016 El Niño and the extreme rainfall events in 2017 and 2019), have a relevant influence on rainfall regime in Southwestern Tropical Atlantic coastal waters. This study aimed to analyze the climatic effects on seasonal and interannual zooplankton abundance and composition and environmental conditions (salinity, temperature and water transparency), considering other factors such as winds, chlorophyll *a*, discharge of river and ENSO index collected on the online dataset in a 7-year time series study.

MATERIALS AND METHODS

Study area

The study area is in Tamandaré Bay (8˚46’07.5” S, 35˚06’03.6” W) which comprises a Marine Protected Area called “Costa dos Corais”. The area receives influence from the Mamucabas and Ilhetas creeks that flow into the south. Sometimes receives strong influence from the Una River in great flood events (Figure 1).

Figure 1. Location of the study area in Tamandaré Bay, northeastern Brazil, showing the sampling stations (St 1, St 2 and St 3).



Fonte: A autora (2022).

The region is characterized by an As’ climate, according to the Köppen classification (ANDRADE; LINS, 1971). The study area belongs to Eastern Northeast Brazil (ENEB) sub-regions (i.e., the May-to-July rainfall anomalies in austral winter which coincides with the southern intertropical convergence zone – SITCZ, (HOUNSOU-GBO et al., 2019). It exhibits two seasons that stand out: a higher rainfall called the rainy season (from March to August) and a lower rainfall called the dry season (September to February). Rainfall data used were five days (the day of sampling and four days before). The previous four days were chosen after correlation analysis between rainfall days and water transparency and salinity data. This analysis was made because rainfall from the previous days can still interfere at the sampling site. Data were obtained from the website of the Pernambuco Agency of Waters and Climate (APAC: http://old.apac.pe.gov.br/meteorologia/monitoramento-pluvio.php). Tidal ranges of all days of sampling campaigns ranged from 1.6 to 2.5 m. The study area has a semidiurnal tide, i.e., the difference between high tide and low tide is approximately 6 hours.

Wind, Una River discharge, chlorophyll *a* and Oceanic Niño Index (ONI) data were collected on the online database, it was chosen date corresponding to the analyzed samples of zooplankton. The ASCAT dataset is a collection of daily averaged gridded wind fields and wind stress estimates over the global oceans. The dataset uses the ASCAT retrievals and ECMWF analysis to determine wind fields at the surface and in space. The spatial resolution of the dataset is 0.25°, and it aims to provide daily average measurements of wind speed, zonal and meridional components, wind stress, and their corresponding components on a global scale (BENTAMY; FILLON, 2012).

The MODIS Aqua Level 3 dataset contains chlorophyll *a* concentration (ocean color) data derived from the NASA MODIS sensor on the Aqua satellite. The chlorophyll *a* concentration information is computed using an empirical relationship derived from in situ chlorophyll *a* concentration measurements and remote sensing reflectances in the blue-to-green region of the visible spectrum. The implementation of this algorithm relies on the availability of three or more sensor bands spanning the 440 - 670 nm spectral regime. The algorithm can be used with all current ocean color sensors. It specifically focuses on deriving chlorophyll *a* (chlor_a) measurements, which are included in both the standard Level-2 OC product suite and the Level-3 CHL product suite. More information about the chlorophyll *a* derivation can be found at https://modis.gsfc.nasa.gov/data/dataprod/chlor_a.php. The data is processed and mapped onto a cylindrical equidistant map projection, with grids of 4.63 km. (NASA Ocean Biology Processing Group, 2015; (SAVTCHENKO et al., 2004)).

The data of the monthly discharges of the UNA river in the fluviometric station 39590000 (BARREIROS) were taken from the national water agency (ANA) that are pre-processed and stored in the MARDAO dataset (VARONA et al., 2022).

The Oceanic Niño Index (ONI) focuses on the same geographic region as the Niño 3.4 index, which spans from 5°N to 5°S latitude and from 170°W to 120°W longitude. However, the ONI employs a different approach to calculating its values (GLANTZ; RAMIREZ, 2020).

It uses a rolling average of sea surface temperature anomalies over a three-month period. To be considered a definitive El Niño or La Niña event, the anomalies must surpass either +0.5°C or -0.5°C, respectively, for a continuous duration of at least five months. This particular criterion is referred to as the operational definition employed by the National Oceanic and Atmospheric Administration (NOAA). It serves as a standardized guideline to determine the presence and intensity of El Niño and La Niña phenomena.

Sampling strategy

This study is part of the long-term St-Esplan-Tropic Project that sampled bi-monthly during the new moon periods at Tamandaré Bay, from June 2013 to August 2019. Zooplankton samplings were carried out at three stations inside Tamandaré Bay, in a gradient from more distant to near Mamucabas and Ilhetas creeks plume (St 1 to St 3, respectively; Figure 1). Tows were performed using a conical-cylindrical plankton net (64 µm mesh size, 0,31 m mouth aperture, 1 m length), by means of subsurface horizontal tows during 5 min at a speed of 2 to 3 knots during new moon spring high tides, between 11 am and 14 pm. A flowmeter (Hydro-Bios) was coupled at the net opening for posterior calculation of the volume of water filtered.

All samples were conditioned in plastic jars and fixed with 4% formalin (final concentration in seawater), buffered with sodium tetraborate (0.5 g*L-1) (OMORI; IKEDA, 1984). A total of 111 samples collected over six years were filed at the Museum of Oceanography at the Federal University of Pernambuco. Temperature (ºC), salinity and depth (m) were measured at each sampling station using a YSI Cast Way CTD probe (SonTek, San Diego, CA, USA) and transparency (m) with a Secchi disk (PREISENDORFER, 1986). The abiotic data of the surface layer (1 m) were obtained from data extracted from CTD files and used for subsequent analyses.

Laboratory analysis

Four campaigns per year were chosen (two for each season), except for the first (2013) and last (2019) sampling years. A total of 68 saplings were analyzed (34 in the dry season and 34 in the rainy season). In 2015, there was only one campaign in the rainy season due to logistical issues and bad weather. Samples were washed and quartered using a Motoda splitter (MOTODA, 1959). Aliquots were taken according to the number of organisms (ranging between 400 to 700 organisms). Thereon, the aliquots of zooplankton were analyzed in a

Sedgwick-Rafter chamber under a binocular microscope. Organisms were identified at the highest taxonomic level possible (BOLTOVSKOY, 1999; YOUNG, 2006).

Data analysis

All environmental and zooplankton abundance (ind.m-3) data were tested for normality using the Shapiro-Wilk test (SHAPIRO; WILK, 1965). Since several data were not normally distributed, a permutational test (PERMANOVA, permutations = 20000, (ANDERSON, 2005)) was performed to detect differences between seasons (dry vs rainy) by using the function “adonis2” with the “vegan” R package (OKSANEN et al., 2019). Kruskal-Wallis test (KRUSKAL; WALLIS, 1952) and Dunn post hoc (DUNN, 1964, method Bonferroni) were used to analyze years (2013-2019) and samplings stations (St 1, St 2 and St 3). Indicator Value was used to find indicator taxa in relation to season, year and ONI data, by using the function “indval” within the “lindicspecies” R package (DUFRÊNE; LEGENDRE, 1997).

Autocorrelation Functions (ACF) were made to observe trends in the series of environmental variables and zooplankton main taxa (Apêndice C). Autocorrelation measured the relationship between the past values of a series and its future values. Lag refers to the delay or time interval (i.e., monthly in this study) between consecutive observations (comparing t with t - 1). For this purpose, the average between stations was calculated. Correlograms were performed using the function “acf” in the “stats” R package (VENABLES et al., 2002). A correlogram (Corrplot) representing the Pearson correlation coefficient (n = 6) matrix between environmental variables and main zooplankton taxa was built using the function “cor” in the “corrplot” R package (FRIENDLY, 2002).

A Redundancy Analysis (RDA) was used to explore the relationship between zooplankton abundance taxa (response variables) vs environmental descriptors (explanatory variables). The zooplankton abundance was transformed by Hellinger (LEGENDRE; GALLAGHER, 2001) and the One-way Variance Analysis (ANOVA) was used to assess the significance of the axis of RDA to test the hypothesis that environmental descriptors are responsible for changes in zooplankton abundance. Due to information gaps in some environmental descriptors, all campaigns of 2013 were removed, and 54 samples (31 in the dry season and 23 in the rainy season) remained to perform the analysis of Corrplot and RDA. All analyses were performed using R version 4.0.5, considering $p < 0.05$ (ZAR, 1999).

RESULTS

Environmental conditions

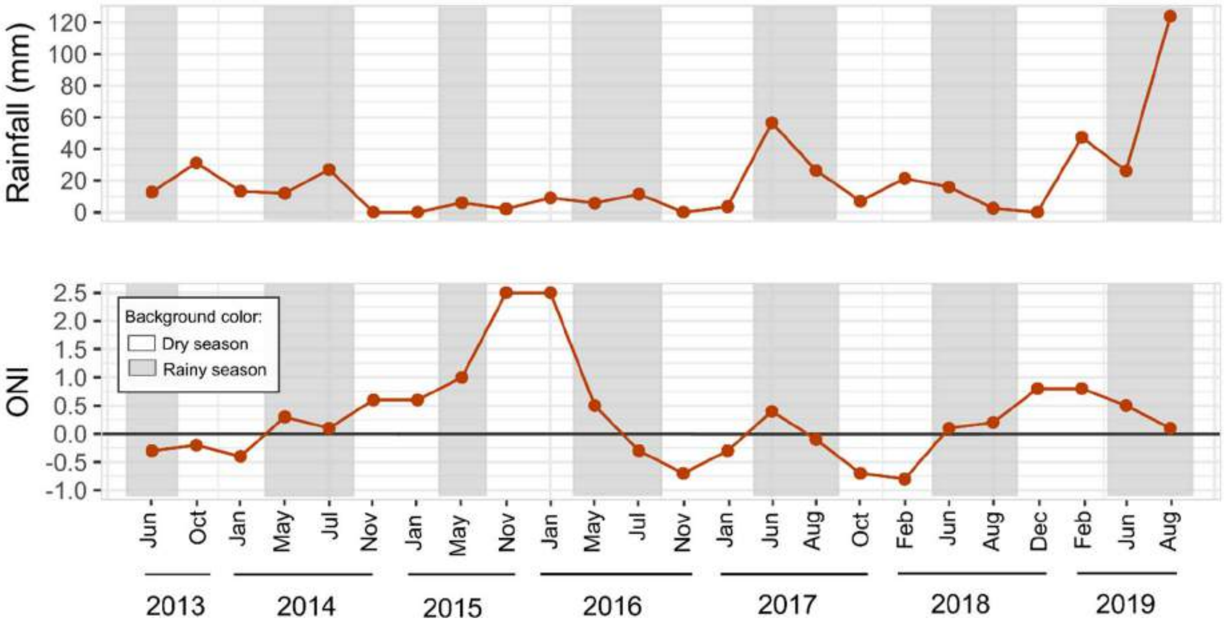
Rainfall showed clear differences between dry and rainy seasons, with peaks in the rainy season. The mean rainfall was 26.3 mm during the rainy season and 8.8 mm during the dry season. Rainfall and abiotic conditions showed marked interannual differences (Table 1, Figures 2 and 3). The sampling campaigns in May 2015 and in July 2016 (during the 2015/16 EN event ONI 2.5 for both Nov/2015 and Jan/2016) displayed local rainfall (max. 6 and 11.4 mm, respectively), and local chlorophyll *a* concentrations below expected for the rainy season (Figures 2 and 3). Conversely, the extreme rainfall events in 2017 and 2019 had conspicuous effects on several abiotic factors (rainfall, Una River discharge, salinity, transparency and chlorophyll a, Figure 2). A significant increase in rainfall was recorded in the year 2019 with a maximum of 123.9 mm in the rainy season. Temperature, salinity, water transparency, river discharge (Una River) and chlorophyll *a* also showed clear patterns between seasons, with low values in the rainy season over the seven years of samplings, except for Una River discharge and chlorophyll *a*, which had high values in the rainy season (Table 1, Figure 3). Except for water transparency and chlorophyll *a*, all environmental descriptors displayed strong and significant interannual differences (Table 1). It was possible to observe an anomaly in the discharge of the Una River in 2017, which may have led to extreme values in chlorophyll *a* and salinity in the same year. Higher rainfall in 2019 also led to lower salinity, temperature and water transparency, and peaks in discharge and chlorophyll *a* (Figure 3). No differences between sampling stations (St 1, St 2 and St 3) were found.

Table 1. General description of the environmental variables by dry and rainy seasons from 2013 to 2019 in Tamandaré Bay (Southwestern Atlantic). SD = Standard deviation. Higher significant values presented in D = Dry season, R = Rainy season, Min = minimum, Max = maximum, NS = Not significant. PERMANOVA was used to detect differences between seasons (dry vs rainy) and the Kruskal-Wallis test and Dunn post hoc were used to analyze differences between years (2013-2019). Significant differences ($p < 0.05$) are indicated in bold.

Environmental variables	Dry			Rainy				Years
	Min	Max	Mean ± SD	Min	Max	Mean ± SD	P Value	P Value
Temperature (ºC)	27.0	30.0	28.7 ± 0.7	26.3	30.7	28.5 ± 1.3	**0.001** $^{\mathrm{D}}$	**0.049** $^{2015 \neq 2017}$
Salinity	29.0	37.1	35.7 ± 1.4	27.0	36.6	34.9 ± 1.8	**0.002** $^{\mathrm{D}}$	**0.023** $^{\mathrm{NS}}$
Water transparency (m)	2.3	7.9	4.0 ± 1.3	0.6	4.7	2.5 ± 1.0	**0.001** $^{\mathrm{D}}$	0.093
Winds (m/s)	4.3	8.7	6.8 ± 1.0	2.3	9.3	6.6 ± 2.0	0.687	**0.016** $^{2018 \neq 2019}$
Una river discharge (m³/s)	5.1	53.0	24.0 ± 15.4	16.4	136.3	62.8 ± 35.3	**0.001** $^{\mathrm{R}}$	**0.001** $^{2015 \neq 2017,\ 2019}$
Rainfall (mm)	0	47.4	8.8 ± 12.8	1.8	123.9	26.3 ± 31.7	**0.006** $^{\mathrm{R}}$	**<0.001**$^{2015 \neq 2013,\ 2019;\ 2019 \neq 2016,\ 2018}$
ONI (index)	-0.8	2.5	0.4 ± 1.1	-0.3	1	0.2 ± 0.4	0.354	**<0.001** $^{2015 \neq 2013,\ 2014,\ 2017,\ 2018}$
Chlorophyll *a* (mg/ m³)	0.1	0.4	0.3 ± 0.1	0.2	3.5	1.2 ± 1.1	**0.001** $^{\mathrm{R}}$	0.415

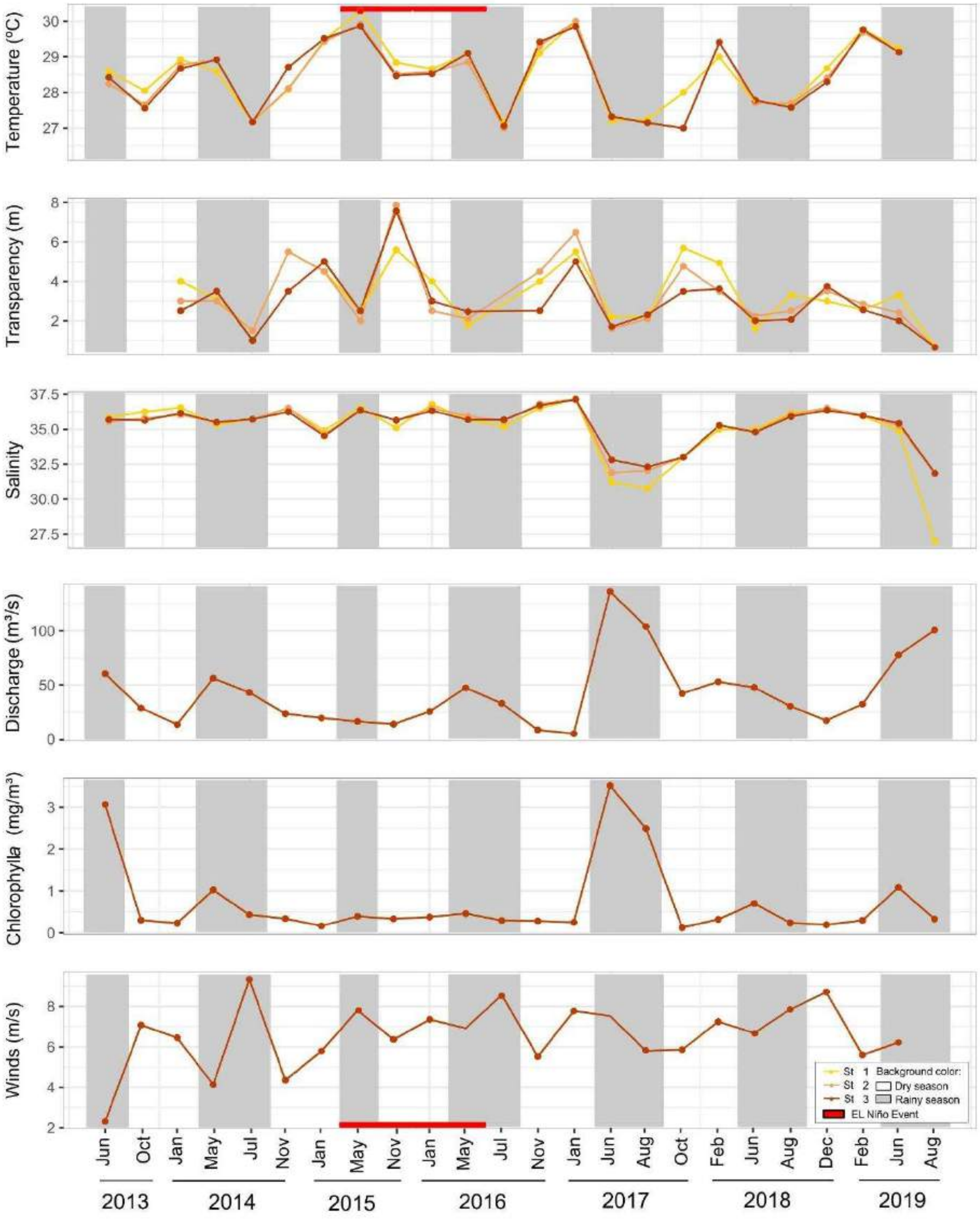
Fonte: A autora (2023).

Figure 2. Rainfall (mm) in Tamandaré Bay (day of samplings and four days before) and ONI (Oceanic Niño Index) in the Pacific Ocean during the months of samplings. Shaded areas represent the rainy season.



Fonte: A autora (2023).

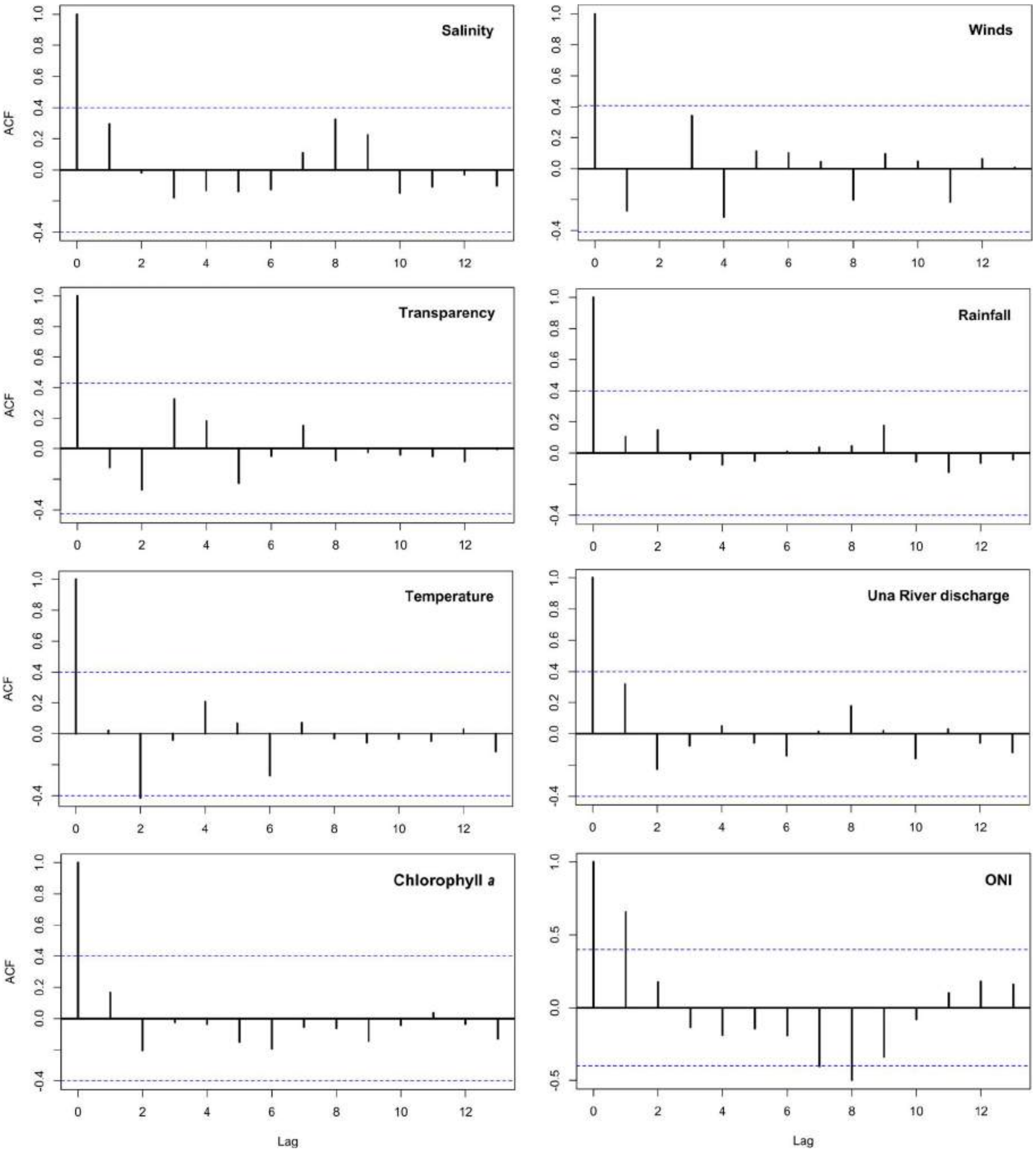
Figure 3. Abiotic data samplings over seven years (2013-2019). Temperature (ºC), salinity, transparency (m), winds (m/s) and Una River Discharge (m³/s) at three stations (St 1, St 2 and St 3) in Tamandaré Bay. Shaded areas represent the rainy season.



Fonte: A autora (2023).

The interpretation of autocorrelation function was more complex, because temporal data in this study are irregular, with months and the number of months varying each year (Figure 2 and 3). Due to this, the results were interpreted in a general way, observing the general pattern of autocorrelation. The abiotic factors that showed significant autocorrelations in lag (in months) were Temperature and ENSO (ONI) (Figure 4). The temperature was negatively autocorrelated in lag 2, indicating a trend reversal. ENSO (ONI) showed a positive autocorrelation in lag 1 and a negative in lag 8 (Figure 4). Positive autocorrelation in lag 1 suggests that the series value is positively related to the value observed a time interval ago. While negative autocorrelation on lag 8 indicates a significant and inverse trend between the time series values (in months) at that time and the values eight time periods ago.

Figure 4. Autocorrelation Functions (ACF) of environmental variables sampled in Tamandaré Bay from 2013 to 2019. Upper and lower blue dashed lines indicate the confidence interval. The vertical lines indicate the correlation coefficient. Lag represents time in months: Lag 0, the autocorrelation of the data, lag 1 (t - 1) onwards.

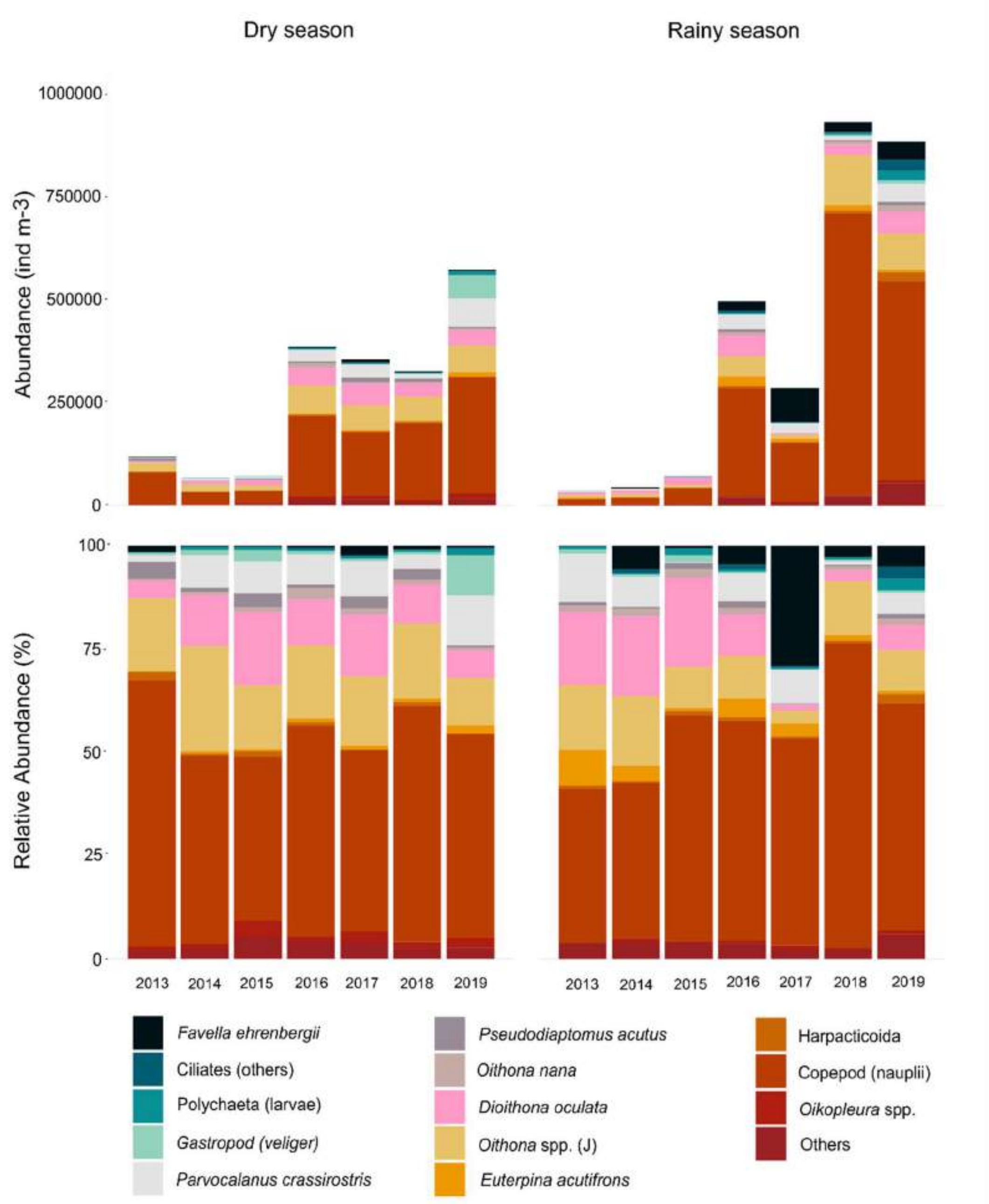


Fonte: A autora (2023).

Zooplankton community

Within the zooplankton community, 72 taxa were identified (Appendix 2, supplementary table). Copepods (adults, juveniles and nauplii) were the clearly dominant taxon, with 90% of total average relative abundance, followed by the abundant ciliate *Favella ehrenbergii* (4.4%), gastropod veligers (1.3%), appendicularians *Oikopleura* spp. (1.1%), polychaete larvae (1.1%) and "other ciliates" (1.0%) (Figure 5). Within the copepod community, the most abundant groups were nauplii (56%), *Oithona* spp. juveniles (12.8%), *Dioithona oculata* (7.8%) *Parvocalanus crassirostris* (5.6%), *Euterpina acutifrons* (1.7%), *Oithona nana* (1.3%), *Pseudodiaptomus acutus* (1.2%), and harpacticoid adults and juveniles (1.1%). The remaining taxa (Others) were below 1.0%. The total zooplankton community abundance ranged from 9,018 to 3,558,957 ind m^{-3}, with a mean value of 353,052 (± 546,717) ind m^{-3}. The extremely high maximum value was observed during the reproduction peaks of copepods, with a high abundance of nauplii in the rainy seasons of 2018 and 2019 (Figure 5).

Figure 5. Abundance (ind.m^{-3}) and relative abundance (%) of the most representative groups of zooplankton in the dry and rainy seasons.



Fonte: A autora (2022).

Seasonal effects were found for *F. ehrenbergii*, “other ciliates” and *E. acutifrons* with significantly higher abundances in the rainy season (PERMANOVA, p = < 0.001, p = 0.015 and p = 0.012, respectively). There was a higher total and relative abundance for *F. ehrenbergii* in the rainy season of 2017, showing that this species was positively affected by the peak of Una River discharge this year (Figures 3 and 5). The rainy season displayed the highest mean abundance of total zooplankton (437,705.8 ± 730,777.7 ind m^{-3}, Appendix 2, supplementary table, Figure 5). Except for three taxa (*P. acutus*, *D. oculata* and *Oikopleura* sp.), all main taxa displayed significant interannual differences (Table 2, Figures 6, 7 and 8). No spatial differences were found (i.e., differences between the three stations).

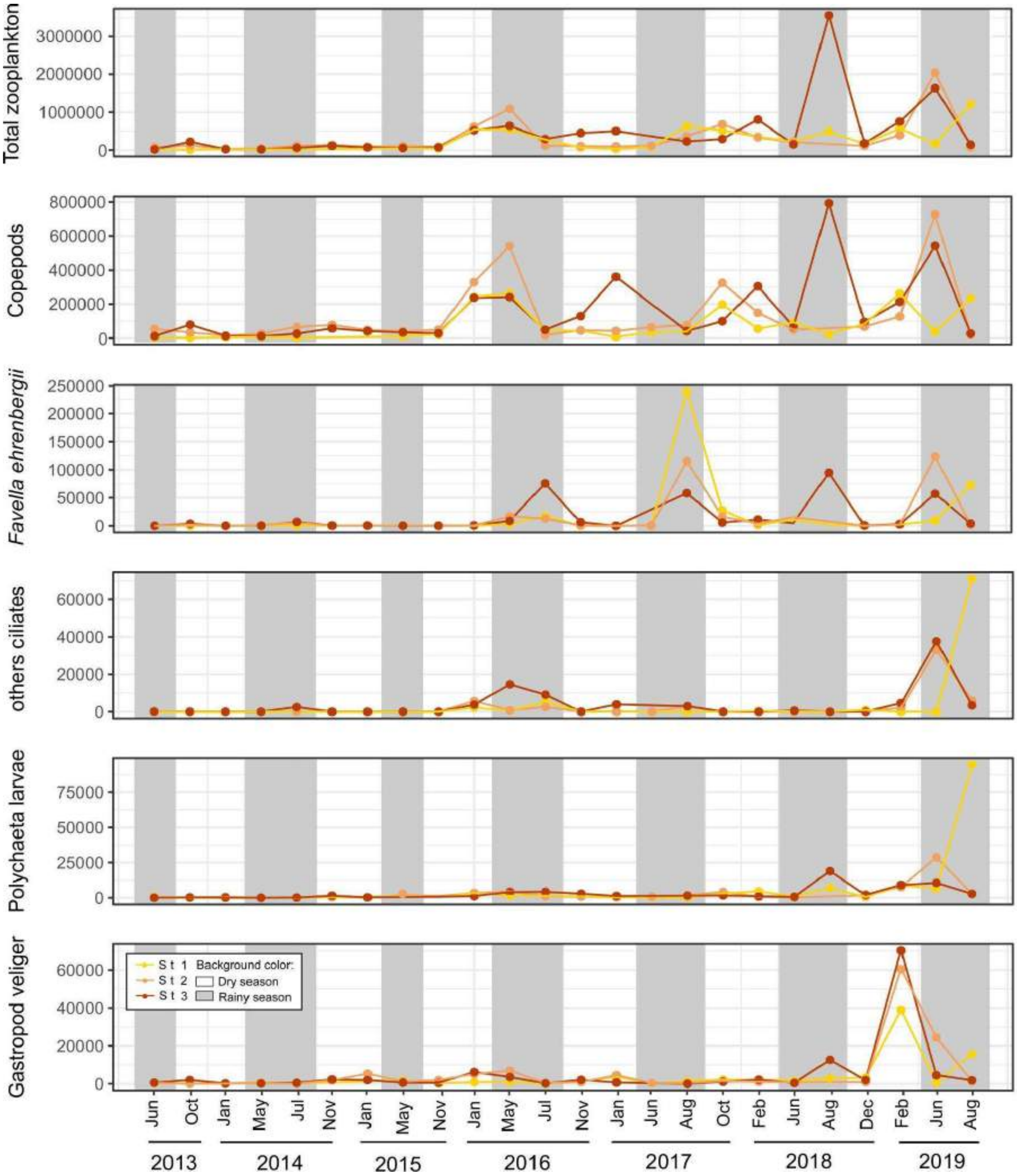
Table 2. P-values results of Indicator values (IndVal) and statistical analyses of main zooplankton taxa and season, year and ENSO index (ONI) in Tamandaré Bay. In statistical analyses, PERMANOVA was used to detect differences between seasons (dry vs. rainy) and the Kruskal-Wallis test and Dunn post hoc were used to analyze differences between years (2013-2019). R = rainy season, D = dry season. Significant differences p < 0.05.

Taxa	Season		Year		ONI	
	IndVal	p values	IndVal	p values	IndVal	p values
Favella ehrenbergii	0.888	0.001			0.641	0.036
Other ciliates	0.524	0.004	0.605	0.003		
Polychaeta larvae			0.682	0.001		
Gastropod veliger			0.725	0.001	0.735	0.012
Parvocalanus crassirostris			0.397	0.001		
Pseudodiaptomus acutus					0.606	0.018
Oithona spp.						
Oithona nana						
Dioithona oculata						
Harpacticoida			0.495	0.019		
Euterpina acutifrons	0.731	0.003				
Copepod nauplii						
Oikopleura spp.						
Others			0.452	0.010		

Taxa	Statistical analyses (“p” values)	
	Season	Year
Favella ehrenbergii	$<0.001^{R}$	$0.004^{2015\neq2019}$
Other ciliates	0.015^{R}	$<0.001^{2013\neq2019;\ 2014\neq2016,\ 2019;\ 2015\neq2016,\ 2019;\ 2018\neq2019}$
Polychaeta larvae		$<0.001^{2013\neq2016,\ 2019;\ 2014\neq2016,\ 2018,\ 2019;\ 2015\neq2019;\ 2017\neq2019}$
Gastropod veliger		$<0.001^{2013\neq2019;\ 2014\neq2019}$
Parvocalanus crassirostris		$<0.001^{2013\neq2019;\ 2014\neq2019;\ 2015\neq2019}$
Pseudodiaptomus acutus		
Oithona spp.		$<0.001^{2014\neq2016,\ 2018}$
Oithona nana		$<0.001^{2013\neq2016;\ 2014\neq2016}$
Dioithona oculata		
Harpacticoida		$0.003^{2014\neq2016,\ 2019}$
Euterpina acutifrons	0.012^{R}	$0.002^{2015\neq2018}$
Copepod nauplii		$<0.001^{2013\neq2019;\ 2014\neq2016,\ 2017,\ 2018,\ 2019;\ 2015\neq2016,\ 2019}$
Oikopleura spp.		
Others		$<0.001^{2013\neq2016,\ 2017,\ 2019;\ 2014\neq2016,\ 2017,\ 2018,\ 2019;\ 2015\neq2019}$

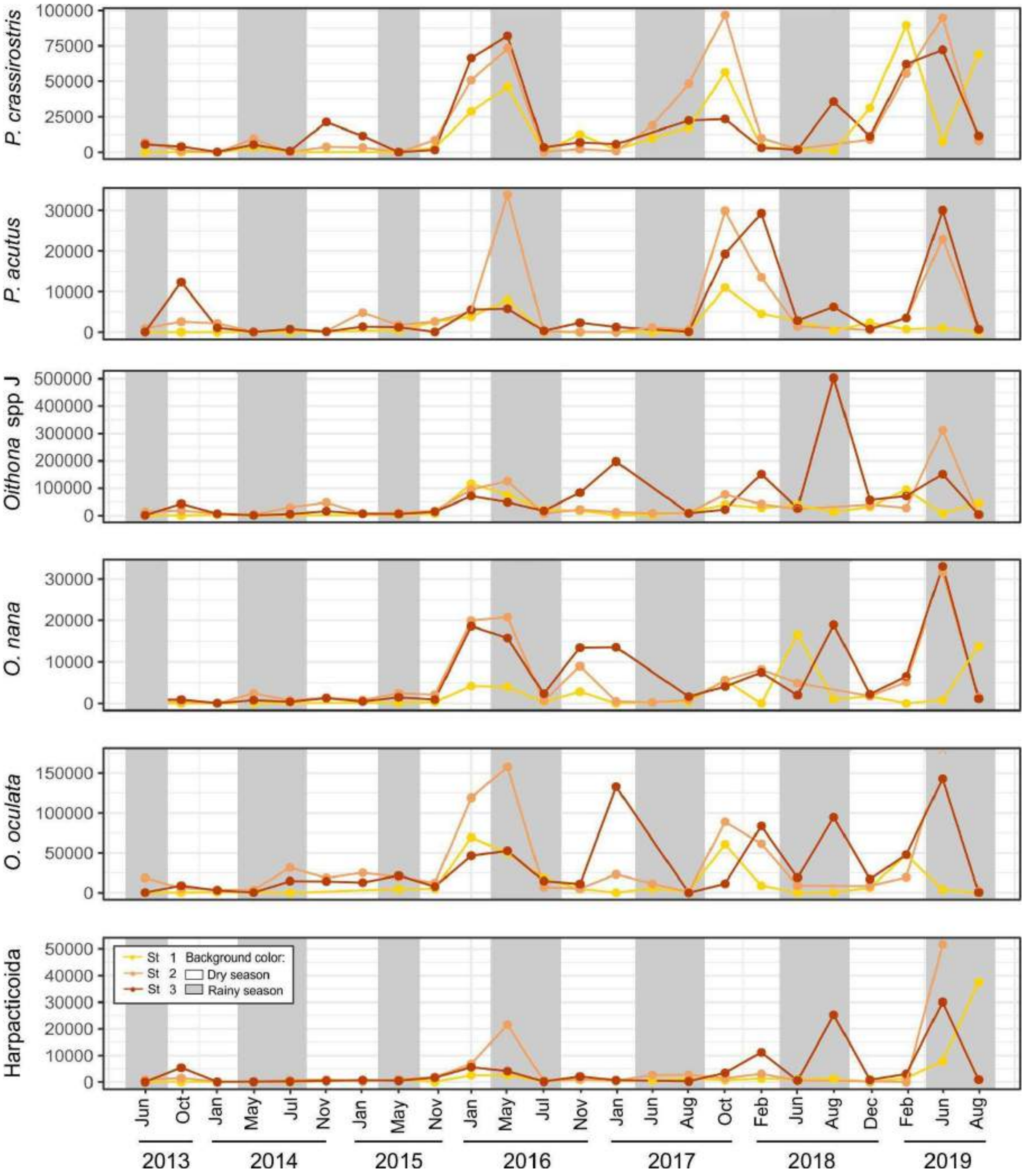
Fonte: A autora (2022).

Figure 6. Variation of the main zooplankton taxa over the seven years (2013-2019) sampled at three stations (St 1, St 2 and St 3) in Tamandaré Bay. Shaded areas represent the rainy season.



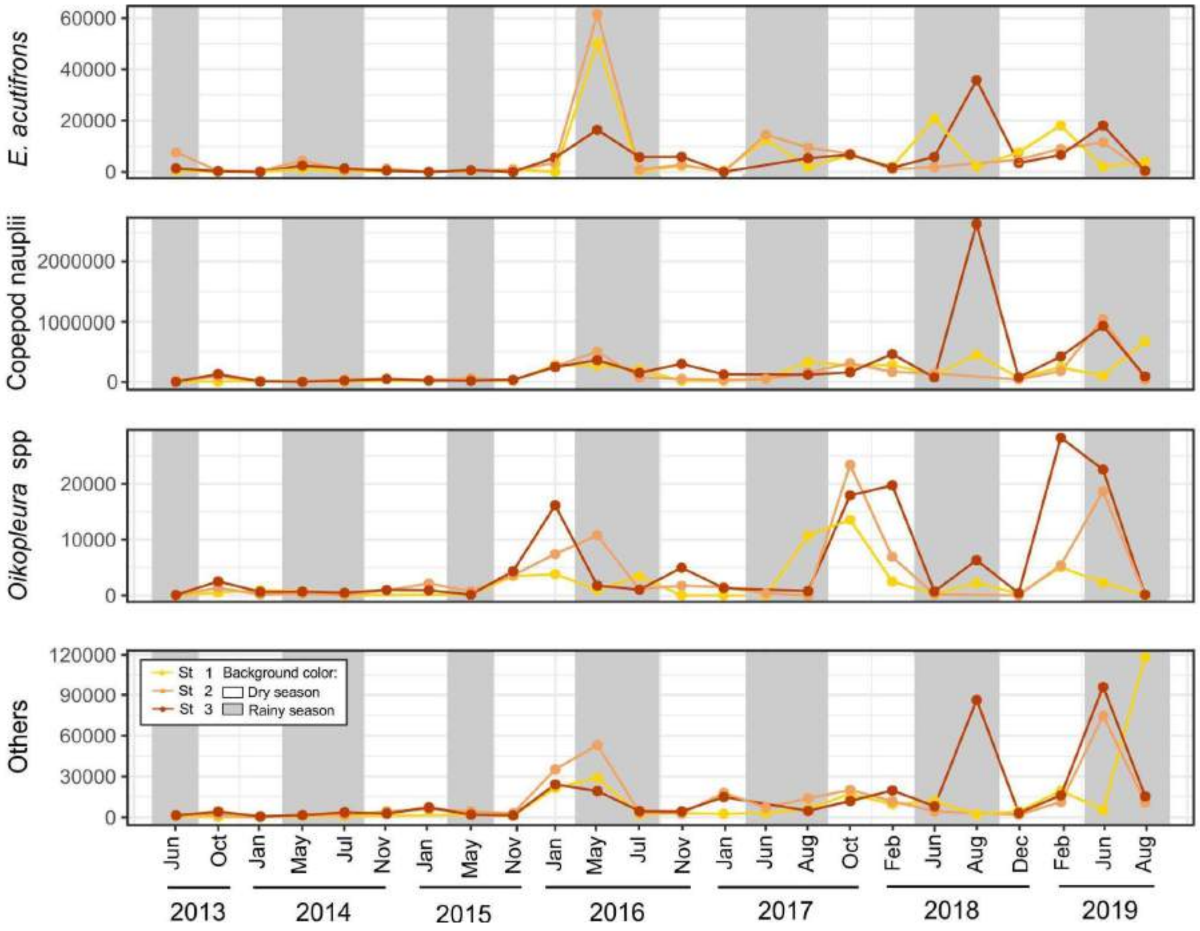
Fonte: A autora (2023).

Figure 7. Variation of the main zooplankton taxa over the seven years (2013-2019) sampled at three stations (St 1, St 2 and St 3) in Tamandaré Bay. Shaded areas represent the rainy season.



Fonte: A autora (2023).

Figure 8. Variation of the main zooplankton taxa over the seven years (2013-2019) sampled at three stations (St 1, St 2 and St 3) in Tamandaré Bay. Shaded areas represent the rainy season.

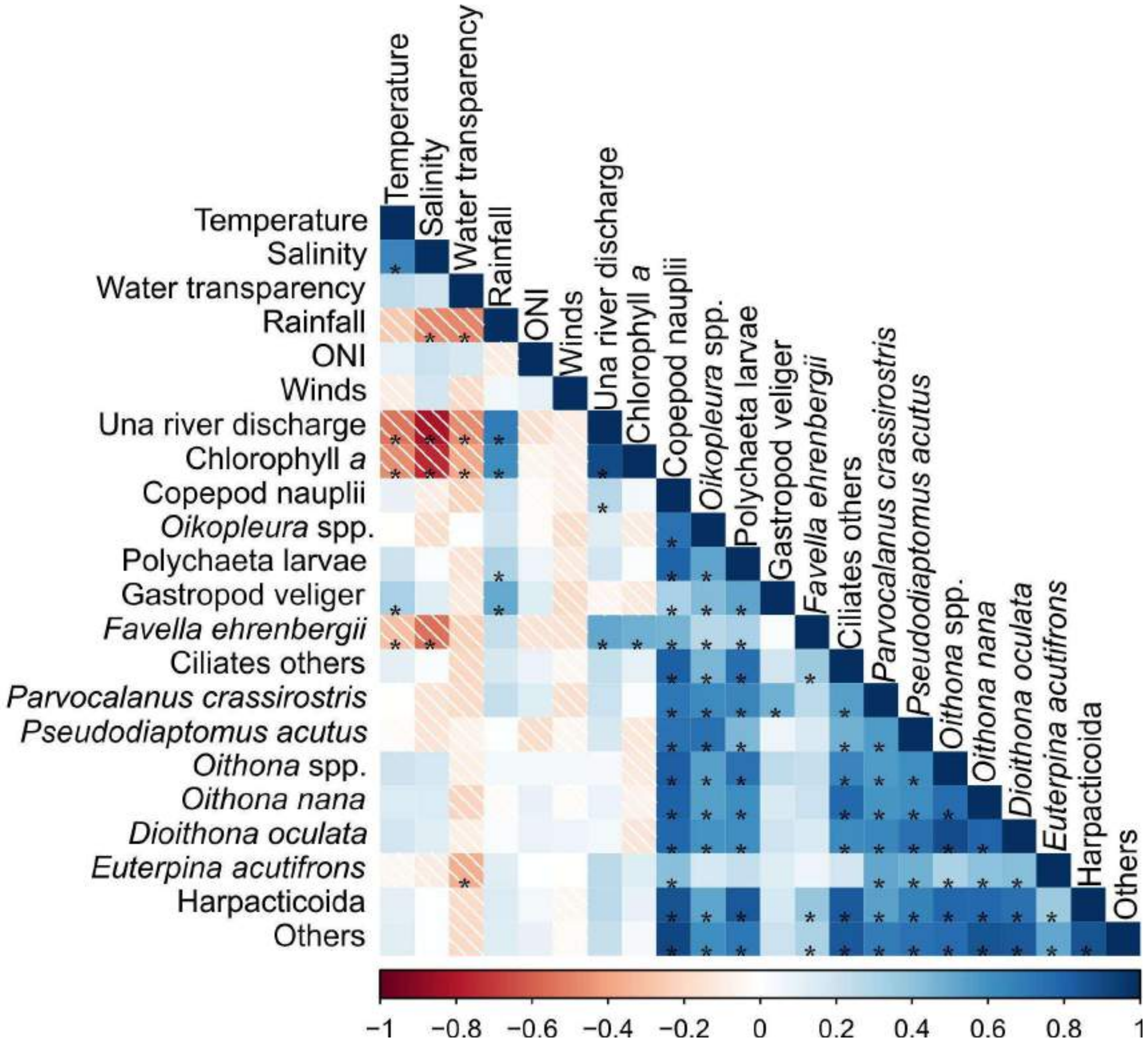


Fonte: A autora (2023).

Indicator ("IndVal") analysis found eight taxa (and "Others") that were significant indicators of seasons, years, or ONI. Indicator taxa for the Rainy Season were *F. ehrenbergii*, *E. acutifrons* and "other ciliates". Indicator taxa for specific years were the most abundant, with "other ciliates", Polychaeta, Gastropoda, *P. crassirostris*, Harpacticoida and "Others". ONI indicator taxa were Gastropod veliger, *F. ehrenbergii* and *P. acutus* (Table 2).

Numerous significant correlations were found between environmental variables and the main zooplankton taxa (Figure 9). Also, many zooplankton taxa were correlated with other taxa. The variable that was mostly correlated with others was "Copepod nauplii" with 14 significant correlations, followed by Polychaeta, with 13 significant correlations and *P. crassirostis*, Harpacticoida, *Oikopleura* sp. and Others with 12 for each taxon. In general, Rainfall was negatively correlated with salinity and water transparency and positively correlated with the discharge of Una River, chlorophyll *a*, Gastropoda and Polychaeta. The zooplankton taxa that were correlated with environmental variables were *F. ehrenbergii*, *E. acutifrons* (both were negatively correlated with environmental variables: temperature and salinity with *F. ehrenbergii* and water transparency with *E. acutifrons*), Gastropoda, Polychaeta and Copepod nauplii (Figure 9). Water transparency, temperature and salinity were negatively correlated with Una River discharge and chlorophyll *a.* Wind speed and ONI were not correlated with any abiotic or biological variables.

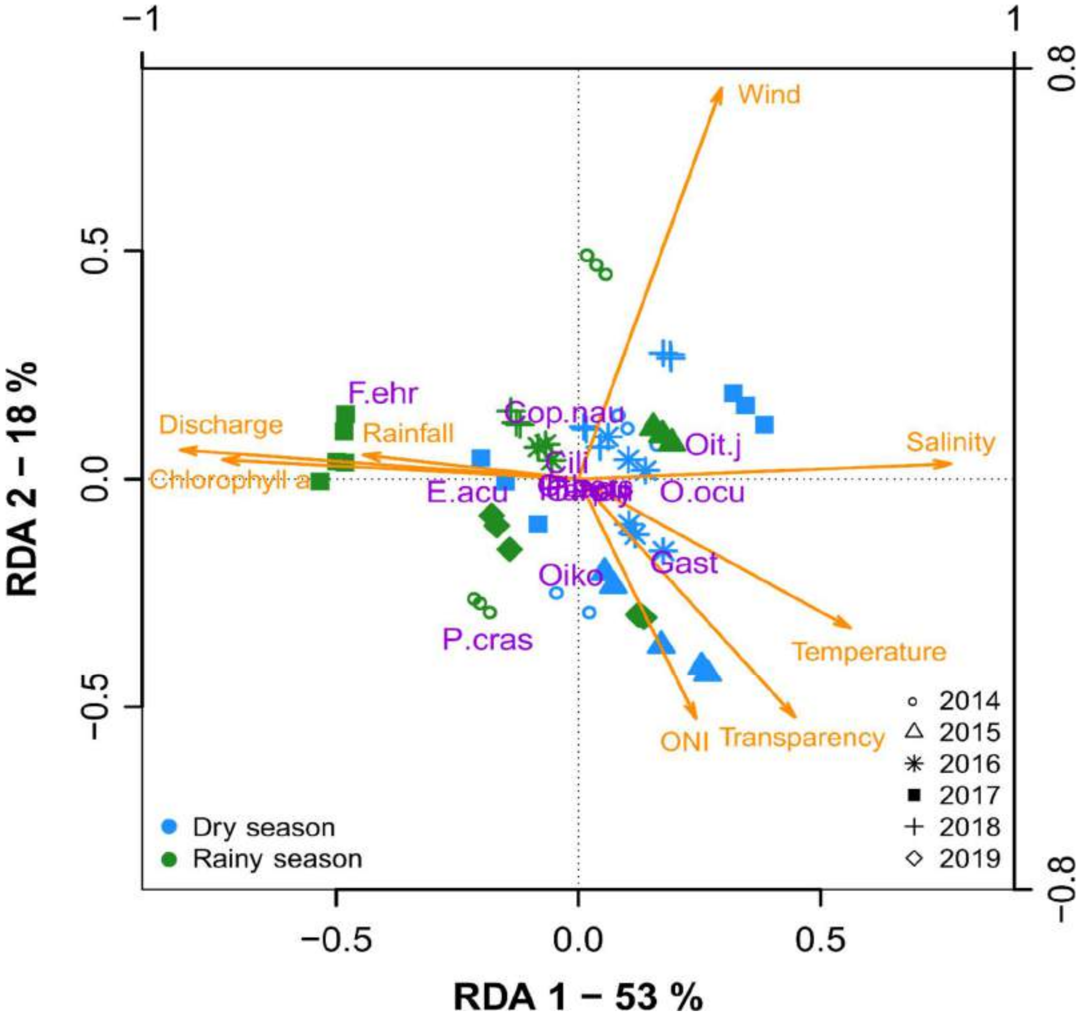
Figure 9. Correlogram representing the correlations between zooplankton main taxa and environmental variables. Asterisks (*) represent the significance of the Pearson correlations ($p < 0.05$). Colours indicate different correlation coefficient values according to the scale bar at the bottom. The intensity of the colour is proportional to the correlation coefficients.



Fonte: A autora (2023).

The global RDA model showed a strong significant relationship ($p = 0.001$) between the zooplankton abundance matrix and environment descriptors. The canonical axes 1 and 2 were statistically significant ($p = 0.001$ and 0.04, respectively) and contributed 71% of the total variance explained by the analyses (Figure 10). Temperature ($p = 0.001$), salinity ($p = 0.001$), water transparency ($p = 0.009$), winds ($p = 0.003$) and Una River discharge ($p = 0.038$) were responsible for the significance of the model. Explanatory variables explained 53% of the total variability of the abundance of zooplankton taxa. *F. ehrenbergii* and *E. acutifrons* were correlated to rainfall, Una River discharge and chlorophyll *a* in the rainy season, while *D. oculata* and *Oithona* spp. were correlated to salinity in the dry season. Copepod nauplii were correlated to wind speed, Gastropoda to transparency and temperature in the dry season and *Oikopleura* spp. to ONI (Figure 10).

Figure 10. Redundancy analysis (RDA) based on abundance (ind.m^{-3}) of main zooplankton and other taxa (response variables) *vs* environmental descriptors (explanatory variables). Cop.nau = Copepod nauplii, Oiko = *Oikopleura* spp., Poly = Polychaeta, Gast = Gastropod, F.ehr = *Favella ehrenbergii*, Cili = Ciliates others, P.cras = *Parvocalanus crassirostris*, P.acu = *Pseudodiaptomus acutus*, Oit.j= *Oithona* spp. juveniles, O.nan = *Oithona nana*, O.ocu = *Oithona oculata*, E.acu = *Euterpina acutifrons*, Harp = Harpacticoida.



Fonte: A autora (2023).

DISCUSSION

This study disclosed the processes and drivers that shape the pelagic ecosystem in a coastal tropical bay, during a seven-year time series. We found a strong influence of rainfall variability on environmental conditions and consequently on the zooplankton taxa from the dry to the rainy season as the long-term study on a coral-reef-lined tropical coastal bay in the southwest Atlantic influenced by variable inputs from estuarine plumes. The rainfall promoted river inputs, significantly altering the physical-chemical processes, inserting freshwater, nutrients, food particles, phytoplankton and organisms from estuaries into this coastal ecosystem.

Zooplankton community and seasonal and interannual variability

Our results disclosed a strong influence of environmental conditions on the zooplankton community, which significantly increases zooplankton abundance from dry to rainy seasons. *Euterpina acutifrons*, *Favella ehrenbergii* and other ciliates were indicators of seasonal variations in this study, with higher abundance in the rainy season. This group are considered euryhaline species and they are found abundantly in both estuarine and coastal regions (STERZA; FERNANDES, 2006; DIAS; ARAUJO; BONECKER, 2009; NASCIMENTO-VIEIRA et al., 2010; MELO JÚNIOR et al., 2013; BRITO-LOLAIA et al., 2020).

E. acutifrons was negatively correlated with water transparency and also correlated with rainfall, Una discharge and chlorophyll *a*. Melo Júnior et al. (2013) observed a positive relation of *E. acutifrons* body length and clutch size to chlorophyll content in a coastal area of Southeastern Brazil. This species is a coastal and omnivore-herbivore species (BROGLIO et al., 2004) and its high abundance in the rainy season, to which chlorophyll *a* was strongly related, corroborates its trophic strategy.

Unlike other studies conducted in temperate areas, using Niskin bottles and buckets, in which the genus *Tintinnopsis* often dominates among the ciliate fauna (HARGRAVES, 1981; MONTI et al., 2012), in this study *Favella ehrenbergii* was the most abundant ciliate. *F. ehrenbergii* and other ciliates presented a relevant contribution to the zooplankton community. *F. ehrenbergii* and other ciliates were considered good indicators of the eutrophic state of the ecosystem (BRITO-LOLAIA et al., 2022). Eskinazi-Sant'anna and Björnberg (2006) found a distinctly seasonal basis for ciliates in a coastal area of the southeast of Brazil. Some species of ciliates occurred primarily at temperatures of < 25º C. However, unlike what was observed by these authors which *F. ehrenbergii* was found in higher abundance in high temperatures and salinity, the present study was the opposite. This could be due to the fact that *F. ehrenbergii* feeds on phytoplankton, preferably dinoflagellate, and it is often associated with dinoflagellate blooms (KAMIYAMA; ARIMA, 2001; STOECKER; GUILLARD; KAVEE, 1981). Two situations can be occurring (1) This ciliate is found in higher abundance in the outer estuary and consequently was carried out in the rainy season from Una River and creeks to the Bay, which was observed by Urrutxurtu et al. (2003) in a eutrophic estuary of the Bay of Biscay and (2) In the rainy season this region has a significative high value of chlorophyll *a*, increasing the food availability to this species and other species of ciliates. In this study, *F. ehrenbergii* was positively correlated with discharge and chlorophyll *a* and it was possible to observe a high relative abundance of *F. ehrenbergii* in 2017, which corresponds to discharge and chlorophyll *a* anomaly in the same year.

Except for the study made by (SANTOS et al. 2019), where meroplankton was the most abundant in Tamandaré Bay due to another type of device and the mesh size used (300 µm), holoplanktonic copepods are the group of numerical dominance in the study area, constituting an important carbon source for upper trophic levels (SANTOS; BRITO-LOLAIA; SCHWAMBORN, 2017; SILVA et al. 2020; BRITO-LOLAIA et al. 2020, BRITO-LOLAIA et al., 2022). Nauplii of copepods contributed to 56% of the all-zooplankton community in this study. It was observed a peak in abundance in the rainy seasons of 2018 and 2019. This fact was also observed by Brito-Lolaia et al. (2020) in Tamandaré Bay. The higher abundance of nauplii can be explained that some of them are from the benthic copepod family, while their copepodites in the pelagic system are rare, as expected (SILVA et al., 2020). Silva et al. (2020) reported that the nauplii stage of the Harpacticoida Longipedidae family was the second most abundant, due to this the authors highlighted the importance of the early stages of the Copepoda benthic contribution to the pelagic food web.

Dioithona oculata and *Oithona* spp. juveniles showed a correlation with salinity in the dry season of 2017 and in the rainy season of 2015 (which in this study had low rainfall values). Although those taxa did not present differences between seasons, this analysis indicated this species has a relationship with the dry season. Brito-Lolaia et al. (2022) concluded in their study *Oithona* spp. juveniles as an indicator of oligotrophic conditions. The genus *Oithona*, adults and copepodites, were found in higher abundance in the area. This genus is the major component of the zooplankton community in the global ocean, independent of environmental conditions (GALLIENNE; ROBINS, 2001). This wide range of sites is related to its feeding habits, i.e., active ambush-feeding omnivores and it is specialized to exploit microbial food web and feed on particles of reduced size spectrum for other copepods (NIELSEN; SABATINI, 1996; BENEDETTI; GASPARINI; AYATA, 2016). In addition, *Oithona* spp. are small size species (mean size of 426 µm for copepodites and 610 µm for adult species; data not shown) and the mesh size used in our study (64 µm) allowed us to effectively capture this genus. Plankton nets of 200 µm and above are widely used in the studies of mesozooplankton, however, they are unable to effectively sample smaller sizes of copepods or early stages of these species, may have a loss of > 90% of abundance (GALLIENNE; ROBINS, 2001). Despite the smaller size, they may contribute significantly to biomass and their nauplii stage serve as a food source prior to the phytoplankton bloom to other planktonic organisms (CASTELLANI et al., 2007; NIELSEN; SABATINI, 1996).

Zooplankton taxa, in general, were correlated with each other. Tropical copepods have distinct types of trophic strategies that allow their co-existence. Omnivorous copepods are the largest proportion, which allows them to occupy different niches in the environment (TEUBER et al., 2019).

The high abundance found in this study in the rainy season may be due to the fact that the area receives a large influx of nutrients and detritus particles from mangroves ecosystems (LINS SILVA; MARCOLIN; SCHWAMBORN, 2019; SCHWAMBORN; BONECKER, 1996) that increase the production of phytoplankton, food source of some zooplankton group, in addition with changes in other parameters leading to a great shift in the system. In a coastal area of the Mediterranean, (D'ALCALA et al., 2004) observed that two of three different phases of growth of zooplankton and phytoplankton in the seasonal cycle depended on the interplay between large-scale meteorological events and local terrestrial impact. In another site of the Mediterranean, the temperature was the main factor for zooplankton species fluctuations (SIOKOU-FRANGOU, 1996). In those sites where there is a high-temperature range, this can be an important factor in the seasonal variability of zooplankton. This type of finding reinforces the importance of studies of long time series to describe other factors governing zooplankton variability in different climates.

Although in this study, the samplings were always carried out during high tide, in order to minimize the influence of the river runoff and capture truly marine zooplankton, the presence of typical species of coastal-estuarine waters highlights the importance of estuarine plumes in this area, even during high tide. The well-represented *E. acutifrons*, *P. crassirostris*, and as well as *F. ehrenbergii*, are typical of this environment along the Brazilian coast influenced by estuarine plume and represent an important food source for upper trophic level in coastal areas (BRITO-LOLAIA et al., 2020; DIAS; BONECKER, 2008; MILSTEIN, 1979; SILVA et al., 2004). Besides that, each species has different life history and ecological functions in the environment (NIELSEN; SABATINI, 1996; BENEDETTI; GASPARINI; AYATA, 2016), which leads to a seasonal change in the trophodynamic structure of the ecosystem.

Environmental conditions

Rainfall showed seasonal and interannual differences, with values below expected for the rainy season of the years 2015 and 2016 that may possibly be related to the record strength El Niño event in this period ("Godzilla El Niño", CORIA-MONTER et al., 2019; SCHIERMEIER, 2015, the peak of ONI 2.5 in November 2015 and January 2016). A warm SST anomaly of Pacific SST (strong El Niño) occurred only once in our time series, hence there was no significant correlation between rainfall and ENSO in this study. Yet, during our sampling campaigns in the rainy seasons of 2015 and 2016, there was conspicuously less rainfall than in the other rainy seasons of our time series. However, due to the low spatial cover of this study and the relatively coarse temporal resolution (twice per season), and the fact that only one strong canonical El Niño event occurred in our time series, we cannot conclusively affirm whether ENSO is the main factor responsible for the observed low rainfall in these years.

Conversely, our data are conclusive in proving that the strong rainfall events in 2017 and 2019 had strong effects on the abiotic conditions and ecosystem structure in the study area. Extreme rainfall events in NEB coastal regions are related to the southwestern Atlantic warm pool (HOUNSOU-GBO et al., 2019). Such events, which cause catastrophic flash floods and landslides in NEB coastal cities, are prone to occur more intensely and frequently with global climate warming (MARENGO et al., 2023). The effects of these extreme rainfall events on coastal ecosystems had been poorly understood, prior to our study.

While ENSO has its central processes occurring in the Pacific Ocean, there are also several potentially relevant regular interannual oscillations that occur mostly in the Atlantic Ocean, such as the Atlantic Niño. The summer Atlantic Niño is a symmetric dominant mode of interannual variability in the tropical Atlantic (LÜBBECKE et al., 2010; LÜBBECKE; MCPHADEN, 2017; ZEBIAK, 1993). A strong and significant relationship between Pacific El Niño events and preceding Atlantic Niño events has been well documented and proven (HOUNSOU-GBO et al., 2020).

The atmosphere-ocean interactions exhibit some features in the tropical Atlantic, the most robust of these is the correlation between tropical Atlantic SST and rainfall that comes over NEB (SARAVANAN; CHANG, 2000). Differences in the length or intensity of the rainy season are due to several processes or a combination of them (KOUADIO et al., 2012). The main mechanism of rainfall in this region is the migration of the Intertropical Convergence Zone across the Equator (HASTENRATH, 1990). Although no correlation was observed between rainfall and the ENSO phenomenon, Saravanan and Chang (2000) concluded in their study that SST anomalies in the Pacific associated with ENSO have a significant remote influence on tropical Atlantic variability and much of this variability in the region can be explained by the conjunction of the ENSO and local atmospheric response to SST anomalies. Also, the southwestern Atlantic warm pool and the SST along the southern branch of the South Equatorial Current have a strong influence on the rainfall in the study area (HOUNSOU-GBO et al., 2019).

The seasonal differences in temperature, salinity, water transparency and chlorophyll *a* indicate a strong influence caused by the discharge of river and creeks as registered previously by other authors in Tamandaré Bay (SILVA et al., 2020; LINS SILVA; MARCOLIN; SCHWAMBORN, 2019).

Water transparency was correlated with rainfall, discharge of the Una River and chlorophyll *a*. There is a relevant supply of continental particles, nutrients and organisms in coastal areas, especially in rainy periods (LINS SILVA; MARCOLIN; SCHWAMBORN, 2019) as discussed above. Low water transparency values in the rainy season in this study indicate a seasonally eutrophic system, with high amounts of phytoplankton (“green water” conditions) during these periods. This result corroborates the fact that this easily obtained environmental variable (water transparency measured through Secchi Depth) is a good proxy to assess the trophic status of a pelagic ecosystem (oligotrophic *vs.* eutrophic state, KIRBY et al., 2021).

Conclusions

Our time series analysis allows the construction of a picture of the seasonal cycle and interannual variations on zooplankton in a tropical coastal area. A sampling effort of only one or two years would not have enabled us to detect the consistent drivers that cause oscillations or shifts in the community structure of the zooplankton. This highlights the importance of this type of long-term study in coastal tropical waters. Further studies of other important climate events and their effects on tropical marine ecosystems are needed to investigate these phenomena and relationships.

REFERENCE

ANDERSON, M. J. Permutational multivariate analysis of variance. **Department of Statistics, University of Auckland, Auckland**, v. 26, p. 32–46, 2005.

ANDRADE, G. O. DE; LINS, R. C. Os climas do Nordeste. **As regiões naturais do Nordeste, o meio e a civilização. CONDEPE, Recife**, v. 3, n. 4, p. 95–138, 1971.

BALASURIYA, A. Coastal area management: Biodiversity and ecological sustainability in Sri Lankan perspective. Em: **Biodiversity and climate change adaptation in tropical islands**. [s.l.] Elsevier, 2018. p. 701–724.

BEAUGRAND, G.; REID, P. C. Long-term changes in phytoplankton, zooplankton and salmon related to climate. **Global Change Biology**, v. 9, n. 6, p. 801–817, 1 jun. 2003.

BENEDETTI, F.; GASPARINI, S.; AYATA, S.-D. Identifying copepod functional groups from species functional traits. **Journal of Plankton Research**, v. 38, n. 1, p. 159–166, 3 nov. 2016.

BENTAMY, A.; FILLON, D. C. Gridded surface wind fields from Metop/ASCAT measurements. **International journal of remote sensing**, v. 33, n. 6, p. 1729–1754, 2012.

BOLTOVSKOY, D. **South Atlantic Zooplankton**. Leiden: Backhuys Publishers, 1999.

BRITO-LOLAIA, M. et al. Micro- and mesozooplankton at the edges of coastal tropical reefs (Tamandaré, Brazil). **Helgoland Marine Research**, v. 74, 1 dez. 2020.

CALBET, A.; LANDRY, M. R.; SCHEINBERG, R. D. Copepod grazing in a subtropical bay: species-specific responses to a midsummer increase in nanoplankton standing stock. **Marine Ecology Progress Series**, v. 193, p. 75–84, 2000.

CASTELLANI, C. et al. Regional and temporal variation of Oithona spp. biomass, stage structure and productivity in the Irminger Sea, North Atlantic. **Journal of Plankton Research**, v. 29, n. 12, p. 1051–1070, 15 out. 2007.

CASTONGUAY, M. et al. Copepod production drives recruitment in a marine fish. **Canadian Journal of Fisheries and Aquatic Sciences**, v. 65, n. 8, p. 1528–1531, 2008.

COLLOCA, F. et al. Structure and evolution of the artisanal fishery in a southern Italian coastal area. **Fisheries Research**, v. 69, n. 3, p. 359–369, 2004.

CORIA-MONTER, E. et al. Satellite observations of the effect of the "Godzilla El Niño" on the Tehuantepec upwelling system in the Mexican Pacific. **Helgoland Marine Research**, v. 73, p. 1–11, 2019.

COYLE, K. O.; PINCHUK, A. I. Annual cycle of zooplankton abundance, biomass and production on the northern Gulf of Alaska shelf, October 1997 through October 2000. **Fisheries Oceanography**, v. 12, n. 4-5, p. 327–338, 2003.

D'ALCALÀ, M. R. et al. Seasonal patterns in plankton communities in a pluriannual time series at a coastal Mediterranean site (Gulf of Naples): an attempt to discern recurrences and trends. **Scientia marina**, v. 68, n. S1, p. 65–83, 2004.

DIAS, C.; BONECKER, S. Inter-annual variability of planktonic copepods in a tropical bay in Southeastern Brazil. **Brazilian Archives of Biology and Technology - BRAZ ARCH BIOL TECHNOL**, v. 51, 1 jul. 2008.

DRIF, K.; AG, H.; HAY, S. Seasonal abundance and egg production rates of *Oithona similis* and *Pseudocalanus elongatus* in the northern North Sea: a first comparison of egg-ratio and incubation methods. **Marine Ecology Progress Series**, v. 415, p. 159–175, 2010.

DUFRÊNE, M.; LEGENDRE, P. Species assemblages and indicator species: The need for a flexible asymmetrical approach. **Ecological Monographs**, v. 67, n. 3, p. 345–366, 1 ago. 1997.

DUNN, O. J. Multiple comparisons using rank sums. **Technometrics**, v. 6, n. 3, p. 241–252, 1964.

DVORETSKY, V. G.; DVORETSKY, A. G. Life cycle of *Oithona similis* (Copepoda: Cyclopoida) in Kola Bay (Barents Sea). **Marine Biology**, v. 156, n. 7, p. 1433–1446, 2009.

ELLIOTT, D. T.; HARRIS, C. K.; TANG, K. W. Dead in the water: the fate of copepod carcasses in the York River estuary, Virginia. **Limnology and Oceanography**, v. 55, n. 5, p. 1821–1834, 2010.

ESKINAZI-SANT'ANNA, E. M.; BJÖRNBERG, T. K. S. Seasonal dynamics of microzooplankton in the São Sebastião Channel (SP, Brazil). **Brazilian Journal of Biology**, v. 66, p. 221–231, 2006.

FEITOSA, J. L. L.; FERREIRA, B. P. Distribution and feeding patterns of juvenile parrotfish on algal-dominated coral reefs. **Marine Ecology**, v. 36, n. 3, p. 462–474, 1 set. 2015.

FERREIRA, B.; MAIDA, M.; CAVA, F. C. Características e perspectivas para o manejo da pesca na APA Marinha Costa dos Corais. p. 50–58, 1 jan. 2000.

FERREIRA, B. P.; MAIDA, M. **Monitoramento dos recifes de coral do Brasil: situação atual e perspectivas**. [s.l.] MMA/SBF, 2006.

FERREIRA, B. P. et al. The effects of sea surface temperature anomalies on oceanic coral reef systems in the southwestern tropical Atlantic. **Coral reefs**, v. 32, p. 441–454, 2013.

FRANGOULIS, C. et al. Importance of copepod carcasses versus faecal pellets in the upper water column of an oligotrophic area. **Estuarine, Coastal and Shelf Science**, v. 92, n. 3, p. 456–463, 2011.

FRIENDLY, M. Corrgrams: Exploratory displays for correlation matrices. **The american statistician**, v. 56, n. 4, p. 316–324, 2002.

GALLIENNE, C. P.; ROBINS, D. B. Is Oithona the most important copepod in the world's oceans? **Journal of Plankton Research**, v. 23, n. 12, p. 1421–1432, 1 dez. 2001.

GASPAR, T. L. et al. Severe coral bleaching of Siderastrea stellata at the only atoll in the South Atlantic driven by sequential Marine Heatwaves. **Biota Neotropica**, v. 21, 2021.

GISMERVIK, I. Top-down impact by copepods on ciliate numbers and persistence depends on copepod and ciliate species composition. **Journal of Plankton Research**, v. 28, n. 5, p. 499–507, 2006.

GLANTZ, M. H.; RAMIREZ, I. J. Reviewing the Oceanic Niño Index (ONI) to enhance societal readiness for El Niño's impacts. **International Journal of Disaster Risk Science**, v. 11, p. 394–403, 2020.

HARGRAVES, P. E. Seasonal variations of tintinnids (Ciliophora: Oligotrichida) in Narragansett Bay, Rhode Island, U.S.A. **Journal of Plankton Research**, v. 3, p. 81–91, 1981.

HARZALLAH, A.; ROCHA DE ARAGÃO, J. O.; SADOURNY, R. INTERANNUAL RAINFALL VARIABILITY IN NORTH-EAST BRAZIL: OBSERVATION AND MODEL SIMULATION. **International Journal of Climatology**, v. 16, n. 8, p. 861–878, 1 ago. 1996.

HASTENRATH, S. Prediction of Northeast Brazil Rainfall Anomalies. **Journal of Climate**, v. 3, n. 8, p. 893–904, ago. 1990.

HAYS, G. C.; RICHARDSON, A. J.; ROBINSON, C. Climate change and marine plankton. **Trends in Ecology & Evolution**, v. 20, n. 6, p. 337–344, 2005.

HEIDELBERG, K. B. et al. Vertical distribution and diel patterns of zooplankton abundance and biomass at Conch Reef, Florida Keys (USA). **Journal of Plankton Research**, v. 32, n. 1, p. 75–91, 2010.

HOLT, J. et al. The potential impacts of climate change on the hydrography of the northwest European continental shelf. **Progress in Oceanography**, v. 86, n. 3–4, p. 361–379, 2010.

HOUNSOU-GBO, A. et al. Summer and winter Atlantic Niño: connections with ENSO and implications. **Climate Dynamics**, v. 55, n. 11, p. 2939–2956, 2020.

HOUNSOU-GBO, G. et al. SST Indexes in the Tropical South Atlantic for Forecasting Rainy Seasons in Northeast Brazil. **Atmosphere**, v. 10, p. 335, 19 jun. 2019.

HOUNSOU-GBO, G. A. et al. Oceanic indices for forecasting seasonal rainfall over the northern part of Brazilian northeast. 2016.

HUANG, B. et al. Extended Reconstructed Sea Surface Temperature Version 4 (ERSST.v4). Part I: Upgrades and Intercomparisons. **Journal of Climate**, v. 28, n. 3, p. 911–930, 4 fev. 2015.

IKEDA, T. Nutritional Ecology of Marine Zooplankton. **Mem. Fac. Fish. Hokkaido Univ.**, v. 22, n. 1, p. 1–97, 1974.

JUSTIC, D.; RABALAIS, N. N.; TURNER, R. E. Impacts of climate change on net productivity of coastal waters: implications for carbon budgets and hypoxia. **Climate research**, v. 8, n. 3, p. 225–237, 1997.

KAMIYAMA, T.; ARIMA, S. Feeding characteristics of two tintinnid ciliate species on phytoplankton including harmful species: effects of prey size on ingestion rates and selectivity. **Journal of Experimental Marine Biology and Ecology**, v. 257, n. 2, p. 281–296, 2001.

KIRBY, R. R. et al. Citizens and scientists collect comparable oceanographic data: measurements of ocean transparency from the Secchi Disk study and science programmes. **Scientific Reports**, v. 11, n. 1, p. 15499, 2021.

KOUADIO, Y. et al. Heavy Rainfall Episodes in the Eastern Northeast Brazil Linked to Large-Scale Ocean-Atmosphere Conditions in the Tropical Atlantic. **Advances in Meteorology**, v. 2012 (2012), p. 16 pages, 10 jul. 2012.

KRUSKAL, W. H.; WALLIS, W. A. Use of ranks in one-criterion variance analysis. **Journal of the American statistical Association**, v. 47, n. 260, p. 583–621, 1952.

LEGENDRE, P.; GALLAGHER, E. D. Ecologically meaningful transformations for ordination of species data. **Oecologia**, v. 129, p. 271–280, 2001.

LINS SILVA, N.; 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.

LÜBBECKE, J. F. et al. On the connection between Benguela and equatorial Atlantic Niños and the role of the South Atlantic Anticyclone. **Journal of Geophysical Research: Oceans**, v. 115, n. C9, 2010.

LÜBBECKE, J. F.; MCPHADEN, M. J. Symmetry of the Atlantic Niño mode. **Geophysical Research Letters**, v. 44, n. 2, p. 965–973, 2017.

LUGOMELA, C. et al. Trichodesmium in coastal waters of Tanzania: diversity, seasonality, nitrogen and carbon fixation. **Hydrobiologia**, v. 477, n. 1, p. 1–13, 2002.

MARENGO, J. A. et al. Variabilidade e mudanças climáticas no semiárido brasileiro. **Recursos hídricos em regiões áridas e semiáridas**, v. 1, p. 385–422, 2011.

MARENGO, J. A. et al. Flash floods and landslides in the city of Recife, Northeast Brazil after heavy rain on May 25–28, 2022: Causes, impacts, and disaster preparedness. **Weather and Climate Extremes**, v. 39, p. 100545, 2023.

MILSTEIN, A. Vertical distribution of Paracalanus crassirostris (Copepoda, Calanoidea): analysis by the general linear model. **Boletim do Instituto Oceanográfico**, v. 28, n. 2, p. 65–78, 1979.

MOLINERO, J. C. et al. Climate control on the long-term anomalous changes of zooplankton communities in the Northwestern Mediterranean. **Global Change Biology**, v. 14, n. 1, p. 11–26, 1 jan. 2008.

MONTI, M. et al. Seasonal and interannual dynamics of microzooplankton abundances in the Gulf of Trieste (Northern Adriatic Sea, Italy). **Estuarine, Coastal and Shelf Science**, v. 115, p. 149–157, dez. 2012.

MOTODA, S. Devices of simple plankton apparatus. **Memoirs of the faculty of fisheries Hokkaido University**, v. 7, n. 1–2, p. 73–94, 1959.

NASCIMENTO-VIEIRA, D. A.; DE FIGUEIREDO, F.; NETO, P. Mesozooplâncton de área recifal do atlântico sudoeste tropical. 2010.

NIELSEN, T.; SABATINI, M. Role of cyclopoid copepods Oithona spp. in North Sea plankton communities. **Marine Ecology-progress Series - MAR ECOL-PROGR SER**, v. 139, p. 79–93, 1 ago. 1996.

NITTROUER, C. A. et al. An introduction to the geological significance of sediment transport and accumulation on the Amazon continental shelf. **Marine Geology**, v. 125, n. 3–4, p. 177–192, 1995.

OKSANEN, J. et al. **vegan: Community Ecology Package. 2019. R package version 2.5-6**. Avilable online at https://CRAN. R-project. org/package= vegan (accessed …, , 2019.

OMORI, M.; IKEDA, T. **Methods in marine zooplankton ecology**. John Wiley and Sons Inc., New York, , 1984.

PITOIS, S.; YEBRA, L. Contribution of marine zooplankton time series to the United Nations Decade of Ocean Science for Sustainable Development. **ICES Journal of Marine Science**, v. 79, n. 3, p. 722–726, 2022.

PLANQUE, B.; TAYLOR, A. H. Long-term changes in zooplankton and the climate of the North Atlantic. **ICES Journal of Marine Science**, v. 55, n. 4, p. 644–654, 1 ago. 1998.

PREISENDORFER, R. W. Secchi disk science: Visual optics of natural waters 1. **Limnology and oceanography**, v. 31, n. 5, p. 909–926, 1986.

ROMAGNAN, J.-B. et al. Comprehensive model of annual plankton succession based on the whole-plankton time series approach. **PLoS One**, v. 10, n. 3, p. e0119219, 2015.

RUIZ-BARRADAS, A.; CARTON, J. A.; NIGAM, S. Structure of interannual-to-decadal climate variability in the tropical Atlantic sector. **Journal of Climate**, v. 13, n. 18, p. 3285–3297, 2000.

SANTANA, C. S. et al. Amazon river plume influence on planktonic decapods in the tropical Atlantic. **Journal of Marine Systems**, v. 212, p. 103428, 2020.

SANTOS, G. S. et al. Are tropical coastal reefs sinks or sources of mesozooplankton? A case study in a Brazilian marine protected area. **Coral Reefs**, v. 38, n. 6, p. 1107–1120, 2019.

SANTOS, G. S.; BRITO-LOLAIA, M.; SCHWAMBORN, R. Two new methods for sampling zooplankton and larval assemblages in tropical reef ecosystems. **Journal of Experimental Marine Biology and Ecology**, v. 491, p. 27–37, 1 jun. 2017.

SARAVANAN, R.; CHANG, P. Interaction between tropical Atlantic variability and El Niño–Southern oscillation. **Journal of climate**, v. 13, n. 13, p. 2177–2194, 2000.

SAVTCHENKO, A. et al. Terra and Aqua MODIS products available from NASA GES DAAC. **Advances in Space Research**, v. 34, n. 4, p. 710–714, 2004.

SCHIERMEIER, Q. Hunting the Godzilla El Niño. **Nature**, v. 526, n. 7574, p. 490, 2015.

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. **Arquivos de Biologia e Technologia**, v. 39, p. 451–462, 1 jan. 1996.

SHAPIRO, S. S.; WILK, M. B. An Analysis of Variance Test for Normality (Complete Samples). **Biometrika**, v. 52, n. 3/4, p. 591, dez. 1965.

SHEAVES, M. et al. True Value of Estuarine and Coastal Nurseries for Fish: Incorporating Complexity and Dynamics. **Estuaries and Coasts**, v. 38, n. 2, p. 401–414, 2015.

SILVA, A. P. et al. Mesozooplankton of an impacted Bay in North Eastern Brazil. **Brazilian Archives of Biology and Technology**, v. 47, n. 3, p. 485–493, 2004.

SILVA, A. J. et al. Non-predatory mortality of planktonic copepods in a reef area influenced by estuarine plume. **Marine Environmental Research**, v. 159, p. 105024, 2020.

SILVA, E.; MANDÚ, T. Rainfall intensity variability in the rainy season in Recife-PE Brazilian Journal of Development. **Brazilian Journal of Development**, v. 6, p. 69044–69053, 16 set. 2020.

SIOKOU-FRANGOU, I. Zooplankton annual cycle in a Mediterranean coastal area. **Journal of Plankton Research**, v. 18, n. 2, p. 203–223, 1996.

SOMMER, U. et al. Beyond the Plankton Ecology Group (PEG) model: mechanisms driving plankton succession. **Annual review of ecology, evolution, and systematics**, v. 43, p. 429–448, 2012.

STOECKER, D.; GUILLARD, R. R. L.; KAVEE, R. M. SELECTIVE PREDATION BY FAVELLA EHRENBERGII (TINTINNIA) ON AND AMONG DINOFLAGELLATES. **The Biological Bulletin**, v. 160, n. 1, p. 136–145, 1 fev. 1981.

URRUTXURTU, I.; ORIVE, E.; SOTA, A. DE LA. Seasonal dynamics of ciliated protozoa and their potential food in an eutrophic estuary (Bay of Biscay). **Estuarine, Coastal and Shelf Science**, v. 57, n. 5, p. 1169–1182, 2003.

VARONA, H. L. et al. Monthly anomaly database of atmospheric and oceanic parameters in the tropical Atlantic Ocean. **Data in Brief**, v. 41, p. 107969, 2022.

VENABLES, W. N. et al. Exploratory multivariate analysis. **Modern applied statistics with S**, p. 301–330, 2002.

YOUNG, C. M. (ED). **Atlas of Marine Invertebrate Larvae**. San Diego, United States.

ZAHEDI, S. Tourism impact on coastal environment. **WIT Transactions on The Built Environment**, v. 99, p. 45–57, 2008.

ZAR, J. H. **Biostatistical Analysis**. Prentice Hall, 1999.

ZEBIAK, S. E. Air–sea interaction in the equatorial Atlantic region. **Journal of Climate**, v. 6, n. 8, p. 1567–1586, 1993.

4 ARTIGO 2 – CAN THE STABLE ISOTOPE VARIABILITY IN A ZOOPLANKTON TIME SERIES BE EXPLAINED BY ITS KEY SPECIES?

Observação: Este artigo foi publicado na revista Marine Environmental Research em 3 de setembro de 2022. https://doi.org/10.1016/j.marenvres.2022.105737. Para seguir o padrão da tese, o abstract, acknowledgements, fundings foram extraídos desse artigo.

INTRODUCTION

Carbon and nitrogen stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) have been used for a variety of purposes in marine ecosystem research (FRY, 2006; OHMAN; RAU; HULL, 2012; POST, 2002; SCHWAMBORN; GIARRIZZO, 2015). $\delta^{13}C$ can be used as a tracer for primary food sources since it is transferred from preys to predators with minor isotopic changes (MCCONNAUGHEY; MCROY, 1979). Conversely, $\delta^{15}N$ values show strong enrichment within food chains and thus can be used as indicators of trophic position (HANNIDES et al., 2009; MINAGAWA; WADA, 1984; POST, 2002). Furthermore, the C/N ratio can be used as a proxy for assessing the lipid content of organisms (SCHWAMBORN; GIARRIZZO, 2015). In contrast to early species-based community descriptors (i.e., abundance, diversity, etc.), the wide use of stable isotopes in the past few decades has promoted a further understanding of trophic relations and food sources in marine ecosystems (HUNT et al., 2015; YANG et al., 2016).

Marine food webs are often regulated by a discrete number of key species (e.g., large-sized apex predators or small-sized, very abundant prey). However, there are still surprisingly few quantitative approaches available that allow the detection of such key species, that determine the temporal variability (time series) in ecosystem stable isotope signatures, and thus, the dynamics of the food web.

Time series play an essential role in the observation of changes in zooplankton community stable isotope signatures, allowing the analysis of cyclic variations such as seasonal and interannual isotopic shifts (GREVE et al., 2004; MULLIN; RAU; EPPLEY, 1984; OHMAN; RAU; HULL, 2012; SHERIDAN; LANDRY, 2004; VANDROMME et al., 2011). Zooplankton often exhibits a seasonal succession driven by biotic and abiotic factors that structure communities (CALBET; LANDRY; SCHEINBERG, 2000; D’ALCALÀ et al., 2004;

ROMAGNAN et al., 2015; SOMMER et al., 2012). Salinity, temperature and food availability are major drivers influencing the abundance and composition of zooplankton communities (BUCKLIN et al., 2019; COYLE; PINCHUK, 2003; D'ALCALÀ et al., 2004; PITOIS; YEBRA, 2022). Zooplankton is an important carbon source for upper trophic levels (TL) and often a good indicator ("signal amplifier") for climate change (BEAUGRAND, 2005; HAYS; RICHARDSON; ROBINSON, 2005).

Most studies on stable isotopes of marine zooplankton are focused on a few species (FOREST et al., 2011; HANNIDES et al., 2009; SANDEL et al., 2015; YANG et al., 2016) or size-fractions (FIGUEIREDO et al., 2020b; FRY; QUIÑONES, 1994; GIERING et al., 2019; YANG et al., 2017). The most common approach in stable isotope ecology studies, including those on zooplankton, is to *a priori* define a small list of species of interest. For each selected species, a few specimens are usually sorted out from plankton net samples and measured for their carbon and nitrogen content, C/N ratio and stable isotope composition (CHOI et al., 2020; MULLIN; RAU; EPPLEY, 1984; OHMAN; RAU; HULL, 2012; SCHWAMBORN et al., 1999). However, this approach may be questionable, especially regarding the potential bias when describing highly complex ecosystems based on a subjectively pre-defined list of a few "favorite" species. Unfortunately, there is no standard method available in the published literature that would allow us to detect which species are the most important in shaping the variability in stable isotope signatures of ecosystems, and thus in its food web structure and dynamics.

Here, we test the hypothesis that the temporal biomass variations of one species (or a set of species) have a significant effect on stable isotope and element ratios of the whole zooplankton community, in order to infer key ecological processes and indices, such as trophic position. One key question for the present study is which taxa affect $\delta^{15}N$, and thus determine the TL of the zooplankton community. We hypothesize that an increase in relative biomass (i.e., % contribution to the total zooplankton biomass) of large-sized carnivores should increase the $\delta^{15}N$ of the pelagic ecosystem (i.e., increase the zooplankton community TL). Also, we intend to investigate the sources of variability in $\delta^{13}C$. Seasonal variations in nutrient inputs should affect the zooplankton carbon isotope signature, assuming that diatom-rich "green waters" are more $\delta^{13}C$-enriched than oligotrophic and flagellate-rich "blue waters" (FRY; WAINRIGHT, 1991). Furthermore, we investigated seasonal variations in C/N ratio (e.g., to assess lipid content, SCHWAMBORN; GIARRIZZO, 2015) and their relationship to the biomass composition of zooplankton, within a novel species-biomass-isotopes-mixture (SBIM) approach.

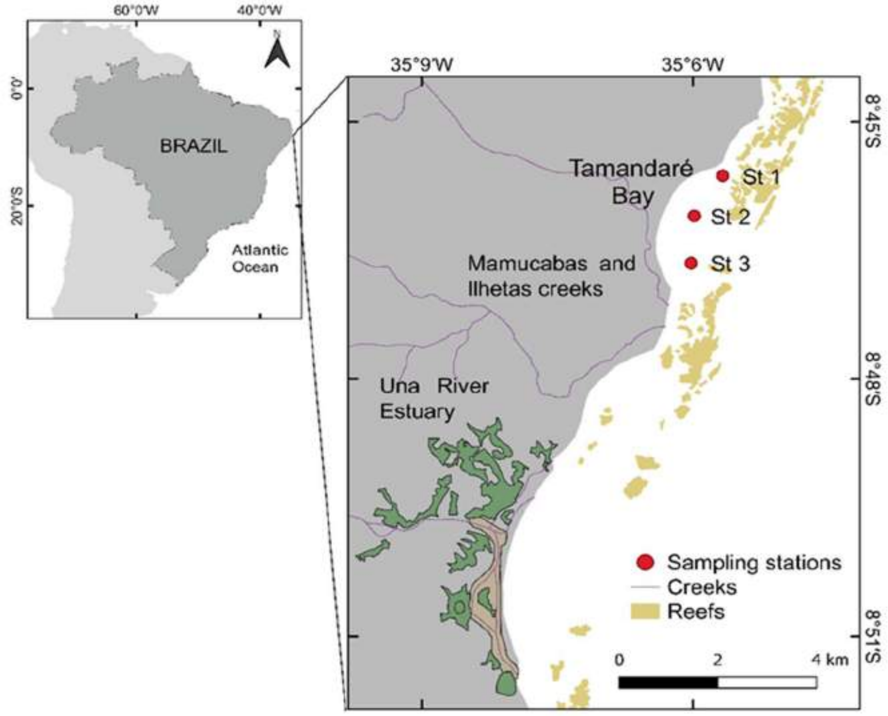
MATERIALS AND METHODS

Study area

Tamandaré Bay (8° 46’ 07.5” S, 35° 06’ 03.6” W) is located in northeastern Brazil (Figure 1). It is a semi-enclosed embayment lined by sandstone reefs that harbour unique endemic corals, zoanthids, and other fauna and flora (SANTOS et al., 2015). The bay is located within the northernmost limit of the Costa dos Corais marine protected area (MPA). In the rainy season, the bay is under direct influence of the Mamucabas-Ilhetas creeks that discharge their plumes in the southern portion of Tamandaré Bay. Occasionally, it may also be influenced by the Una River (Figure 1) plume during extreme discharge events.

The study area is characterized by an As’ climate, according to the Köppen classification (ANDRADE; LINS, 1971). The rainy season is typically from March to August, while the dry season is from September to February. Local tides are semidiurnal with mesotidal ranges from 1.6 to 2.5 m. Coastal drift is usually wind-driven and predominantly in a south-north direction. Thus, the discharge of the Una River (located south of Tamandaré Bay) is especially important for the coastal waters on the continental shelf off the study area (Figure 1). Coastal winds are usually in the onshore direction (SE, NE and E) and stronger in June-October (GREGO et al., 2009), roughly coinciding with the rainy season.

Figure 1. Geographical setting of Tamandaré Bay and its surroundings. Red dots depict sampling stations in Tamandaré Bay.



Fonte: A autora (2022).

Sampling strategy

Regular sampling campaigns were carried out every other month over six years, during spring tides (new moon) from June 2013 to August 2019. Zooplankton was collected at three stations in Tamandaré Bay (Figure 1). Mean depths at stations 1, 2 and 3 were 4.2m, 6.5m and 7.4m, respectively. In order to avoid terrigenous and freshwater inputs and to allow monitoring of marine coastal water masses, sampling was always carried out around high tide. Subsurface (0 to 0.3 m deep) horizontal tows were performed for 5 min at speeds of 2-3 knots using a conical-cylindrical plankton net (64 µm mesh size, 0.31 m mouth ring diameter, 1 m length). All tows were conducted during daytime spring high tides. A flow meter was attached to the net mouth for calculating the volume of filtered seawater.

Samples were fixed with 4% formalin (final concentration in seawater) buffered with sodium tetraborate (0.5 g L^{-1}, HANNIDES et al., 2009; MULLIN; RAU; EPPLEY, 1984; OHMAN; RAU; HULL, 2012; OMORI; IKEDA, 1984; RAU; OHMAN; PIERROT-BULTS, 2003). Sea surface (1 m) temperature (SST), salinity and depth were recorded at each sampling station using a CTD probe (SonTek model CastAway, San Diego, CA, USA). Water transparency was estimated using a Secchi disk (Preisendorfer, 1986). Secchi depth can be used to assess transparency and may be a good proxy for the trophic status (oligotrophic *vs* eutrophic state) of pelagic ecosystems (KIRBY et al., 2021).

We used accumulated rainfall over a five-day period (i.e., on the sampling day and on four preceding days) as an explaining variable in our analysis. This period was chosen after running a multi-lag correlation analysis between rainfall, water transparency and salinity. Local rainfall data sets were obtained from the Pernambuco State Agency for Water and Climate (APAC, https://www.apac.pe.gov.br/).

Laboratory analyses

A total of 111 plankton samples were successfully collected over seven years, as part of the ST-ESPLAN-Tropic project, and archived at the Museum of Oceanography of the Federal University of Pernambuco (Recife, Brazil). Four sampling campaigns were chosen each year for stable isotope analysis. Two campaigns were selected for each season (rainy/dry), except for the first (2013) and last (2019) sampling years. In 2015, there was only one campaign in the rainy season due to logistical issues and bad weather. Thus, 66 zooplankton samples were selected for stable isotope analysis (34 obtained in the dry season and 32 in the rainy season).

All samples were washed with filtered tap water and split using a Motoda splitter (MOTODA, 1959). In each aliquot, approximately 500 to 1000 individuals were randomly selected for investigating the zooplankton community and for stable isotope analysis. Identification, counting and measurements (body width and total length from the tip of the rostrum to the rear end of the telson, not including setae) were conducted on a Sedgwick-Rafter chamber under a binocular microscope. Organisms were identified to the lowest possible taxonomic level (BOLTOVSKOY, 1999; YOUNG; SEWELL, 2006). Zooplankton biomass ($mg\ C\ m^{-3}$) was estimated using the following equation: ln (copepod biomass) = 1.82 * ln (S) + 1.28 for copepods (including adults and copepodites), and ln (non-copepod biomass) = 1.46 * ln (S) + 1.03 for other taxa, where S is total body size in mm (HEIDELBERG et al., 2010; HEIDELBERG; SEBENS; PURCELL, 2004). Average taxon-specific carbon values ($\mu g\ C\ ind^{-1}$) of all taxa were multiplied by their abundance ($ind\ m^{-3}$) in each sample in order to calculate total zooplankton biomass ($\mu g\ C\ m^{-3}$).

From each subsample, a small aliquot (i.e., qualitative subsample) was further washed with distilled water prior to stable isotope analysis. Zooplankton organisms were inserted into silver capsules that were previously weighed on a micro-analytical balance (accuracy: 0.001 mg) and then oven-dried at 60 ºC for 24 hours. The dried samples were left to cool in a desiccator at room temperature and weighed again for determining dry weights (which ranged between 0.151 and 3.386 mg). Finally, silver capsules were wrapped up and placed in the autosampler of an elemental analyzer (EA, EuroVector, model EA3000 Single) coupled to an isotope ratio mass spectrometer (IRMS, Thermo Scientific, model DELTA V Advantage).

In zooplankton isotope studies, sample acidification is necessary for removing inorganic carbon prior to $\delta^{13}C$ analysis. However, this procedure may interfere with $\delta^{15}N$ values (JACOB et al., 2005). So, ten samples were chosen for assessing the influence of sample acidification in $\delta^{15}N$: five samples with the highest $\delta^{13}C$ values and five samples with the lowest $\delta^{13}C$ values. Following the recommendations of Jacob et al. (2005), these samples were acidified with drops of hydrochloric acid (1 M) until bubble formation ceased. After this procedure, all capsules were oven-dried, wrapped up and placed in the EA-IRMS autosampler. PERMANOVA did not show any significant differences in $\delta^{13}C$ and $\delta^{15}N$ between decarbonated and non-decarbonated zooplankton samples. In contrast, C/N ratios were different ($p < 0.001$) with higher values in samples not acidified as expected. Therefore, subsequent stable isotope analyses in zooplankton were done without acidifying samples.

Stable isotopes values are reported according to the delta notation: $\delta^{13}C$ (or $\delta^{15}N$) = $[R_{sample}/R_{standard} - 1] \times 1000$, where $R = {}^{13}C/{}^{12}C$ (or ${}^{15}N/{}^{14}N$). The international standards for carbon and nitrogen are Vienna Pee Dee Belemnite (VPDB) and atmospheric air (AIR), respectively. A certified reference material (casein) purchased from Elemental Microanalysis UK (P/N B2155) was employed for checking analytical precision. The standard deviation (SD) of stable isotope analysis was 0.13‰ ($n = 9$) for both $\delta^{13}C$ and $\delta^{15}N$. SD for elemental analysis was 2.5% for carbon ($n = 9$) and 0.79% for nitrogen ($n = 9$).

Data analysis

All data were tested for normality using the Shapiro-Wilk test (SHAPIRO; WILK, 1965). Since they were not normally distributed, univariate PERMANOVA (ANDERSON, 2001) was used to test for differences between seasons (dry *vs* rainy), years (2013, 2014, 2015, 2016, 2017, 2018 and 2019) and sampling stations (St. 1, St. 2 and St. 3), by using the function “adonis2” with the “vegan” R package (OKSANEN et al., 2019). Spearman rank correlation was used to assess correlations between variables. PERMANOVA was based on Euclidean distances, with 20,000 permutations.

All multivariate analyses (linear models) were conducted with the aim of testing the hypothesis that stable isotope ($\delta^{13}C$ and $\delta^{15}N$) and elemental composition (C/N ratio) of zooplankton samples can be explained by their taxonomic composition. We verified which taxonomic groups are more relevant for predicting the zooplankton stable isotope composition. We tested whether specific taxa in the samples were related to lower (or higher) values of stable isotope ($\delta^{13}C$ and $\delta^{15}N$) and C/N ratios.

These analyses were conducted within a novel species-biomass-isotopes-mixture (SBIM) approach. It consists in using a species-specific relative biomass matrix to explain the stable isotope signature of the total zooplankton community (i.e., the mixture of species). The underlying rationale is similar to that of any common stable isotope mixing model: instantaneous linear change in the stable isotope signature of a mixture (e.g., $\delta^{13}C$ of the total zooplankton community) is linearly proportional to the change in relative biomass of the components of the mixture (i.e., the relative biomass of the species). Thus, SBIM is a simple combination of multiple linear regression and common linear mixing models. It consists in finding the multiple linear regression models that best explain the variability in stable isotope signatures ($\delta^{13}C$ and $\delta^{15}N$) and C/N ratios, stepwise backward selecting significant variables (see below), combined with post-hoc nonparametric permutation tests.

Prior to the SBIM analysis, zooplankton biomass (mg C m^{-3}) was transformed into relative units (% biomass). A simple composite index (frequency of occurrence * biomass of each taxonomic group) was used to select the 15 most relevant taxa prior to multivariate analyses. All other taxonomic groups were pooled together as “others”. For multiple linear models, stepwise backward regression was used for selecting the significant variables using the function “stepAIC” in the R Package “MASS” (VENABLES et al., 2002). The significance of linear models (either univariate or multivariate) was checked with nonparametric permutation tests using the function “lmp” (Permutation Tests for Linear Models) within the R package “lmPerm” (WHEELER; TORCHIANO; TORCHIANO, 2016). The contribution of each taxonomic group to the overall variability in stable isotopes explained by linear models was assessed with the “Relative importance” approach, by calculating the “lmg” index (R^2 partitioned by averaging over orders, (LINDEMAN; MERENDA; GOLD, 1980), within the R package “Relaimpo” (GROEMPING, 2006). Significance levels were set at $\alpha = 0.05$ (ZAR, 1999), reporting different grades of evidence (AMRHEIN; GREENLAND; MCSHANE, 2019; MUFF et al., 2021). Thus, for significant results, we used a scale from “moderate evidence” ($0.05 > p > 0.01$) to “strong evidence” ($0.01 > p > 0.001$) and “very strong evidence” ($p < 0.001$, MUFF et al., 2021).

RESULTS

Environmental conditions

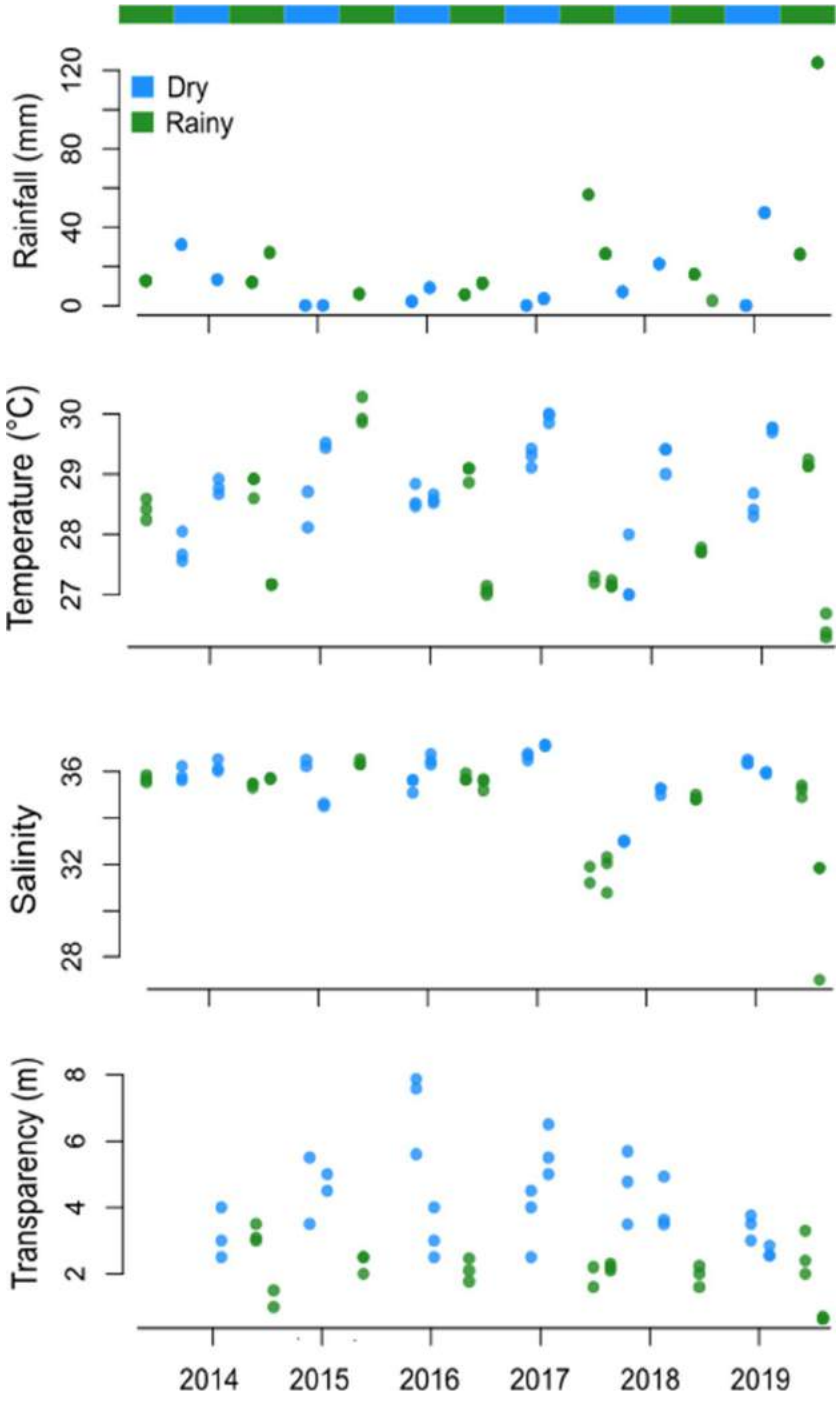
All abiotic parameters (rainfall, salinity, temperature and water transparency) showed significant differences between seasons (Table 1). Median accumulated rainfall was 7.0 and 14.3 mm in dry and rainy seasons, respectively (Table 1). The five-day accumulated rainfall had a significant effect on both salinity and transparency. Seasonally increasing rainfall clearly reduced the water transparency (turbid "green water" conditions) in Tamandaré Bay, during the rainy seasons, in all years (Figure 2). Furthermore, high rainfall events led to a decrease in salinity, especially in 2017 and 2019 (Figure 2). Also, there was strong evidence for seasonal differences in salinity (PERMANOVA, $p < 0.001$) and temperature (PERMANOVA, $p = 0.003$), with lower values in the rainy season. Higher rainfall was observed in 2019 while lower salinity was observed in 2017 and 2019 (Figure 2), although salinity was always above 26. In almost all (97%) of sampling campaigns, conditions were clearly euhaline (salinity > 30), except in August 2019, when it was exceptionally rainy, leading to minimum values of temperature, salinity and water transparency. Environmental parameters did not show any significant differences between sampling stations. Also, there were no significant interannual differences in temperature and water transparency.

Table 1. Descriptive statistics of environmental variables at three sampling stations of Tamandaré Bay (northeastern Brazil) in dry and rainy seasons from 2013 to 2019. Significant differences ($p < 0.05$) are indicated in bold (Permutation test).

Environmental variables	Dry			Rainy			
	Min	Max	Median	Min	Max	Median	P-Value
Temperature (ºC)	27.0	30.0	28.7	26.3	30.7	27.8	**0.003**
Salinity	29.0	37.1	36.1	27.0	36.6	35.4	**<0.001**
Transparency (m)	2.3	7.9	4.0	0.6	4.7	2.1	**<0.001**
Rainfall (mm)	0	47.4	7.0	1.8	123.9	14.3	**0.010**

Fonte: A autora (2022).

Figure 2. Time series (2013-2019) of abiotic parameters (rainfall, salinity, temperature and Secchi depth) were recorded in the dry (blue dots) and rainy (green dots) seasons in Tamandaré Bay, northeastern Brazil.

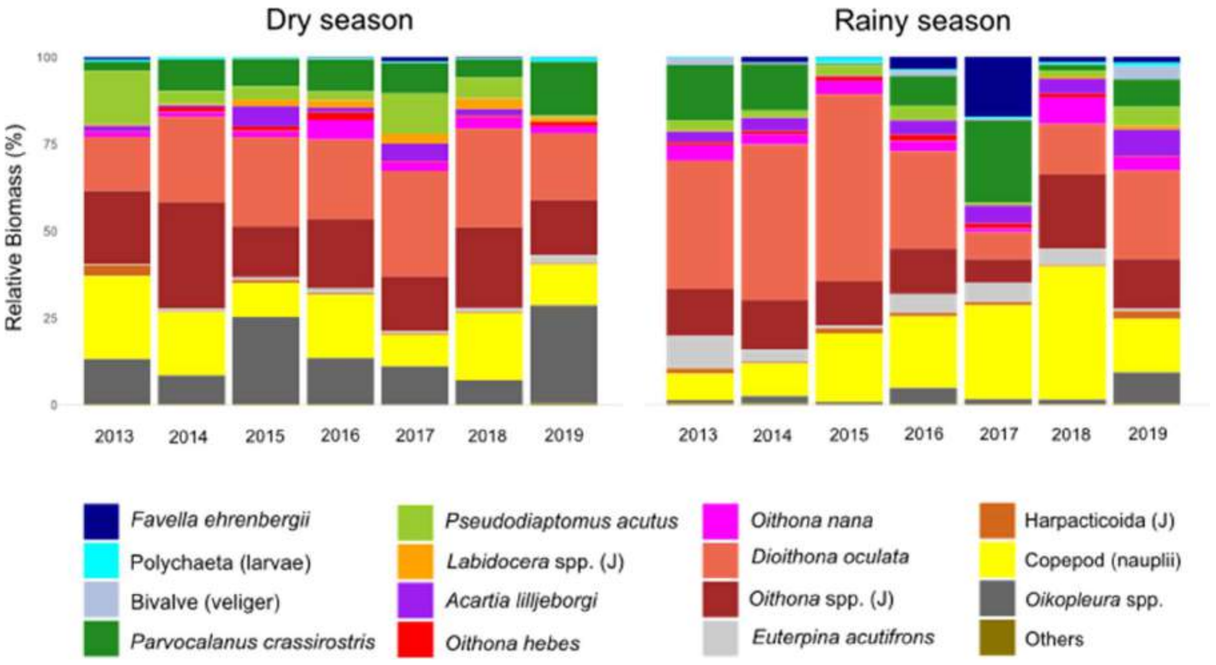


Fonte: A autora (2022).

Zooplankton composition and biomass

A total of 72 zooplankton taxa were identified in this study. Zooplankton composition varied considerably between seasons and years (Figure 3). Copepods (adults, juveniles and nauplii) were dominant in terms of both abundance and biomass. Based on relative biomass, the most important taxa were the cyclopoid copepods *Dioithona oculata* (adults, mean: 28% relative biomass) and *Oithona* spp. (juveniles, 17%), copepod nauplii (19%), appendicularians *Oikopleura* spp. (11%), calanoid copepods *Parvocalanus crassirostris* (adult and juveniles, 9%), *Pseudodiaptomus acutus* (adults and juveniles, mean, 3%, st. dev. 4%: max: 22%), and *Acartia lilljeborgi* (adult and juveniles, 3%), the cyclopoid *Oithona nana* (adults, 3%), the harpacticoid *Euterpina acutifrons* (adult and juveniles, 2%), the tintinnid *Favella ehrenbergii* (1%), bivalve larvae (veliger stages, 1%), polychaete larvae (1%), other harpacticoid copepods (juveniles, 1%, mostly Longipediidae), the cyclopoid copepod *Oithona hebes* (adults, 1%), and the calanoid copepod *Labidocera* spp. (juveniles, 1%). Other taxa comprised less than 1% of total biomass.

Figure 3. Relative biomass of zooplankton taxa sampled in rainy and dry seasons in Tamandaré Bay from 2013 to 2019.



Fonte: A autora (2022).

There was strong evidence that total zooplankton wet biomass differed between seasons (PERMANOVA, $p < 0.001$) and between sampling stations (PERMANOVA, $p < 0.01$). Also, zooplankton wet biomass differed significantly between years (PERMANOVA, $p = 0.015$). There was also a significant interaction between year and season (PERMANOVA, $p = 0.002$) (Table 2).

Table 2. Outcome (p-values) of the three-way PERMANOVA on zooplankton relative biomass. Explanatory variables are year, season, and sampling station. Differences between factor levels are identified in brackets. The full model tested all possible interactions (year:season, year:station, season:station, and year:season:station). Significant values ($P < 0.05$) are in bold.

Variables	Zooplankton Biomass
	PERMANOVA
Year	**0.015** (2016 ≠ 2017)
Season	**0.001** (dry < rainy)
Station	**0.018** (St 1 ≠ St 2 = St 3)
Year:Season	**0.002**
Year:Station	0.454
Season:Station	0.926
Year:Season: Station	0.424

Fonte: A autora (2022).

Ten taxa were significantly ($p < 0.05$) associated with seasonality (PERMANOVA, Table 3). For three of these taxa (*Labidocera* spp. juveniles, *Oithona* spp. and *Oikopleura* spp.), there was very strong evidence ($p < 0.001$, PERMANOVA) for higher relative biomass in the dry season. Also, for three taxa (*F. ehrenbergii*, bivalves and *E. acutifrons*) there was very strong evidence ($p < 0.001$, PERMANOVA) that they had higher relative biomass in the rainy season (Table 3). There were significant interannual differences for copepod nauplii (max. in 2018), *D. oculata* (max. in 2015) and “others” (max in 2019), however with moderate evidence only (Table 3, Figure 3).

Table 3. Outcome ("p"-values) of the PERMANOVA of relative biomass of the most relevant taxa, in relation to the explanatory variables "Year", "Season" and the interaction "Year:Season". "R", (or "D"): Higher relative abundance in the Rainy (or Dry) Season. Significant values ($p < 0.05$) are in bold. J: juveniles.

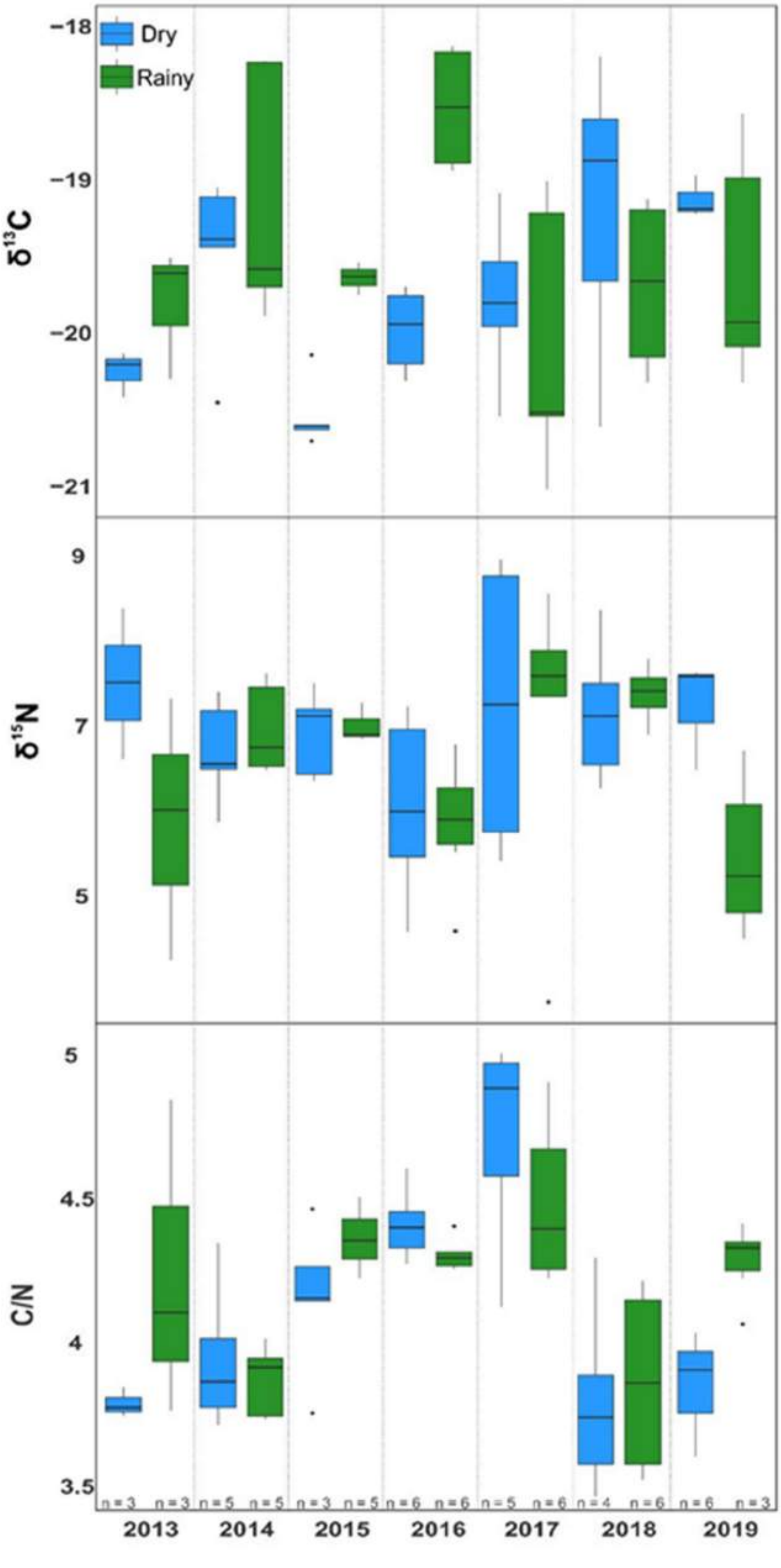
Variables	Year	Season	Year:Season
Favella ehrenbergii	0.366	**<0.001** (R)	0.460
Polychaeta (larvae)	0.063	0.065	0.239
Bivalve (veliger)	0.919	**<0.001** (R)	0.849
Parvocalanus crassirostris	0.761	0.121	0.064
Pseudodiaptomus acutus	0.581	**0.028** (D)	0.142
Labidocera spp. (J)	0.262	**<0.001** (D)	0.889
Acartia lilljeborgi	0.615	**0.028** (R)	0.272
Oithona hebes	0.726	0.217	0.755
Oithona nana	0.458	0.274	0.865
Dioithona oculata	**0.025** (max. 2015)	0.113	**0.025**
Oithona spp. (J)	0.541	**<0.001** (D)	0.647
Euterpina acutifrons	0.600	**<0.001** (R)	**0.001**
Harpacticoida (J)	0.112	**0.035** (R)	**<0.001**
Copepod (nauplii)	**0.047** (max. 2018)	**0.045** (R)	**0.003**
Oikopleura spp.	0.339	**<0.001** (D)	0.154
Others	**0.019** (max. 2019)	0.114	0.417

Fonte: A autora (2022).

Zooplankton stable isotope signature

The $\delta^{13}C$ values of zooplankton showed a small variation, ranging from -21.0 to -18.2‰ (mean ± standard deviation: -19.7 ± 0.7‰ in the dry season, and -19.4 ± 0.8‰ in the rainy season, Figure 4). Zooplankton $\delta^{15}N$ values varied across a wide range, from 3.8 to 9.0‰ (mean ± standard deviation: 7.0 ± 1.0‰ in the dry season, and 6.5 ± 1.2‰ rainy season). There were no significant differences in zooplankton $\delta^{15}N$ between seasons. C/N ratios of zooplankton ranged from 3.5 to 5.0 (mean ± standard deviation: 4.2 ± 0.4 in the dry season and 4.2 ± 0.3 in the rainy season, Figure 4). Since there were no significant stable isotope differences between sampling stations, they were considered replicates in subsequent analyses.

Figure 4. δ^{13}C, δ^{15}N and C/N ratios of zooplankton in the dry and rainy season, from 2013 to 2019.



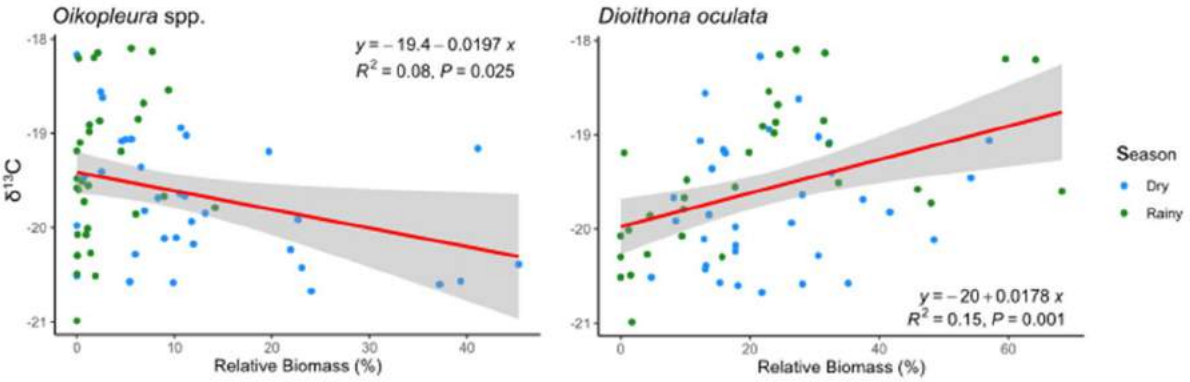
Fonte: A autora (2022).

$\delta^{13}C$ and zooplankton relative biomass

The “best” multiple linear model (backward selection with permutation tests) obtained within the SBIM analysis explained 41% of the variability in $\delta^{13}C$ using relative biomass of key zooplankton taxa as explanatory variables. Backward selection yielded a linear model with the relative biomasses of six key taxa as dependent variables: bivalve larvae, *E. acutifrons,* copepod nauplii, *O. nana, D. oculata* and *Oithona* spp. ($p < 0.001$, $R^2 = 0.41$). The relative importance analysis (Relaimpo package) confirmed *D. oculata* as the most important organism for explaining $\delta^{13}C$ (17.7% of the total variability).

Simple univariate linear models revealed significant relationships between zooplankton $\delta^{13}C$ and relative biomass for two taxa: *Oikopleura* spp. and *D. oculata* ($p = 0.025$, $R^2 = 0.08$ and $p = 0.001$, $R^2 = 0.15$, respectively). *D. oculata* showed a significantly positive correlation with $\delta^{13}C$ (Figure 5). Conversely, the appendicularian *Oikopleura* spp. showed a significantly negative correlation with $\delta^{13}C$. Furthermore, a seasonal effect was observed since low $\delta^{13}C$ and high relative biomass of *Oikopleura* spp. were found in the dry season (Figure 5) along with high transparency (“blue waters”) and oligotrophic conditions.

Figure 5. Significant simple linear regressions between $\delta^{13}C$ and relative biomass of *Oikopleura* spp. and *D. oculata*. Blue and green dots denote dry and rainy seasons, respectively.



Fonte: A autora (2022).

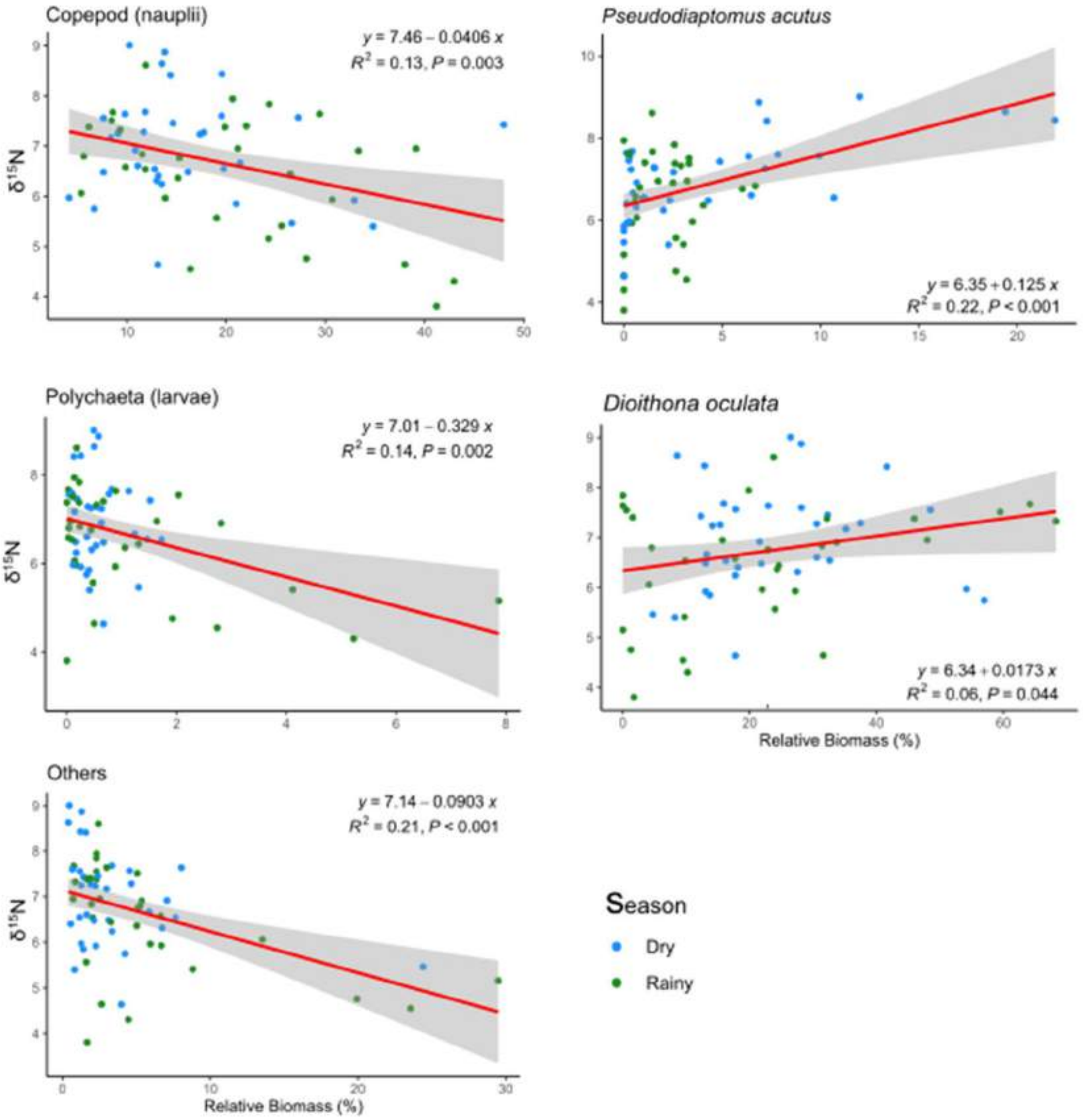
$\delta^{15}N$ and zooplankton relative biomass

Within the SBIM analysis, the "best" linear model for zooplankton $\delta^{15}N$ and the relative biomass of key taxa explained 42% of the variability. Seven key taxa were selected as significant variables: *E. acutifrons,* copepod nauplii, *Oikopleura* spp., *D. oculata, P. crassirostris,* polychaete larvae and *P. acutus* ($p < 0.001$, $R^2 = 0.42$). The Relaimpo analysis, using the lmg index, confirmed *P. acutus* as the most important variable for $\delta^{15}N$. Based on the lmg index, 20.5% of the total variability in $\delta^{15}N$ was explained by *P. acutus* in the multiple linear model.

Simple linear regressions between relative biomass and $\delta^{15}N$ were significant for the following taxa: copepod nauplii ($p = 0.003$, $R^2 = 0.13$), *D. oculata* ($p = 0.044$, $R^2 = 0.06$), polychaete larvae ($p = 0.002$, $R^2 = 0.14$) and *P. acutus* ($p < 0.001$, $R^2 = 0.22$) (Figure 6). *D. oculata* and large-sized *P. acutus* showed positive correlations with $\delta^{15}N$. Conversely, copepod nauplii, polychaete larvae and "others" were negatively correlated with $\delta^{15}N$ (Figure 6). Copepod nauplii and polychaete larvae showed a highly significant correlation with each other (Spearman correlation, $p = 0.00012$), indicating a strong temporal covariation.

The univariate linear model with *P. acutus* explained 22% of the $\delta^{15}N$ variability. Relaimpo results provided a similar outcome, indicating that *P. acutus* dominated the $\delta^{15}N$ variability. Thus, higher $\delta^{15}N$ values (i.e., zooplankton with higher TL) were found in samples with higher relative biomass of *P. acutus,* especially in the dry season (Figure 6). Fourteen samples (8% of 111 samples) had high (> 5%) biomass of *P. acutus,* with high abundances of this species and high $\delta^{15}N$ (above 6 ‰). Among these *P. acutus*-rich, high-$\delta^{15}N$ samples, the vast majority (86%, twelve samples) were collected in the dry season.

Figure 6. Significant simple linear regressions between δ^{15}N and relative biomass of copepod nauplii, *P. acutus*, polychaete larvae, *D. oculata* and "others" (pooled taxa with low relative biomass in the data set). Blue and green dots denote dry and rainy seasons, respectively.

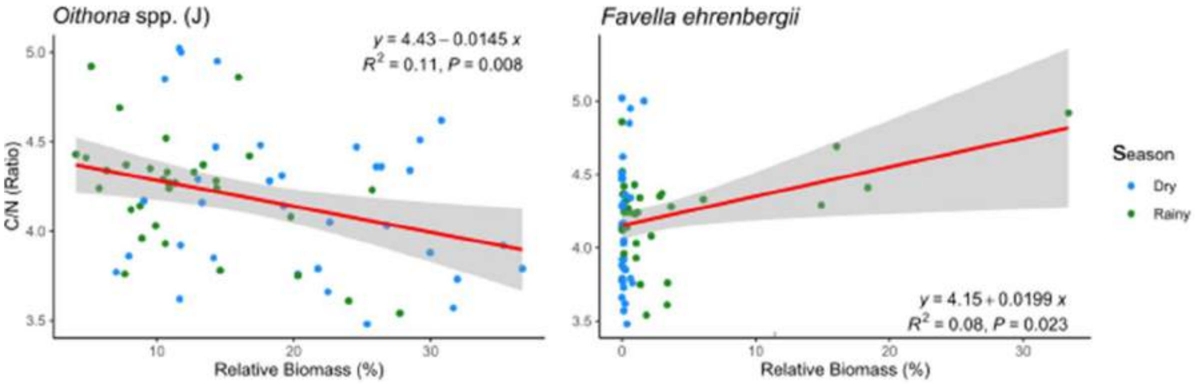


Fonte: A autora (2022).

C/N ratio

The "best" multiple linear model, within SBIM analysis, explained 26% of the variability in zooplankton C/N ratio based on the relative biomass of five taxa: *F. ehrenbergii, Labidocera* spp. (juveniles), Polychaeta, *Oithona* spp (juveniles) and others ($p < 0.001$, $R^2 = 0.26$). The Relaimpo analysis confirmed *Oithona* spp. (juveniles) as the most important group for C/N ratio (8.1% of the total variability). Relative biomass of two taxa exhibited significant linear relationships with zooplankton C/N ratio: *Oithona* spp. showed a negative correlation ($p = 0.008$, $R^2 = 0.11$) and *F. ehrenbergii* showed a positive correlation ($p = 0.023$, $R^2 = 0.08$) (Figure 7). In the rainy season, *F. ehrenbergii* showed higher relative biomass associated with higher zooplankton C/N values (Figure 7). *F. ehrenbergii* was also positively correlated to water transparency ($p = 0.0028$, $R^2 = 0.15$, for log[x+1] - transformed relative biomass), showing that high relative biomass of *F. ehrenbergii* occurred in turbid "green waters", during the rainy season.

Figure 7. Significant simple linear regressions between C/N ratio and relative biomass of *Oithona* spp. and *F. ehrenbergii*. Blue and green dots denote dry and rainy seasons, respectively.



Fonte: A autora (2022).

DISCUSSION

This study presents and combines two unique datasets within the SBIM approach: 1.) a time series of zooplankton community structure and species relative biomass composition and 2.) a time series of zooplankton stable isotope signatures. This novel approach, which combines these two datasets, was used to detect key taxa that have a strong and significant effect on community stable isotope signature. They were not outstanding by their mean abundance, or mean biomass, but rather by their variability in relative biomass, and their extreme position in isotope signature (far above or far below the community mean, as in the calanid copepod *P. acutus*). Also, these key taxa may be bioindicators of a specific ecosystem state (as in the tintinnid *F. ehrenbergii*).

Contribution of *Pseudodiaptomus acutus* and *Dioithona oculata* to zooplankton δ^{15}N

One of the most surprising findings of this study was that the relative biomass of the copepod *Pseudodiaptomus acutus* showed a high significant positive correlation with zooplankton δ^{15}N, being responsible for a considerable portion (22%) of the variability in δ^{15}N. Since δ^{15}N can be used as a proxy of TL (POST, 2002), the large-sized calanid *P. acutus* was the single most important species in defining the TL of the zooplankton community. This result was unexpected, considering its very small contribution in units of abundance (2%) and biomass (5%). Based on its numbers and average biomass, it would seem absurd to think that *P. acutus* could ever be the single most important species in determining the TL of this pelagic ecosystem. No previous study has ever highlighted this species as a potential key species in tropical coastal food webs. Yet, in our study, *P. acutus* accounted for approximately half of the overall variability that can be explained by the zooplankton biomass composition in linear models (Overall R^2: 42%).

The strong positive correlation with community δ^{15}N indicates that *P. acutus* occupies a very high trophic position, far above the average zooplankton. This species is a relatively large-sized copepod (mean total length: 830 µm) within the community sampled with a 64 µm mesh (i.e., when compared to cyclopoids of the genus *Oithona*, with a mean total length of 670 µm, found with very high relative biomass in this study). A strong size-TL relationship was also supported by the findings of Figueiredo et al. (2020b), who detected a positive relationship between δ^{15}N and zooplankton body size in tropical marine plankton.

Copepods can actively search for, capture and choose to ingest or reject potential food particles (KLEPPEL, 1993). *P. acutus* can be detritivorous and selective and probably chooses food items (e.g., tintinnids) with greater protein potential (ESKINAZI-SANT'ANNA; BJÖRNBERG, 2000; VERITY; LAGDON, 1984). Furthermore, *P. acutus* showed very high variability in abundance and biomass, with significantly higher relative contributions to the zooplankton in the dry season. Our study showed that *P. acutus* has a strong influence on the variability in ecosystem TL, which, considering its relatively small numbers, can only be achieved through a combination of three factors: 1.) body size above average (i.e., relatively high individual biomass), 2.) consistently high TL, and 3.) highly variable abundance (i.e., if it was appearing in constant numbers, its effect would be zero). The main factor seems to be a TL far above average, given its relatively low numbers. To our knowledge, this is the first study to detect the importance of this ubiquitous species, which is surprising, considering the plethora of studies on tropical zooplankton. In a common stable isotope study, where a few specimens of a list of subjectively pre-selected species are usually sorted out of a sample (FOREST et al., 2011; HANNIDES et al., 2009; OHMAN; RAU; HULL, 2012; SANDEL et al., 2015; SCHWAMBORN et al., 1999; YANG et al., 2016), this key species, that is not the largest one (e.g., adults of the ubiquitous copepods *Labidocera fluviatilis* and *Acartia lilljeborgi* have longer total lengths than *P. acutus*) nor the most abundant, would certainly not be analyzed at all, due to its very small abundance and relative biomass. Conversely, the congener *Pseudodiaptomus koreanus* showed the lowest $\delta^{15}N$ and thus a very low TL (below average zooplankton) in a recent study in South Korean estuarine and coastal waters, using a similar approach (CHEN et al., 2018). Yet, Chen et al. (2018) did not investigate the stable isotope dynamics of the total zooplankton community (as in this study), but rather the stable isotope signatures of copepod subsamples only. The striking discrepancies between two studies using a similar, novel approach, are possibly due to differences in feeding behavior between these two species (*P. acutus vs P. koreanus*) or in differences in the available food spectrum and seasonal cycles (tropical *vs* temperate) in these ecosystems and highlight the need for further studies on these little investigated key calanoid copepods, and comparisons between ecosystems. A common denominator for these two studies may be the high seasonal variability in relative biomass of *Pseudodiaptomus* spp.

Pseudodiaptomus spp. are relatively rare and large copepods that may have been neglected in many previous zooplankton SI studies. Other, very large and rare zooplankton groups (e.g., large-sized medusae) have also been detected as relevant drivers of variability in pelagic food webs (BOERO et al., 2008; FIGUEIREDO et al., 2020a; LIRA et al., 2017;

PURCELL; WHITE; ROMAN, 1994), but these extremely large-sized mega- and macrozooplankton taxa were not considered in the present study, which focused on the micro- and mesozooplankton communities.

Relative biomass of the cyclopoid *Dioithona oculata* also showed a significant positive correlation with δ^{15}N, indicating that this species has a TL above average. However, its contribution to the overall variability in δ^{15}N was very small, which is probably due to its consistently high numbers throughout our study, and possibly a change in TL according to environmental conditions (CHOI et al., 2020). Similarly, to our results, the recent study by Chen et al. (2018) also indicated that cyclopoids have a very high TL in the waters off South Korea.

A recent study in polar waters (CHOI et al., 2020) also compared the stable isotope-based TL of small-sized oithonid and large-sized calanid copepods. In their study, *Calanus* spp. also had an unexpectedly high TL and *Oithona similis* showed strong changes in TL between seasons. Cyclopoids employ a variety of different feeding strategies, and one species may shift feeding strategies seasonally, additionally to ontogenetic shifts. Copepod feeding behavior is extremely complex and often depends intrinsically on the available food composition and density (CHEN et al., 2018).

Contribution of small-sized larvae to zooplankton δ^{15}N - bioindicators or determinants of ecosystem state?

Small-sized copepod nauplii (mean total length: 144 μm) and small-sized polychaete larvae (mean total length: 263 μm) presented highly significant negative correlations with δ^{15}N, which corroborates the fact that these small-sized larval organisms feed on small particles, that are likely more basal in the food chain, such as phytoplankton (PHILLIPS; PERNET, 1996; TURNER et al., 2001; VOGT; PERES-NETO; BEISNER, 2013). This is explained by their maximum relative biomass occurring in zooplankton samples with low δ^{15}N (i.e., low TL).

However, the detailed analysis and comparison of copepod nauplii and polychaete larvae reveal intrinsic differences between these two taxa, in our dataset, and in the possible interpretations of SBIM results. While copepod nauplii are very abundant and thus have a very large relative biomass (mean: 19%, max: 76%), and are obviously relevant contributors to the variability in zooplankton δ^{15}N, this is not possible for polychaete larvae, due to their minuscule, irrelevant relative biomass (mean: 0.8%, max: 8%).

Thus, for polychaete larvae, it is likely that they are useful bio-indicators for a specific ecosystem state (i.e., for zooplankton with low mean TL). Polychaete larval relative biomass and zooplankton community TL are linked within the temporal variability in our time series, but their low biomass implies that they cannot have a causal linear influence on zooplankton $\delta^{15}N$, even though there was a significant linear regression (Figure 6). Polychaete larvae showed a highly significant correlation with copepod nauplii (synchronized reproduction), which did represent a significant biomass contribution to the community sampled in 64-micron mesh nets. Synchronized spawning has already been observed for other invertebrate taxa in tropical coastal areas (SCHWAMBORN et al., 2001).

For the interpretation of SBIM results in general, this means that there are several possible interpretations, additionally to the inherent challenges in the evaluation of causal relations in any complex systems. Obviously, statistical correlations observed in natural ecosystems cannot be used to prove any causal relationship, and the likelihood of a given species being a determinant of stable isotope signatures must be evaluated carefully in each case, considering the statistical significance, magnitude of effects, mean and maximum relative biomass, and the variability (e.g., st. dev.) in relative biomass.

Contributions of *Dioithona oculata* and *Oikopleura* spp. to zooplankton $\delta^{13}C$

The relative biomass of *Dioithona oculata* was positively correlated with $\delta^{13}C$. AMBLER; ALCALA-HERRERA; BURKE (1994) found in their study a variation from -15.2 to -13.8‰ for *D. oculata* which is more ^{13}C-enriched (enrichment > 2‰) than its potential food as a potential consumer of detritus and dinoflagellates. In Tamandaré Bay, diatoms are generally predominant (81.18%, with high abundances of two very large diatom species, *Chaetoceros lorenzianus* (size 9 - 35 µm) and *Coscinodiscus centralis* (diameter 100 - 300 µm)) among other phytoplankton groups (SILVA et al., 2005) and they were probably used as a food source by *D. oculata*. This conclusion is in line with the findings of Figueiredo et al. (2020b) who observed a discrepancy between POM and ^{13}C-enriched zooplankton, indicating that tropical marine zooplankton selectively uses $\delta^{13}C$-rich phytoplankton (e.g., diatoms) as a food source. Furthermore, our $\delta^{13}C$ values for zooplankton (from -21.0 to -18.2‰) confirm what was found for copepods (from -19.5 to -18.7‰) in a previous study conducted on the northeastern Brazil shelf (SCHWAMBORN et al., 1999). In a recent study in Tamandaré Bay (BRITO-LOLAIA et al., 2020) *D. oculata* was also found to dominate in units of abundance. *D. oculata* is widely found in many tropical coastal areas, often forming swarms near coral reefs

(AMBLER; FERRARI; FORNSHELL, 1991; BUSKEY; PETERSON; AMBLER, 1996), which can be an important carbon source for fish larvae and other planktivores in coastal areas.

Conversely, the appendicularian *Oikopleura* spp. showed a negative relationship with $\delta^{13}C$ in this study. These organisms feed by means of a complex, fragile gelatinous house (TROEDSSON et al., 2009), which filters particles of very small sizes, down to 0.15 µm (FLOOD; DEIBEL, 1998). The filter-feeding house can capture particles much smaller than diatoms, which can quickly clog the filtering structure. Fry and Wainright (1991) observed ^{13}C-depleted values in other (non-diatom) phytoplankton and most particulate organic matter. The filter-feeding mechanism enables them to survive in extremely oligotrophic waters with low food concentrations (ACUÑA, 2001) and explains their higher relative abundance in the dry season ("blue water" conditions) in our study.

C/N ratio

It is well established that the C/N ratio can be used as a proxy for lipid content (POST et al., 2007; SCHWAMBORN; GIARRIZZO, 2015; SWEETING; POLUNIN; JENNINGS, 2006). Two taxa showed a significant linear relationship between their relative biomass and zooplankton C/N ratios: *Oithona* spp. juveniles showed a negative correlation with zooplankton C/N ratios, thus being an indicator for oligotrophic conditions and lipid-poor zooplankton, while *F. ehrenbergii* showed a positive correlation with zooplankton C/N ratios.

Samples with very high relative biomass of the tintinnid *F. ehrenbergii* occurred in turbid "green waters", during the rainy season, when the ecosystem was in a eutrophic state, with high lipid contents in a "well-fed" zooplankton community, which can lead to an increase in lipid content in tintinnids (VERITY; LAGDON, 1984) and many other zooplankton groups. In Tamandaré Bay, this species was significantly ($p < 0.001$) more abundant during the rainy season. This highly palatable tintinnid species is the preferred prey for many meso- and macrozooplankton taxa (SCHWAMBORN et al., 2006). Its high abundance indicates the plentiful availability of food in a hypereutrophic pelagic ecosystem, such as the extremely polluted urban ecosystem of Guanabara Bay, in southeastern Brazil (SCHWAMBORN et al., 2006).

Temporal and environmental variability of zooplankton biomass and stable isotope signatures

Zooplankton stable isotopes and C/N ratios did not show any consistent spatial, seasonal or annual variability.

However, in 2015 and 2016, we observed a ^{13}C-enrichment in the rainy season, probably due to a stronger influence of "green waters" that receive continental runoff. The input of nutrients and organisms from estuaries, as well as higher resuspension of sediments, boost the primary production (DELL'AQUILA et al., 2017; PAHLOW; RIEBESELL; WOLF-GLADROW, 1997; SCHWAMBORN et al., 1999) in the rainy season. In study area, there is a predominance of diatoms (SILVA et al., 2005). This phytoplankton is a ^{13}C-rich carbon source for many marine food webs (FRY; WAINRIGHT, 1991) and the observed increase in ^{13}C may be related to a greater supply of this food source to the ecosystem. The ^{15}N-enrichment in 2013 and 2019 in the dry season may be related to the species *P. acutus* being positively correlated with δ^{15}N and having high relative biomass in the dry season (see above).

Also, the non-expressive spatial, seasonal and interannual variability of stable isotope signatures found here can be explained by the high variability of taxa present in this study. We observed a seasonal faunistic succession between seasons. The dry season showed higher relative biomass for the appendicularian *Oikopleura* spp. and the copepods *P. acutus* and *Labidocera* spp. (juv.), while in the rainy season, there was higher relative biomass of bivalves, *F. ehrenbergii*, copepod nauplii, *A. lilljeborgi* and *E. acutifrons*. All taxa found in higher relative biomass in the rainy season are typical of coastal-estuarine waters (BRITO-LOLAIA et al., 2020; DIAS; BONECKER, 2008).

In the present study, rainfall was the main factor acting on seasonal and interannual variability in environmental conditions (salinity and transparency) in the study area. Spatial variability was generally negligible (at least in environmental conditions and stable isotope signatures), due to the proximity of the stations and the high temporal variability within a time series in a highly dynamic coastal area. Although this study was always conducted at maximum spring high tide in order to allow for a maximum oceanic influence in the bay (and avoid sampling inside any estuarine plumes), the seasonal differences in salinity and water transparency indicate an influence caused by the discharge of rivers and creeks, as was registered previously by other authors in Tamandaré bay (SILVA et al., 2020; LINS SILVA; MARCOLIN; SCHWAMBORN, 2019) and elsewhere (DIAS; BONECKER, 2008; JYOTHIBABU et al., 2008).

This sampling strategy (sampling at high tide) explains why we did not find any δ^{13}C values influenced by estuarine plumes with ^{13}C-depleted mangrove carbon, as found in tropical estuaries and in the plumes that are found at river mouths, during low tide (SCHWAMBORN et al., 1999). In almost all sampling campaigns (except one, in August 2019), conditions were clearly euhaline, further supporting the observations that we did not sample any “brown-water”, turbid estuarine plumes. This is why our interpretation and analysis of the $\delta^{13}C$ data were not conducted within the traditional dichotomy of terrigenous (i.e., mangrove) carbon *vs* marine (i.e., phytoplankton) carbon sources (GIARRIZZO; SCHWAMBORN; SAINT-PAUL, 2011; SCHWAMBORN et al., 2002). The obvious absence of any detectable mangrove carbon in our samples (when considering the sampling strategy, water color, salinity, and especially the $\delta^{13}C$ data) led us towards a new interpretation, comparing diatom-rich (^{13}C-enriched) marine plankton *vs* other marine plankton. Our sampling strategy (sampling at high tide, far away from any river mouths) allowed us to sample marine zooplankton communities that are influenced under seasonally varying complex nutrient input and processing dynamics (i.e., with nutrients being sedimented, resuspended and diluted) in the coastal boundary layer. The higher rainfall and stronger winds in the rainy season increase productivity and modify the structure of the community, which is reflected in the isotopic variation in this region.

Conclusions and Outlook

The combined analysis of zooplankton stable isotopes and taxonomic composition of the biomass (“species-biomass-isotopes-mixture” - SBIM approach) proved to be useful to describe the structure and temporal dynamics of food webs. A previous study, which was also based on a similar approach, investigated the trophic relations between POM and subsamples of copepods only (not the whole zooplankton community, as in our study) in South Korea (CHEN et al., 2018). Thus, this is the first study to analyze stable isotopes of a complex zooplankton community within a time series, using the SBIM approach.

This new approach allowed us to successfully assess the relative TL of key taxa (i.e., the TL of key taxa relative to the mean TL of the zooplankton community), which would be impossible to achieve in traditional “pick-and-measure” studies of selected taxa, mainly due to their small size (e.g., for copepod nauplii and polychaete larvae) and the extremely high species richness of tropical plankton. Also, it allowed us to detect key taxa (e.g., *P. acutus*), that would otherwise not be highlighted nor analyzed separately in traditional stable isotope studies, based on the analysis of a few specimens (sometimes only one specimen, e.g., one bat in SCHWAMBORN; GIARRIZZO, 2015) in a subjective list of pre-selected species. This new, statistically sound and robust approach paves the way for novel ecosystem models and a new area of stable isotope research.

REFERENCES

ACUÑA, J. L. Pelagic Tunicates: Why Gelatinous? **The American Naturalist**, v. 158, n. 1, p. 100–107, 1 jul. 2001.

AMBLER, J.; FERRARI, F.; FORNSHELL, J. Population structure and swarm formation of the cyclopoid copepod Dioithona oculata near mangrove cays. **Journal of Plankton Research**, v. 13, 1 nov. 1991.

AMBLER, J. W.; ALCALA-HERRERA, J.; BURKE, R. Trophic roles of particle feeders and detritus in a mangrove island prop root ecosystem. **Hydrobiologia**, v. 292, n. 1, p. 437–446, 1994.

AMRHEIN, V.; GREENLAND, S.; MCSHANE, B. Retire statistical significance. **Nature**, v. 567, p. 305–307, 20 mar. 2019.

ANDERSON, M. J. A new method for non-parametric multivariate analysis of variance. **Austral Ecology**, v. 26, n. 1, p. 32–46, 1 fev. 2001.

ANDRADE, G. O. DE; LINS, R. C. Os climas do Nordeste. **As regiões naturais do Nordeste, o meio e a civilização. CONDEPE, Recife**, v. 3, n. 4, p. 95–138, 1971.

BEAUGRAND, G. Monitoring pelagic ecosystems using plankton indicators. **ICES Journal of Marine Science**, v. 62, n. 3, p. 333–338, 2005.

BOERO, F. et al. Gelatinous plankton: Irregularities rule the world (sometimes). **Marine Ecology Progress Series**, v. 356, p. 299–310, 18 mar. 2008.

BOLTOVSKOY, D. **South atlantic zooplankton**. 1999.

BRITO-LOLAIA, M. et al. Micro- and mesozooplankton at the edges of coastal tropical reefs (Tamandaré, Brazil). **Helgoland Marine Research**, v. 74, 1 dez. 2020.

BUCKLIN, A. et al. Time-series metabarcoding analysis of zooplankton diversity of the NW Atlantic continental shelf. **ICES Journal of Marine Science**, v. 76, n. 4, p. 1162–1176, 2019.

BUSKEY, E. J.; PETERSON, J. O.; AMBLER, J. W. he swarming behavior of the copepod Dioithona oculata: In situ and laboratory studies. **Limnology and Oceanography**, v. 41, n. 3, p. 513–521, 1996.

CALBET, A.; LANDRY, M. R.; SCHEINBERG, R. D. Copepod grazing in a subtropical bay: species-specific responses to a midsummer increase in nanoplankton standing stock. **Marine Ecology Progress Series**, v. 193, p. 75–84, 2000.

CHEN, M. et al. Variability in copepod trophic levels and feeding selectivity based on stable isotope analysis in Gwangyang Bay of the southern coast of the Korean Peninsula. **Biogeosciences**, v. 15, n. 7, p. 2055–2073, 2018.

CHOI, H. et al. Trophic dynamics of zooplankton before and after polar night in the Kongsfjorden (Svalbard): Evidence of trophic position estimated by δ15N analysis of amino acids. **Frontiers in Marine Science**, v. 7, p. 489, 2020.

COYLE, K. O.; PINCHUK, A. I. Annual cycle of zooplankton abundance, biomass and production on the northern Gulf of Alaska shelf, October 1997 through October 2000. **Fisheries Oceanography**, v. 12, n. 4-5, p. 327–338, 2003.

D'ALCALÀ, M. R. et al. Seasonal patterns in plankton communities in a pluriannual time series at a coastal Mediterranean site (Gulf of Naples): an attempt to discern recurrences and trends. **Scientia marina**, v. 68, n. S1, p. 65–83, 2004.

DELL'AQUILA, G. et al. Nutrient consumption and chain tuning in diatoms exposed to storm-like turbulence. **Scientific Reports**, v. 7, p. 1828, 12 maio 2017.

DIAS, C.; BONECKER, S. Inter-annual variability of planktonic copepods in a tropical bay in Southeastern Brazil. **Brazilian Archives of Biology and Technology - BRAZ ARCH BIOL TECHNOL**, v. 51, 1 jul. 2008.

FIGUEIREDO, G. et al. New records of the mollusk Firoloida desmarestia Lesueur, 1817 (Gastropoda: Pterotracheidae) off Fernando de Noronha Archipelago and Northeastern Brazilian continental slope, Tropical Atlantic. **Tropical Oceanography**, v. 48, 21 jul. 2020a.

FIGUEIREDO, G. G. A. A. et al. Body size and stable isotope composition of zooplankton in the western tropical Atlantic. **Journal of Marine Systems**, v. 212, p. 103449, 2020b.

FLOOD, P. R.; DEIBEL, D. **The appendicularian house**. 1998.

FOREST, A. et al. Biogenic carbon flows through the planktonic food web of the Amundsen Gulf (Arctic Ocean): A synthesis of field measurements and inverse modeling analyses. **Progress in Oceanography**, v. 91, n. 4, p. 410–436, 2011.

FRY, B. **Stable isotope ecology**. [s.l.] Springer, 2006. v. 521

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 13C-rich carbon in marine food webs. **Marine Ecology Progress Series**, v. 76, p. 149–157, 1991.

GIARRIZZO, T.; SCHWAMBORN, R.; SAINT-PAUL, U. Utilization of carbon sources in a northern Brazilian mangrove ecosystem. **Estuarine, Coastal and Shelf Science**, v. 95, n. 4, p. 447–457, 2011.

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.

GREGO, C. et al. Fitoplâncton do ecossistema estuarino do rio Ariquindá (Tamandaré, Pernambuco, Brasil): variáveis ambientais, biomassa e produtividade primária. Atlantica 31. https://doi.org/10.5088/ atl.2009.31.2.183. 2009.

GREVE, W. et al. Helgoland Roads meso-and macrozooplankton time-series 1974 to 2004: lessons from 30 years of single spot, high frequency sampling at the only off-shore island of the North Sea. **Helgoland Marine Research**, v. 58, p. 274–288, 2004.

GROEMPING, U. Relative Importance for Linear Regression in R: The Package relaimpo. **Journal of Statistical Software**, v. 17, n. 1, p. 1–27, 1 set. 2006.

HANNIDES, C. C. S. et al. Quantification of zooplankton trophic position in the North Pacific Subtropical Gyre using stable nitrogen isotopes. **Limnology and oceanography**, v. 54, n. 1, p. 50–61, 2009.

HAYS, G. C.; RICHARDSON, A. J.; ROBINSON, C. Climate change and marine plankton. **Trends in ecology & evolution**, v. 20, n. 6, p. 337–344, 2005.

HEIDELBERG, K. B. et al. Vertical distribution and diel patterns of zooplankton abundance and biomass at Conch Reef, Florida Keys (USA). **Journal of Plankton Research**, v. 32, n. 1, p. 75–91, 2010.

HEIDELBERG, K. B.; SEBENS, K. P.; PURCELL, J. E. Composition and sources of near reef zooplankton on a Jamaican forereef along with implications for coral feeding. **Coral Reefs**, v. 23, n. 2, p. 263–276, 2004.

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.

JACOB, U. et al. Stable isotope food web studies: A case for standardized sample treatment. **Marine Ecology Progress Series**, v. 287, p. 251–253, 18 fev. 2005.

JYOTHIBABU, R. et al. Seasonal variation of microzooplankton (20–200µm) and its possible implications on the vertical carbon flux in the western Bay of Bengal. **Continental Shelf Research**, v. 28, n. 6, p. 737–755, 2008.

KIRBY, R. R. et al. Citizens and scientists collect comparable oceanographic data: measurements of ocean transparency from the Secchi Disk study and science programmes. **Scientific Reports**, v. 11, n. 1, p. 15499, 2021.

KLEPPEL, G. S. On the diets of calanoid copepods. **Marine Ecology Progress Series**, v. 99, p. 183–195, 1993.

LINDEMAN, R. H.; MERENDA, P. F.; GOLD, R. Z. **Introduction to Bivariate and Multivariate Analysis**. [s.l.] Scott, Foresman, 1980.

LINS SILVA, N.; 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.

LIRA, S. et al. New records of the larval forms Cerataspis monstrosa and Amphionides reynaudii (Crustacea: Decapoda) from the western tropical Atlantic. **Zootaxa**, v. 4237, p. 335 – 346, 27 fev. 2017.

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

MINAGAWA, M.; WADA, E. Stepwise enrichment of 15N along food chains: further evidence and the relation between δ15N and animal age. **Geochimica et cosmochimica acta**, v. 48, n. 5, p. 1135–1140, 1984.

MOTODA, S. Devices of simple plankton apparatus. **Memoirs of the faculty of fisheries Hokkaido University**, v. 7, n. 1–2, p. 73–94, 1959.

MUFF, S. et al. Rewriting results sections in the language of evidence. **Trends in Ecology & Evolution**, v. 37, 1 nov. 2021.

MULLIN, M. M.; RAU, G. H.; EPPLEY, R. W. Stable nitrogen isotopes in zooplankton: Some geographic and temporal variations in the North Pacific 1. **Limnology and Oceanography**, v. 29, n. 6, p. 1267–1273, 1984.

OHMAN, M. D.; RAU, G. H.; HULL, P. M. Multi-decadal variations in stable N isotopes of California Current zooplankton. **Deep Sea Research Part I: Oceanographic Research Papers**, v. 60, p. 46–55, 2012.

OKSANEN, J. et al. **vegan: Community Ecology Package. 2019. R package version 2.5-6**. Avilable online at https://CRAN. R-project. org/package= vegan (accessed …, , 2019.

OMORI, M.; IKEDA, T. **Methods in marine zooplankton ecology**. John Wiley and Sons Inc., New York, , 1984.

PAHLOW, M.; RIEBESELL, U.; WOLF-GLADROW, D. A. Impact of cell shape and chain formation on nutrient acquisition by marine diatoms. **Limnology and Oceanography**, v. 42, n. 8, p. 1660–1672, 1 dez. 1997.

PHILLIPS, N. E.; PERNET, B. Capture of Large Particles by Suspension-Feeding Scaleworm Larvae (Polychaeta: Polynoidae). **The Biological Bulletin**, v. 191, n. 2, p. 199–208, 1 out. 1996.

PITOIS, S.; YEBRA, L. Contribution of marine zooplankton time series to the United Nations Decade of Ocean Science for Sustainable Development. **ICES Journal of Marine Science**, v. 79, n. 3, p. 722–726, 2022.

POST, D. et al. Getting to the fat of the matter: Models, methods and assumptions for dealing with lipids in stable isotope analyses. **Oecologia**, v. 152, p. 179–189, 1 jun. 2007.

POST, D. M. USING STABLE ISOTOPES TO ESTIMATE TROPHIC POSITION: MODELS, METHODS, AND ASSUMPTIONS. **Ecology**, v. 83, n. 3, p. 703–718, 1 mar. 2002.

PURCELL, J.; WHITE, J.; ROMAN, M. Predation by gelatinous zooplankton and resource limitation as potential controls of Acartia tonsa copepod populations in Chesapeake Bay. **Limnology and oceanography**, v. 39, 1 mar. 1994.

RAU, G. H.; OHMAN, M. D.; PIERROT-BULTS, A. Linking nitrogen dynamics to climate variability off central California: a 51 year record based on 15N/14N in CalCOFI zooplankton. **Deep Sea Research Part II: Topical Studies in Oceanography**, v. 50, n. 14–16, p. 2431–2447, 2003.

ROMAGNAN, J.-B. et al. Comprehensive model of annual plankton succession based on the whole-plankton time series approach. **PLoS One**, v. 10, n. 3, p. e0119219, 2015.

SANDEL, V. et al. Nitrogen fuelling of the pelagic food web of the tropical Atlantic. **PLoS One**, v. 10, n. 6, p. e0131258, 2015.

SANTOS, G. S. et al. The Impact of Trampling on Reef Macrobenthos in Northeastern Brazil: How Effective are Current Conservation Strategies? **Environmental Management**, v. 56, n. 4, p. 847–858, 2015.

SCHWAMBORN, R. et al. Stable isotope composition of paniculate organic matter and Zooplankton in North-East Brazilian shelf waters. **Archive of Fishery and Marine Research**, v. 47, p. 201–210, 1 jan. 1999.

SCHWAMBORN, R. et al. Distribution And Dispersal of Decapod Crustacean Larvae and Other Zooplankton In The Itamaracá Estuarine System, Brazil. **Tropical Oceanography**, v. 29, p. 1–17, 1 jan. 2001.

SCHWAMBORN, R. et al. How important are mangroves as a carbon source for decapod crustacean larvae in a tropical estuary? **Marine Ecology-progress Series - MAR ECOL-PROGR SER**, v. 229, p. 195–205, 20 mar. 2002.

SCHWAMBORN, R. et al. Ingestion of Large Centric Diatoms, Mangrove Detritus, and Zooplankton by Zoeae of Aratus pisonii (Crustacea: Brachyura: Grapsidae). **Hydrobiologia**, v. 560, n. 1, p. 1–13, 2006.

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, p. 813–825, 2015.

SHAPIRO, S. S.; WILK, M. B. An analysis of variance test for normality (complete samples). **Biometrika**, v. 52, n. 3/4, p. 591–611, 1965.

SHERIDAN, C. C.; LANDRY, M. R. A 9-year increasing trend in mesozooplankton biomass at the Hawaii Ocean Time-series Station ALOHA. **ICES Journal of Marine Science**, v. 61, n. 4, p. 457–463, 2004.

SILVA, A. J. et al. Non-predatory mortality of planktonic copepods in a reef area influenced by estuarine plume. **Marine Environmental Research**, v. 159, p. 105024, 2020.

SILVA, M. S. et al. Estrutura da comunidade fitoplanctônica na baía de Tamandaré (Pernambuco, nordeste do Brasil). **Tropical Oceanography**, v. 33, 2005.

SOMMER, U. et al. Beyond the Plankton Ecology Group (PEG) model: mechanisms driving plankton succession. **Annual review of ecology, evolution, and systematics**, v. 43, p. 429–448, 2012.

SWEETING, C.; POLUNIN, N.; JENNINGS, S. Effects of chemical lipid extraction and arithmetic lipid correction on stable isotope ratios of fish tissues. **Rapid communications in mass spectrometry : RCM**, v. 20, p. 595–601, 28 fev. 2006.

TROEDSSON, C. et al. Regulation of filter-feeding house components in response to varying food regimes in the Appendicularian, Oikopleura dioica. **Journal of Plankton Research**, v. 31, p. 1453–1463, 1 dez. 2009.

TURNER, J. et al. Zooplankton feeding ecology: Grazing on phytoplankton and predation on protozoans by copepod and barnacle nauplii in Disko Bay, West Greenland. **Marine Ecology-progress Series - MAR ECOL-PROGR SER**, v. 221, p. 209–219, 18 out. 2001.

VANDROMME, P. et al. Inter-annual fluctuations of zooplankton communities in the Bay of Villefranche-sur-mer from 1995 to 2005 (Northern Ligurian Sea, France). **Biogeosciences**, v. 8, n. 11, p. 3143–3158, 2011.

VENABLES, W. N. et al. Exploratory multivariate analysis. **Modern applied statistics with S**, p. 301–330, 2002.

VERITY, P. G.; LAGDON, C. Relationships between lorica volume, carbon, nitrogen, and ATP content of tintinnids in Narragansett Bay. **Journal of Plankton Research**, v. 6, p. 859–868, 1984.

VOGT, R. J.; PERES-NETO, P. R.; BEISNER, B. E. Using functional traits to investigate the determinants of crustacean zooplankton community structure. **Oikos**, v. 122, n. 12, p. 1700–1709, 2013.

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.

YOUNG, C. M.; SEWELL, M. A. **Atlas of Marine Invertebrate Larvae**. [s.l.] Elsevier Science, 2006.

ZAR, J. H. **Biostatistical analysis**. [s.l.] Pearson Education India, 1999.

5 ARTIGO 3 – THE FUNCTIONAL RESPONSE OF TROPICAL COASTAL COPEPODS TO ENVIRONMENTAL FORCINGS

INTRODUCTION

Functional diversity indices and functional trait-based indices are recent and relevant approaches to ecological studies of marine zooplankton and represent additional ecological tools to traditional studies (BECKER et al., 2021; CAMPOS et al., 2017; LI et al., 2022; POMERLEAU; SASTRI; BEISNER, 2015). Usually, studies of communities in an ecosystem are based on traditional analyses, such as morphology. While these taxonomic classifications are essential, they may not be suitable for many ecological assessments, specifically for the evaluation of specific functions with the food web (BARNETT; FINLAY; BEISNER, 2007; POMERLEAU; SASTRI; BEISNER, 2015).

The attribution of functional traits is generally based on morphological features, life history, and behavioral and physiological characteristics of organisms (e.g., body size, reproduction, feeding strategy and feeding rates, respectively), which are the most common traits used to analyze functional biodiversity (LITCHMAN; OHMAN; KIØRBOE, 2013; SODRÉ; BOZELLI, 2019). In addition, environmental drivers (e.g., water temperature, salinity and food availability), as well as seasonality are responsible for response in functional traits (LI et al., 2022; SODRÉ; BOZELLI, 2019). However, until now, there are no time-series studies focusing on the functional diversity of copepods and ecosystem functioning in the coastal Tropical Southwestern Atlantic (TSWA).

Tropical marine environments show slight changes in environmental conditions throughout the year, in contrast to temperate and polar systems, where strong seasonal variations led to an adaptation of copepod species to periods of food paucity (TEUBER et al., 2019). However, previous studies observed differences in the abundance and biomass of copepods between dry and wet seasons in the tropical regions, especially in coastal areas with estuarine plume influence (BRITO-LOLAIA et al., 2022; DA SILVA et al., 2020).

Typically, copepods are numerically dominant in marine waters, including the TSWA coast (DA SILVA et al., 2020; DIAS; ARAUJO; BONECKER, 2009; PINTO et al., 2004; VALENTIN; MONTEIRO-RIBAS, 1993). They are also generally the main contributors to the biomass of zooplankton < 2000 µm (BRITO-LOLAIA et al., 2020; DA ROCHA MARCOLIN et al., 2013). Copepods serve as prey for higher trophic levels of organisms such as planktivorous fishes and macroinvertebrates (CASTONGUAY et al., 2008; NAGATA; MORANDINI, 2018). Their remains are a source of energy for necrophagous animals, the microbial loop and benthic communities through the sinking of carcasses and faecal pellets (ELLIOTT; HARRIS; TANG, 2010; FRANGOULIS et al., 2011).

Tropical regions are notoriously characterized by the presence of small-sized copepods (< 1mm in length), probably due to the metabolic and food-web effects of high temperatures (BRUN; PAYNE; KIØRBOE, 2016; HOPCROFT; ROFF; CHAVEZ, 2001). Within functional traits, the body size is a “master trait”, that determines many of the vital functions (e.g., feeding, growth, metabolism, mortality, etc.) and influences many other traits (KIØRBOE; VISSER; ANDERSEN, 2018; LITCHMAN; OHMAN; KIØRBOE, 2013). For this reason, we emphasize the importance of choosing the mesh size of the net (e.g., 64 µm mesh size) in ecological analyzes of small-sized copepod communities, especially for early larval stages of copepods (DA SILVA et al., 2020).

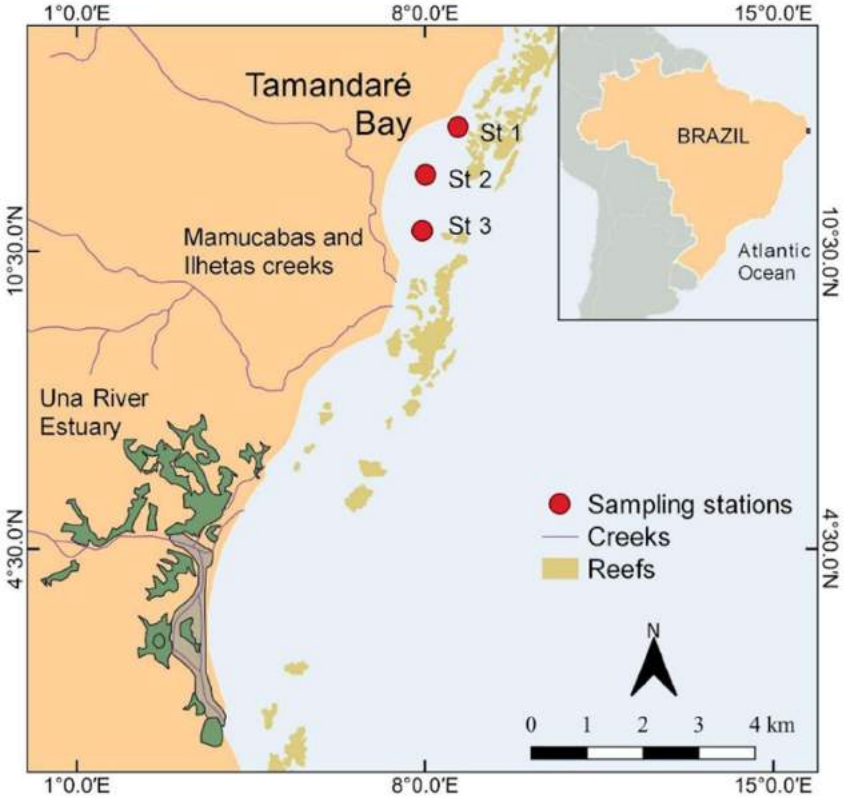
Two previous studies of zooplankton functional diversity conducted in the TSWA focused on spatial (inner, middle and outer shelf) analysis on the continental shelf on only two occasions during the dry season (CAMPOS et al., 2017), and on a latitudinal gradient sampled in the austral summer (BECKER et al., 2021). Also, functional traits were used to investigate ecological processes, such as human-induced disturbance in estuaries and Amazon plume influences (NEUMANN LEITÃO et al., 2019; NEUMANN-LEITÃO et al., 2018; VERÍSSIMO et al., 2017). These previous studies showed interesting results regarding spatial patterns, but it is still unclear how functional traits of copepod assemblages respond to changes in environmental conditions over the years. In the present study, we hypothesize that (1) functional traits, functional groups, functional diversity indices and abundance of copepod assemblages exhibit seasonal and interannual variations and (2) environmental and hydrological variations significantly influence the abundance, composition and functional descriptors of copepods. For the first time, this study intends to assess the importance of environmental variations in a time-series study for the knowledge of the functional diversity of copepods in TSWA.

MATERIALS AND METHODS

Study area

Tamandaré Bay (8˚46’07.5” S, 35˚06’03.6” W) is located on the Northeastern Brazilian coast (Figure 1). The study area is part of the Coral Coast Marine Protected Area (“APA Costa dos Corais”), which is lined by sandstone reefs that form a semi-closed embayment. The reefs harbour unique corals, zoanthids, macroalgae, and other endemic fauna and flora (SANTOS et al., 2015).

Figure 1. Map of the study area in Tamandaré Bay, northeastern Brazil, showing the sampling stations on red dots (St 1, St 2 and St 3).



Fonte: A autora (2023).

The study area is characterized by an As’ climate, according to the Köppen classification (ANDRADE; LINS, 1971). The region exhibits two clear seasons: dry and rainy. The rainy season is typically from March to August, while the dry season is from September to February. In the rainy season, the bay is influenced by the Mamucabas-Ilhetas creeks that discharge in the southern portion. Coastal drift is usually wind-driven and predominantly in a south-north direction. Therefore, occasionally, in storm events, the bay may also be influenced by the nearby large-scale Una River plume (Figure 1). Coastal winds are usually in the onshore direction (SE, NE and E) and stronger in June-October (SILVA et al., 2011), roughly coinciding with the rainy season.

Sampling strategy and laboratory analysis

Sampling campaigns were carried out bi-monthly over six years, during daytime high tides (new moon) from June 2013 to August 2019. A total of 111 plankton samples were collected at three stations in Tamandaré Bay (Figure 1). Subsurface (0 to 0.3 m deep) horizontal tows were performed for 5 min at speeds of 2-3 knots using a conical-cylindrical plankton net (64 µm mesh size, 0.31 m mouth ring diameter, 1 m length). A flow meter was attached to the net mouth to calculate the filtered seawater volume.

Samcples were fixed with 4% formalin (final concentration in seawater) buffered with sodium tetraborate (0.5 g L-1, (OMORI; IKEDA, 1984). Sea surface (1 m) temperature (SST), and sea surface salinity (SSS) were recorded at each sampling station using a CTD probe (SonTek model CastAway, San Diego, CA, USA). The transparency of water (TW) was estimated using a Secchi disk (PREISENDORFER, 1986). Secchi depth can be used to assess transparency and may be a good proxy for the trophic status of the pelagic ecosystem (oligotrophic vs. eutrophic state) (KIRBY et al., 2021).

The rainfall data used in the analysis of this study were collected as follows: rainfall over five days (i.e., at the sampling day and four preceding days) after running a multi-lag correlation analysis between rainfall, TW and SSS. This data was used as an explaining variable in our analysis. Local rainfall data sets were obtained from the Pernambuco State Agency for Water and Climate (APAC, https://www.apac.pe.gov.br/).

Four sampling campaigns were chosen each year for performing functional diversity analysis. Two campaigns were selected for each season (rainy/dry), except for the first (2013) and last (2019) sampling years. In 2015, there was only one campaign in the rainy season due to logistical issues and bad weather.

In functional diversity and abundance analysis, 68 zooplankton samples were selected (34 obtained in the dry season and 34 in the rainy season), except for the analysis of the environmental descriptors, which due to information gaps, some campaigns were removed, e.g., all campaigns of 2013, remained 57 samples (31 in the dry season and 26 in the rainy season). Zooplankton sample aliquots were taken with a Motoda splitter (MOTODA, 1959) to obtain 300 to 400 organisms per counting and spilt on the Sedgewick-Rafter counting chamber. Copepods were counted, identified and measured under a Zeiss Axiostar plus binocular microscope.

Functional traits analysis

A literature review of the functional traits of marine copepods was carried out, resulting in a matrix for assessing functional traits (based mainly on BENEDETTI; GASPARINI; AYATA, 2016 and CAMPOS et al., 2017). The following traits were included: (i) origin (neritic, composed of oceanic and coastal origin species, neritic-estuarine, euryhaline species found in both environments; (ii) feeding strategy (active ambush feeding, filter-feeding, cruise feeding, mixed feeding); (iii) trophic group (carnivore, omnivore, omnivore-herbivore, omnivore-carnivore, omnivore-detritivore); (iv) size classes formed by maximum total body length measured with an ocular micrometer under the microscope from 10 to 30 specimens of each specie and classified into three categories (small: 0.5 – 0.9 mm, medium: 0.9 – 1.2 mm, large: 1.2 – 1.5 mm); (v) reproduction strategy (broadcaster, sac-spawner).

Different indices of functional diversity (FD) were calculated, and their values ranged between 0 and 1. Functional Richness (FRic) is the amount of functional space occupied by the community. Functional Evenness (FEve) measures the regularity of the relative abundance distribution in a functional space. Functional Dispersion (FDis) represents the mean distance of each individual species to the centre of multidimensional functional space (BECKER et al., 2021; MOUILLOT et al., 2013).

Data analysis

The functional diversity of copepod assemblages was identified based on their functional traits. Major groups of copepod species were analyzed from a cluster dendrogram calculated using Ward’s hierarchical clustering of species, whose dissimilarity matrix was based on the Gower distance (GOWER, 1971). Four functional groups were identified from their similar features. The functional diversity indices (FRic, FEve, FDis) were calculated using the “dbFD” function in the FD package in R (LALIBERTÉ et al., 2014). Species diversity indices included species richness (*S*), evenness (J'), and the Shannon–Wiener index (H').

Simple linear models were conducted to evaluate the relationship between the functional and species diversity indices.

A Redundancy Analysis (RDA) was applied to explore the relationship between copepod abundance and functional groups (response variables) *vs.* environmental descriptors (explanatory variables). The copepod abundance and the functional traits were transformed by Hellinger (LEGENDRE; GALLAGHER, 2001). The One-way Variance Analysis (ANOVA) was used to assess the significance of the axis of RDA to test the hypothesis that environmental descriptors are responsible for changes in copepod abundance and functional groups.

Functional traits data, functional diversity indices and copepod abundance (ind.m^{-3}) were tested for normality using the Shapiro-Wilk test (SHAPIRO; WILK, 1965). Since they were not normally distributed, univariate PERMANOVA (ANDERSON, 2005) was used to test for differences between seasons (dry vs rainy), by using the function "adonis2" with the "vegan" R package (OKSANEN et al., 2020). PERMANOVA was based on Euclidean distances, with 20,000 permutations. Kruskal-Wallis and Dunn post hoc (ZAR, 1999) were used to test differences between years (2013, 2014, 2015, 2016, 2017, 2018 and 2019) and sampling stations (St. 1, St. 2 and St. 3). All analyses were performed using R version 4.0.5, with a level of significance of 5%.

RESULTS

Environmental variables

Environmental conditions varied considerably between seasons (Table 1). SSS and TW showed a strong difference between the dry and rainy seasons (PERMANOVA, $p < 0.001$) as well as SST (PERMANOVA, $p = 0.003$), with lower values in the rainy season. The mean of five days of accumulated rainfall was 8.8 and 26.3 mm in the dry and rainy seasons, respectively (Table 1) with a maximum of 123.9 mm in Aug 2019. There was a significant difference in seasonality in rainfall (PERMANOVA, $p = 0.010$). Environmental variables did not show any significant differences between sampling stations. Also, SST and TW had no significant differences between years (from 2013 to 2019).

Table 1. Variations (Min, Max, Median) in environmental descriptors by a dry and rainy season from 2013 to 2019 samplings at three stations at Tamandaré Bay (Northeastern Atlantic). SST, sea surface temperature (°C); SSS, sea surface salinity; TW, transparency of water (m) and rainfall (mm).

Environmental variables	Dry			Rainy			
	Min	Max	Median	Min	Max	Median	P-Value
SST (ºC)	27.0	30.0	28.7	26.3	30.7	27.8	**0.003**
SSS	29.0	37.1	36.1	27.0	36.6	35.4	**<0.001**
TW (m)	2.3	7.9	4.0	0.6	4.7	2.1	**<0.001**
Rainfall (mm)	0	47.4	7.0	1.8	123.9	14.3	**0.010**

Fonte: A autora (2022).

Abundance and composition of Copepod assemblages

A total of 22 taxa of adults and juveniles of copepods were analyzed in this study (Table 2). The highest copepod abundance was recorded in the rainy season with total abundance ranging from 856 to 59,776 ind.m^{-3}, while the dry season was ranging from 549 to 34,031 ind.m^{-3}.

Table 2. Abundance (ind.m^{-3}) and relative abundance (%) of copepods in dry and rainy seasons. RA: Relative abundance.

	Taxa	Dry season		Rainy season	
		Mean ± St. Dev.	RA (%)	Mean ± St. Dev.	RA (%)
1	*Acartia (Odontocartia) lilljeborgii*	271.7 ± 359.9	1.9	351.7 ± 604.7	2.5
2	*Centropages velificatus*	0		1.2 ± 4.9	< 0.1
3	*Clausocalanus* sp.	0.8 ± 5.0	< 0.1	0	
4	*Corycaeus* spp. juveniles	7.6 ± 15.0	< 0.1	51.3 ± 108.2	0.4
5	*Dioithona oculata*	3733.5 ± 2839.0	25.6	4143.4 ± 5599.1	29.9
6	*Ditrichocorycaeus amazonicus*	8.5 ± 23.3	< 0.1	47.4 ± 154.8	0.3
7	*Euterpina acutifrons*	309.0 ± 338.6	2.1	1188.0 ± 1667.5	8.6
8	*Farranula* sp.	1.6 ± 6.6	< 0.1	3.9 ± 22.9	< 0.1
9	*Labidocera* spp.	146.2 ± 137.3	1.0	41.0 ± 115.5	0.3
10	*Macrosetella gracilis*	0		0.7 ± 3.9	< 0.1
11	*Microsetella rosea*	1.7 ± 9.9	< 0.1	1.3 ± 6.1	< 0.1
12	*Oithona hebes*	153.6 ± 227.1	1.0	154.9 ± 249.1	1.1
13	*Oithona nana*	424.6 ± 381.5	2.9	586.0 ± 765.3	4.2
14	*Oithona* spp. juveniles	6268.4 ± 5060.1	43.0	4513.3 ± 5877.2	32.6
15	*Oncaea* sp.	0.9 ± 5.4	< 0.1	1.9 ± 10.9	< 0.1
16	*Onychocorycaeus giesbrechti*	3.0 ± 10.3	< 0.1	3.9 ± 16.0	< 0.1
17	*Paracalanus aculeatus*	3.9 ± 14.2	< 0.1	3.8 ± 21.9	< 0.1
18	*Paracalanus quasimodo*	31.7 ± 54.1	0.2	46.4 ± 104.9	0.3
19	*Paracalanus* spp. juveniles	70.1 ± 118.0	0.5	65.5 ± 167.3	0.5
20	*Parvocalanus crassirostris*	2280.1 ± 2532.9	15.6	2207.1 ± 2664.2	15.9
21	*Pseudodiaptomus acutus*	856.6 ± 1233.1	5.9	411.0 ± 742.6	2.9
22	*Temora turbinata*	7.7 ± 19.5	< 0.1	9.1 ± 20.8	< 0.1

Fonte: A autora (2022).

Eight species dominated in the study area: *Oithona* spp. juveniles (38%) followed by *Dioithona oculata* (28%), *Parvocalanus crassirostris* (16%), *Euterpina acutifrons* (5%), *Pseudodiaptomus acutus* (4%), *Oithona nana* (4%), *Acartia (Odontocartia) lilljeborgii* (2%) and *Oithona hebes* (1%). The remaining species corresponded to < 1% of relative abundance.

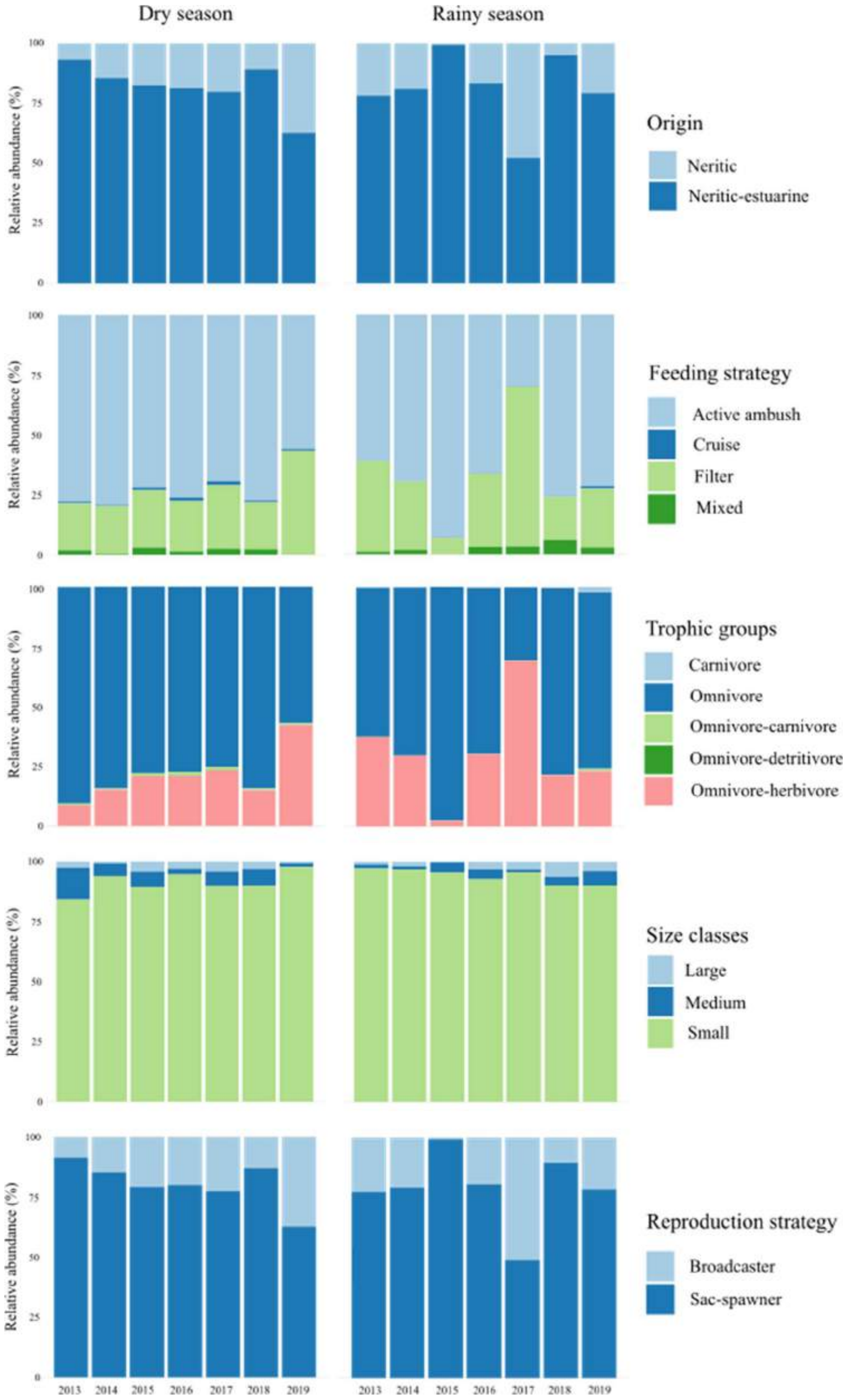
There were significant differences in abundance between seasons for *Corycaeus* spp. juveniles (PERMANOVA, $p = 0.007$) and *E. acutifrons* (PERMANOVA, $p < 0.001$), with higher abundance in the rainy season. Conversely, *Labidocera* spp. and *Microsetella rosea* showed higher abundance in the dry season (PERMANOVA, $p < 0.001$ and $p = 0.047$, respectively). Only *Corycaeus* spp. juveniles differed between years (PERMANOVA, $p = 0.020$), with higher values in 2019. Significant differences between stations were found in genus *Oithona* (*D. oculata*, ($p = 0.005$), *O. nana*, ($p = 0.004$) and *Oithona* spp. juveniles ($p = 0.027$)), with low values in St 1, and in species *Paracalanus aculeatus* ($p = 0.030$) and *Onychocorycaeus giesbrechti* ($p = 0.025$) and with high values in St 2 and St 3, respectively.

Functional trait composition and functional groups

Strong seasonality was observed for functional trait composition. Regarding the feeding strategy, cruise-feeding species were more abundant in the dry season (PERMANOVA, $p = 0.001$). Equally, for the trophic group, omnivore-carnivore species were more abundant in the dry season (PERMANOVA, $p < 0.001$). Conversely, carnivore species were more abundant in the rainy season (PERMANOVA, $p = 0.002$) and also showed differences between years (PERMANOVA, $p = 0.009$), with higher abundance in 2019.

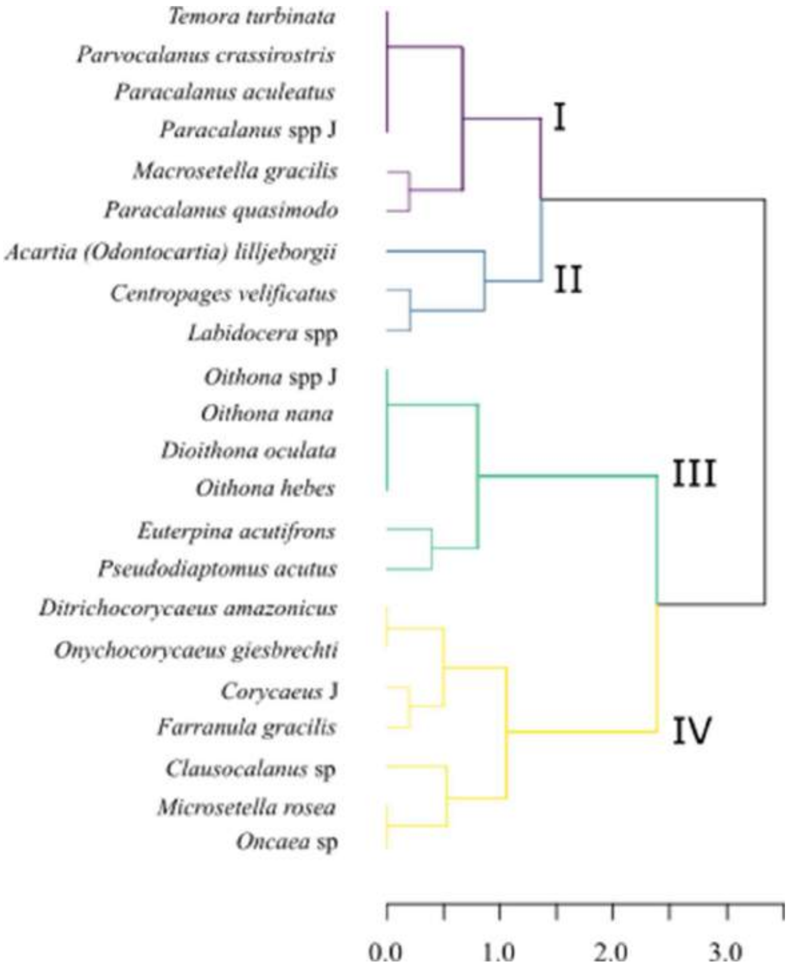
The copepod assemblage in the study area mainly consisted of neritic-estuarine origin, active-ambush, omnivore, small size and sac-spawner species (> 71% for each trait, Figure 2). Based on functional traits, four functional groups of copepod assemblages were identified (Fig 3, Table 3). Initially, the species were sorted by reproduction strategy and then by four groups according to the origin and trophic groups. Group I was composed of neritic, filter-feeding and omnivore-herbivore copepods, mainly of small size (0.5 – 0.9 mm) and broadcaster, except for *Macrosetella gracilis* (medium size and sac-spawner). Group II was formed by neritic, cruise feeding and omnivore-carnivore species, except for *A. lilljerborgii* which is neritic-estuarine, mixed feeding strategy and omnivore-herbivore. This group is formed by broadcaster and large species (1.2 – 1.5 mm) *A. lilljerborgii* and *Labidocera* spp. and small *Centropages velificatus*. Group III is composed of the most abundant species (80%, Fig 4), all are neritic-estuarine and sac-spawner, mostly active-ambush, omnivore and small size. Group IV had the highest number of species among the four groups; however, it had less abundance, < 1% (Figure 3 and 4). It is formed by a mixed trait sac-spawner from neritic origin species, with active-ambush and cruise feeding strategy, carnivore, omnivore-herbivore and omnivore-detritivore, with small, medium (0.9 – 1.2 mm) and large-sized copepods. Group IV differed significantly between seasons and years (PERMANOVA, $p = 0.005$ and $p = 0.012$, respectively), with high abundance in the rainy season of 2016 and 2019. Group III showed differences between stations (PERMANOVA, $p = 0.005$), due to this group being mostly formed by the abundant genus *Oithona,* which exhibited the lowest abundance at St 1.

Figure 2. Relative abundance of each type for functional traits of copepod assemblages between dry and rainy seasons from 2013 to 2019.



Fonte: A autora (2022).

Figure 3. Cluster of functional groups of Copepod assemblages identified based on functional traits.



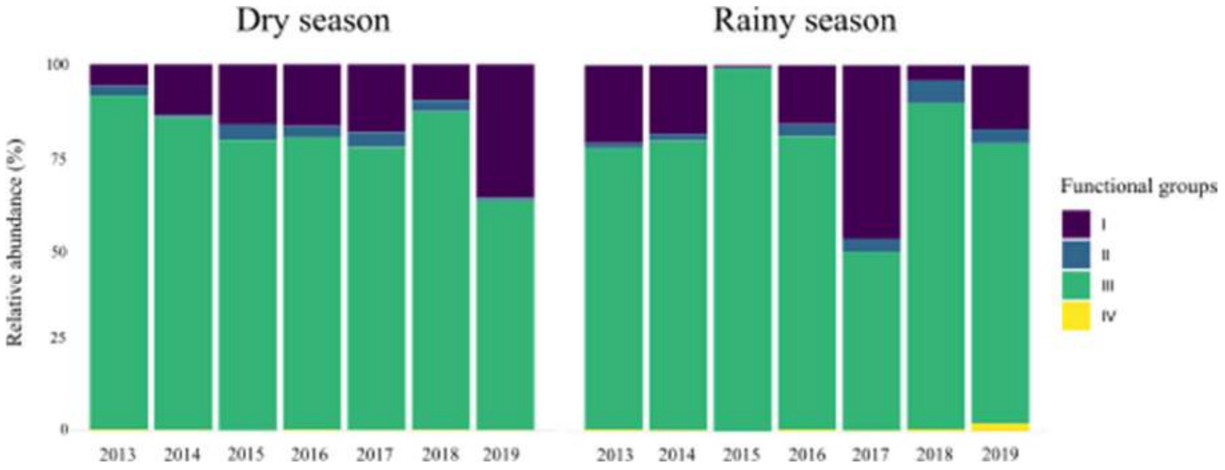
Fonte: A autora (2022).

Table 3. Trait characteristics of the four identified functional groups and their number of copepod species.

Functional Trait	Category	Functional groups				
		Group I	Group II	Group III	Group IV	Total number of species
Origin	Neritic	6	2	0	7	15
	Neritic-estuarine	0	1	6	0	7
Feeding strategy	Active ambush	0	0	4	3	7
	Cruise	0	2	0	4	6
	Filter	6	0	2	0	8
	Mixed	0	1	0	0	1
Trophic group	Carnivore	0	0	0	4	4
	Omnivore-carnivore	0	2	0	0	2
	Omnivore	0	0	5	0	5
	Omnivore-herbivore	6	1	1	1	9
	Omnivore-detritivore	0	0	0	2	2
Reproduction strategy	Broadcaster	5	3	0	0	8
	Sac-spawner	1	0	6	7	14
Maximum total body length	Small	4	1	5	4	14
	Medium	2	0	1	2	5
	Large	0	2	0	1	3

Fonte: A autora (2022).

Figure 4. Relative abundance (%) of each functional group between dry and rainy seasons from 2013 to 2019.



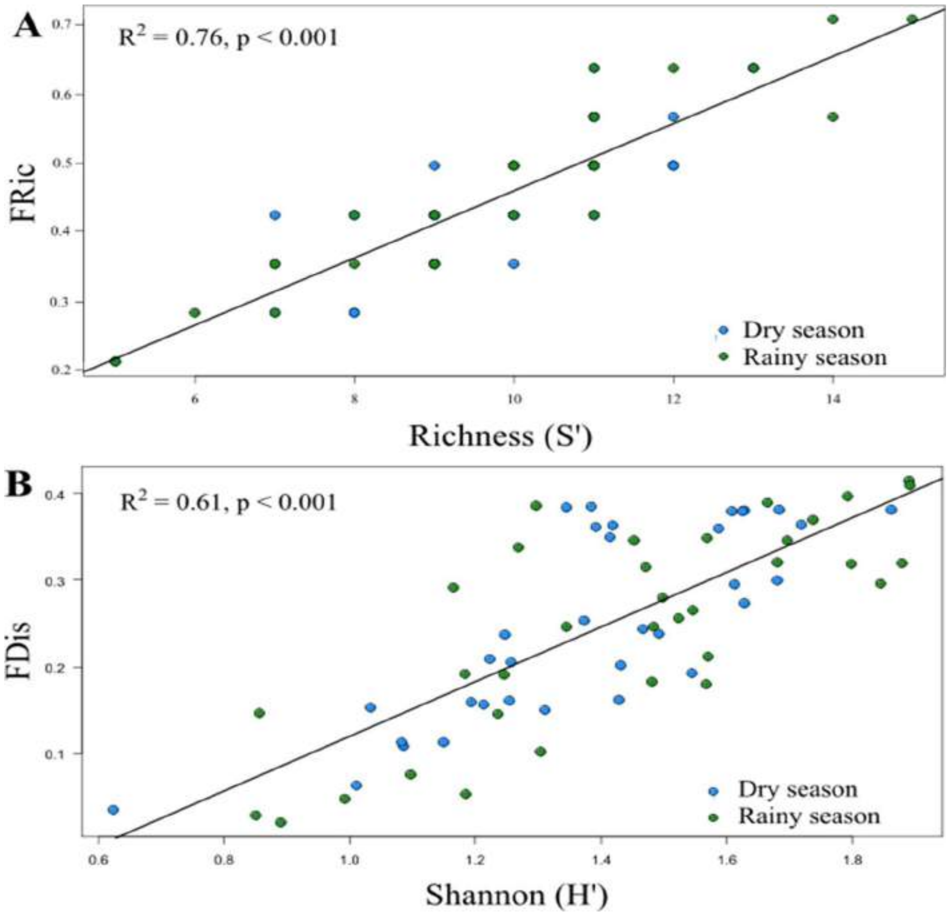
Fonte: A autora (2022).

Functional diversity and species diversity

The functional dispersion (FDis) showed differences between years (2014, 2015, 2018 ≠ 2019, $p = 0.002$), with high values in 2019. The same result was found for Shannon species diversity ($p = 0.002$). FDis ranged from 0.02 to 0.38 (mean = 0.19) in 2014 and 0.25 to 0.42 (mean = 0.36) in 2019. No significant results were found between seasons for functional and species diversity.

A simple linear model revealed a significant relationship between functional richness (FRic) and copepod species richness (S') ($p < 0.001$, $R^2 = 0.76$), with high values in the rainy season, and functional dispersion (FDis) and copepod Shannon diversity (H') ($p < 0.001$, $R^2 = 0.61$) (Figure 5). The functional evenness did not show any correspondence with copepod abundance evenness.

Figure 5. Significant simple linear regression between A: Functional Richness and Richness (S') and B: Functional Dispersion (FDis) and Shannon diversity (H'). Blue and green dots denote the dry and rainy seasons, respectively.

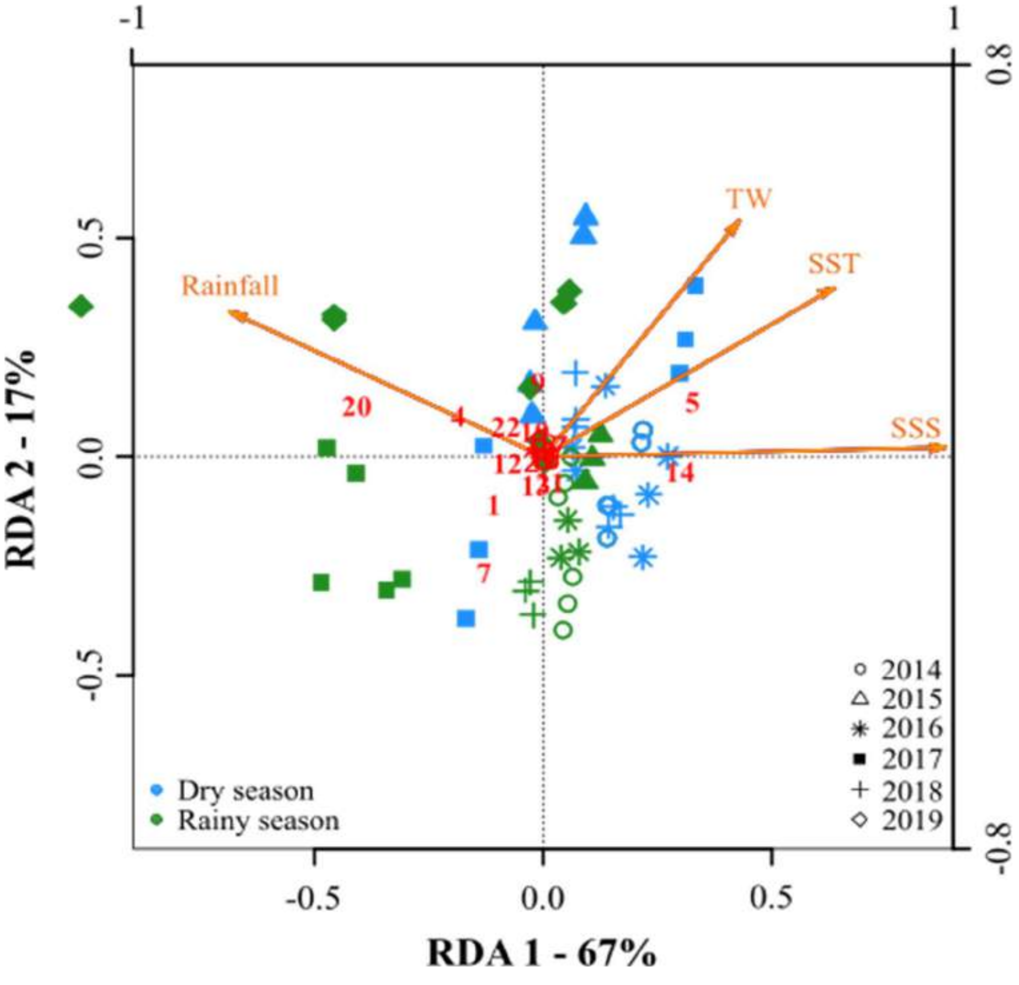


Fonte: A autora (2022).

Effect of environmental descriptors on Abundance and functional diversity of copepod assemblages

The global RDA model that investigated the relationship between copepod assemblages and environment descriptors showed a strong significance ($p = 0.001$). SST and SSS were responsible for the significance of the model ($p = 0.001$, for both). Explanatory variables explained 67% of the total variability of the abundance of copepod assemblages. Axis 1 and 2 contributed 84% of the total variance explained by the analyses (Figure 6). *P. crassirostris*, *Corycaeus* juveniles and *Temora turbinata* were more correlated to rainfall, while *D. oculata* was more correlated to SST and *Oithona* spp. to SSS in the dry season.

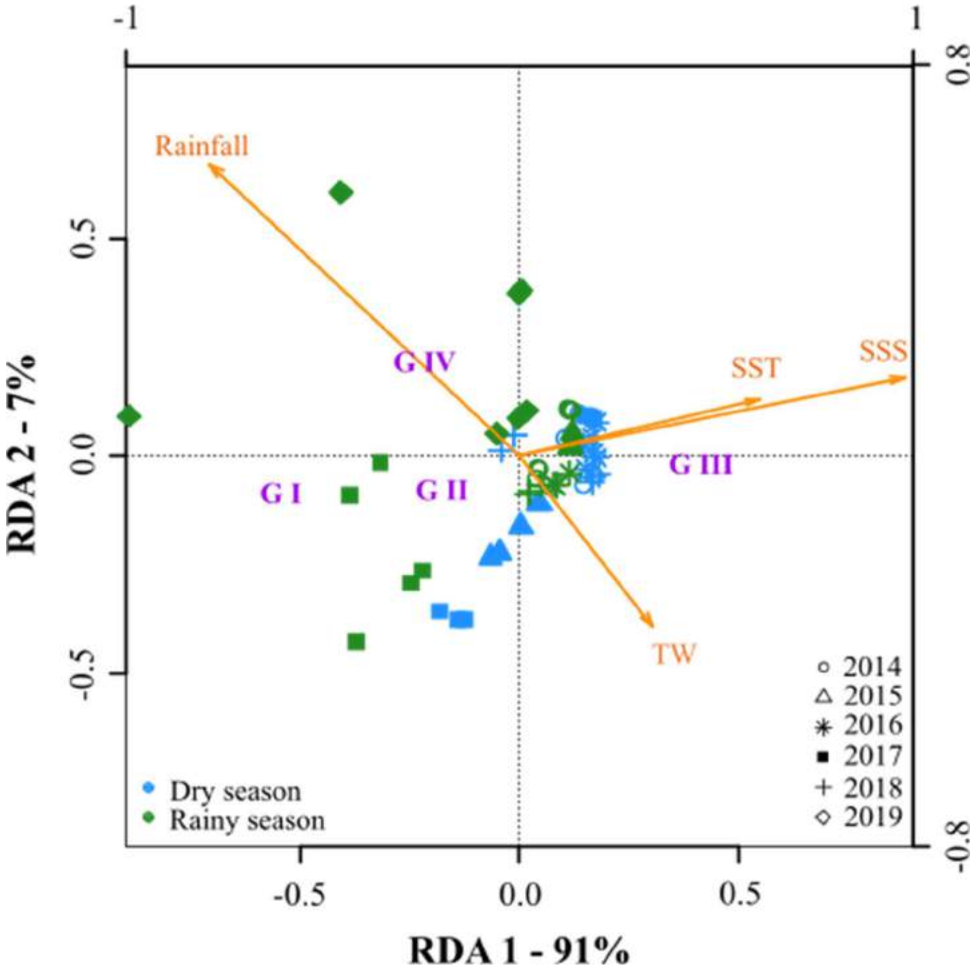
Figure 6. Redundancy analysis (RDA) based on abundance (ind.m^{-3}) of copepod assemblages (response variables) *vs* environmental descriptors (explanatory variables). SST: Sea surface temperature; SSS: sea surface salinity; TW: transparency of water. Copepod species are numbered alphabetically from 1 to 22 (see Table 2).



Fonte: A autora (2022).

RDA of Functional groups showed that the canonical axis was statically significant (p = 0.001) for SST (p = 0.004) and SSS (p = 0.001). The explanatory variables explained 91% of the total variability of the abundance of functional groups. Axis 1 and 2 contributed 98% of the total variance explained by the analyses (Figure 7). Group III was more associated with SST and SSS in the dry season, while Group IV was more associated with rainfall in the rainy season.

Figure 7. Redundancy analysis based on abundance (ind.m^{-3}) of functional groups of copepod assemblages (response variables) *vs* environmental descriptors (explanatory variables). SST: Sea surface temperature; SSS: sea surface salinity; TW: transparency of water; G I: group I; G II: group II; G III: group III; G IV: group IV.



Fonte: A autora (2022).

DISCUSSION

This study presented an overview of the temporal variability and environmental and hydrological variations on the functional diversity of the copepods in the coastal TSWA pelagic system. Notwithstanding, the fact that the ranges of variations in environmental parameters (e.g., SST with a minimum of 26.3 °C and maximum of 30.7 °C in the rainy season) in such a "constant" tropical coastal ecosystem are low, even a minimal change affected the structure of functional groups and copepod assemblages. Also, the oligotrophic environment and high variability of the tropical coast allowed the presence of a highly dominant and well-adapted group to those conditions. Here, we also discuss the importance of small copepods in the functional diversity of tropical coastal waters and the functional traits responsible for adaptation in this complex coastal environment.

Small environmental variations - high effects on Abundance and Functional Diversity of Copepod Assemblages

The environmental descriptors explained 91% of the variability in the abundance of functional groups in this study. Temperature and salinity were the main environmental factors contributing to the variability of copepods, especially for the most abundant group (Group III) in the dry season. This is a surprising result since variations in temperature and salinity are not as high as those occurring in regions of high latitudes and in estuaries, respectively. These factors also influence the composition and abundance of communities of zooplankton on the northern shelf of the Gulf of Alaska (COYLE; PINCHUK, 2003) and in the Mediterranean Sea (BENEDETTI et al., 2018). Unlike what happens in regions like the Yellow Sea, where ocean currents are also responsible for the variation in abiotic factors (LI et al., 2022), here the rainfalls and consequently more significant river outflows in coastal areas are responsible for the abiotic variation, decreasing the temperature, salinity and transparency of the water in the region (BRITO-LOLAIA et al., 2022). This result showed that a small variation in environmental conditions was significant to the copepod functional group, much higher when compared to species alone, highlighting the importance of this study.

The genus *Oithona* was more associated with SST (*Dioithona oculata*) and SSS (*Oithona* spp. juveniles) in the dry season. It can suggest that this abundant taxon is capable of tolerating high temperatures (maximum 30 °C in this study) and salinities. A study with *Oithona nana* showed although it had the ability to withstand abrupt changes in salinity, its optimal salinity level was 20, which achieved the highest population growth (MAGOUZ et al., 2021). Another study observed a salinity tolerance range of 6–40 in *Oithona davisae* (SVETLICHNY; HUBAREVA; UTTIERI, 2021). *Oithona* is a thermophilic genus that tolerates a wide range of temperatures. Svetlichny et al. (2021) demonstrated that the swimming behaviour and respiration rate of *O. davisae* increased with temperatures reaching higher values in higher temperatures.

Copepod functional groups and traits

This study in a tropical coastal area showed the dominance of a group of well-adapted copepods to the ecosystem with variations in salinity and food availability, also presenting an advantageous morphological feature and reproduction strategy. Group III consisted mainly of neritic-estuarine origin, active-ambush, omnivore, small size and sac-spawner species that comprised 80% of relative abundance and showed > 71% of each functional trait. The main functional traits found in this study were constituted mostly by the genus *Oithona*, found in higher abundance and biomass in Tamandaré Bay (BRITO-LOLAIA et al., 2020, 2022) in both dry and rainy seasons. This genus is widely found in many coastal areas, mainly forming swarms near reefs (AMBLER; FERRARI; FORNSHELL, 1991; BUSKEY; PETERSON; AMBLER, 1996) and composes an important carbon source for the upper trophic level in this coastal area. As they are of neritic-estuarine origin, they were found in lower abundance in the station (St 1) furthest from the plume of the Mamucabas-Ilhetas creeks. Their advantageous features are discussed below.

Neritic-estuarine copepods are found in higher abundance in Tamandaré Bay and elsewhere along the Brazilian coast with estuarine influence (BRITO-LOLAIA et al., 2020; DIAS; BONECKER, 2008; PINTO et al., 2004). These euryhaline copepods can be found in estuaries (e.g., *D. oculata*, AMBLER; FERRARI; FORNSHELL, 1991) and coastal areas even with high salinity and no detectable freshwater outflow (BRITO-LOLAIA et al., 2020). Previous studies observed that the genus *Oithona* displayed a striking osmotic control, being capable of withstanding abrupt changes in the salinity (MAGOUZ et al., 2021; SVETLICHNY; HUBAREVA; UTTIERI, 2021). The feeding strategy, Active ambush (i.e., organisms that may swim through the water or generate a feeding current and thereby actively encounter their prey), is considered a useful trait, being more efficient than passive ambush feeding that target only motile prey (KIØRBOE; VISSER; ANDERSEN, 2018). Although this type of feeding can generate much larger fluid disturbances by both feeding and propulsion, making them susceptible to predators (KIØRBOE; VISSER; ANDERSEN, 2018), the active feeders are favoured in environments with low concentrations of both prey and predators (MARIANI et al., 2013). The benefits of feeding depend on the availability of food and the risk of feeding in places with a high abundance of predators. Since the environment favours traits that optimize the trade-offs (KIØRBOE; VISSER; ANDERSEN, 2018), this must be what happened in the studied environment. Tropical calanoid copepods present different feeding strategies to occupy different niches, being the omnivore the trophic strategy with a higher proportion (TEUBER et al., 2019). In this study, there is a higher proportion of omnivores also considering omnivore-herbivore, omnivore-carnivore, and omnivore-detritivore. This strategy increases the chance of survival in a wide range of ecological niches.

Regarding the highest abundance of small-sized copepods, the microzooplankton dominant copepods throughout our study are composed of both adults and different developmental stages of mesozooplankton species, some of which predominate in oligotrophic areas, and are key components in the microbial loop (CALBET et al., 2001; TURNER, 2004) and vital intermediates between the classical and microbial food webs (HOPCROFT; ROFF; LOMBARD, 1998; NAKAMURA; TURNER, 1997; TURNER, 2004). Small adult copepods and juvenile stages were numerically dominant. A previous study observed that small-sized copepods (< 1 mm in length) were up to a maximum of seven times the abundance of large-sized forms in tropical coastal water from India (RAKHESH et al., 2013). Li et al. (2022) concluded that their community was controlled by small copepods in the Yellow Sea. These copepods have a very superior growth rate (HOPCROFT; ROFF; LOMBARD, 1998; PETERSON; TISELIUS; KIØRBOE, 1991) and impact the efficacy of trophic coupling in food webs (ZERVOUDAKI et al., 2007). The largest (> 200 µm) mesh size is historically widely used to assess the pelagic zooplankton, however, this resulted in an underestimation of the importance of small copepods such as the genus *Oithona* (TEROL, 2013).

Another advantageous feature is being sac spawner, although the rate of egg production is lower by almost an order of magnitude in sac spawner when compared to the broadcaster, the broadcaster egg mortality is much greater than the post-hatch mortality (observed broadcaster egg mortality is up to 3 orders of magnitude larger than post hatch rates, (HIRST; KIØRBOE, 2002). Also, Hirst and Kiørboe (2002) observed, in their laboratory study, the largest broadcast and sac-spawning copepods have mortality rates that fall very close to the pelagic pattern, while the smaller broadcast and sac-spawning copepods have lower rates. They also concluded that the smallest copepods avoid mortality, unlike other pelagic organisms of similar size.

The copepod assemblages were also mainly separated by the trophic strategy trait (herbivorous, omnivorous-detritivorous, carnivorous), a similar performance recorded in the Amazon reef system (NEUMANN-LEITÃO et al., 2018) and Northeast coastal area (NEUMANN-LEITÃO et al., 2019). Trophic strategies are commonly regulated by female weight, environmental temperature, and food (BLAXTER et al., 1998; BUNKER; HIRST, 2004).

Regarding seasonality, the cruise-feeding species (i.e., species that swim actively through the water and capture individual prey) showed high abundance in the dry season. This feeding mechanism requires the organism to perceive the prey remotely (KIØRBOE, 2011). This is not an easy task in an environment with more disturbance caused by sediment in the water column brought by river runoff in rainy seasons. Also, copepods can feed on large particles (known as marine snow) and may be guided by the chemical trail or hydrodynamic when these large particles sink into the bottom (KIØRBOE, 2011). These large aggregates can be formed from the houses of the appendicularians, which are very abundant in the dry season in Tamandaré Bay (BRITO-LOLAIA et al., 2022).

Group IV presented a higher number of carnivore species (*Ditrichocorycaeus amazonicus, Onychocorycaeus Giesbrecht, Corycaeus* spp. juveniles and *Farranula gracilis*). Both group IV and the trait carnivore showed higher abundance in the rainy season mainly in 2019, which corroborates with higher rainfall in 2019 (probably caused by the high abundance of *Corycaeus* spp., which also showed high abundance in the rainy season and 2019). *Microsetella rosea, Ditrichocorycaeus amazonicus* and *Onychocorycaeus giesbrecht* were known, in general, to cling to the cyanobacteria *Trichodesmium* and to fragments of Larvacea discharged houses. These species use *Trichodesmium* to stay with their oral appendages to help their movements (BJÖRNBERG, 1981) and eat these cyanobacteria, consuming substantial quantities (O'NEIL; ROMAN, 1994). However, these cyanobacteria are found in oligotrophic waters with poor nutrients. Probably these species are feeding on ciliates (e.g., *Favella ehrenbergii*) or copepod nauplii (TURNER, 1984) very abundant in the rainy season in Tamandaré Bay (BRITO-LOLAIA et al., 2022). They also usually present uneven distribution, forming patches in tropical neritic and oceanic waters (BJÖRNBERG, 1981). In contrast, Omnivore-carnivore (mainly carnivorous species that sometimes eat phytoplankton and organic detritus) showed seasonality with higher abundance in the dry season. Probably this occurred due to the oligotrophic waters (blue water conditions) with a low abundance of food that favors species that feed on a wide range of food available in the environment.

Group I was the second group more abundant. Several copepods from the tropical and subtropical regions have distinct types of swimming and acquiring food that allows their co-existence. *Paracalanus aculeatus* and *P. quasimodo* go slowly and frequently produce currents for feeding, being selective in the food catch and ingestion, getting particles at a distance (PAFFENHÖFER et al., 1995). *Paracalanus* juveniles and females are able to collect very small-sized particles (<̲ 5µm) passively (PRICE; PAFFENHÖFER; STRICKLER, 1983). *Temora turbinata* shows incessant, gradual, linear movement, employing food currents (MAZZOCCHI; PAFFENHÖFER, 1999). This species is an exotic species in Northeastern Brazil that now is widespread in coastal and oceanic, is abundant on the middle shelf and mainly on the inner shelf (CAMPOS et al., 2017)

Parvocalanus crassirostris is a very significant copepod in the microzooplankton fraction of coastal areas, commonly occurring in most Brazilian estuaries (BJÖRNBERG, 1981), even in immensely impacted estuaries (PINTO et al., 2004; SCHWAMBORN et al., 2004) found also estuarine plumes along with coastal areas. This species behaves as opportunistic feeding mainly on picoplankton and nanoplankton, presenting great ingestion rates of the dominant cells (2-5 µm size) (CALBET; LANDRY; SCHEINBERG, 2000). *Parvocalanus crassirostris* is an indicator of eutrophic condition, showing the influence of estuarine plume in the coastal studied area. The dominance of Paracalanidae is typical of inshore tropical waters in Brazil (BJÖRNBERG, 1981).

Functional diversity and species diversity

FDis and Shannon diversity showed differences between years, with higher values in 2019. FDis refers to the variability of traits within a community. Low FDis suggests similar trait types among species in a sample. This low value can occur in environmental adversity situations, under generally oligotrophic conditions (VOGT; PERES-NETO; BEISNER, 2013) or El Niño events (POMERLEAU; SASTRI; BEISNER, 2015). Conversely, high FDis indicates high variability across trait types (CÔTE; KUCZYNSKI; GRENOUILLET, 2018; LI et al., 2022b) and with increasing values, the species assemblage of functional traits can become overdispersed due to the larger number of functional traits represented (WIEDMANN et al., 2014). 2019 had the highest rainfall (123.9 mm) registered when compared to other years in this study. This suggests that although there are no differences between the rainy and dry seasons, the high precipitation observed in 2019 may have led to a high FDis value. Li et al. (2022) observed a high FDis in the Yellow Sea during cold water mass when the environment was relatively stable, providing a suitable living habitat for species with distinctive traits. In this study, probably high precipitation increases the entry of species from the estuarine system (e.g., *E. acutifrons*) in the coastal area, raising the variability of species and trait types.

Copepod species richness and functional richness (FRic) were strongly correlated indicating that a larger number of species fill a greater volume of trait space (POMERLEAU; SASTRI; BEISNER, 2015; VILLÉGER; MASON; MOUILLOT, 2008), especially in the rainy season. This result corroborates what we have seen in this study. The rainy season had a higher abundance of copepods and indirectly showed higher values in FRic and FDis. In other words, the rainy season probably presents complex and diverse traits that rule the system. The Shannon diversity index (H’) is the taxonomic analogue of FDis. The strong and positive relationship between Shannon diversity and FDis indicates that within our marine copepod assemblage, a high species diversity value also reflects in a greater variety of traits, as seen by Pomerleau et al. (2015).

Conclusions

The results of this study showed that a low variation in temperature and salinity is highly responsible for the variability in the functional groups of copepods in the TWSA. The environmental forcings are more important on functional groups than copepod species alone. Also, the coastal area is dominated by a small group of species with high abundance and well-adapted to hydrological and climatic variations. However, in rainy seasons there is an increase in the diversity of functional traits and species. Strong rainfalls cause a shift in the system that allows the presence of other species (e.g., *Centropages velificatus* and *Macrosetella gracilis*) and a higher abundance of less abundant species, for example, group IV with higher abundance in the rainy season of 2019.

REFERENCES

AMBLER, J.; FERRARI, F.; FORNSHELL, J. Population structure and swarm formation of the cyclopoid copepod Dioithona oculata near mangrove cays. **Journal of Plankton Research**, v. 13, 1 nov. 1991.

ANDERSON, M. J. Permutational multivariate analysis of variance. **Department of Statistics, University of Auckland, Auckland**, v. 26, p. 32–46, 2005.

ANDRADE, G. O. DE; LINS, R. C. Os climas do Nordeste. **As regiões naturais do Nordeste, o meio e a civilização. CONDEPE, Recife**, v. 3, n. 4, p. 95–138, 1971.

BARNETT, A. J.; FINLAY, K.; BEISNER, B. E. Functional diversity of crustacean zooplankton communities: towards a trait-based classification. **Freshwater Biology**, v. 52, n. 5, p. 796–813, 2007.

BECKER, É. et al. Latitudinal gradient of copepod functional diversity in the South Atlantic Ocean. **Progress in Oceanography**, v. 199, p. 102710, 1 nov. 2021.

BENEDETTI, F. et al. Climate change may have minor impact on zooplankton functional diversity in the Mediterranean Sea. **Diversity and Distributions**, v. 25, p. 1–14, 15 nov. 2018.

BENEDETTI, F.; GASPARINI, S.; AYATA, S.-D. Identifying copepod functional groups from species functional traits. **Journal of Plankton Research**, v. 38, n. 1, p. 159–166, 2016.

BLAXTER, J. H. S. et al. **The biology of calanoid copepods**. [s.l.] Academic Press, 1998.

BRITO-LOLAIA, M. et al. Micro- and mesozooplankton at the edges of coastal tropical reefs (Tamandaré, Brazil). **Helgoland Marine Research**, v. 74, 1 dez. 2020.

BRITO-LOLAIA, M. et al. Can the stable isotope variability in a zooplankton time series be explained by its key species? **Marine Environmental Research**, v. 181, p. 105737, 2022.

BRUN, P.; PAYNE, M. R.; KIØRBOE, T. Trait biogeography of marine copepods–an analysis across scales. **Ecology Letters**, v. 19, n. 12, p. 1403–1413, 2016.

BUNKER, A. J.; HIRST, A. G. Fecundity of marine planktonic copepods: global rates and patterns in relation to chlorophyll a, temperature and body weight. **Marine Ecology Progress Series**, v. 279, p. 161–181, 2004.

BUSKEY, E. J.; PETERSON, J. O.; AMBLER, J. W. he swarming behavior of the copepod Dioithona oculata: In situ and laboratory studies. **Limnology and Oceanography**, v. 41, n. 3, p. 513–521, 1996.

CALBET, A. et al. Annual zooplankton succession in coastal NW Mediterranean waters: the importance of the smaller size fractions. **Journal of Plankton research**, v. 23, n. 3, p. 319–331, 2001.

CALBET, A.; LANDRY, M. R.; SCHEINBERG, R. D. Copepod grazing in a subtropical bay: species-specific responses to a midsummer increase in nanoplankton standing stock. **Marine Ecology Progress Series**, v. 193, p. 75–84, 2000.

CAMPOS, C. C. et al. Ecological indicators and functional groups of copepod assemblages. **Ecological Indicators**, v. 83, p. 416–426, 2017.

CASTONGUAY, M. et al. Copepod production drives recruitment in a marine fish. **Canadian Journal of Fisheries and Aquatic Sciences**, v. 65, n. 8, p. 1528–1531, 2008.

CÔTE, J.; KUCZYNSKI, L.; GRENOUILLET, G. Spatial patterns and determinants of trait dispersion in freshwater fish assemblages across Europe. **Global Ecology and Biogeography**, v. 28, 10 dez. 2018.

COYLE, K. O.; PINCHUK, A. I. Annual cycle of zooplankton abundance, biomass and production on the northern Gulf of Alaska shelf, October 1997 through October 2000. **Fisheries Oceanography**, v. 12, n. 4-5, p. 327–338, 2003.

DA ROCHA MARCOLIN, C. 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.

DA SILVA, A. J. et al. Non-predatory mortality of planktonic copepods in a reef area influenced by estuarine plume. **Marine Environmental Research**, v. 159, p. 105024, 2020.

DIAS, C.; BONECKER, S. Inter-annual variability of planktonic copepods in a tropical bay in Southeastern Brazil. **Brazilian Archives of Biology and Technology - BRAZ ARCH BIOL TECHNOL**, v. 51, 1 jul. 2008.

DIAS, C. DE O.; ARAUJO, A. V. DE; BONECKER, S. L. C. Seasonal variability of planktonic copepods (Copepoda: Crustacea) in a tropical estuarine region in Brazil. **Zoologia (Curitiba)**, v. 26, 2009.

ELLIOTT, D. T.; HARRIS, C. K.; TANG, K. W. Dead in the water: the fate of copepod carcasses in the York River estuary, Virginia. **Limnology and Oceanography**, v. 55, n. 5, p. 1821–1834, 2010.

FRANGOULIS, C. et al. Importance of copepod carcasses versus faecal pellets in the upper water column of an oligotrophic area. **Estuarine, Coastal and Shelf Science**, v. 92, n. 3, p. 456–463, 2011.

GOWER, J. C. A general coefficient of similarity and some of its properties. **Biometrics**, p. 857–871, 1971.

HIRST, A.; KIØRBOE, T. Mortality of marine planktonic copepods: Global rates and patterns. **Marine Ecology-progress Series - MAR ECOL-PROGR SER**, v. 230, p. 195–209, 5 abr. 2002.

HOPCROFT, R. R.; ROFF, J. C.; CHAVEZ, F. P. Size paradigms in copepod communities: a re-examination. **Hydrobiologia**, v. 453, p. 133–141, 2001.

HOPCROFT, R. R.; ROFF, J. C.; LOMBARD, D. Production of tropical copepods in Kingston Harbour, Jamaica: the importance of small species. **Marine Biology**, v. 130, p. 593–604, 1998.

KIØRBOE, T. How zooplankton feed: mechanisms, traits and trade-offs. **Biological Reviews**, v. 86, n. 2, p. 311–339, 1 maio 2011.

KIØRBOE, T.; VISSER, A.; ANDERSEN, K. H. A trait-based approach to ocean ecology. **ICES Journal of Marine Science**, v. 75, n. 6, p. 1849–1863, 1 dez. 2018.

KIRBY, R. R. et al. Citizens and scientists collect comparable oceanographic data: measurements of ocean transparency from the Secchi Disk study and science programmes. **Scientific Reports**, v. 11, n. 1, p. 15499, 2021.

LALIBERTÉ, E. et al. Package 'fd'. **Measuring functional diversity from multiple traits, and other tools for functional ecology**, v. 1, p. 0–12, 2014.

LEGENDRE, P.; GALLAGHER, E. D. Ecologically meaningful transformations for ordination of species data. **Oecologia**, v. 129, p. 271–280, 2001.

LI, Y. et al. Functional diversity and groups of crustacean zooplankton in the southern Yellow Sea. **Ecological Indicators**, v. 136, p. 108699, 2022a.

LI, Y. et al. Functional diversity and groups of crustacean zooplankton in the southern Yellow Sea. **Ecological Indicators**, v. 136, p. 108699, 2022b.

LITCHMAN, E.; OHMAN, M. D.; KIØRBOE, T. Trait-based approaches to zooplankton communities. **Journal of plankton research**, v. 35, n. 3, p. 473–484, 2013.

MAGOUZ, F. I. et al. Effect of Different Salinity Levels on Population Dynamics and Growth of the Cyclopoid Copepod Oithona nana. **Diversity**, v. 13, n. 5, 2021.

MARIANI, P. et al. Control of plankton seasonal succession by adaptive grazing. **Limnology and Oceanography**, v. 58, n. 1, p. 173–184, 1 jan. 2013.

MAZZOCCHI, M. G.; PAFFENHÖFER, G.-A. Swimming and feeding behaviour of the planktonic copepod Clausocalanus furcatus. **Journal of Plankton Research**, v. 21, n. 8, 1999.

MOTODA, S. Devices of simple plankton apparatus. **Memoirs of the faculty of fisheries Hokkaido University**, v. 7, n. 1–2, p. 73–94, 1959.

MOUILLOT, D. et al. A functional approach reveals community responses to disturbances. **Trends in ecology & evolution**, v. 28, n. 3, p. 167–177, 2013.

NAGATA, R. M.; MORANDINI, A. C. Diet, prey selection, and individual feeding rates of the jellyfish Lychnorhiza lucerna (Scyphozoa, Rhizostomeae). **Marine biology**, v. 165, n. 12, p. 187, 2018.

NAKAMURA, Y.; TURNER, J. T. Predation and respiration by the small cyclopoid copepod Oithona similisr: How important is feeding on ciliates and heterotrophic flagellates? **Journal of Plankton Research**, v. 19, n. 9, p. 1275–1288, 1997.

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. Zooplankton from a reef system under the influence of the Amazon River plume. **Frontiers in microbiology**, v. 9, p. 355, 2018.

OMORI, M.; IKEDA, T. **Methods in marine zooplankton ecology**. John Wiley and Sons Inc., New York, , 1984.

O'NEIL, J. M.; ROMAN, M. R. Ingestion of the cyanobacterium Trichodesmium spp. by pelagic harpacticoid copepods Macrosetella, Miracia and Oculosetella. **Hydrobiologia**, v. 292, p. 235–240, 1994.

PAFFENHÖFER, G.-A. et al. Rates of ingestion and their variability between individual calanoid copepods: direct observations. **Journal of Plankton Research**, v. 17, n. 7, p. 1573–1585, 1995.

PETERSON, W. T.; TISELIUS, P.; KIØRBOE, T. Copepod egg production, moulting and growth rates, and secondary production, in the Skagerrak in August 1988. **Journal of Plankton Research**, v. 13, n. 1, p. 131–154, 1991.

PINTO, A. et al. Mesozooplankton of an impacted Bay in North Eastern Brazil. **Brazilian Archives of Biology and Technology - BRAZ ARCH BIOL TECHNOL**, v. 47, 1 jul. 2004.

POMERLEAU, C.; SASTRI, A. R.; BEISNER, B. E. Evaluation of functional trait diversity for marine zooplankton communities in the Northeast subarctic Pacific Ocean. **Journal of Plankton Research**, v. 37, n. 4, p. 712–726, 2015.

PREISENDORFER, R. W. Secchi disk science: Visual optics of natural waters 1. **Limnology and oceanography**, v. 31, n. 5, p. 909–926, 1986.

PRICE, H. J.; PAFFENHÖFER, G.-A.; STRICKLER, J. R. Modes of cell capture in calanoid copepods 1. **Limnology and Oceanography**, v. 28, n. 1, p. 116–123, 1983.

RAKHESH, M. et al. Small copepods structuring mesozooplankton community dynamics in a tropical estuary-coastal system. **Estuarine, Coastal and Shelf Science**, v. 126, p. 7–22, 2013.

SANTOS, G. S. et al. The Impact of Trampling on Reef Macrobenthos in Northeastern Brazil: How Effective are Current Conservation Strategies? **Environmental Management**, v. 56, n. 4, p. 847–858, 2015.

SCHWAMBORN, R. et al. Mesozooplankton grazing under conditions of extreme eutrophication in Guanabara Bay, Brazil. **Journal of plankton research**, v. 26, n. 9, p. 983–992, 2004.

SHAPIRO, S. S.; WILK, M. B. An analysis of variance test for normality (complete samples). **Biometrika**, v. 52, n. 3/4, p. 591–611, 1965.

SILVA, A.C. et al. Característicasdas ondas "sea" and "swell" observadas no litoral do Ceará - Brasil: variabilidade anual e interanual. Trop. Oceanogr. 39, 123–132.

SODRÉ, E. DE O.; BOZELLI, R. L. How planktonic microcrustaceans respond to environment and affect ecosystem: a functional trait perspective. **International Aquatic Research**, v. 11, n. 3, p. 207–223, 2019.

SVETLICHNY, L.; HUBAREVA, E.; UTTIERI, M. Ecophysiological and behavioural responses to salinity and temperature stress in cyclopoid copepod Oithona davisae with comments on gender differences. **Mediterranean Marine Science**, v. 22, n. 1, p. 89–101, 27 jan. 2021.

TEROL, S. Z. **Ecology of the marine copepod genus Oithona**. 2013.

TEUBER, L. et al. Who is who in the tropical Atlantic? Functional traits, ecophysiological adaptations and life strategies in tropical calanoid copepods. **Progress in Oceanography**, v. 171, p. 128–135, 2019.

TURNER, J. T. Zooplankton feeding ecology: contents of fecal pellets of the copepods Temora turbinata and T. stylifera from continental shelf and slope waters near the mouth of the Mississippi River. **Marine Biology**, v. 82, p. 73–83, 1984.

TURNER, J. T. The importance of small planktonic copepods and their roles in pelagic marine food webs. **Zool. Stud**, v. 43, n. 2, p. 255–266, 2004.

VALENTIN, J. L.; MONTEIRO-RIBAS, W. M. Zooplankton community structure on the east-southeast Brazilian continental shelf (18–23°S latitude). **Continental Shelf Research**, v. 13, n. 4, p. 407–424, 1993.

VERÍSSIMO, H. et al. Functional diversity of zooplankton communities in two tropical estuaries (NE Brazil) with different degrees of human-induced disturbance. **Marine environmental research**, v. 129, p. 46–56, 2017.

VILLÉGER, S.; MASON, N. W. H.; MOUILLOT, D. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. **Ecology**, v. 89, n. 8, p. 2290–2301, 2008.

VOGT, R. J.; PERES-NETO, P. R.; BEISNER, B. E. Using functional traits to investigate the determinants of crustacean zooplankton community structure. **Oikos**, v. 122, n. 12, p. 1700–1709, 2013.

WIEDMANN, M. A. et al. Functional diversity of the Barents Sea fish community. **Marine Ecology Progress Series**, v. 495, p. 205–218, 2014.

ZAR, J. H. **Biostatistical analysis**. [s.l.] Pearson Education India, 1999.

ZERVOUDAKI, S. et al. The importance of small-sized copepods in a frontal area of the Aegean Sea. **Journal of Plankton Research**, v. 29, n. 4, p. 317–338, 2007.

6 CONSIDERAÇÕES FINAIS

O estudo desenvolvido nesta tese ofereceu um vislumbre sobre os fatores ecológicos que regem a variabilidade do microzooplâncton no ecossistema costeiro de Tamandaré. E teve como propósito entender essas variações, estabelecendo uma *baseline* para que outros pesquisadores possam entender e avaliar outras comunidades que habitam o ecossistema da Baía de Tamandaré. Uma vez que o microzooplâncton é fonte alimentar de peixes e crustáceos de grande importância econômica nessa região, este estudo tem em si uma grande relevância. A Baía de Tamandaré faz parte de uma área marinha protegida de uso sustentável, a APA Costa dos Corais, criada para proteção dos recursos naturais e que nos últimos anos tem mostrado dados de recuperação muito significativos. O ecossistema local é fonte de renda de pescadores que se beneficiam da pesca, elemento importante para a economia local. Portanto, este estudo visou analisar e entender como funciona o ecossistema marinho de uma região costeira tropical, observando e comparando com variações climáticas ao longo de uma série temporal.

Neste estudo não foi possível observar variações significativas dos fatores ambientais e da comunidade do microzooplâncton durante o evento de El Niño (2015-2016), sendo necessário a observação de outros eventos de El Niño para afirmar que não há efeitos sobre o zooplâncton da área costeira do nordeste do Brasil. Como perspectivas futuras a continuação de estudo de longo prazo é importante para a observação não só dos efeitos de outras anomalias climáticas como também para observar os impactos em campo das mudanças climáticas sobre o microzooplâncton do ambiente pelágico marinho do nordeste do Brasil.

REFERÊNCIAS

BAKKER, C.; PHAFF, W. J. Tintinnida from coastal waters of the S.W.-Netherlands I. The genus Tintinnopsis stein. **Hydrobiologia**, v. 50, p. 101–111, 1976.

BARNETT, A. J.; FINLAY, K.; BEISNER, B. E. Functional diversity of crustacean zooplankton communities: towards a trait-based classification. **Freshwater Biology**, v. 52, n. 5, p. 796–813, 2007.

BEAUGRAND, G. Monitoring pelagic ecosystems using plankton indicators. **ICES Journal of Marine Science**, v. 62, n. 3, p. 333–338, 2005.

BRITO-LOLAIA, M. et al. Micro- and mesozooplankton at the edges of coastal tropical reefs (Tamandaré, Brazil). **Helgoland Marine Research**, v. 74, 1 dez. 2020.

BRITO-LOLAIA, M. et al. Can the stable isotope variability in a zooplankton time series be explained by its key species? **Marine Environmental Research**, v. 181, p. 105737, 2022.

CALAZANS, D.; MUELBERT, J.; MUXAGATA, E. Organismos PlanctÔnicos. Em: **Estudos Oceanográficos: Do Instrumental ao Prático**. [s.l: s.n.]. p. 163–232.

CAMPOS, C. C. et al. Ecological indicators and functional groups of copepod assemblages. **Ecological Indicators**, v. 83, p. 416–426, 2017.

COYLE, K. O.; PINCHUK, A. I. Annual cycle of zooplankton abundance, biomass and production on the northern Gulf of Alaska shelf, October 1997 through October 2000. **Fisheries Oceanography**, v. 12, n. 4-5, p. 327–338, 2003.

DA ROCHA MARCOLIN, C. 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.

DA SILVA, A. J. et al. Non-predatory mortality of planktonic copepods in a reef area influenced by estuarine plume. **Marine Environmental Research**, v. 159, p. 105024, 2020.

D'ALCALÀ, M. R. et al. Seasonal patterns in plankton communities in a pluriannual time series at a coastal Mediterranean site (Gulf of Naples): an attempt to discern recurrences and trends. **Scientia marina**, v. 68, n. S1, p. 65–83, 2004.

DE SANTANA, C. S. et al. Amazon river plume influence on planktonic decapods in the tropical Atlantic. **Journal of Marine Systems**, v. 212, p. 103428, 2020.

DI LORENZO, E.; OHMAN, M. D. A double-integration hypothesis to explain ocean ecosystem response to climate forcing. **Proceedings of the National Academy of Sciences**, v. 110, n. 7, p. 2496–2499, 2013.

DIAS, C.; BONECKER, S. Inter-annual variability of planktonic copepods in a tropical bay in Southeastern Brazil. **Brazilian Archives of Biology and Technology - BRAZ ARCH BIOL TECHNOL**, v. 51, 1 jul. 2008.

ELLIOTT, D. T.; HARRIS, C. K.; TANG, K. W. Dead in the water: the fate of copepod carcasses in the York River estuary, Virginia. **Limnology and Oceanography**, v. 55, n. 5, p. 1821–1834, 2010.

ESKINAZI-SANT’ANNA, E. M.; BJÖRNBERG, T. K. S. Seasonal dynamics of microzooplankton in the São Sebastião Channel (SP, Brazil). **Brazilian Journal of Biology**, v. 66, p. 221–231, 2006.

FEITOSA, J. L. L.; FERREIRA, B. P. Distribution and feeding patterns of juvenile parrotfish on algal-dominated coral reefs. **Marine Ecology**, v. 36, n. 3, p. 462–474, 2015.

FERREIRA, B. P.; MAIDA, M. **Monitoramento dos recifes de coral do Brasil**. [s.l.] MMA, Secretaria de Biodiversidade e Florestas Brasília, DF, 2006.

FERREIRA, B. P.; MAIDA, M.; CAVA, F. **Características e perspectivas para o manejo da pesca na APA Marinha Costa dos Corais**. Congresso Brasileiro de Unidades de Conservação. **Anais**...2001.

FRANGOULIS, C. et al. Importance of copepod carcasses versus faecal pellets in the upper water column of an oligotrophic area. **Estuarine, Coastal and Shelf Science**, v. 92, n. 3, p. 456–463, 2011.

FRY, B. **Stable isotope ecology**. Springer, 2006. v. 521

HAMNER, W. M. et al. Zooplankton, planktivorous fish, and water currents on a windward reef face: Great Barrier Reef, Australia. **Bulletin of Marine Science**, v. 42, n. 3, p. 459–479, 1988.

HARRIS, R. et al. **ICES Zooplankton Methodology Manual**. Academic Press, 2000.

HAYS, G. C.; RICHARDSON, A. J.; ROBINSON, C. Climate change and marine plankton. **Trends in ecology & evolution**, v. 20, n. 6, p. 337–344, 2005.

HOLT, J. et al. The potential impacts of climate change on the hydrography of the northwest European continental shelf. **Progress in Oceanography**, v. 86, n. 3–4, p. 361–379, 2010.

HOUNSOU-GBO, G. A. et al. Oceanic indices for forecasting seasonal rainfall over the northern part of Brazilian northeast. 2016.

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

JUSTIC, D.; RABALAIS, N. N.; TURNER, R. E. Impacts of climate change on net productivity of coastal waters: implications for carbon budgets and hypoxia. **Climate research**, v. 8, n. 3, p. 225–237, 1997.

JYOTHIBABU, R. et al. Seasonal variation of microzooplankton (20–200µm) and its possible implications on the vertical carbon flux in the western Bay of Bengal. **Continental Shelf Research**, v. 28, n. 6, p. 737–755, 2008.

LANDRY, M. R.; HASSETT, R. P. Estimating the grazing impact of marine micro-zooplankton. **Marine Biology**, v. 67, n. 3, p. 283–288, 1982.

LITCHMAN, E.; OHMAN, M. D.; KIØRBOE, T. Trait-based approaches to zooplankton communities. **Journal of plankton research**, v. 35, n. 3, p. 473–484, 2013.

MACKAS, D. L.; BEAUGRAND, G. Comparisons of zooplankton time series. **Journal of Marine Systems**, v. 79, n. 3–4, p. 286–304, 2010.

MASON, N.; MOUILLOT, D. Functional Diversity Measures. Em: **Encyclopedia of Biodiversity**. [s.l: s.n.]. p. 597–608.

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

MELO, P. A. M. C. et al. Demersal zooplankton communities from tropical habitats in the southwestern Atlantic. **Marine Biology Research**, v. 6, n. 6, p. 530–541, 2010.

MINAGAWA, M.; WADA, E. Stepwise enrichment of 15N along food chains: further evidence and the relation between δ15N and animal age. **Geochimica et cosmochimica acta**, v. 48, n. 5, p. 1135–1140, 1984.

MONTI, M. et al. Seasonal and interannual dynamics of microzooplankton abundances in the Gulf of Trieste (Northern Adriatic Sea, Italy). **Estuarine, Coastal and Shelf Science**, v. 115, p. 149–157, dez. 2012.

NIBAKKEN, J.W. **Marine Biology: an ecological approach** 3rd. ed. New York: Harper Colling College, 1993.

NITTROUER, C. A. et al. An introduction to the geological significance of sediment transport and accumulation on the Amazon continental shelf. **Marine Geology**, v. 125, n. 3–4, p. 177–192, 1995.

OHMAN, M. D.; RAU, G. H.; HULL, P. M. Multi-decadal variations in stable N isotopes of California Current zooplankton. **Deep Sea Research Part I: Oceanographic Research Papers**, v. 60, p. 46–55, 2012.

OUBA, A.; ABBOUD-ABI SAAB, M.; STEMMANN, L. Temporal Variability of Zooplankton (2000-2013) in the Levantine Sea: Significant Changes Associated to the 2005-2010 EMT-like Event? **PLoS One**, v. 11, n. 7, p. e0158484, 2016.

PINTO, M. F.; MOURÃO, J. S.; ALVES, R. R. N. How do artisanal fishermen name fish? An Ethnotaxonomic study in Northeastern Brazil. **Journal of Ethnobiology**, v. 36, n. 2, p. 348–381, 2016.

POMERLEAU, C.; SASTRI, A. R.; BEISNER, B. E. Evaluation of functional trait diversity for marine zooplankton communities in the Northeast subarctic Pacific Ocean. **Journal of Plankton Research**, v. 37, n. 4, p. 712–726, 2015.

POST, D. M. USING STABLE ISOTOPES TO ESTIMATE TROPHIC POSITION: MODELS, METHODS, AND ASSUMPTIONS. **Ecology**, v. 83, n. 3, p. 703–718, 1 mar. 2002.

RAU, G. H.; OHMAN, M. D.; PIERROT-BULTS, A. Linking nitrogen dynamics to climate variability off central California: a 51 year record based on 15N/14N in CalCOFI zooplankton. **Deep Sea Research Part II: Topical Studies in Oceanography**, v. 50, n. 14–16, p. 2431–2447, 2003.

ROMAGNAN, J.-B. et al. Comprehensive model of annual plankton succession based on the whole-plankton time series approach. **PLoS One**, v. 10, n. 3, p. e0119219, 2015.

SANTOS, G. S. et al. The Impact of Trampling on Reef Macrobenthos in Northeastern Brazil: How Effective are Current Conservation Strategies? **Environmental Management**, v. 56, n. 4, p. 847–858, 2015.

SANTOS, G. S. et al. Response of the zooxanthellae of Palythoa caribaeorum (Cnidaria: Zoanthidea) to different environmental conditions in coastal and oceanic ecosystems of the Tropical Atlantic. **Helgoland Marine Research**, v. 70, p. 1–7, 2016.

SANTOS, G. S. et al. Are tropical coastal reefs sinks or sources of mesozooplankton? A case study in a Brazilian marine protected area. **Coral Reefs**, v. 38, p. 1107–1120, 2019.

SANTOS, G. S.; BRITO-LOLAIA, M.; SCHWAMBORN, R. Two new methods for sampling zooplankton and larval assemblages in tropical reef ecosystems. **Journal of Experimental Marine Biology and Ecology**, v. 491, p. 27–37, 2017.

SARAVANAN, R.; CHANG, P. Interaction between tropical Atlantic variability and El Niño–Southern oscillation. **Journal of climate**, v. 13, n. 13, p. 2177–2194, 2000.

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, p. 813–825, 2015.

SCHWAMBORN, R. et al. Ingestion of Large Centric Diatoms, Mangrove Detritus, and Zooplankton by Zoeae of Aratus pisonii (Crustacea: Brachyura: Grapsidae). **Hydrobiologia**, v. 560, n. 1, p. 1–13, 2006.

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.

SIOKOU-FRANGOU, I. Zooplankton annual cycle in a Mediterranean coastal area. **Journal of Plankton Research**, v. 18, n. 2, p. 203–223, 1996.

SIVASANKAR, R. et al. Loricate ciliates as an indicator of eutrophication status in the estuarine and coastal waters. **Marine Pollution Bulletin**, v. 129, n. 1, p. 207–211, 2018.

SODRÉ, E. DE O.; BOZELLI, R. L. How planktonic microcrustaceans respond to environment and affect ecosystem: a functional trait perspective. **International Aquatic Research**, v. 11, n. 3, p. 207–223, 2019.

TILMAN, D. Functional diversity. **Encyclopedia of biodiversity**, v. 3, n. 1, p. 109–120, 2001.

TURNER, J. T.; TESTER, P. A. Zooplankton feeding ecology: bacterivory by metazoan microzooplankton. **Journal of Experimental Marine Biology and Ecology**, v. 160, n. 2, p. 149–167, 1992.

UNESCO. **Zooplankton Sampling**. [s.l.] Unesco, 1968.

APÊNDICE A – ARTIGO PUBLICADO NA MARINE ENVIRONMENTAL RESEARCH

Marine Environmental Research 181 (2022) 105737

Contents lists available at ScienceDirect

Marine Environmental Research

journal homepage: www.elsevier.com/locate/marenvrev

Can the stable isotope variability in a zooplankton time series be explained by its key species?

Morgana Brito-Lolaia, Gabriela Guerra Araújo Abrantes de Figueiredo, Sigrid Neumann-Leitão, Gilvan Takeshi Yogui, Ralf Schwamborn *

Dept. of Oceanography, Federal University of Pernambuco (UFPE), Av. Arquitetura s/n, Cidade Universitária, Recife, PE, 50740-550, Brazil

A R T I C L E I N F O

Keywords:
Species-biomass-isotopes-mixture approach
$\delta^{13}C$
$\delta^{15}N$
C/N ratio
Variability
Bioindicators
Food webs
Time series
Mixing models
Linear models
Zooplankton

A B S T R A C T

Stable isotope (SI) analysis is a standard tool to study marine food webs, usually based on the measurement of a few individuals from a small list of subjectively pre-defined species. The main objective of this study was to find out which species are significantly associated with the temporal variability of the SI composition of zooplankton in a tropical marine ecosystem. We investigated this by means of a novel species-biomass-isotopes-mixture (SBIM) approach that uses a relative biomass matrix to explain the SI signature of the zooplankton community. Furthermore, SBIM was applied to detect key taxa that can be considered bioindicators for important descriptors of ecosystem state (e.g., oligotrophy, carbon sources, mean trophic level). Plankton samples (64 μm mesh size) were obtained in Tamandaré Bay (northeastern Brazil) from June 2013 to August 2019. One aliquot of each sample was taken for stable isotope measurements and one for taxonomic identification and estimation of size and relative biomass. Total zooplankton biomass differed significantly between years, seasons and stations. Total zooplankton $\delta^{13}C$ values ranged from −21.0 to −18.2‰ (mean ± standard deviation: −19.7 ± 0.7‰ in the dry season, and −19.4 ± 0.8‰ in the rainy season). Total zooplankton $\delta^{15}N$ values ranged from 3.8 to 9.0‰ (7.0 ± 1.0‰ in the dry season, and 6.5 ± 1.2‰ rainy season). Total zooplankton C/N ratios ranged from 3.5 to 5.0 (4.2 ± 0.4 in the dry season and 4.2 ± 0.3 in the rainy season). The sparsely abundant and relatively large-sized copepod *Pseudodiaptomus acutus* was the most important species for explaining the variability in $\delta^{15}N$ (22% of the total variability). Relative biomass (%) of *P. acutus* showed a strong positive correlation with $\delta^{15}N$, indicating a high trophic level (TL). Our results highlight the importance of less abundant taxa for marine food webs. Small-sized invertebrate larvae were negatively correlated with $\delta^{15}N$, indicating a TL below average. The copepod *Dioithona oculata* was the most important organism in explaining the $\delta^{13}C$ of zooplankton (17.7% of the total variability, positive correlation with $\delta^{13}C$), indicating possible selective use of a ^{13}C-enriched food source (e.g., diatoms) by this cyclopoid copepod. *Oithona* spp. juveniles showed a negative relationship with zooplankton C/N ratio, which can be indicators of an oligotrophic ecosystem state and lipid-poor zooplankton. The tintinnid *F. ehrenbergii* showed a positive correlation with C/N, being an indicator for turbid "green waters", during the rainy season, when the ecosystem was in a eutrophic state, with high lipid contents in the zooplankton community. The proposed SBIM approach opens up a novel pathway to understanding the factors and species that shape the temporal variability of food webs.

1. Introduction

Carbon and nitrogen stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) have been used for a variety of purposes in marine ecosystem research (Fry, 2006; Ohman et al., 2012; Post, 2002; Schwamborn and Giarrizzo, 2015). $\delta^{13}C$ can be used as a tracer for primary food sources since it is transferred from preys to predators with minor isotopic changes (McConnaughey and McRoy, 1979). Conversely, $\delta^{15}N$ values show strong enrichment within food chains and thus can be used as indicators of trophic position (Hannides et al., 2009; Minagawa and Wada, 1984; Post, 2002). Furthermore, the C/N ratio can be used as a proxy for assessing the lipid content of organisms (Schwamborn and Giarrizzo, 2015). In contrast to early species-based community descriptors (i.e., abundance, diversity, etc.), the wide use of stable isotopes in the past few decades has

---

* Corresponding author:
E-mail address: ralf.schwamborn@ufpe.br (R. Schwamborn).

https://doi.org/10.1016/j.marenvres.2022.105737
Received 14 April 2022; Received in revised form 20 August 2022; Accepted 23 August 2022

APÊNDICE B – TABELA SUPLEMENTAR

Table A. Abundance (mean ± standard deviation), relative abundance (%) and ratio D/R (dry/rainy season) of zooplankton sampled at Tamandaré Bay (northeast Brazil). NP: Not present; Some taxa have been separated into adults and juveniles (J).

Taxa	Dry season		Rainy season		Ratio
	Ind m^{-3}	%	Ind m^{-3}	%	D/R
CILIOPHORA					
Favella ehrenbergii	2,640.3 ± 5,666.3	1.0	28,295.7 ± 51,325.9	6.5	0.1
Tintinopsis fimbriata	208.0 ± 689.6	< 0.1	603.6 ± 1531.7	0.1	0.3
Tintinopsis compressa	NP		363.9 ± 1331.2	< 0.1	
Tintinopsis acuminata	56.8 ± 331.5	< 0.1	347.7 ± 1967.9	< 0.1	0.2
Tintinopsis spp.	71.7 ± 340.1	< 0.1	542.5 ± 2090.0	0.1	0.1
Condonellopsis schabi	12.4 ± 72.5	< 0.1	26.4 ± 154.0	< 0.1	0.5
Condonellopsis ostenfeldi	308.4 ± 1123.5	0.1	2047.4 ± 9804.9	0.5	0.2
Condonellopsis sp.	NP		97.7 ± 404.0	< 0.1	
Rhabdonella spiralis	12.2 ± 71.1	< 0.1	2.8 ± 16.1	< 0.1	4.4
Rhabdonella brandti	6.1 ± 35.6	< 0.1	93.5 ± 335.9	< 0.1	0.1
Leprotintinnus nordqvisti	14.9 ± 86.6	< 0.1	1,505.1 ± 4,731.5	0.3	< 0.1
Tintinna (others)	NP		42.7 ± 161.3	< 0.1	
ROTIFERA					
Brachionus plicatilis	51.1 ± 251.9	< 0.1	435.8 ± 1827.4	< 0.1	0.1
FORAMINIFERA	763.8 ± 2418.2	0.3	752.5 ± 1407.5	0.2	1.0
BRYOZOA	33.3 ± 117.6	< 0.1	22.3 ± 62.9	< 0.1	1.5
CNIDARIA					
Hydromedusae	48.8 ± 182.2	< 0.1	0.7 ± 4.3	< 0.1	66.8
Siphonophora (Nectophore)	136.7 ± 638.7	< 0.1	NP		
ECHINODERMATA					
Ophiuroidea	NP		30.1 ± 134.9	< 0.1	
Echinoidea	21.3 ± 110.9	< 0.1	144.6 ± 548.3	< 0.1	0.1
NEMATODA	10.7 ± 35.0	< 0.1	35.9 ± 87.1	< 0.1	0.2
NEMERTEA	19.9 ± 90.6	< 0.1	42.2 ± 246.1	< 0.1	0.5
ANNELIDA					
Polychaeta (larvae)	1,977.7 ± 2,388.9	0.7	5,907.6 ± 16,753.9	1.3	0.3
MOLLUSCA					
Gastropoda (veliger)	6,663.5 ± 16,308.4	2.5	2,559.3 ± 5,185.9	0.6	2.6
Bivalve (veliger)	837.8 ± 1,200.7	0.3	2,688.8 ± 5,721.6	0.6	0.3
CRUSTACEA					
Copepoda (adults and juveniles)					
Calanidae	35.7 ± 145.2	< 0.1	7.5 ± 43.7	< 0.1	4.8
Paracalanidae (J)	7.7 ± 36.4	< 0.1	40.3 ± 173.6	< 0.1	0.2
Clausocalanus sp.	16.7 ± 97.6	< 0.1	NP		
Paracalanus spp. (J)	509.9 ± 807.3	0.2	616.5 ± 1,720.7	0.1	0.8
Paracalanus aculeatus	15.9 ± 41.4	< 0.1	42.2 ± 246.1	< 0.1	0.4
Paracalanus quasimodo	309.5 ± 825.8	< 0.1	762.9 ± 2070.4	< 0.1	0.4
Parvocalanus crassirostris	20,231.9 ± 27,082.8	7.5	19,447.8 ± 27,877.1	4.4	1.0
Centropages velificatus	NP		14.9 ± 60.2	< 0.1	
Pseudodiaptomus acutus	4,926.4 ± 7,674.3	1.8	3,691.8 ± 8,318.9	0.8	1.3
Temora turbinata	65.7 ± 200.8	< 0.1	121.5 ± 367.8	< 0.1	0.5
Labidocera spp. (J)	1,288.7 ± 1,857.4	0.5	673.1 ± 1,843.2	< 0.1	1.9
Acartia lilljeborgi	2,062.6 ± 3239.7	0.8	4,114.8 ± 8656.9	0.9	0.5
Oithona spp. (J)	44,433.3 ± 45,377.0	16.5	45,916.8 ± 100,646.3	10.5	1.0
Oithona hebes	1,229.4 ± 2,082.3	0.4	1,435.8 ± 2,864.2	0.3	0.9
Oithona nana	4,101.6 ± 5,331.5	1.5	5,377.3 ± 9,029.2	1.2	0.8
Dioithona oculata	29,259.3 ± 34,843.7	10.9	25,913.5 ± 46,083.8	5.9	1.1
Harpacticoida (adults and juveniles)	319.7 ± 544.4	0.9	443.6 ± 929.5	1.0	0.7
Harpacticidae	224.2 ± 359.2	< 0.1	412.5 ± 1,506.0	< 0.1	0.5
Longipediidae	167.9 ± 392.0	< 0.1	438.1 ± 1,211.0	0.1	0.4
Tegastidae	7.5 ± 43.8	< 0.1	26.2 ± 133.0	< 0.1	0.3
Tisbidae	NP		5.8 ± 23.8	< 0.1	

Laophontidae	103.7 ± 212.2	< 0.1	322.5 ± 1,116.6	< 0.1	0.3
Ectinosomatidae	23.8 ± 81.6	< 0.1	186.2 ± 1,082.7	< 0.1	0.1
Diosaccidae	NP		11.2 ± 65.2	< 0.1	
Thalestridae	94.8 ± 195.6	< 0.1	110.3 ± 199.1	< 0.1	0.9
Microsetella rosea	18.9 ± 110.5	< 0.1	3.5 ± 15.7	< 0.1	5.3
Macrosetella gracilis	NP		7.5 ± 43.7	< 0.1	
Euterpina acutifrons	2,907.7 ± 3,848.1	1.1	8,863.8 ± 14,291.3	2.0	0.3
Ditrichocorycaeus amazonicus	41.3 ± 102.4	< 0.1	441.5 ± 1,723.5	0.1	0.1
Corycaeus giesbrechti	23.6 ± 96.3	< 0.1	252.8 ± 1,443.1	< 0.1	0.1
Corycaeus (J)	78.2 ± 197.8	< 0.1	1,450.3 ± 6,120.7	0.3	0.1
Oncea sp.	18.2 ± 106.4	< 0.1	5.6 ± 32.6	< 0.1	3.3
Farranula	18.0 ± 74.2	< 0.1	44.2 ± 257.8	< 0.1	0.4
Copepoda (nauplii)	134,417.2 ± 128,562.2	50.1	259,913.7 ± 490,656.4	59.4	0.5
Cirripedia (nauplii)	374.7 ± 696.9	0.1	940.9 ± 3425.2	0.2	0.4
Cirripedia (cypris)	56.4 ± 141.5	< 0.1	10.3 ± 37.1	< 0.1	5.5
Decapoda (nauplii)	101.7 ± 390.3	< 0.1	542.8 ± 2712.5	0.1	0.2
Ostracoda	3.7 ± 21.7	< 0.1	65.6 ± 338.5	< 0.1	0.1
Cladocera	2.2 ± 12.9	< 0.1	NP		
Decapoda (larvae)	1.9 ± 10.8	< 0.1	NP		
Brachyura (zoea)	7.9 ± 36.8	< 0.1	132.6 ± 487.7	< 0.1	0.1
Belzebub faxoni	5.0 ± 29.3	< 0.1	NP		
Isopoda (manca)	69.0 ± 134.7	< 0.1	143.7 ± 371.6	< 0.1	0.5
CHAETOGNATHA	44.8 ± 149.7	< 0.1	87.7 ± 346.0	< 0.1	0.5
CHORDATA					
APPENDICULARIA					
Oikopleura spp.	5,371.2 ± 7365.0	2.0	2,579.8 ± 5,316.5	0.6	2.1
Ascidiacea	7.5 ± 28.3	< 0.1	7.8 ± 36.0	< 0.1	1.0
Teleostei (eggs)	58.7 ± 136.2	< 0.1	1.4 ± 6.0	< 0.1	10.8
Teleostei (larvae)	0.5 ± 3.0	< 0.1	60.7 ± 338.3	< 0.1	0.0
TOTAL	268,397.9 ± 240,945.5	100	437,705.8 ± 730,777.7	100	0.8

APÊNDICE C – FIGURAS DE FUNÇÃO DE AUTOCORRELAÇÃO DOS PRINCIPAIS TÁXONS DO ZOOPLÂNCTON

Figure A. Autocorrelation Functions (ACF) of zooplankton taxa sampled in Tamandaré Bay from 2013 to 2019. Upper and lower blue dashed lines indicate the confidence interval. The vertical lines indicate the correlation coefficient. Lag represents time in months: Lag 0, the autocorrelation of the data, lag 1 (t-1) onwards.

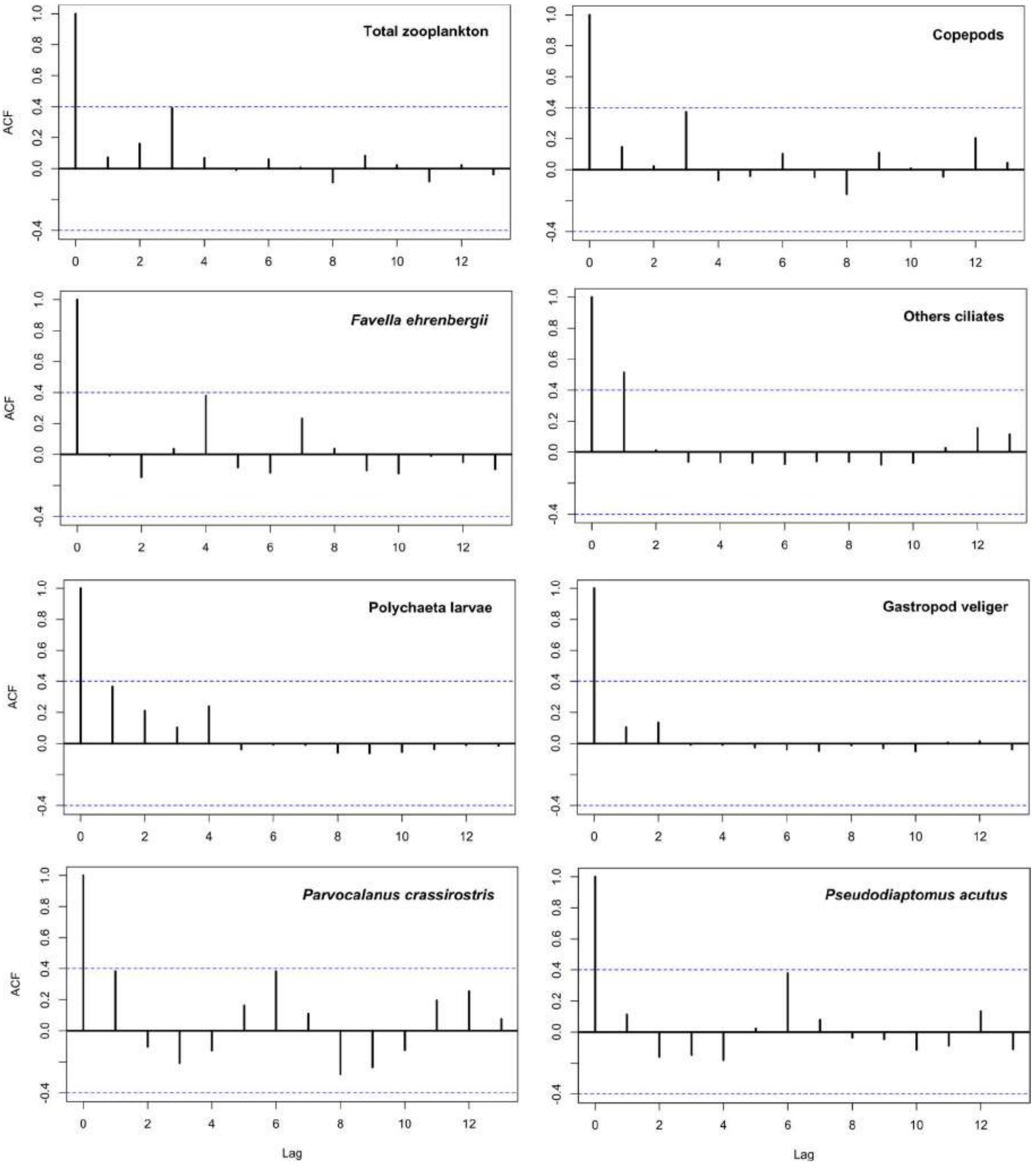


Figure B. Autocorrelation Functions (ACF) of zooplankton taxa sampled in Tamandaré Bay from 2013 to 2019. Upper and lower blue dashed lines indicate the confidence interval. The vertical lines indicate the correlation coefficient. Lag represents time in months: Lag 0, the autocorrelation of the data, lag 1 (t-1) onwards. J = juveniles.