



UNIVERSIDADE FEDERAL DE SANTA CATARINA
CENTRO DE CIÊNCIAS BIOLÓGICAS
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

Érica Caroline Becker

**Gradientes latitudinais de copépodes epipelágicos no Oceano Atlântico Sul:
diversidade funcional e tamanho corporal**

Florianópolis

2022

Érica Caroline Becker

**Gradientes latitudinais de copépodos epipelágicos no Oceano Atlântico Sul:
diversidade funcional e tamanho corporal**

Tese submetida ao Programa de Pós-graduação em
Ecologia da Universidade Federal de Santa Catarina
para obtenção do título de Doutora em Ecologia.
Orientadora: Prof.^a Dra. Andrea Santarosa Freire

Florianópolis

2022

Ficha de identificação da obra elaborada pelo autor,
através do Programa de Geração Automática da Biblioteca Universitária da UFSC.

Becker, Érica Caroline

Gradientes latitudinais de copépodes epipelágicos no Oceano Atlântico Sul: diversidade funcional e tamanho corporal / Érica Caroline Becker ; orientador, Andrea Santarosa Freire, 2022.

125 p.

Tese (doutorado) - Universidade Federal de Santa Catarina, Centro de Ciências Biológicas, Programa de Pós Graduação em Ecologia, Florianópolis, 2022.

Inclui referências.

1. Ecologia. 2. Biodiversidade. 3. Funcionamento do ecossistema. 4. Traços funcionais. 5. Regra de Bergmann. I. Freire, Andrea Santarosa. II. Universidade Federal de Santa Catarina. Programa de Pós-Graduação em Ecologia. III. Título.

Érica Caroline Becker

**Gradientes latitudinais de copépodes epipelágicos no Oceano Atlântico Sul:
diversidade funcional e tamanho corporal**

O presente trabalho em nível de doutorado foi avaliado e aprovado por banca examinadora composta pelos seguintes membros:

Prof., Dr. Eduardo Marcelo Acha
Universidad Nacional de Mar del Plata

Prof.^a, Dra. Áurea Luiza Lemes da Silva
Universidade Federal de Santa Catarina

Prof., Dr. Mauro de Melo Junior
Universidade Federal Rural de Pernambuco

Certificamos que esta é a **versão original e final** do trabalho de conclusão que foi julgado adequado para obtenção do título de doutora em Ecologia.

Prof., Dr. Nei Kavaguichi Leite
Coordenação do Programa de Pós-Graduação

Prof.^a, Dra. Andrea Santarosa Freire
Orientadora

Florianópolis, 2022.

Minha mãe dizia que eu tinha uma alma de camaleão
Sem uma bússola apontando pro Norte, sem personalidade fixa
Apenas uma indecisão interior
Tão ampla e ondulante como o oceano

« À memória de minha mãe »

AGRADECIMENTOS

Este foi um trabalho de muita dedicação e amadurecimento científico e pessoal. Gostaria de começar agradecendo ao Programa de Pós-graduação em Ecologia da Universidade Federal de Santa Catarina e aos seus coordenadores ao longo desses anos. Obrigada por me permitir realizar a minha tese neste Programa, no qual passei anos fantásticos da minha vida acadêmica. Gostaria de agradecer a CAPES (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior) pela concessão da bolsa de doutorado no Brasil e doutorado sanduíche na Itália.

Ter mentoras que apoiam faz toda a diferença na jornada acadêmica. Agradeço do fundo do coração as minhas duas orientadoras de tese. Andrea, a nossa bagagem já soma desde o mestrado (uma década!), o que meu deu muita segurança e certeza de fazer o doutorado com você também. Você fez muito para garantir que minha tese ocorresse nas melhores condições possíveis. Obrigada por todas as oportunidades, seus conselhos e orientações extraordinárias, por me dar a liberdade de expressar minhas ideias e guiar esta tese na direção de minha escolha. Aprendi muito sobre o trabalho de pesquisador e sobre mim mesma. Agradeço a Maria Grazia, que me recebeu com muito carinho e dedicação durante o doutorado sanduíche na Stazione Zoologia de Nápoles. Obrigada pelos ensinamentos em taxonomia de copépodes, pude crescer muito em poucos meses, sua opinião e visão sempre contaram e enriqueceram muito esta tese. Obrigada por acompanhar meu trabalho com atenção e interesse apesar da distância. Sou muito grata também pela rede de pesquisadores apaixonados por copépodes que pude conhecer a partir de você (curso AZC1). Carinho enorme por essas pessoas incríveis que torcem muito uns pelos outros e fazem um trabalho maravilhoso.

Sinto muito orgulho e satisfação em fazer parte do Laboratório de Crustáceos e Plâncton, acompanhar projetos incríveis que me permitiram florescer cientificamente, com muitos jovens cientistas chegando, me apoiando e trocando ideias fascinantes. Obrigada Déia, Thais, Isis, Vanessa, Fernando, Mariana, Gabriela. E em especial a « velha guarda », Luis, Manu, Babi, Mari Teschima, Tammy e Flora. Tenho muitas recordações lindas e sinto muita falta de vocês.

Sou extremamente grata a outros pesquisadores notáveis que contribuíram em algumas etapas pontuais, em discussões, análises de laboratório ou estatística, conselhos e por aí vai. Catarina Marcolin, Iole Di Capua, Cristina Dias, Marco Uttieri, Wiebe Kooistra,

Amanda Elineau, Yawouvi Dodji Soviadan, vocês têm minha eterna gratidão por tudo que me ensinaram, espero que possamos continuar a trabalhar juntos no futuro.

Obrigada aos meus amigos durante o estágio na Itália, foram uma verdadeira rede de apoio emocional durante os meses longe da minha família. Lorena, Louise, Hung, Flo e Fred, vocês me ajudaram a me superar, fora do casulo Joinville-Florianópolis, tenho muita saudade dos finais de semana descontraídos com aperol de vinho e queijo e das pequenas trips na região da Campânia da bela capital Napoli.

Agradeço a Marê e Talminha, minhas amigas da vida, graduação, pós-graduação e maternidade. Vocês são minhas parceiras de vida, ponta firme sempre. Sou a última do trio a ser doutora, mas represento com muita responsa haha muito obrigada por me escutar, me aconselhar, colocar meus pés no chão de vez em quando e por estarem presentes em momentos bons e ruins da minha vida. Amo vocês.

Gostaria de agradecer a minha família, minhas três irmãs «Ana Cláudia, Roberta e Isabella», ao meu compadre «Erich», e aos meus companheiros de vida «Marcelo e nosso filhote Miguel». É muito gostoso compartilhar a vida com vocês. Obrigada por ser suporte, por ser amor, minhas risadas e companhia de todos os dias. Fui muito feliz de estar em casa com vocês e terminar a redação da tese de um modo leve e saudável próximo de quem eu amo.

Eu dedico essa tese com todo o meu amor a minha mãe, que se foi no final desse processo. Minha mãe foi a minha rede de apoio incondicional, minha referência de mulher, minha base, meu suporte em momentos de indecisão, me cuidou tanto. Eu sinto muita saudade, mãe. E o que eu mais queria na vida é que visse eu terminar o doutorado, infelizmente não foi possível. Mas eu fiz. Terminei. E dedico do fundo do meu coração para você.

RESUMO

Copépodes têm um papel central na bomba biológica de carbono e no funcionamento dos oceanos globais. Sua notável diversidade taxonômica levanta questões sobre os mecanismos que permitem a coexistência de espécies e o papel dessa alta diversidade no funcionamento da comunidade. A diversidade de copépodes pode ser dividida em múltiplas facetas que incluem uma ampla gama de características morfológicas, histórias de vida, hábitos tróficos, comportamentais, distribuições verticais e geográficas. Assim, os copépodes epipelágicos são um modelo interessante para estudar como as condições ambientais moldam traços funcionais, o acoplamento de grupos funcionais a mecanismos ecológicos, e como o tamanho corporal, que é considerado o principal traço funcional, varia ao longo do gradiente latitudinal do Atlântico Sul ao Oceano Antártico. Os objetivos específicos foram: (1) identificar diferentes grupos funcionais de copépodes no Oceano Atlântico Sul e Oceano Antártico (Capítulo I), (2) identificar se os grupos funcionais são diferentes ao longo do gradiente latitudinal e zonas biogeográficas (Capítulo I), (3) modelar a estrutura de tamanho da comunidade de copépodes em relação as variáveis ambientais ao longo do gradiente latitudinal (Capítulo II), (4) discutir os padrões macroecológicos de diversidade funcional e estrutura de tamanho de copépodes pelágicos e os mecanismos ecológicos associados à biodiversidade e funcionamento do ecossistema (Capítulo I e II). Nossa hipótese é que comunidades com maior riqueza de espécies suportam alta riqueza funcional e ambas devem diminuir em direção aos polos. Além disso, testamos a tendência geral de que o tamanho do corpo de copépodes, em nível de família, seguirá a regra de Bergmann, com tamanhos maiores em direção às regiões polares. Nossos resultados permitiram descrever pela primeira vez em larga escala os grupos funcionais de copépodes do Atlântico Sul. A diversidade funcional de aproximadamente 100 espécies de copépodes mostrou como as condições ambientais controlam a distribuição dos diferentes grupos e, portanto, potencialmente a expressão das funções que eles fornecem, ou seja, a relação da biodiversidade e o funcionamento do ecossistema (BEF). Mecanismos ecológicos destacaram o papel da complementariedade funcional na estrutura da comunidade de copépodes. Espécies de hábitos alimentares carnívoros e detritívoros, ao contrário de espécies com hábitos omnívoros-herbívoros, diminuem ao longo do gradiente latitudinal, levando a uma queda substancial na riqueza funcional polar. No entanto, o tamanho médio de copépodes aumentou ao longo do gradiente latitudinal, ou seja, com a diminuição da temperatura e aumento do oxigênio. A resposta do tamanho corporal de copépodes ao longo do gradiente latitudinal teve uma forte assinatura taxonômica. De forma geral, o aumento da abundância de copépodes grandes pertencente à família Calanidae impulsionou esse padrão de aumento na região temperada e polar. Por outro lado, copépodes pequenos foram extremamente importantes em termos de abundância e biomassa principalmente em regiões tropicais e subtropicais, porém apresentaram pouca ou nenhuma variação de tamanho ao longo do gradiente latitudinal. A estabilidade de tamanhos médios dessas populações, juntamente com seus amplos nichos ambientais, pode ser uma característica proeminente nos ecossistemas do Oceano Atlântico Sul e Oceano Antártico. Além disso, a modelagem do tamanho corporal, em nível de família, mostrou que cada família responde de maneira diferente ao gradiente térmico e a outros fatores ambientais projetados, demonstrando as contribuições relativas de diferentes estratégias de história de vida. Finalmente, grupos funcionais de copépodes não apenas aprofundam nossa compreensão do funcionamento dos ecossistemas pelágicos a partir da abordagem de índices de diversidade funcional, mas também melhorarão a representação de famílias de copépodes em estudos sobre o papel da estrutura de tamanho do zooplâncton em modelos regionais e globais.

Palavras-chave: biodiversidade, funcionamento do ecossistema, traços funcionais, Regra de Bergmann, gradiente de temperatura, Copepoda

ABSTRACT

Copepods play a central role in the biological carbon pump and the functioning of the global oceans. Their remarkable taxonomic diversity raises questions on the mechanisms enabling species coexistence and the role of this high diversity in community functioning. Copepod diversity can be divided into multiple facets that include a wide array of morphological features, life histories, trophic habits, behaviors, vertical and geographic distributions. Thus, epipelagic copepods have emerged as an interesting model to study how environmental conditions shape functional traits, the coupling of functional groups to ecological mechanisms, and how body size, which is considered a master trait, varies along the latitudinal gradient of South Atlantic to the Southern Ocean. The specific goals were: (1) to identify different functional groups of copepods in the South Atlantic Ocean and Southern Ocean (Chapter I), (2) to identify whether the functional groups are different along the latitudinal gradient and biogeographic zones (Chapter I), (3) model the size structure of the copepod community in relation to environmental variables along the latitudinal gradient (Chapter II), (4) discuss the macroecological patterns of functional diversity and size structure of pelagic copepods, and the ecological mechanisms associated with the biodiversity and ecosystem functioning (Chapters I and II). We hypothesize that species-rich communities support high functional richness and both should be conversely lower poleward than in tropical waters. Furthermore, we tested the general trend that the body size of copepods, at the family level, will follow Bergmann's rule, with increasing contribution of larger copepods poleward. Our results allowed us to describe for the first time the copepod functional groups of South Atlantic. The functional diversity of approximately 100 species of copepods showed how environmental conditions control the distribution of the different groups and, therefore, potentially the expression of the functions they provide, i.e. the relationship between biodiversity and ecosystem functioning (BEF). Ecological mechanisms have highlighted the role of functional complementarity in the structure of the copepod community. Copepod species with carnivorous and detritivorous trophic groups, unlike species with omnivorous-herbivorous habits, decrease along the latitudinal gradient, leading to a substantial drop in polar functional richness. However, the average size of copepods increased along the latitudinal gradient, that is, with decreasing temperature and increasing oxygen. The body size response of copepods along the latitudinal gradient had a strong taxonomic signature. In general, the increase in the abundance of large copepods belonging to the family Calanidae enhanced the increasing pattern of body size towards the temperate and polar regions. On the other hand, small copepods were extremely important in terms of abundance and biomass mainly in tropical and subtropical regions, but showed little or no size variation along the latitudinal gradient. The stability of populations with small average sizes, together with their wide environmental niches, may be a prominent feature in the ecosystems of the South Atlantic Ocean and Southern Ocean. Furthermore, modeling the family level average body size showed that each family responds differently to the thermal gradient, and to other projected environmental factors, demonstrating the relative contributions of different life history strategies. Finally, copepod functional groups will not only deepen our understanding of the pelagic ecosystem functioning applying the functional diversity approach, but will also improve the representation of copepod families in studies on the role of zooplankton size structure in regional and global models.

Keywords: Biodiversity, Ecosystem functioning, Functional traits, Bergmann's Rule, Temperature gradient, Copepoda

LISTA DE FIGURAS

Introdução geral

Figura 1 – Modelo conceitual do espaço funcional e seleção de traços funcionais ao longo do gradiente ambiental. Os pontos representam os valores de traços funcionais hipotéticos. Espécies que correspondem a combinação de traços similares são consideradas uma entidade funcional, que estão ordenadas no plano do espaço (n) em função dos traços. Combinações de traços se distribuem ao longo do gradiente ambiental selecionando grupos funcionais, que são identificados através da análise de agrupamento hierárquico.....15

Figura 2 – Distribuição da riqueza de espécies global de copépodes planctônicos, 4 mostrando o número total de espécies e a porcentagem em cada bacia oceânica em relação 5 ao pool de espécies global. A ligação entre regiões geográficas mostra o número de 6 espécies compartilhada entre as regiões. Dados obtidos em: Razouls et al., (2005-2021).....21

Capítulo I

Figure 1 – South Atlantic and Southern Ocean circulation, sampling stations and SST satellite image based on the average records from October 2010 to January 2011. The sampling stations are depicted by different colors, according to the six biogeographic zones.....29

Figure 2 – Violin plots of the environmental variables throughout the different biogeographic zones, from 12° to 64°S, in the South Atlantic and Southern Ocean. It highlights the distribution ranges, the outliers and, the relation of the different variables with each other. Its width is related to the frequency of data. TRJ: Tropical Rio de Janeiro; TSC: Tropical Santa Catarina.....35

Figure 3 – Variation in species richness (SR; A, B), functional richness (FRic; C, D), evenness (FEve; E, F), divergence (FDiv; G, H), and dispersion (FDis; I, J) of copepod community among the six biogeographic zones. Significant differences between biogeographic zones revealed by ANOVA and the Scott-Knott clustering algorithm was used to multiple comparisons (all $p \leq 0.05$, except FDiv) illustrated by the letters (a,b,c,d). Generalized Least Squares (GLS) model and a t -test pair-wise comparisons was applied only for FEve (see Methods). Points show the mean index value of each biogeographic zone. Biogeographic zones sharing a letter are not significantly different ($P < 0.05$), those not sharing a letter are significantly different.....37

Figure 4 – Multidimensional trait space occupied by copepod community in six biogeographic zones in the Southwestern Atlantic and Southern Ocean (12°-64°S). **A** Geographic location of the six biogeographic zones depicted in the sampling area (Fig. 1). **B** Functional space of the species pool ($n = 94$; PCoA biplot), with colored polygon indicating the biogeographic zones: tropical gyre (red), tropical Rio de Janeiro (pink), tropical Santa Catarina (orange), subtropical (yellow), temperate (light blue), and polar (dark blue). Each point represents a species and is colored according to the biogeographic zones, while each gray cross represents species absence therein. **C** Bubble sizes are

proportional to species abundance in the functional space. Copepod shapes were chosen to illustrate the main abundant genera. **D** Barplots show copepod functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), and functional dispersion (FDis).....39

Figure 5 – Copepod functional groups in the RLQ analysis based on the covariation between traits (size, trophic group, foraging behavior, myelination and reproduction mode) and environmental variables (temperature, oxygen, silicate, dissolved inorganic nitrogen (NID), chl-a at DCM) among the 94 copepod species of the Southwestern Atlantic and Southern Ocean. UPGMA hierarchical clustering was defined in the functional dendrogram and the best partition of groups A-D is presented by distinct colors (see Fig. S1). In detailed, functional space with trait vectors (upper right) and with functional groups (lower right). Copepod shapes were chosen to illustrate the position of the main copepod genera in the functional space.....40

Figure 6 – RLQ biplot showing the correlation between environmental variables (R-Table 5 x 30) and trait attributes (Q-Table 94 x 5), constrained by species abundance (L-Table 30 x 94). Clustered points identify functional groups (A-D, Fig. 5). Each point represents the species or subgroup of species (species in the same level of similarity) position on the RLQ Axis 1 and 2. Stations are plotted accordingly to the different biogeographic zones. Barplots and the boxplot represent the trait contribution within each functional group.....41

Figure 7 – Schematic illustration of the oceanographic conditions and the major functional traits related to ecological mechanisms, that can explain the relationship between copepods functional diversity and ecosystem functioning in the South Atlantic Ocean and Southern Ocean.....45

Figure S1 – The optimal number of clustering groups determined via Calinski and Harabasz's index in the functional dendrogram of the relation between five functional traits and five environmental variables using average linkage clustering of 94 copepod species.....51

Capítulo II

Figure 1 – South Atlantic and Southern Ocean circulation, including some of the key oceanographic features and its connection to the neighboring basins (adapted from Peterson & Stramma,1991; Stramma & England, 1999; Garzoli & Matano, 2011; Villar et al., 2015; Campos et al., 2017). A map of the South Atlantic bathymetry and the sampling stations from *TARA Oceans* and *Cruzeiro do Sul* expeditions is detailed. The stations here considered as representative of the main basins are (i) TARA_073 to TARA_080 for the South Atlantic Ocean, and (ii) TARA_082 to TARA_089 for the Southern Ocean. BC: Brazil Current; SCZ: Subtropical Confluence Zone; SAW: Subantarctic Water; ACC: Antarctic Circumpolar Current.....80

Figure 2 – (a) Surface temperature (°C), (b) salinity, (c) oxygen (mg l⁻¹) and (d) deep chlorophyll-a maximum (mg m⁻³) along the latitudinal gradient of the South Atlantic and Southern Ocean (13°-64°S). Black ellipses in temperature values delimits the

oceanographic features considered in this study. BC: Brazil Current; SCZ: Subtropical Confluence Zone; SAW: Subantarctic Water; ACC: Antarctic Circumpolar Current.....84

Figure 3 – Copepod imaged with the ZooScan System. A representative collection of copepod families from the South Atlantic and Southern Ocean. Scale bar: 1 mm.....85

Figure 4 – Relative abundance and biomass of the main copepod families and life stages along the latitudinal gradient in the South Atlantic and Southern Ocean (13°-64°S).....86

Figure 5 – Body size frequency distribution of copepod families, both copepodite and adult, along the latitudinal gradient of the South Atlantic and Southern Ocean (13°-64°S).....87

Figure 6 – (a) Individual body size, (b) mean family and (c) community body size of the copepod community along the latitudinal gradient in the South Atlantic and Southern Ocean (13°-64°S). Circles are displayed over a designated geographical region with the size and color proportional to its value in the sampling station.....88

Figure 7 – Mean body size (ESD mm, dots) of copepod families along the temperature (°C) gradient in the South Atlantic and Southern Ocean (13°-64°S). Solid lines represent the fitted values (\pm 95% CI, colored shading) predicted for each family from GLMM models. Respective *p* values are shown in the top left corners. Note that the y-axis scale is different among the families, given the various body size ranges.....89

Figure 8 – Mean body size (ESD mm, dots) of copepod families along the oxygen (mg l^{-1}) gradient in the South Atlantic and Southern Ocean (13°-64°S). Solid lines represent the fitted values (\pm 95% CI, colored shading) predicted for each family from GLMM models. Respective *p* values are shown in the top left corners. Note that the y-axis scale is different among the families, given the various body size ranges.....90

Figure 9 – Mean body size (ESD mm, dots) in copepod families along the deep chlorophyll-*a* maximum (mg l^{-3}) gradient in the South Atlantic and Southern Ocean (13°-64°S). Solid lines represent the fitted values (\pm 95% CI, colored shading) predicted for each family from GLMM models. Respective *p* values are shown in the top left corners. Note that the y-axis scale is different among the families, given the various body size ranges.....91

Figure S1 – Relative copepod abundance according to the life stages along the latitudinal gradient of the South Atlantic and Southern Ocean (13°-64°S).....96

Figure S2 – Body size frequency distribution of the main copepod families and life stages along the latitudinal gradient in the South Atlantic and Southern Ocean (13°-64°S).....97

Figure S3 – Abundance (ind.m^{-3}) of the main copepod families along the latitudinal gradient in the South Atlantic and Southern Ocean (13°-64°S). Circles are displayed over a designated geographical region with the size and color proportional to its value in the sampling station.....97

Figure S4 – Biomass ($\mu\text{gC m}^{-3}$) of the main copepod families along the latitudinal gradient in the South Atlantic and Southern Ocean (13°-64°S). Circles are displayed over

a designated geographical region with the size and color proportional to its value in the sampling station.....98

Figure S5 – Mean body size (ESD mm, dots) of copepod families along the salinity gradient in the South Atlantic and Southern Ocean (13°-64°S). Solid lines represent the fitted values (\pm 95% CI, colored shading) predicted for each family from GLMM models. Respective *p* values are shown in the top left corners. Note that the y-axis scale is different among the families, given the various body size ranges.....98

LISTA DE TABELAS

Capítulo I

Table S1 – Main features of the sampling design in the different expeditions.....	52
Table S2 – Functional traits of the 94 selected copepod species from the South Atlantic and Southern Ocean. References are listed in the supplemental table S7. Body size represents the average adult female body length.....	52
Table S3 – Species with trait gaps not included in the statistical analysis. NA: not available. Body size: mean female size.....	55
Table S4 – Copepod species mean (\pm standard deviation) abundances and presence (1) or absence (0) in the different biogeographic zones. TGY: Tropical gyre; TRJ: Tropical Rio de Janeiro; TSC: Tropical Santa Catarina; SUB: Subtropical; TEM: Temperate; POL: Polar. Abundant species are highlighted in bold.....	56
Table S5 – Species and functional indices in the different biogeographic zones – mean (\pm standard deviation).....	59
Table S6 – RLQ axes correlations with each environmental variable. DCM: depth chlorophyll-a maximum. NID: dissolved inorganic nitrogen.....	60
Table S7 – Results of standard effect sizes (SES) based on the null model for functional richness. ns.: non significant; ***: $P < 0.05$	60
Table S8 – Copepod trait references.....	61

Capítulo II

Table S1 – Generalized linear mixed model (GLMM) accounting the effects of the Temperature ($^{\circ}\text{C}$), Salinity, Oxygen (mg.l^{-1}) and Chlorophyll-a (mg.m^{-3}) on mean body size (ESD mm) within different copepod families along the latitudinal gradient in the South Atlantic and Southern Ocean (13° - 64°S). Models also accounted the different life stages (adult and copepodite) as random effects.....	99
Table S2 – Competing models selection using the ranked Akaike's Information Criterion (AIC) in GLMM analysis. The models accounted the effects of environmental variables on mean body size (ESD mm) within different copepod families along the latitudinal gradient in the South Atlantic and Southern Ocean (13° - 64°S). Models also accounted the different life stages (adult and copepodite) as random effects. *: interaction.....	100

SUMÁRIO

1 INTRODUÇÃO GERAL	13
1.1 TRAÇOS FUNCIONAIS NA PESQUISA DO PLÂNCTON	13
1.2 DIVERSIDADE FUNCIONAL DE COPÉPODES E OS MECANISMOS ECOLÓGICOS	14
1.3 O TAMANHO COMO O PRINCIPAL TRAÇO FUNCIONAL	17
1.4 FATORES QUE CONTRIBUEM PARA OS PADRÕES DE BIODIVERSIDADE PELÁGICA EM GRANDE ESCALA NO OCEANO ATLÂNTICO	19
1.5 HIPÓTESE GERAL.....	21
1.6 OBJETIVO GERAL	22
1.7 HIPÓTESES ESPECÍFICAS.....	22
1.8 OBJETIVOS ESPECÍFICOS	22
1.9 ESTRUTURA DA TESE	23
2 INTRODUÇÃO AO CAPÍTULO I	24
3 CAPÍTULO I.....	25
4 TRANSIÇÃO PARA O CAPÍTULO II.....	74
5 CAPÍTULO II	75
6 CONCLUSÃO	108
7 DIVULGAÇÃO CIENTÍFICA.....	111
8 ANEXO I.....	113
8.1 LISTA DE MANUSCRITOS EM PREPARAÇÃO, SUBMETIDOS E PUBLICADOS	113
8.2 LISTA DE COMUNICAÇÕES CIENTÍFICAS	113
8.3 MÍDIAS SOCIAIS E WEBSITE.....	114
8.4 GRANTS DE PESQUISA.....	114
9 REFERÊNCIAS.....	116

1 INTRODUÇÃO GERAL

1.1 TRAÇOS FUNCIONAIS NA PESQUISA DO PLÂNCTON

Nos últimos 40 anos, as imagens *in situ* e laboratoriais de organismos do plâncton se desenvolveram rapidamente (Ortner et al., 1979; Davis et al., 1992; Benfield et al., 2007; Gorsky et al., 2010, Picheral et al., 2010; Ohman et al., 2018) e provou seu potencial de descrever a distribuição de organismos planctônicos em escalas e resoluções espaço-temporais anteriormente inacessíveis (Sieracki et al., 2010). Dispositivos de imagem de plâncton são atualmente bastante variados e oferecem uma ampla gama de possibilidades técnicas e ecológicas: amostras preservadas e vivas, medições laboratoriais e *in situ*, *snapshots* ou gravação contínua de vídeo, imagens coloridas ou escala em cinza, e holografia (Benfield et al., 2007, Lombard et al., 2019). Cada ferramenta é limitada a uma porção específica do espectro de tamanho do plâncton. A combinação dessas modalidades permite aos ecologistas aquáticos estudar todo o espectro das comunidades planctônicas e fornecer uma visão holística do ecossistema planctônico (Stemmann & Boss, 2012, Romagnan et al., 2015, Lombard et al., 2019). Esses sistemas de imagem permitem a estimativa simultânea da estrutura taxonômica de uma comunidade e a medição das características morfológicas de organismos individuais. A quantidade e qualidade de dados registrados aumentou imensamente, devido a melhorias na instrumentação e desenvolvimentos no pós-processamento de imagens, projetando a comunidade oceanográfica em uma nova era de riqueza de dados. Além disso, o uso de técnicas de imagem em amostras de plâncton preservadas em redes ou garrafas deu aos cientistas a oportunidade de revisitar arquivos históricos (García-Comas et al., 2011, Peacock et al., 2014).

Abordagens baseadas em traços funcionais que descrevem ecossistemas de plâncton foram desenvolvidas em paralelo com avanços em sistemas de imagem (Litchman & Klausmeier, 2008, Litchman et al., 2013, Kiørboe et al., 2018, Martini et al., 2021). Em vez de considerar a identidade taxonômica de um organismo, a abordagem funcional os caracteriza por sua combinação de traços funcionais – características de organismos que impactam sua aptidão por meio da aquisição de recursos, crescimento, reprodução e sobrevivência (Violle et al., 2007). A informação de traços transcende os táxons e pode ter várias vantagens sobre a informação taxonômica: (i) os organismos são distribuídos no ambiente principalmente de acordo com seus traços; (ii) as funções do ecossistema dependem dos traços dos organismos constituintes; e (iii) embora os

ecossistemas marinhos são habitados por uma miríade de espécies (de Vargas et al., 2015), os principais traços que transcendem os táxons são poucos (Martini et al., 2021). Descrições baseadas em traços, portanto, têm o potencial de encapsular a complexidade dos ecossistemas marinhos em um número conciso de métricas (Kjørboe et al., 2018).

1.2 DIVERSIDADE FUNCIONAL DE COPÉPODES E OS MECANISMOS ECOLÓGICOS

O uso da abordagem funcional tem se mostrado cada vez mais eficiente para o entendimento dos padrões de biodiversidade, pela intrínseca relação dos traços funcionais com o ambiente que os seleciona (Quesado, 2017). Existe uma relação na qual os níveis de biodiversidade influenciam o funcionamento geral do ecossistema (BEF) (Walker, 1992; Jones & Lawton, 1995; Johnson et al., 1996). Em um ecossistema, indivíduos e espécies fornecem contribuições únicas para diferentes processos ecológicos de acordo com seu conjunto particular de características e, muitas vezes, influenciando vários processos ao mesmo tempo. Altos níveis de biodiversidade ajudam a sustentar um grande número de processos do ecossistema, melhorando o funcionamento e a produtividade geral do ecossistema. Declínios na biodiversidade podem reduzir o funcionamento do ecossistema, diminuindo suas provisões de bens e serviços. Embora os cientistas tenham observado os processos do ecossistema afetados negativamente pelos declínios da biodiversidade, nem sempre é esse o caso. Uma correlação depende do processo considerado e dos indivíduos e espécies envolvidos. Além da diversidade, a composição específica de uma assembleia de organismos influencia o sucesso dos processos ecológicos (Hooper et al., 2005). As relações entre BEF são de interesse crescente no campo da ecologia, especialmente por causa da urgência da crise da biodiversidade e até que ponto a perda de biodiversidade afetará processos ecológicos essenciais para o funcionamento do ecossistema.

A diversidade funcional é geralmente medida como grupos funcionais ou índices. Grupos funcionais são grupos de espécies ecologicamente semelhantes e podem ser definidos a priori ou a posteriori baseado em dendrogramas (Fig. 1) (Pla et al., 2012). Índices são valores calculado com base nas características funcionais presentes na comunidade. Vários índices funcionais foram propostos: riqueza funcional, uniformidade funcional, divergência funcional, dispersão funcional, redundância funcional, entre outros (Petchey & Gaston, 2002; Laliberté & Legendre, 2010; Mason et al., 2005). Todas as

abordagens, dependem da seleção de traços funcionais (Leps^ˇ et al., 2006; Poos et al., 2009). Para que uma medida de diversidade funcional seja ecologicamente relevante, os traços utilizados devem refletir os processos ecológicos de interesse (Rosado et al., 2013), sejam assembleia de comunidades (*community assembly*; Pavoine & Bonsall, 2011) ou funções do ecossistema (Cadotte et al., 2011). Esta abordagem explica que os traços específicos de um organismo dentro de um ecossistema as configuram para papéis funcionais específicos que dão suporte ao funcionamento geral do ecossistema.

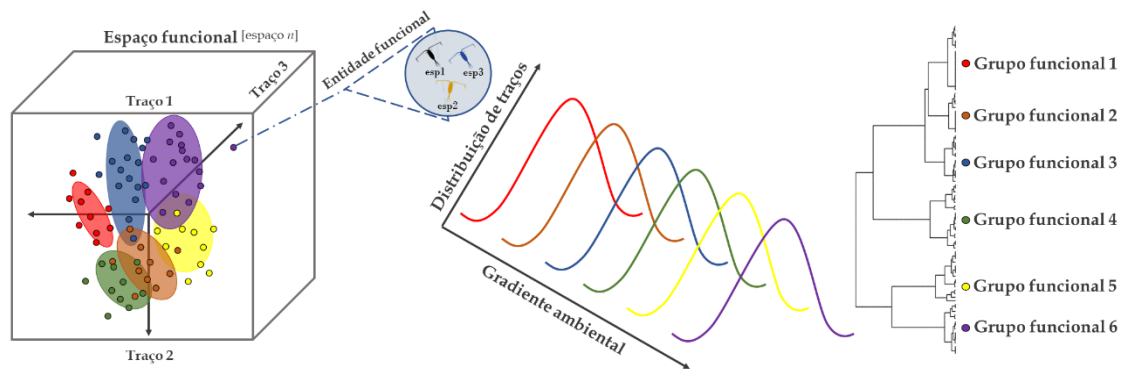


Figura 1: Modelo conceitual do espaço funcional e seleção de traços funcionais ao longo do gradiente ambiental. Os pontos representam os valores de traços funcionais hipotéticos. Espécies que correspondem a combinação de traços similares são consideradas uma entidade funcional, que estão ordenadas no plano do espaço (n) em função dos traços. Combinações de traços se distribuem ao longo do gradiente ambiental selecionando grupos funcionais, que são identificados através da análise de agrupamento hierárquico.

Os traços funcionais do zooplâncton são fortemente regulados pelas condições ambientais em escalas local e global (Barton et al., 2013, Brun et al., 2016). Características como tamanho do corpo, hábitos alimentares e comportamentos de acasalamento, bem como capacidades de dispersão, desempenham papéis importantes nas funções ecológicas do zooplâncton (Litchman et al., 2013) e, assim, determinam a resposta potencial às mudanças climáticas atuais e futuras no oceano (Benedetti et al., 2018). Além disso, a abordagem funcional do zooplâncton tem sido aplicada para investigar processos ecológicos, como a perturbação antrópica em estuários e na influência da pluma amazônica no Atlântico Tropical (Veríssimo et al., 2017, Neumann Leitão et al., 2018, Neumann Leitão et al., 2019), a crescente tropicalização das assembleias de copépodes no Mar Mediterrâneo (Benedetti et al., 2018), e a significativa expansão em direção ao pólo de copépodes carnívoros em detrimento dos herbívoros em altas latitudes (McGinty et al., 2021). Como resultado, relações complexas entre traços e

ambiente mantêm a diversidade e a estrutura da comunidade, e certas combinações de traços são selecionados sob gradientes ambientais.

As assembleias de copépodes têm um papel central na bomba biológica de carbono e no funcionamento dos oceanos globais (Steinberg & Landry, 2017). Sua notável diversidade taxonômica levanta questões sobre os mecanismos que permitem a coexistência de espécies e o papel dessa diversidade no funcionamento da comunidade. A diversidade de copépodes pode ser dividida em múltiplas facetas que incluem uma ampla gama de características morfológicas, histórias de vida, hábitos tróficos, comportamentos, distribuições verticais e geográficas (Kiørboe, 2011, Hébert et al., 2017). Assim, os copépodes planctônicos surgiram como um modelo interessante para estudar como as condições ambientais moldam características funcionais e o acoplamento de grupos funcionais a mecanismos ecológicos (Barton et al., 2013; Benedetti et al., 2018b).

A enorme diversidade de espécies mostrada pelo plâncton, especialmente copépodes, intriga os ecologistas há décadas. A exclusão competitiva, ou seja, o domínio de poucas espécies mais adaptadas, não se aplica a um ambiente não estruturado e homogêneo como o habitat planctônico, sendo esta é a principal questão introduzida pelo renomado artigo '*O paradoxo do plâncton*' por Hutchinson (Hutchinson, 1961). As observações experimentais explicaram o paradoxo, sugerindo que a coexistência estável de espécies distintas no mesmo nível trófico é um resultado provável de processos de competição de recursos (Tilman, 1977, 1990). No entanto, pode ocorrer o acréscimo de espécies sem alteração das funções existentes ocorrendo a redundância funcional, que é o resultado da interação entre competição e complementariedade entre as espécies coexistentes. Em gradientes latitudinais, devido a maior heterogeneidade ambiental, a complementariedade das espécies entre as regiões biogeográficas aumenta as funções dos ecossistemas gradualmente com o aumento de novas espécies (Dolédec & Bonada, 2013). Neste contexto, aproximadamente 500 táxons são conhecidos no Golfo de Nápoles e a maioria deles tem papéis ecológicos aparentemente semelhantes (Mazzocchi et al., 2012; Piredda et al., 2017). Hoje em dia sabemos que uma elevada redundância funcional ao nível da comunidade não é incomum por natureza (Lefcheck et al., 2015), pode surgir mesmo em condições ambientais estáveis, e seu principal papel ecológico é garantir a sobrevivência de grupos funcionais em caso de extinção de espécies (Rosenfeld, 2002).

Os efeitos de complementariedade estão relacionados ao aprimoramento de um processo de ecossistema pela riqueza de espécies. Deste modo, as diferentes espécies se

facilitam ou se complementam, e a soma da contribuição complementar de cada espécie é maior do que a de uma única espécie. Quando as interações entre as espécies são facilitadoras, ao invés de complementares, seu desempenho coletivo é maior do que se fosse simplesmente aditivo. Por outro lado, o mecanismo ecológico de partição de nicho envolve um efeito de complementaridade resultante de interações facilitadoras. Este mecanismo ocorre quando espécies diferentes ocupam nichos únicos, ou tipos de habitat, dentro de um ambiente de forma complementar para que o uso de recursos coletivos seja, em última instância, potencializado. Comunidades com mais espécies podem utilizar um maior número de oportunidades de nicho disponíveis em um ambiente do que comunidades com menos espécies e, como resultado, essas comunidades diversas podem capturar mais recursos biológicos ativos.

1.3 O TAMANHO COMO O PRINCIPAL TRAÇO FUNCIONAL

A estrutura de tamanho de toda a comunidade de organismos é reconhecida como uma propriedade estruturante que explica a organização e o funcionamento das redes tróficas desde o início dos anos 1970 (Sheldon et al., 1972). O tamanho individual é um traço funcional que pode ser medido facilmente a partir de imagens e é utilizado para apoiar abordagens taxonômicas, uma vez que muitas espécies com formas corporais semelhantes são frequentemente discriminadas por suas distribuições de frequência de tamanho (Parent et al., 2011). Além disso, o tamanho do corpo individual é descrito como o traço de escalonamento de processos fisiológicos, tróficos e de história de vida, como metabolismo, desenvolvimento, alimentação e mobilidade (Platt & Denman, 1978; Hansen et al., 1994; Litchman et al., 2013; Blanchard et al., 2017). Os organismos planctônicos desempenham funções ecológicas distintas de acordo com seu tamanho e como (em termos de manuseio e eficiência) convertem alimentos em energia (respiração), sua própria biomassa ou material exportado disponível para outros níveis tróficos (Moreno-Ostos et al., 2015; García-Comas et al., 2016; Guidi et al., 2016). Tamanho, é na verdade, uma característica que transcende as escalas de organização dos sistemas biológicos, desde o indivíduo até todo o ecossistema por meio de relações alométricas que envolvem todas as funções biológicas (Litchman et al., 2013). Por isso, é muitas vezes referido como um “*master trait*”.

As descobertas recentes relacionadas às mudanças climáticas revitalizaram o interesse na relação entre o tamanho do corpo e a temperatura (Sommer et al., 2017), uma

vez que o aumento da temperatura pode selecionar tamanhos corporais menores (Daufresne et al., 2009, Beaugrand et al., 2010, Campbell et al., 2021). Conseqüentemente, isso afetará a influência que a estrutura de tamanho de comunidades marinhas exerce sobre a produtividade da pesca regional e a eficiência de transporte do carbono vertical (Beaugrand & Kirby, 2010; Bi et al., 2011). Regras ecogeográficas de décadas atrás postulam gradientes latitudinais de tamanho corporal, de modo que é esperado que espécies nos trópicos tenham tamanhos de corpo menores do que suas contrapartes em latitudes mais altas (Bergmann, 1847). Originalmente restrita aos homeotérmicos, a regra de Bergmann propõe que o padrão é pensado para resultar da seleção favorecendo tamanhos maiores em ambientes mais frios, o que minimiza a perda de calor através das superfícies do corpo, reduzindo as relações superfície/volume e dando-lhes uma vantagem energética em ambientes frios (Salewski & Watt, 2017). No entanto, foi demonstrado que se aplica amplamente a ectotérmicos, mas através de mecanismos diferentes.

Para a grande maioria dos animais ectotérmicos (83,5%), a relação entre a temperatura é particularmente importante e difundida nas diferenças de tamanho (Atkinson, 1994), visto que a diminuição da temperatura é o principal fator de aumento do tamanho corporal em crustáceos marinhos ao longo de gradientes latitudinais e de profundidade (Timofeev, 2001). As comunidades zooplânctônicas apresentam maior tamanho e abundância em direção aos polos e regiões tropicais de ressurgência, um padrão que é amplamente impulsionado pelos copépodes (San Martín et al., 2006, Brandão & Benedetti et al., 2021). A força da resposta temperatura-tamanho em copépodes é dependente de mudanças sazonais na densidade de espécies dominantes, com reduções cerca de 3% a 10% da massa de carbono $^{\circ}\text{C}^{-1}$ (Corona et al., 2021). Conseqüentemente, a base da relação global interespecífica temperatura-tamanho dos copépodes é apoiada pela dominância de grandes Calanidae que impulsionam o aumento latitudinal do tamanho médio em direção aos pólos (Evans et al., 2020, Brandão & Benedetti et al., 2021), onde eles são bem conhecidos por aumentar a produção de níveis tróficos mais altos devido ao maior teor lipídico (Record et al., 2018). Por outro lado, pequenos onívoro-carnívoros Cyclopoida (ou seja, Oithonidae, Oncaidae e Corycaidae) seguem o padrão oposto e aumentam de tamanho dos pólos para os trópicos (Brandão & Benedetti et al., 2021).

A resposta do tamanho corporal a gradientes ambientais pode variar entre e dentro de grupos taxonômicos, pois diferentes tamanhos corporais podem estar associados a

diferentes estratégias ecofisiológicas adotadas pelos organismos para lidar com o ambiente (Ackerly & Cornwell, 2007). As características adaptativas dos copépodes que causam sua dominância incluem a forma hidrodinâmica do corpo, suas capacidades musculares e sensoriais, que os tornam altamente eficientes em atacar presas e escapar de predadores, e sua capacidade de detectar parceiros remotamente (Kiorboe, 2011). As estratégias de alimentação também desempenham um papel significativo em ditar a magnitude das respostas temperatura-tamanho sazonais em copépodes, ao qual é negativa em aproximadamente 90% das espécies de copépodes e exibem uma redução quatro vezes maior da massa corporal adulta por °C em copépodes calanóides que se alimentam através de correntes de alimentação em comparação a ciclopóides de alimentação de emboscada (Horne et al., 2016). Essas descobertas recentes destacam que, embora os gradientes latitudinais no tamanho corporal tenham sido aplicados igualmente a toda a comunidade de copépodes (Campbell et al., 2021), isso pode não ser necessariamente o caso devido a diferenças biológicas fundamentais entre as populações com diferentes estratégias de história de vida em resposta a gradientes ambientais e pode modificar as respostas espaço-temporais de organismos planctônicos ao aquecimento climático (Evans et al., 2020).

1.4 FATORES QUE CONTRIBUEM PARA OS PADRÕES DE BIODIVERSIDADE PELÁGICA EM GRANDE ESCALA NO OCEANO ATLÂNTICO

O Oceano Atlântico é um pilar da economia marítima global. Estima-se que o valor anual acrescentado pela economia marítima atlântica dos países que fazem fronteira nos últimos 20 anos ultrapassa os 400 bilhões de dólares (Ecorys, 2014), o que corresponde a ~30% do valor agregado pela economia marítima para o mesmo período à escala global (~1500G\$), com um aumento contínuo esperado (OECD, 2016).

O Oceano Atlântico também é um componente chave do sistema terrestre. A convecção do Atlântico Norte é o gatilho da circulação meridional (Marshall et al., 2012), componente fundamental do sistema climático. Os nutrientes limitantes primários exibem variações latitudinais, que afetam a estrutura das cadeias alimentares enquanto sustentam florações de fitoplâncton com um forte impacto nos estoques de peixes (Pershing et al., 2020). A dinâmica física interna e forçantes em larga escala produzem um regime bem documentado de mudanças na bacia do Norte, até agora, mas provavelmente afetando toda a bacia, com consequências sobre os recursos bióticos (Reid et al., 2003). Os processos biogeoquímicos impulsionam mais de 30% da redução global de CO₂

atmosférico nos oceanos, com uma possível diminuição nas próximas décadas (Barange et al., 2017). Séries temporais são essenciais para avaliar o efeito de longo prazo das mudanças climáticas nas comunidades planctônicas. O *Continuous Plankton Recorder* (CPR) é o único programa de monitoramento científico desse tipo no mundo, sem nenhum programa equivalente existente. Abrange uma importante escala de tempo, de 1948 até o presente, ainda ativa, com uma grande escala espacial cobrindo todo o Oceano Atlântico Norte e seus mares adjacentes (Kléparsi et al., 2021), sendo considerado “o mais extenso levantamento de longo prazo de organismos marinhos do mundo” (Reid et al., 2003). No entanto, nossa compreensão dos efeitos das mudanças climáticas antropogênicas na biodiversidade atlântica e nas funções dos ecossistemas associadas permanece muito assimétrica em comparação ao hemisférico norte e sul. Existe uma grande lacuna de informações no Atlântico Sul, devido à falta de monitoramento contínuo.

Um inventário de 2692 espécies marinhas de copépodes planctônicos em todos os oceanos e mares do mundo, foi estabelecido a partir do trabalho de Giesbrecht (1892) até o momento. Metade da riqueza taxonômica global de copépodes está registrada na bacia Atlântica – 53%, 1348 espécies (Fig. 2; Razouls et al., 2005-2021). Entre as 25 zonas geográficas arbitrariamente definidas, o número de formas inventariadas é máximo para o Oceano Índico e mínimo para o Oceano Ártico. O número médio de espécies por zona é de 17,2% do total (média: 463 espécies \pm s.d: 198) (Fig. 2; Razouls et al., 2005-2021).

A circulação oceânica tem uma forte assinatura regional ou local na biodiversidade planctônica (Longhurst, 1998; Boltovskoy & Valentin, 2018). A influência da circulação oceânica é crucial na escala da Bacia do Atlântico, e a diferença na biodiversidade do Atlântico Sul é claramente explicada pelo giro subtropical anticiclônico, que é formado pela Corrente de Benguela, Corrente Sul Equatorial, a Corrente do Brasil (CB) e a Corrente do Atlântico Sul. Ao longo do lado oeste, a coluna d'água superficial é representada pela BC fluindo para o sul, trazendo mais espécies de água quente em direção ao pólo sul. A Corrente das Malvinas (CM) flui para o norte transportando águas da Corrente Circumpolar Antártica e trazem espécies típicas de águas frias. A CM encontra a BC (~36-38°S), formando a Zona de Confluência Subtropical (Garzoli & Matano, 2011), região conhecida pela convergência de comunidades biológicas. As conexões dos três principais oceanos estão no Atlântico Sul. As lacunas meridionais entre os continentes do hemisfério sul e a Antártica permitem a livre troca de massas d'água entre as bacias, através da Passagem de Drake do Oceano Pacífico (Campos et al., 2017) e a Corrente das Agulhas contribui com as águas do Oceano Índico

através dos anéis desprendidos de sua retroflexão (Villar et al., 2015). A Frente Polar Antártica tem uma grande influência ao separar a baixa biodiversidade do bioma polar das regiões de maior biodiversidade dos biomas temperados da América e África do Sul, e Atlântico Tropical (sensu Longhurst, 1998). Portanto, a biodiversidade do plâncton no Oceano Atlântico Sul é impulsionada principalmente pela temperatura e circulação oceânica, e também a batimetria que controla mais diretamente a advecção do plâncton.

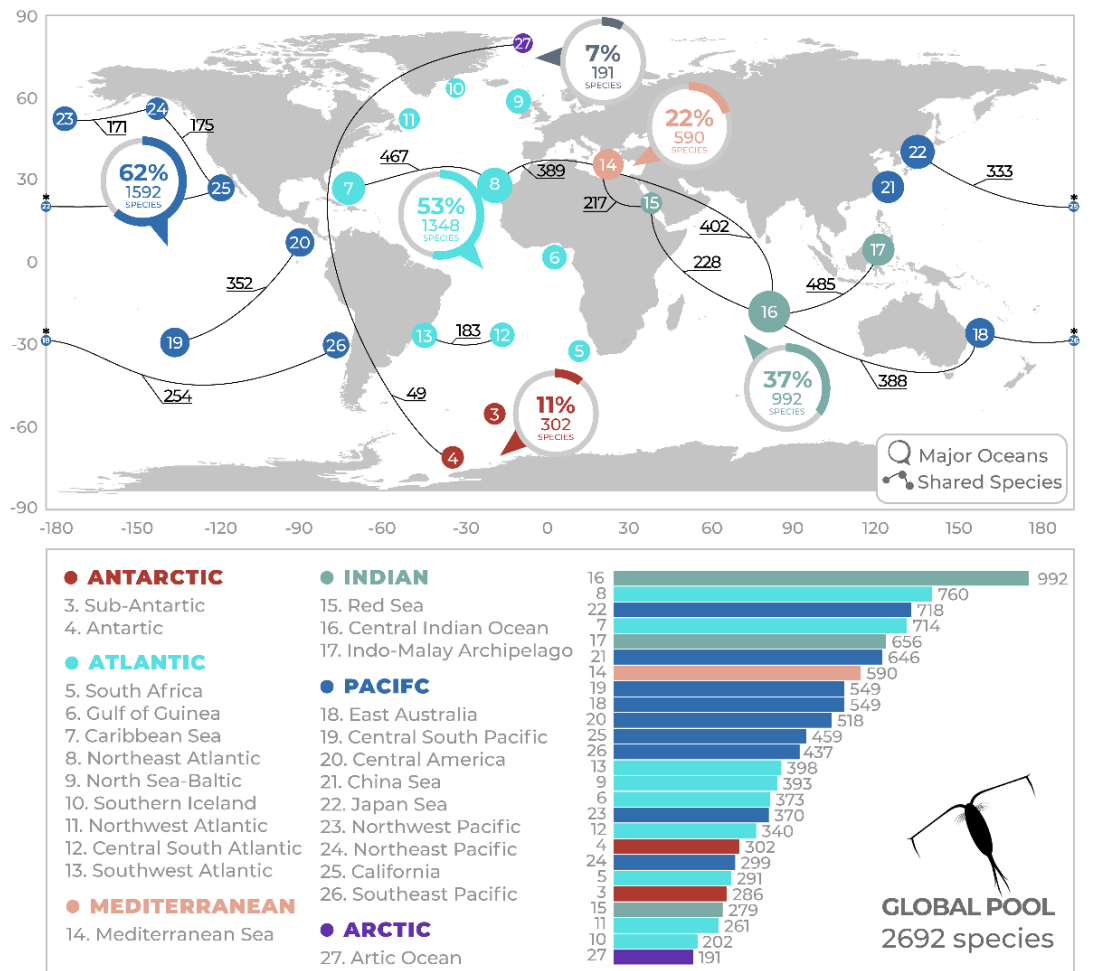


Figura 2: Distribuição da riqueza global de espécies de copépodes planctônicos, mostrando o número total de espécies e a porcentagem em cada bacia oceânica em relação ao pool de espécies global. A ligação entre regiões geográficas mostra o número de espécies compartilhada entre as regiões. Dados obtidos em: Razouls et al., (2005-2021).

1.5 HIPÓTESE GERAL

A relação entre os componentes da biodiversidade de copépodes varia de acordo com o gradiente latitudinal no ecossistema pelágico, onde espera-se que a relação entre a diversidade funcional e a estrutura de tamanho corporal seja negativa. Assim, o aumento da diversidade na região tropical está associado a menores tamanhos médios de

copépodes. Em contraste, em direção a região polar a diversidade funcional diminui em paralelo ao aumento do tamanho do corpo dos organismos.

1.6 OBJETIVO GERAL

Este estudo avalia a relação do gradiente latitudinal de diversidade taxonômica e funcional, em paralelo à estrutura de tamanho de copépodes e como as relações de composição taxonômica e tamanho influenciam no funcionamento do ecossistema pelágico no oceano Atlântico Sul e Antártico.

1.7 HIPÓTESES ESPECÍFICAS

1. Nossa primeira hipótese é que comunidades ricas em espécies suportam alta riqueza funcional e ambas diminuem em direção aos polos.
2. A segunda hipótese diz que o tamanho corporal das famílias mais abundantes de copépodes segue a regra de Bergmann, com maior contribuição de organismos menores em regiões mais quentes e de organismos maiores em regiões frias. Adicionalmente, espera-se que a influência de processos oceanográficos regionais impulsiona esse padrão ao longo do gradiente latitudinal dos oceanos Atlântico Sul e Antártico.

1.8 OBJETIVOS ESPECÍFICOS

1. Identificar diferentes grupos funcionais de copépodes no Oceano Atlântico Sul e Oceano Antártico (Capítulo I)
2. Identificar se os grupos funcionais são diferentes ao longo do gradiente ambiental e zonas biogeográficas (Capítulo I)
3. Modelar a estrutura de tamanho da comunidade de copépodes em relação as variáveis ambientais ao longo do gradiente latitudinal (Capítulo II)
4. Discutir os mecanismos ecológicos associados às relações da biodiversidade e o funcionamento do ecossistema nos padrões macroecológicos da diversidade funcional e estrutura de tamanho de copépodes pelágicos (Capítulo I e II)

1.9 ESTRUTURA DA TESE

Esta tese está apresentada sob forma de capítulos, cada um contendo um manuscrito científico. Todos os dados utilizados para a elaboração dessa tese foram coletados durante o ano de 2010/2011, durante a expedição brasileira MCTII e a expedição global *Tara Oceans*. A seção intitulada “Introdução Geral” apresentou os principais referenciais teóricos e problemas ecológicos que motivaram a elaboração dessa tese, juntamente com a hipótese geral e as específicas, e o objetivo geral e os específicos. Segue-se os capítulos intitulados: I) *Latitudinal gradient of copepod functional diversity in the South Atlantic Ocean*, manuscrito publicado na *Progress in Oceanography* em novembro de 2021; II) *Copepod body size latitudinal patterns and their environmental drivers in the South Atlantic*, manuscrito em preparação para ser submetido no *Journal of Biogeography*. Uma “Introdução ao Capítulo I” e uma “Transição para o Capítulo II” são apresentadas para fazer a ligação entre os capítulos. Finalmente, uma seção intitulada “Conclusão” tem quatro objetivos principais: (i) integrar os resultados obtidos nos Capítulos I e II; (ii) aprofundar estes resultados para fornecer uma visão mais completa sobre o papel dos grupos funcionais do mesozooplâncton nos ecossistemas no Oceano Atlântico Sul e Oceano Antártico; (iii) discutir certas escolhas que foram feitas ao longo da tese e que levaram a (iv) perspectivas de pesquisas futuras. Por último, é apresentado um texto de divulgação científica, e o anexo I, onde encontra-se os produtos gerados ao longo do doutorado.

2 INTRODUÇÃO AO CAPÍTULO I

No primeiro capítulo desta tese, buscaremos identificar grupos funcionais de copépodes planctônicos marinhos, a partir dos valores de traços funcionais de diferentes espécies de copépodes. Traços funcionais são características fenotípicas que têm um impacto no valor adaptativo dos organismos e que são relevantes para o funcionamento dos ecossistemas. Portanto, grupos funcionais agrupam espécies que desempenham um papel semelhante em diferentes ecossistemas e/ou reagem de forma análoga às mudanças ambientais.

Aproximadamente 100 espécies de copépodes que dominam a composição das comunidades zooplancônicas superficial dos oceanos Atlântico Sul e Antártico foram identificadas por taxonomia morfológica. Para definir esses grupos, usamos um banco de dados de 5 traços funcionais já bem estabelecido por Benedetti et al. (2018) para copépodes marinhos – com base no tamanho médio da espécie, regime trófico, estratégia de alimentação, presença/ausência de mielina e a estratégia de desova. Usamos análises de agrupamento para descrever os grupos funcionais de espécies que compartilham combinações semelhantes de valores de traços funcionais. Investigamos o nível de sobreposição entre os espaços funcionais de espécies pertencentes a diferentes grupos funcionais de copépodes, para responder a seguinte pergunta: os traços funcionais e os índices de diversidade funcional variam ao longo do gradiente latitudinal definido por diferentes regiões biogeográficas? Os grupos funcionais estão distribuídos igualmente em diferentes condições ambientais?

Em seguida, discutimos a importância desses grupos funcionais nos ecossistemas pelágicos do oceano Atlântico Sul e comparamos com o oceano mundial.

3 CAPÍTULO I

Latitudinal gradient of copepod functional diversity in the South Atlantic Ocean

Érica Caroline Becker^{a,*}, Maria Grazia Mazzocchi^b, Luis Carlos Pinto de Macedo-Soares^a, Manoela Costa Brandão^a, Andrea Santarosa Freire^a

a Universidade Federal de Santa Catarina, Campus Universitário, 88010-970 Florianópolis, Brazil

b Stazione Zoologica Anton Dohrn, Villa Comunale, 80121 Naples, Italy

Manuscript published in *Progress in Oceanography* (2021)

* Corresponding author: ericabeckker@gmail.com

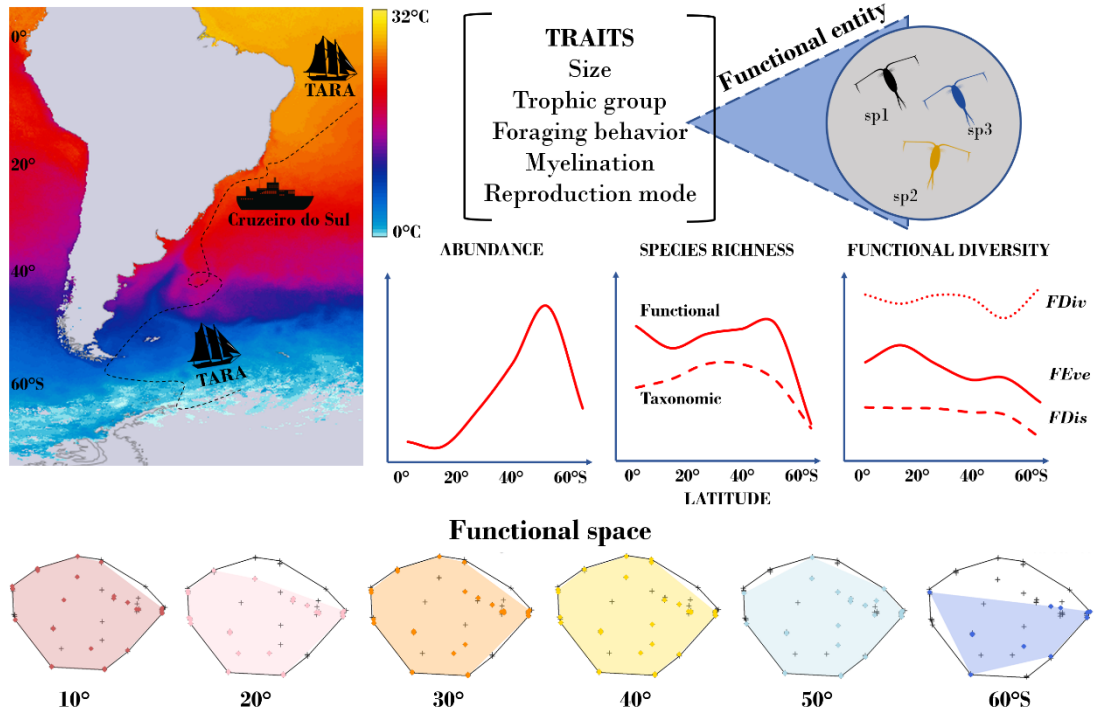
Abstract

There is a growing consensus for assessing the multifaceted marine biodiversity by analyzing morphological taxonomy and biological traits to link the biodiversity and ecosystem functioning relationships (BEF) to environmental variability. We applied taxonomic and functional diversity indices to relate copepod biodiversity with ecosystem functioning along different biogeographic zones from the Southwestern Atlantic to the Southern Ocean. To assess the link between functional traits and environmental gradients, we clustered 94 species into functional groups based on the combination of five functional traits. Taxonomic and functional diversity showed a linear decreasing trend along the latitudinal gradient. Species richness peaked at the subtropical latitude (~30°S), while the functional richness was similar from the tropical up to the temperate region (~45°S), which hosted on average 70% of the total pool of species, and dropped to only 16% in polar waters. We found that small- and medium-bodied broadcasting, large cruising carnivorous and detritivorous copepods contributed mostly to the larger functional space in tropical and subtropical zones. In turn, dominant copepod species with contrasting traits enhanced the functional divergence and decreased functional evenness poleward. Our results indicate that distinct copepod functional groups with specific environmental preferences are influenced by ecological mechanisms that promote functional richness through complementary resource use and niche partitioning. These findings highlight the relationship between species diversity and ecosystem functioning, which might contribute to ecosystem stability and resilience along environmental gradients.

Keywords: Zooplankton, Copepods, Biodiversity, Functional traits, Functional groups, Biogeography, Environmental gradients

Graphical abstract

COPEPOD FUNCTIONAL DIVERSITY



1. Introduction

Biodiversity can influence ecosystem functioning through changes in the complementary resource use among species (Petchey et al., 2004). Biodiversity and ecosystem functioning (BEF) relationships are of growing interest from the ecological standpoint, especially owing to the urgency of the biodiversity crisis (Beaugrand et al., 2010). BEF studies are currently focused on explaining ecological mechanisms applying functional diversity approach to marine ecosystems. The importance of BEF relies on the fact that changes in functional diversity rather than changes in taxonomic composition are likely to affect the stability, resistance and resilience of species assemblages (Rosenfeld, 2002).

In recent decades, compelling evidence of BEF relationships showed shifts in the partitioning of energy and biomass among plankton components (Hébert et al., 2016). Accordingly, the latitudinal increase in phytoplankton and zooplankton biodiversity in the extratropical North Atlantic is coupled to a decrease in mean species body size

(Beaugrand et al., 2010). Given that climate models predict increasingly warmed and stratified oceans, it is suggested that zooplankton communities will shift towards smaller organisms, and thus weaken their contribution to the biological carbon pump (Brandão et al., 2021). These changes may have multiple consequences for marine ecosystem functioning, and future projections suggest that severe warming of the surface ocean by the end of the 21st century could lead to tropicalization of the diversity of most planktonic groups in temperate and polar regions (Ibarbalz et al. 2019).

BEF relationships are influenced by functional diversity, i.e. the range and distribution of functional traits (Hooper et al., 2005; Song et al., 2014). Functional traits link individual performance and fitness to ecosystem functions (Hébert et al., 2016). Further resolution of the BEF relationships through the scope of taxonomic diversity, functional diversity, and community structure is important for identifying mechanisms of biodiversity effects in key community functions (Cardinale et al., 2002), and, ultimately, emerging properties of ecosystem processes within environmental gradients (Walker, 1992).

Zooplankton functional traits are strongly regulated by environmental conditions at local and global scales (Barton et al. 2013, Brun et al. 2016). Traits such as body size, feeding habits, and mating behaviors as well as dispersal capabilities, play important roles in zooplankton ecological functions (Litchman et al., 2013), and thus determine the potential response to current and future climate changes in the ocean (Benedetti et al., 2018a). Furthermore, the zooplankton functional trait approach are applied to investigate ecological processes, such as the human-induced disturbance in estuaries and in the Amazon plume influence in the Tropical Atlantic (Veríssimo et al. 2017, Neumann-Leitão et al. 2018, Neumann Leitão et al. 2019), the increasing tropicalization of copepod assemblages in the Mediterranean Sea (Benedetti et al., 2018a), and the significant poleward expansion of carnivorous copepods at the expense of herbivorous ones at high latitudes (McGinty et al., 2021). As a result, complex trait-environment relationships maintain community diversity and structure, and certain trait combinations are selected under environmental gradients. Most studies to date have investigated zooplankton functional structure, limiting the scope to functional trait combinations (Benedetti et al., 2016; Pomerleau et al., 2015; Menezes et al., 2019), without addressing functional diversity indices neither associating to large-scale BEF relationships and environmental gradients.

Copepod assemblages have a central role in the biological carbon pump and in the functioning of global oceans (Steinberg & Landry, 2017). Their remarkable taxonomic diversity raises questions on the mechanisms enabling species coexistence and the role of this diversity in community functioning. Copepod diversity can be divided into multiple facets that include a wide array of morphological features, life histories, trophic habits, behaviors, vertical and geographic distributions (Hébert et al., 2016). Thus, planktonic copepods have emerged as an interesting model to study how environmental conditions shape functional traits and the coupling of functional groups to ecological mechanisms (Barton et al., 2013; Benedetti et al., 2018b). In the present study, we aim to understand (1) the latitudinal patterns of copepod composition, species diversity and functional diversity along biogeographic zones, and (2) how the environmental gradients influence copepod BEF relationships in the latitudinal gradient from South Atlantic to Southern Ocean. This approach allows us to detect if a particular trait is selected to dominate in a certain biogeographical zone and to compare trait-based community structuring throughout latitudinal gradients. We hypothesize that species-rich communities support high functional richness and both should be conversely lower poleward than in tropical waters.

2. Materials and methods

2.1 Study Area

The sampling locations covered an extended area from the Southwestern Atlantic (SAO; 12°S-60°S) to the Southern Ocean (SO; 60°S-64°S) (Fig. 1). Based on biogeographical features (Acha et al., 2004, Longhurst, 2006, Spalding et al., 2007), the area was divided into four oceanic zones: tropical (12°S-30°S), subtropical (30°S-40°S), temperate (40°S-60°S), and polar waters (> 60°S). Additionally, the tropical area was divided into three subzones: tropical gyre (TGY, 12°-20°S), tropical ocean Rio de Janeiro (TRJ, 20°-25°S), and tropical ocean Santa Catarina (TSC, 25°-30°S), considering boundaries between major water masses and oceanographic features (Acha et al., 2004).

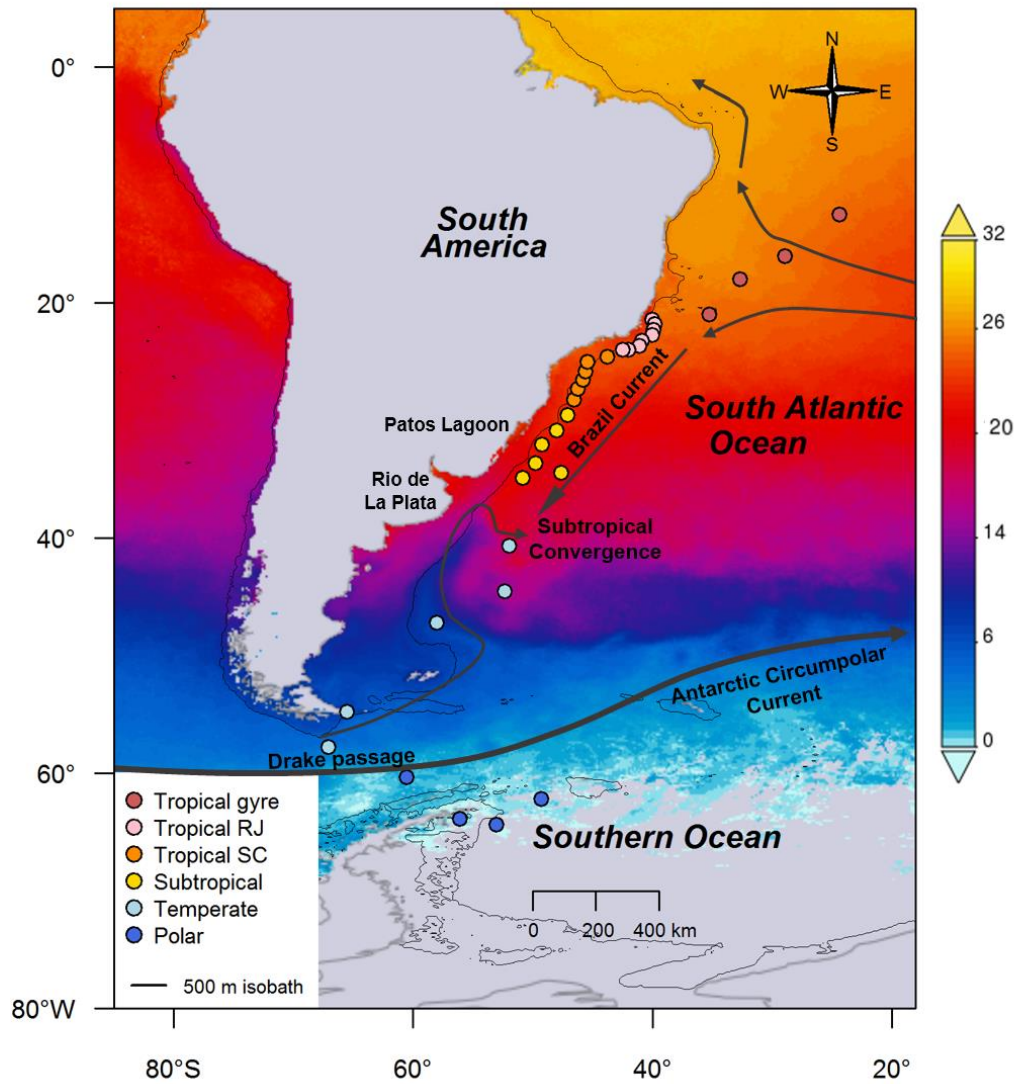


Figure 1. South Atlantic and Southern Ocean circulation, sampling stations and SST satellite image based on the average records from October 2010 to January 2011. The sampling stations are depicted by different colors, according to the six biogeographic zones.

The SAO basin is separated into a western and eastern sector by the mid-Atlantic ridge. Meso- and large-scale oceanographic features influence the tropical and subtropical waters, which are predominantly warm and oligotrophic, characterized by the strong influence of the tropical water driven by the Brazil Current (Stramma & England 1999, Silveira et al., 2000). However, a series of quasi-permanent or episodic oceanographic processes disrupt the vertical stability of the water column significantly increasing the availability of nutrients in the upper layers (Acha et al., 2004). Among them, it is worth highlighting the upwelling events of cold and nutrient rich waters (Campos *et al.*, 2013) off Rio de Janeiro (~ 22°S) and off Santa Catarina (~ 27°S), the massive freshwater discharge of the estuarine complex of the Rio de La Plata and Patos Lagoon in the

subtropical shelf (Piola et al. 2005), and the large circulation shaping the oligotrophic South Atlantic Gyre. In temperate waters, the Subtropical Convergence of Brazil-Malvinas currents is an extensive region where the subantarctic and subtropical waters converge horizontally and vertically creating a region of strong mesoscale variability. Out of the Subtropical Convergence, there is a surface frontal system with strong temperature gradients at around 40-60°S with the formation of the Subantarctic Front (48-50°S) and the Polar Front (55-60°S) (Combes & Matano, 2014).

In the SO, the Antarctic Circumpolar Current is the only global current, flowing eastwards around the entire Antarctica ring in a closed circulation, uninterrupted by continents. The winds reverse easterly, south of 65°S, forcing westward flow alongshore Antarctica, augmented by buoyancy from ice melt and generating cyclonic gyres, particularly in the Weddell and Ross Seas (Orsi et al., 1995, Miller, 2009).

2. Field Sampling

A total of 37 stations were sampled during two cruises conducted in the South Atlantic and the Atlantic sector of the Southern Ocean from October 2010 to January 2011 (Fig. 1 and Table S1). The first cruise MCT-II *Cruzeiro do Sul* was conducted off the Brazilian tropical and subtropical continental shelves (December 6th 2010 to January 11th 2011). The second cruise was part of the *Tara Oceans* expedition, in the tropical Atlantic gyre, and from the temperate shelf to the southern polar waters (October 9th 2010 to January 27th 2011). Both cruises were sampled in the austral summer following similar field protocols.

Vertical profiles of temperature, salinity, fluorescence and dissolved oxygen were obtained with a SeaBird CTD profiler and coupled sensors. In the MCT-II expedition, water samples were collected with 5-L Niskin bottles to determine nutrients (ammonium, nitrite, nitrate, phosphate and silicate) and chlorophyll-a (chl-a) concentrations at selected depths: at 3 m or 5 m, the chl-a maximum depth (DMC) and at the base of the mixed layer. Nutrients were determined using the methods described by Grasshoff et al. (1983) and Strickland and Parsons (1968), and chl-a according to Welschmeyer (1994). In the *Tara Oceans* sampling, chl-a concentrations were measured using high-performance liquid chromatography (HPLC; Van Heukelem & Thomas, 2001; Ras et al., 2008). Nutrient concentrations were determined using segmented flow analysis (Aminot et al., 2009). We compared chl-a data from fluorometric and HPLC methods. Despite the

different chl-a methods, the comparison remains useful as a coarse proxy for phytoplankton biomass (Pinckney et al., 1994).

During both expeditions, zooplankton samples were collected using a WP-2 net of 200 μm mesh size towed vertically from 100 m depth to the surface. The samples were fixed and preserved on-board with buffered formaldehyde (4% final concentration) for later analyses. The net was equipped with a flowmeter to measure the volume of filtered seawater. In the laboratory, the preserved zooplankton samples were fractionated into aliquots using a Folsom splitter (McEwen et al., 1954). In each subsample, at least 100 copepod individuals were sorted (Frontier, 1981) under the stereomicroscope and identified morphologically to the species level according to the literature (e.g., Björnberg, 1981, Bradford-Grieve et al., 1999, and Razouls et al., 2005-2020). A complete overview of the *Tara Oceans* sampling strategy and methodologies is provided in Pesant et al. (2015) and, the oceanography in the environmental context is available in Villar et al. (2015). The full methods of the MCT-II *Cruzeiro do Sul* expedition and main oceanographic features associated to the zooplankton distribution for the South Brazilian shelf are described in Macedo-Soares et al. (2014), Brandão et al. (2015) and Becker et al. (2018).

2.3 Data Analysis

Sea surface temperature (SST) data from satellite images were analyzed to feature the biogeographic zones. We used SST images based on the MODIS/Aqua sensor, downloaded from the GIOVANNI web site (giovanni.gsfc.nasa.gov/giovanni/), with a 4 km spatial resolution. The monthly SST features in each biogeographic zone at the cruise time were similar to the average feature for the whole period. We used the average SST image from October 2010 to January 2011, depicting the latitudinal temperature gradient throughout the SAO and SO.

The variability of the environmental conditions along the latitudinal gradient and biogeographic zones was depicted in violin plots of the following environmental variables: temperature, salinity, chl-a at DCM, oxygen, phosphate, silicate, ammonium, nitrite and nitrate. A violin plot gives the shape of the distribution, i.e., if is multimodal or long tail pattern, showing the whole range of data, including the outliers, and its width is related to the data frequency.

2.4 Functional Diversity

Five functional traits that are frequently used in zooplankton trait-based approaches due to data availability were retained in the present study (see Table S8 for trait references): (i) trophic group (herbivorous, carnivorous, omnivorous, detritivorous, herbivorous–omnivorous, omnivorous–carnivorous, detritivorous–carnivorous); (ii) foraging behavior (ambush-feeding, current-feeding, cruise-feeding, mixed); (iii) average adult female body length (mm) from the literature; (iv) spawning mode (broadcasting or sac-spawning); and (v) myelination of the nervous system (myelinated or amyelinated). Additionally, the vertical distribution preference (epipelagic, epi-mesopelagic and epi-bathypelagic) was used to support the results in the discussion section.

Major functional groups of copepod species were identified in the cluster dendrogram calculated using UPGMA's hierarchical clustering of species based on the Gower dissimilarity matrix for mixed variables (Gower, 1971). The five functional categories and their respective number of traits yielded combinations of trait values called functional entities (Mouillot et al., 2013). Then, the functional entities coordinates on the first four axes of the Principal Coordinates Analysis (PCoA) were kept to build a multidimensional functional space for each biogeographic zone defined by the latitudinal range (Villéger et al., 2008; Mouillot et al., 2013). Trait scores on the first two axes were further retained to plot in the functional space.

We calculated the different indices of Functional Diversity (FD), whose values range between 0 and 1. Functional Richness (*FRic*) represents the amount of the functional space filled in a community by the FEs; Functional Evenness (*FEve*) measures the regularity of the abundance distribution of the species along the minimum spanning tree that links the species points in multidimensional functional space; Functional Dispersion (*FDis*) is the mean distance of individual species to the centroid of all species in the multidimensional trait space; Functional Divergence (*FDiv*) represents the proportion of the total abundance that is supported by the species with the most extreme functional traits, that is, the species making up the edges of the functional space (Mouillot et al., 2013).

One-way Analysis of Variance was applied to test differences in functional diversity indices (*SR*, *FRic*, *FEve*, *FDiv*, *FDis*) among biogeographical zones. Fligner-Killeen test was used to check homogeneity of variances assumption and Kolmogorov-Smirnov to check normality (Zar, 2010). Both tests were applied in ANOVA residuals,

together with graphical inspection (residuals vs. fitted values, normal Q-Q plot). A Generalized Least Squares (GLS) model was applied in *FEve* measures, since Fligner-Killen test and visual inspection found violation in homogeneity of variances assumption (Zuur et al., 2009). A variance structure was added to model residuals, given different variances by biogeographical zones. Whenever significant differences were detected by ANOVA, Scott-Knott Clustering Algorithm was applied to multiple comparisons (Scott and Knott, 1974). In the GLS case, a *t*-test via contrasts analysis was applied to compare pairs of means (Zuur et al., 2009).

The FD indices and validation test were calculated using the ‘FD’ (Laliberté et al., 2015), ‘vegan’ (Oksanen et al., 2019), and ‘ScottKnott’ (Jelihovschi et al., 2014) packages in R software (R Core Team, 2019).

2.5 Null model and randomization tests

As *FRic* tends to be positively correlated with the species richness, we generated null models to remove biases due to differences in species richness (Swenson, 2014). We used a randomization procedure to test whether changes in diversity result from either random or deterministic processes, such as limiting similarity or environmental filtering. To generate null models for *FRic*, we performed 999 constrained randomizations of the community data matrix using the independent swap method (Gotelli & Entsminger, 2001). The independent swap method randomizes the community data matrix while maintaining the original species richness (Swenson, 2014). The standardized effect size (SES) of observed *FRic* (*SESFRic*), was calculated based on the distribution of the following null model index:

$$SES = (I_{mean_{obs}} - I_{mean_{sim}}) / SD_{sim}$$

where I_{obs} is the observed index, and I_{sim} and SD_{sim} are the mean and the standard deviation of simulated null model indices, respectively. Negative SES values indicate trait convergence, while positive values indicate trait divergence (Götzenberger et al., 2012). The null hypothesis is that the average *SESFRic* equals 0 and that ~95% of the observations would fall between -2 and 2. We used *SESFRic* values to determine whether the observed *FRic* values were significantly different from the null hypothesis. The significance of the difference from null expectations was tested using the one-tailed test

($P < 0.05$) proposed by Swenson (2014). SESFRic was computed using ‘picante’ (Kembel et al., 2010) and ‘FD’ (Laliberté et al., 2015) packages in R software (R Core Team, 2019).

2.6 Trait-Environment Relationships

We performed the RLQ (R, environment; L, abundance; Q, traits matrix) analysis (Dolédec et al., 1996), which is a three-table ordination method that allows the simultaneous analysis of tables R, L and Q in order to express the main patterns of covariation between environmental variables (R), species (L), and traits (Q).

Prior to the RLQ analysis, correlation ratios were computed to measure the degree of correlation between species traits and response groups (Kleyer et al., 2012). The Variance Inflation Factor (VIF) was applied to test and remove collinearity ($VIF > 10$) between explanatory variables (Borcard et al., 2011). All explanatory variables were kept in the analysis according to the VIF. From the RLQ analysis, we extracted the correlations between traits and environment parameters (Table S6) to investigate the potential environmental drivers of the observed latitudinal gradients. Outputs of RLQ analysis were used to define functional groups. Euclidean distances between species were computed on the first two axes of RLQ analysis and the UPGMA’s hierarchical clustering was then performed. Clusters were extracted from the dendrogram and the optimal number of groups was determined with the Calinsky-Harabasz stopping criterion (Kleyer et al., 2012). The functional traits table was converted into a binary matrix (except for body size, which was the solely numerical variable). Barplots and boxplots were drawn to represent the trait contribution considering the proportion of species within each functional group.

There were trait gaps in the current literature for ten species recorded in the sampling area and a few samples had missing environmental data (Table S3). Then, the copepod data used in the analysis include: R (5 environmental characteristics of 30 samples), L (94 species distribution across 30 samples), and Q (5 species traits of 94 species) (Table S2).

The RLQ analysis was performed using the ‘ade4’ (Kleyer et al., 2012) package in R software (R Core Team, 2019).

3. Results

3.1 Environmental Variability

Environmental conditions in the water column differed between the biogeographic zones (Fig. 2). High temperature and salinity values concomitant with low oxygen and phosphate concentrations characterized the tropical and subtropical zones. Large environmental variability was observed in the temperate and polar waters. Maximum temperature (24.84 °C) and salinity (37.26) were observed in the tropical gyre (~18°S), while the lowest values were -1.69°C in the polar waters and salinity 32.95 in the temperate zone (Fig. 2A, B). The average oxygen concentration was similar (5-6 mg L⁻¹) from the tropical zones to subtropics and peaked (11.2 mg L⁻¹) in polar waters (Fig. 2C). The chl-a at the DCM (~100 m) increased slightly along the latitudinal gradient and presented a peak of 2 mg m⁻³ in the tropical limit around ~25°S as well as in the polar waters (Fig. 2D). The nitrate at the DCM (~100 m) increased along the latitudinal gradient and presented a peak of 20 μmol l⁻¹ in the tropical limit around ~25°S as well as in the polar waters (Fig. 2G). Nitrite at the DCM (~100 m) increased along the latitudinal gradient and presented a peak of 0.25 μmol l⁻¹ in the tropical limit around ~25°S as well as in the polar waters (Fig. 2H). Ammonium at the DCM (~100 m) increased along the latitudinal gradient and presented a peak of 0.2 μmol l⁻¹ in the tropical limit around ~25°S as well as in the polar waters (Fig. 2I).

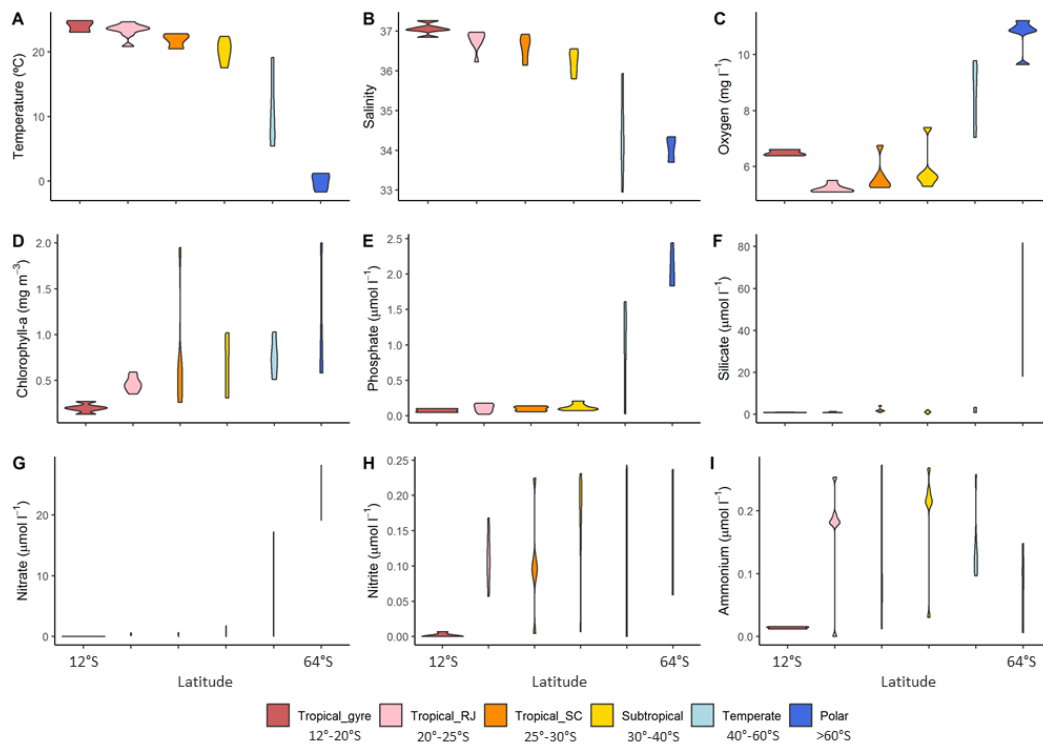


Figure 2. Violin plots of the environmental variables throughout the different biogeographic zones, from 12° to 64°S, in the South Atlantic and Southern Ocean. It highlights the distribution ranges, the outliers and, the relation of the different variables with each other. Its width is related to the frequency of data. TRJ: Tropical Rio de Janeiro; TSC: Tropical Santa Catarina.

Phosphate and nitrate concentrations followed a similar pattern in tropical to subtropical zones, with low concentrations and a sharp increase from temperate to polar zones (Fig. 2E and G). Very high silicate concentrations were found in the polar waters only (Fig. 2G). Nitrite and ammonium showed a strong variability between the biogeographic zones, except in the tropical gyre, where the lowest values ($0.01 \mu\text{mol L}^{-1}$) were recorded (Fig. 2H and I). High ammonium concentrations were consistently observed from the tropical region close to Rio de Janeiro to temperate waters ($\sim 21^\circ$ to 57°S).

3.2 Functional and Taxonomic Diversity

A total of 104 copepod species were identified from tropical to polar oceanic waters (Table S4). The highest copepod abundances were recorded in the temperate zone, although the variance was high, with total abundance ranging from 206 to 2259 ind.m^{-3} (Table S4). The subtropical region also had relatively high copepod abundance with a mean of 1055 ind.m^{-3} . The tropical zone had low abundance, with a mean of 227 ind.m^{-3} and a minimum of 65 ind.m^{-3} in the TRJ. Interestingly, polar waters also had low abundance, with a mean of 518 ind.m^{-3} .

In terms of species relative abundance, 12 species dominated in the tropical and subtropical zones: *Clausocalanus furcatus* (17%), *Oncaea venusta* (8%), *Farranula gracilis* (6%), *Calocalanus pavoninus* (4%), *Oithona plumifera* (4%), *Mecynocera clausi* (2%), *Corycaeus giesbrechti* (2%), *Temora stylifera* (2%), *Oncaea media* (1.6%), *Corycaeus (Corycaeus) speciosus* (1.5%), *Oithona tenuis* (1.3%) and *Nannocalanus minor* (1%). In the temperate and polar zones, seven species were dominant: *Oithona similis* complex (22%), *Calanus simillimus* (14%), *Clausocalanus brevipes* (11%), *Oithona atlantica* (4%), *Ctenocalanus citer* (1.7%), *Paracalanus parvus* complex (1.5%) and *Scolecithricella minor* (1.5%).

There were significant differences in species richness ($F = 7.06$, $P < 0.0001$), functional richness ($F = 9.93$, $P < 0.0001$), functional evenness ($F = 4.46$, $P < 0.0001$), and functional dispersion ($F = 4.93$, $P < 0.002$) between biogeographic zones, but there were no significant differences in functional divergence ($F = 1.44$, $P = 0.24$) (Figs. 3B, D, F, H, J). Mean species richness (SR) decreased with latitude, from 19 ($\pm 6\text{SD}$) in the TGY, 16 ($\pm 3\text{SD}$) in the TRJ, and 22 ($\pm 7\text{SD}$) in the TSC, to 20 ($\pm 7\text{SD}$) in the subtropical, 11 ($\pm 7\text{SD}$) in the temperate, and only 5 ($\pm 3\text{SD}$) in the polar zone (Fig. 3A). *FRic*

followed a similar decreasing pattern as SR, but *FRic* decreased more gradually with latitude than SR, and both presented a dip in TRJ (Fig. 3C). *FEve* decreased poleward, ranging from 0.5 and 0.6 ($\pm 0.03SD$) in the tropical subzones, 0.4 ($\pm 0.15SD$) in the subtropical and temperate zones to 0.3 ($\pm 0.19SD$) in the polar waters (Fig. 3E). In turn, *FDiv* was generally high, but slightly higher in the polar zone (0.97 ± 0.03) (Fig. 4G). *FDis* varied between the zones with greater dispersion in tropical subzones (0.26 to $0.22 \pm 0.03SD$) than subtropical to polar waters (Fig. 4I), and it sharply decreased in polar waters ($0.08 \pm 0.08SD$). Overall, tropical subzones together with subtropical waters supported taxonomic and functionally richer copepod assemblages more evenly distributed than both temperate and polar zones. Despite *FDiv*, all the other three functional diversity indices were lower in the polar zone (Table S5).

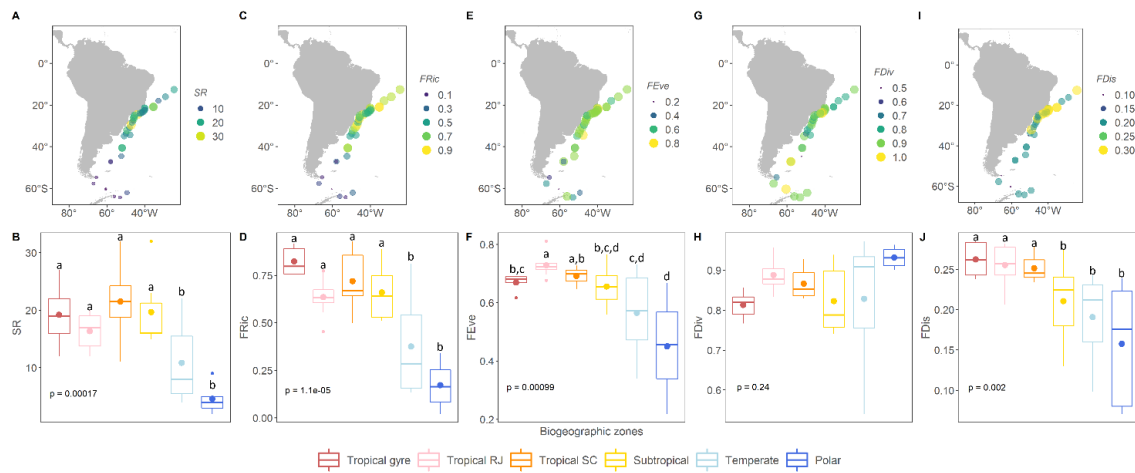


Figure 3. Variation in species richness (SR; A, B), functional richness (FRic; C, D), evenness (FEve; E, F), divergence (FDiv; G, H), and dispersion (FDis; I, J) of copepod community among the six biogeographic zones. Significant differences between biogeographic zones revealed by ANOVA and the Scott-Knott clustering algorithm was used to multiple comparisons (all $p \leq 0.05$, except FDiv) illustrated by the letters (a,b,c,d). Generalized Least Squares (GLS) model and a *t*-test pair-wise comparisons was applied only for FEve (see Methods). Points show the mean index value of each biogeographic zone. Biogeographic zones sharing a letter are not significantly different ($P < 0.05$), those not sharing a letter are significantly different.

FRic was evenly higher from the TGY to temperate zone (75% to 61%) followed by a sharp decrease in the polar zone (16%) (Fig. 4B). The functional space decrease poleward was related to particular traits: (1) nearly the absence of the large carnivorous species (*Euchaeta* spp., *Candacia* spp., *Heterorhabdus* spp., *Scaphocalanus* spp., *Sapphirina* spp., *Undinula vulgaris*, and Corycaeidae species), except the medium

cyclopoid *Corycaeus flaccus*; (2) the scarcity of detritivorous species (*Oncaea* spp., Scolecitrichidae species, and the harpacticoids *Clytemnestra scutellata* and *Microsetella rosea*), except the small cyclopoid *Oncaea waldemari*; (3) and the decreasing contribution of predominantly small and medium size broadcasting copepods (*Clausocalanus* spp., *Paracalanus* spp., *Acartia* spp., *Temora* and large Calanidae species) (Fig. 4B). The abundance distribution was similar from tropical to subtropical zones, and most of the species that achieved higher abundances were sac-spawning species (*Euchaeta* spp., *Clausocalanus furcatus*, *Farranula* spp., *Corycaeus* spp., *Oncaea* spp.), leading to the dominance of *Oithona similis* complex in the polar region. Moreover, broadcasting species reached high abundances in temperate (*Clausocalanus brevipes* and *Calanus simillimus*) and polar (*Ctenocalanus citer*) zones (Fig. 4C).

The comparison with the null model revealed different trait assembly patterns between the biogeographic zones. Positive values indicated that SESFRic were significantly higher than expected at random (SESFRic > 2), suggesting that limiting similarity is the predominant force in the community (trait divergence, i.e. species coexist by exploiting the biogeographic zones differently). On the other hand, few geographic locations down to 47°S in temperate (2 sites) and polar waters (2 sites), showed lower SESFRic values non-significant different from the null model, suggesting that the copepod communities may have been more stochastically structured consistently with the random distribution in these sites (Table S7).

The trait distribution in the functional space (Fig. 5; upper right) was strongly related to traits linked to behavioral and life history traits. In the first PCoA axis (PCoA1), herbivorous-omnivorous and myelinated broadcasting performing current-feeding foraging behavior contrasted to sac-spawning with higher contribution of carnivory and ambush behavior. The second axis (PCoA2) was mainly related to traits representing distribution of cruising detritivorous and particle-feeding in opposition to body size, which had a minor contribution in the trait space. Carnivory and cruise functional traits had a great projection on both axes. Overall, the PCoA axes suggest a trade-off between resource acquisition and trophism (both PCoA axes) and reproduction strategy and myelination mainly in PCoA 1.

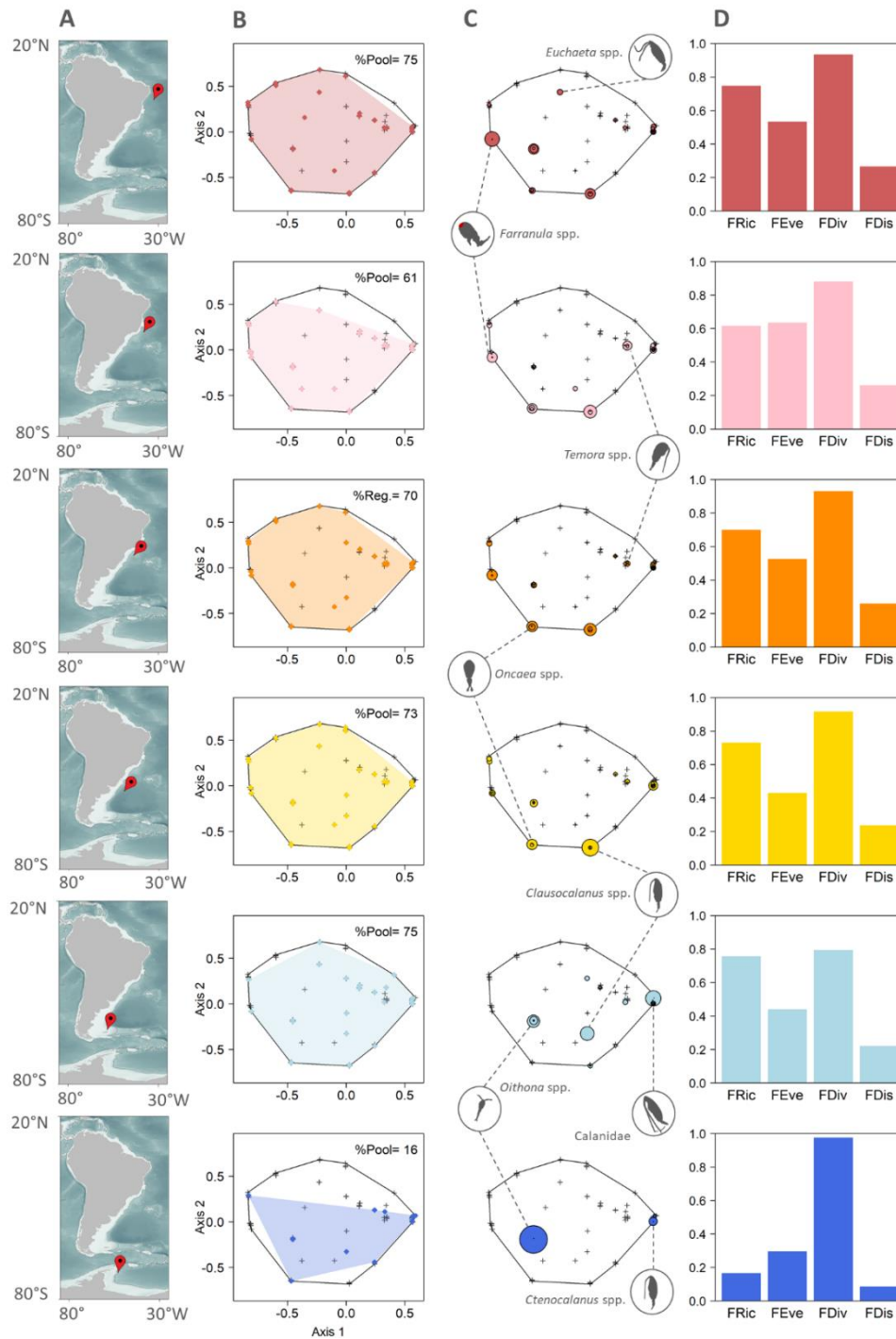


Figure 4. Multidimensional trait space occupied by copepod community in six biogeographic zones in the Southwestern Atlantic and Southern Ocean (12° - 64° S). **A** Geographic location of the six biogeographic zones depicted in the sampling area (Fig. 1). **B** Functional space of the species pool ($n = 94$; PCoA biplot), with colored polygon indicating the biogeographic zones: tropical gyre (red), tropical Rio de Janeiro (pink), tropical Santa Catarina (orange), subtropical (yellow), temperate (light blue), and polar (dark blue). Each point represents a species and is colored according to the biogeographic zones, while each gray cross represents species absence therein. **C** Bubble sizes are proportional to species abundance in the functional space. Copepod shapes were chosen to illustrate the main abundant genera. **D** Barplots show copepod functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), and functional dispersion (FDis).

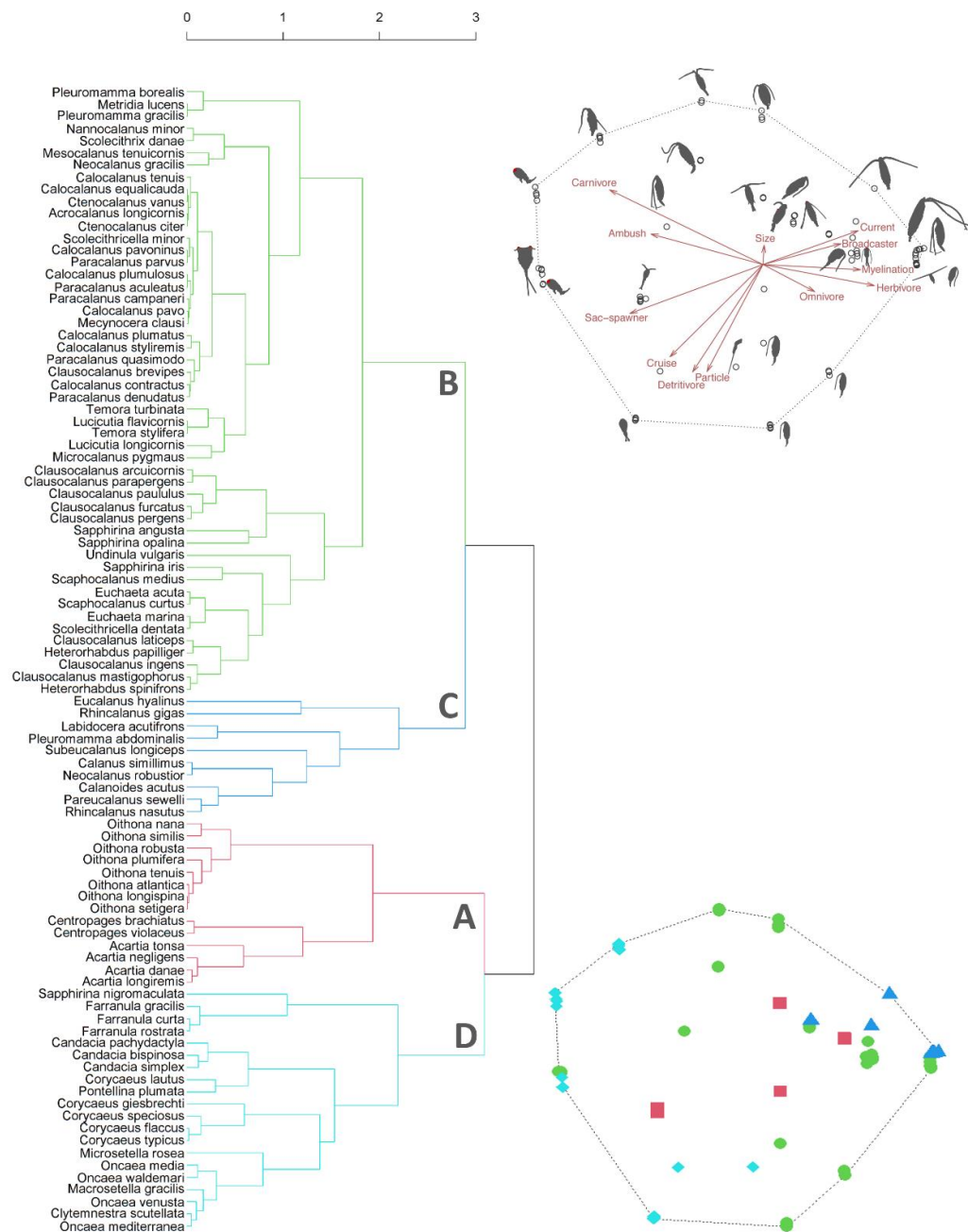


Figure 5. Copepod functional groups in the RLQ analysis based on the covariation between traits (size, trophic group, foraging behavior, myelination and reproduction mode) and environmental variables (temperature, oxygen, silicate, dissolved inorganic nitrogen (NID), chl-a at DCM) among the 94 copepod species of the Southwestern Atlantic and Southern Ocean. UPGMA hierarchical clustering was defined in the functional dendrogram and the best partition of groups A-D is presented by distinct colors (see Fig. S1). In detailed, functional space with trait vectors (upper right) and with functional groups (lower right). Copepod shapes were chosen to illustrate the position of the main copepod genera in the functional space.

3.3 Trait-Environment Relationships

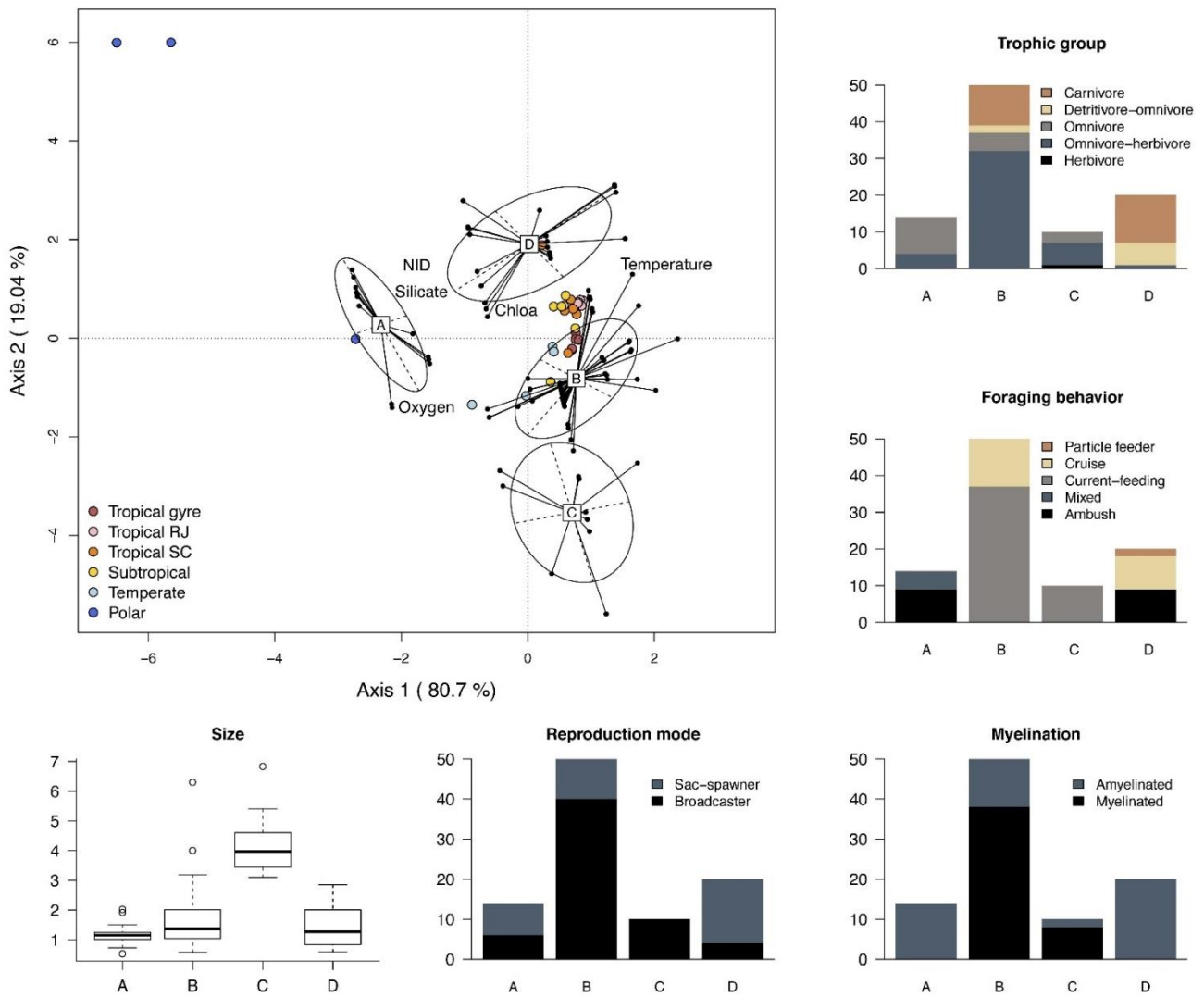


Figure 6. RLQ biplot showing the correlation between environmental variables (R-Table 5 x 30) and trait attributes (Q-Table 94 x 5), constrained by species abundance (L-Table 30 x 94). Clustered points identify functional groups (A-D, Fig. 5). Each point represents the species or subgroup of species (species in the same level of similarity) position on the RLQ Axis 1 and 2. Stations are plotted accordingly to the different biogeographic zones. Barplots and the boxplot represent the trait contribution within each functional group.

We identified four distinct functional groups in the cluster dendrogram based on functional traits dissimilarity (Fig. 5 and Fig. 6 barplots and boxplot). The first level of the functional dendrogram (Fig. 5) distinguished groups according to the presence of myelin. Among myelinated species, most are broadcasting copepods (groups B and C), while amyelinated species are mainly sac-spawning (A and D). The large group B contains 50 species, which mainly belong to the families Paracalanidae, Calocalanidae,

Temoridae and Clausocalanidae. Considering the functional traits, these copepods are medium-sized omnivorous-herbivorous, mainly current- and cruising-feeding, with both spawning strategies, though most species are myelinated broadcasting. Group C was constituted by 10 species, exclusive broadcasting and mainly large myelinated current-feeding from diverse trophic groups. The species from both groups B and C are mostly epi-mesopelagic copepods. Group D is composed of 20 species, which are mostly small sac-spawning, ambush, or cruise-feeding. These copepod species are predators, i.e. the families Corycaeidae, Sapphirinidae, and Candaciidae, and detritivorous species, i.e. *Microsetella rosea* and the family Oncaeidae. Group A contains 14 species with two main trait combinations: 1) omnivorous-herbivorous, mixed feeding strategies and broadcasting amyelinated copepods, 2) the whole family Oithonidae with omnivorous and ambush-feeding, and sac-spawning species. The functional groups A and D encompass amyelinated copepods.

The relationship between copepod traits and environmental features was mainly decomposed onto the two first axes of RLQ analysis (80.7% and 19%, respectively) (Fig. 6). The poleward latitudinal gradient was depicted in the first axis, being positively correlated to temperature (0.92) and negatively correlated to NID (-0.95), silicate (-0.92) and oxygen (-0.89; Table S6). The second axis is positively correlated to chl-a (0.39) and defined by the reproduction mode, where C is exclusively broadcasting and D only sac-spawning. High water temperature was associated with tropical conditions, dominated by small and medium-size broadcasting (B) and sac-spawning (D) epipelagic copepods (Fig. 6). In contrast, the cold and rich water conditions were related to large broadcasting and current-feeding copepods (C), also in addition to the medium-size ambush-feeding *Oithona* species from polar zone (A). This latter group encloses all the *Oithona* species recorded in the sampling area, also including the epipelagic ones from tropical to temperate zones. Additionally, the large body size (range of 4-8 mm) was associated with two outlier stations from polar waters in the Weddell Sea, where adults of *Calanoides acutus* had high abundances related to the peak of DCM (2 mg m^{-3} ; Fig. 2D).

4. Discussion

We presented, for the first time, a detailed overview of the latitudinal distribution of epipelagic copepods from the South Atlantic (SAO) to the Southern Ocean (SO) by focusing on their taxonomic and functional diversity. The biogeographic zones crossed

during this study follow the major provinces of the Atlantic and Antarctic oceans defined by Longhurst (2007). Species richness peaked in the transition of tropical to subtropical areas, which leads to increased functional richness that sharply decreased in the SO. Morphological and behavioral traits enhanced the functional richness equatorward: large cruising carnivorous, detritivorous and, small and medium-size broadcasting. In contrast, two copepod typologies representing different life histories were common in cold conditions, i.e., small *Oithona* species and large calanoid copepods (Atkinson, 1998). The finding that polar communities are nested within tropical communities, rather than placed separately in the trait space, illustrates a maintenance of the core functional structure in the two oceanic regions, despite declines in functional richness. Together, the functional metrics reveal that the polar assemblages contain more functionally contrasting species, but retain a similar functional framework. Our findings imply that there are ecologically distinct copepod functional groups with specific environmental preferences and ecological functions. We have outlined the ecological mechanisms responsible for the biodiversity and ecosystem functioning (BEF) relationships, and unveil the underlying latitudinal gradient of copepod functional diversity, which are discussed in the following sections.

4.1 General Trends of Copepod Taxonomic and Functional Diversity

The pattern of copepod richness observed along a latitudinal gradient peaked in the tropical zone, similar to the latitudinal trend observed in the AMT cruise (Woodd-Walker et al., 2002). However, our finer scale resolution of the tropical zone resulted in the highest species diversity not in the lower tropical latitudes as in AMT, but around 25°S to 40°S (Fig. 4B, Table S5), where the shelf break upwelling and the Subtropical Brazil/ Malvinas Convergence allow the mixing of cold and warm species (Acha et al., 2020). A slight increase in zooplankton richness occurred also at 35°N in the North Atlantic (Woodd-Walker et al., 2002; Rombouts et al., 2009). It seems therefore that copepods in the Atlantic Ocean have also a bimodal richness pattern, with peaks at mid-latitudes and a dip at the equator, as the general pattern of marine species richness (Chaudhary et al., 2016).

Hutchinson (1959) plankton paradox hypothesis explained the coexistence of species in the oligotrophic ocean by the difference of body size among species in a functional group, i.e., groups of co-occurring species using the same resources (Miller,

2009). Although the *Oithona* species are closely related and probably share the same functional group, we observed that each species represented more FEs in the tropical functional space. The species shaping close FEs (Fig. S1) had different mean body sizes: *Oithona nana* (0.53 mm), *Oithona tenuis* (1.15 mm) and *Oithona robusta* (1.51 mm), which likely coupled with slightly different motion behaviors as observed in *O. plumifera* (Paffenhöfer and Mazzocchi, 2002) and *O. similis* (Svensen and Kiørboe, 2000) and might account for differences in resource exploitation, preventing niche overlap as hypothesized by Hutchinson (1959). Coexistence of congeners with niche partitioning has been also reported for other copepods (e.g., Lakkis, 1994; Peralba et al., 2017).

In fact, the functional diversity pattern from tropics to temperate zones points towards a complementarity use of resources (Fig. 7). This ecological mechanism assumes that the variety of traits increases with the regional pool of species, thus the complexity of the ecosystem processes might be enhanced by species richness (Mayfield et al., 2010). In the upper tropical ocean, the high copepod species richness allows a higher trait combination of feeding and trophic traits (Fig. 6; barplots B and D), and therefore, different trophic interactions and food web structures. Previous studies on zooplankton in the tropical Atlantic (Veríssimo et al., 2017) and reef fish in the Eastern Pacific (Mouillot et al., 2014) showed that communities with few species can maintain the range of ecological processes necessary for growth and persistence because their species share most of the functional traits present in richer assemblages.

Marine resilience may be enhanced by maintaining habitat connectivity as well as functional redundancy, environmental heterogeneity, and biological diversity (Pelletier et al., 2020). *FRic* was evenly higher from tropical to temperate regions (~45°S), while species richness peaked at the subtropical latitudes (~30°S), resulting in higher *FEve* (Table S5). In general, a higher *FEve* indicates a regular abundance distribution, and thus, that species are using the resources complementarily (Veríssimo et al., 2017). In contrast, *FDiv* was higher in polar conditions while *FEve* was lower there (Table S5), which suggests that resources are being used more effectively by species with the most extreme traits. In this biogeographic zone there is a higher spread of species in the functional space with fewer species in comparison to richer assemblages in low latitudes. In addition, there is a higher degree of niche differentiation, hence lower resource competition (Mouillot et al., 2013; Veríssimo et al., 2017). We conclude that functional diversity patterns are different along the latitudinal gradient, and therefore, that complementarity and dominance effects may both ensure marine resilience.

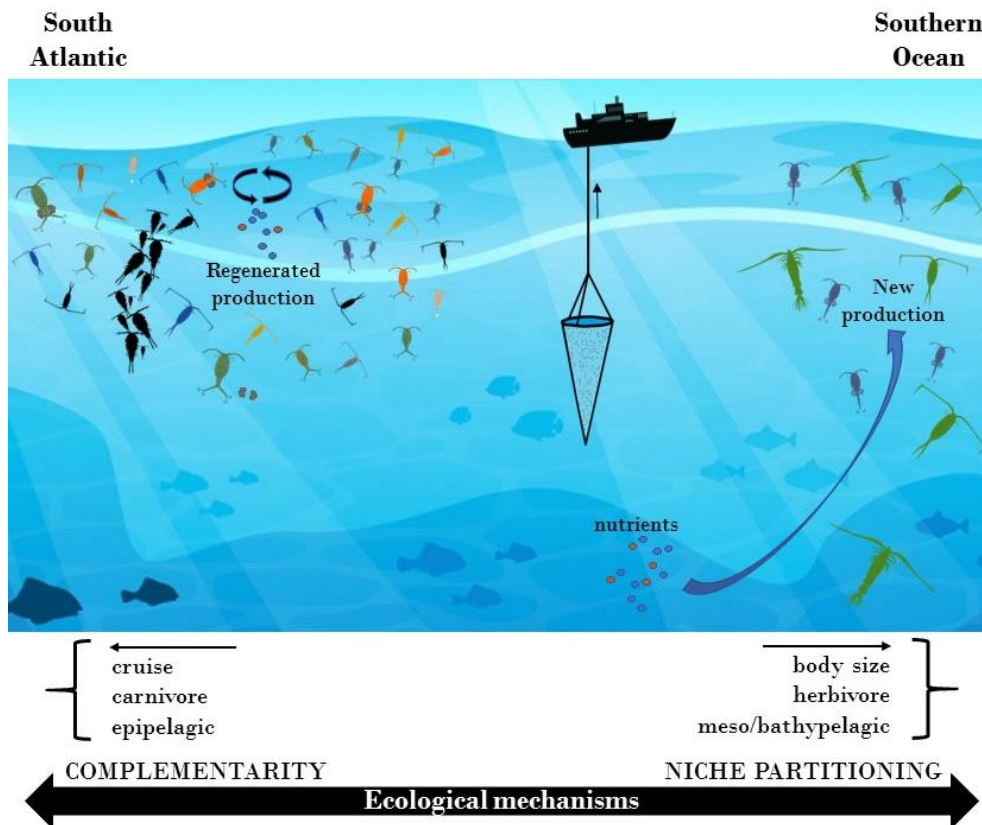


Figure 7. Schematic illustration of the oceanographic conditions and the major functional traits related to ecological mechanisms, that can explain the relationship between copepods functional diversity and ecosystem functioning in the South Atlantic Ocean and Southern Ocean.

4.2 Functional groups, Biodiversity and Ecosystem Functioning, and community assembly processes along Environmental Gradients

The oligotrophic tropical/subtropical waters with high temperature and salinity were opposed to the nutrient-rich and oxygenated waters towards temperate and polar latitudes (Figs. 2 and 6; Table S6). Wind-driven oceanographic processes, such as the South Atlantic Central Water intrusion during summer and the La Plata Plume Water northward displacement during winter, are important mixing processes that fertilize the shelf and enhance the primary production (Bordin et al., 2019). In contrast, the oligotrophic oceans are typical areas of ammonium-based regenerated production (Metzler et al., 1997), where the supply of autochthonous nutrients by regeneration processes supports primary production, with the regenerated ammonium readily oxidized to nitrite and nitrate (Brandini et al., 2018). In our study, high values of ammonium were

recorded from tropical Rio de Janeiro to temperate waters. South of this zone, the increase of nitrate from deep water masses fuels new primary production mainly in subantarctic and Antarctic waters (Fig. 2), which are productive owing to the influence of oceanic frontal systems, the Subtropical Confluence Zone and the Antarctic Polar Front (Lopes et al., 2016).

Oligotrophic conditions characterized by low nutrient and chl-a concentrations in the regenerated system of the tropical waters, to the new production system of high chl-a and nutrient rich waters poleward, depicted the different trophic regimes within the biogeographic zones. It is noteworthy that the latitudinal decrease of the functional space poleward may be related to the decreasing contribution of cruising carnivorous species in relation to herbivorous and omnivorous species (Figs. 4 and 6). Tropical and subtropical zooplankton communities are mainly characterized by high species diversity, complex trophic networks with abundant carnivorous copepods leading to top-down dominated systems (Hébert et al., 2016). Tropical calanoid copepods have adopted different feeding strategies and occupy a wide range of ecological niches, characterized by a large proportion of omnivorous species and many opportunistic predators (Teuber et al., 2014; da Rosa et al., 2016). Carnivorous functional groups mostly found in significantly warmer and less productive areas were found worldwide in the Atlantic Ocean (Woodd-Walker et al., 2002), North Atlantic and the Southern Ocean (McGinty et al., 2018) and in the Mediterranean Sea (Benedetti et al., 2018b). In contrast, cooler seasonal areas tend to be dominated by herbivorous copepods as primary consumers in systems driven by bottom-up processes (Hébert et al., 2016). Herbivorous-omnivorous species display life strategies that are adapted to conditions of strong seasonal variations in temperature but also primary productivity (Atkinson, 1998; Cornils et al., 2018; McGinty et al., 2018).

Environmental gradients filter different sets of species traits defining functional groups that are likely to share similar roles in ecosystem processes (Fig. 7). Myelination was found to be the functional trait driving the first-order separation in the functional space (Fig. 5). Myelin greatly enhances nervous system function, but requires the production and maintenance of large amounts of cell membranes (Lenz et al., 2012). Among myelinated species, most of them are broadcasting copepods (groups B and C), while amyelinated species are mainly sac-spawning (A and D). Group A comprises essentially of *Oithona* spp., *Acartia* spp. and *Centropages* spp. These are small ambush-feeding omnivorous that carry their eggs and they are in turn preyed upon by large carnivorous zooplankton and epipelagic fishes (Mackas and Coyle, 2005). Group D

comprised small and large visual predators and cruising detritivorous, all ambush-feeding and mainly sac-spawning. Detritivorous species feed on copepod carcasses and aggregates of marine snow and contribute to recycling of organic matter (*Oncaea* spp., *Clytemnestra scutellata*; Yamaguchi et al., 2002). Carnivorous species that capture and feed on metazoan prey (*Corycaeus* spp., *Farranula* spp. and *Candacia* spp.), and contribute to the top-down control of mesozooplankton. Group B is the largest group and comprises almost all current-feeding and cruising, mostly omnivorous-herbivorous and carnivorous species ranging from small to large animals. This group are mainly epipelagic species, from small copepod families Paracalanidae, Clausocalanidae and Temoridae to large Calanidae species. They are the most important contributors to secondary production as they are among the most numerically abundant taxa from tropical and subtropical oceans (Napp et al., 2005; Lopes et al., 2015). Besides, it is also a group of diverse carnivorous species, including *Euchaeta* spp., *Sapphirina* spp., *Scaphocalanus* spp., *Heterorhabdus* spp. and *Undinula vulgaris*. Group C is distinguished by the presence of large-bodied organisms (> 3mm), gathering the families Calanidae, Eucalanidae and Rhincalanidae, with typical species from cold water conditions. These species have very special adaptations to float and spare energy, to respond swiftly to temporally and spatially variable phytoplankton pulses initiated by local events and they may find refuge from predation and avoid competition by less hypoxia-tolerant species within the oxygen minimum zone (Teuber et al., 2019). Before the phytoplankton bloom in spring, large antarctic and sub-antarctic copepods (e.g. *Calanoides acutus*) store large amount of lipids and greatly contribute to a massive biomass production being the preferential prey items for both larval and juvenile of mesopelagic fishes (Atkinson, 1998).

Both spawning modes seem to be successful in all parts of the environmental gradients examined, even though sac-spawning species were the most abundant in most of the biogeographic zones, depicted by the dominance of *Clausocalanus furcatus* (group B) in the tropical/subtropical waters and of *Oithona similis* in the polar zone (group A). Although the small sac-spawning *C. furcatus* is well adapted to low phytoplankton concentrations (Mazzocchi and Paffenhoefer, 1999), their success can be attributed to the presence of myelin and the consequent ability to escape predation and relative longevity of the adults (Calbet and Agustí, 1999). Enhanced escape responses and more efficient energy use may promote the success of myelinated calanoids in habitats characterized by high predation risk and low standing stocks of phytoplankton. However, environments

with low food quality may favor amyelinated species, given the cost of producing large quantities of lipid-rich membranes (Lenz et al., 2012), which may be an advantage for *C. furcatus* in tropical and subtropical waters.

Environmental heterogeneity seems to select plastic traits, e.g., size, feeding and trophic group that may vary ontogenetically (e.g. across nauplii, copepodite and adult stages), with season and biogeographic regions (Pomerleau et al., 2015), rather than fixed reproductive and myelination traits. Evidence of stability and resilience in copepod assemblages were associated to high biological plasticity of key species, suggesting that mechanisms of functional diversification are probably acting to allow the persistence of taxonomically diverse copepod assemblages (Mazzocchi et al., 2012). Species diversity is likely to promote ecosystem functioning when differences in species resource acquisition in space and time allow a more complete utilization of resources (Sonkoly et al., 2019). A high proportion (89%) of the assemblages had significantly higher functional richness than expected according to their species richness, i.e. their SESFRic (Table S7), in addition to, the overall high *FDiv* values within the biogeographic zones and the lack of significant differences between them. These findings suggest that limiting similarity might be the dominant assembly rule in copepod assemblages, i.e. species are functionally more distinct from one another (Mouchet et al., 2010), reinforcing that complementarity (equatorward) and niche partitioning (poleward; Fig. 7) may both contribute to marine stability and resilience along environmental gradients.

4.3 The Role of Small-size Copepods in Cold Waters

The increase in the use of fine-mesh nets has led to re-evaluate the importance of small-size species at higher latitudes (Prowe et al., 2019), particularly in the temperate South Atlantic (Cepeda et al., 2020) and in the Southern Ocean (Atkinson et al., 2012; Cornils et al., 2018), as those recorded in our study, i.e., the dominant but distinct FEs, *Oithona similis* and *Ctenocalanus citer*. In the Antarctic Polar Front, downwelling and meandering features increase the residence and retention of small copepod populations within a food-enriched environment, and allow strong biomass accumulation during the productive spring and summer seasons, favoring *O. similis* and *C. citer* breeding during early summer (Dubischar et al., 2002). In our study, *O. similis* peaked in the Antarctic waters (Fig. 4c), which might represent the summer phytoplankton blooming in SO. Apparently, environmental variability is not the most important driver of *Oithona* spp.

population dynamics since species from different biogeographic zones clustered in the same functional group (Fig. 5).

As seen across the North Atlantic, there has been a decrease in overall copepod densities over the past 30 years (Edwards et al., 2020). However, densities and phenological timings of the *O. similis* population have remained stable (Cornwell et al., 2018). This is considered one of the most abundant species in temperate to polar oceans acting as an important link in the trophic network between the microbial loop and higher trophic levels (Cornils et al., 2017). *Oithona* spp. population benefits from the increased abundance of motile prey, such as ciliates and dinoflagellates, throughout the year (Zamora-Terol et al., 2013; Kenitz et al., 2017). Other factors, such as vertical niche partitioning of life stages (Prowe et al., 2019) and contrasting functional traits between *O. similis* with the large, biomass-dominant copepod *Calanus helgolandicus* contribute to both species' populations stability and resilience to climatic variability (Cornwell et al., 2020). Here, *Calanus simillimus* and *Calanoides acutus* are the ecological equivalents in the Southern compared to the Northern hemisphere strengthening the functional divergence especially in the southernmost polar regions. We further validate the main findings of Prowe et al. (2019) which identified the poleward abundance increase of ambush-feeding copepods over the cruising ones, giving the highest abundance of *O. similis* populations in polar waters (Fig. 3C).

Even within regions of high krill abundance, copepod production in summer roughly triples that of post larval *Euphausia superba* (Atkinson et al., 2012). Dominant grazers are small calanoid and cyclopoid copepods removing up to 40% of the total chlorophyll stock in the Subtropical Convergence Zone, and 22% in the Antarctic Polar Front, on a daily basis (Lopes et al., 2016), reflecting a large flow of energy through multiple trophic levels via copepods. Copepod sloppy feeding, excretion and sinking fecal pellets contribute to the flux of particulate carbon and nitrogen below the epipelagic zone, which support bacterial growth and fuel the microbial loop (Saba et al., 2011). Given the large population of *O. similis* throughout the year (Atkinson, 1998) and the great contribution of ciliate microzooplankton in most pelagic ecosystems (Dolan et al., 2012), microbial loop involving small metazoans seems important not only in the regenerated ecosystem in the SAO, but also in the new production system of SO. Still, microbial food webs may represent a form of resilience to populations that should lead to the maintenance of ecosystem functioning in the SO.

5. Conclusions

Copepod assemblages from the Southwest Atlantic and Southern Ocean were characterized by functional groups strongly imposed by environmental gradients. Higher species richness enhanced species trait combinations, especially behavioral traits – trophic habits and foraging behavior – and supported greater functional richness in warm conditions. We showed a decline of functional diversity (*FRic*, *FEve*, *FDis*) mainly driven by the decreasing contribution of cruising carnivorous, small and medium-size broadcasting copepods poleward. Alternatively, higher environmental variability and strong seasonality in food supply at temperate and polar waters favor two types of life-history strategies: small ambush-feeding copepods (dominated by *Oithona similis* complex) and large herbivorous lipid-storing calanoids. Our study fills an important gap in our knowledge of global functional diversity in the poorly investigated South Atlantic Ocean, matching findings with the temperate latitudes in the North Atlantic and Mediterranean Sea, and Pacific sector of the Southern Ocean.

The impact of community processes, and the choice of FD indices may be strongly influenced by species richness. For instance, *FRic* was higher than expected under a random distribution, and *FDiv* was generally high in all biogeographic zones. Consequently, the dominant assembly rule seems to promote functional dissimilarity, thus driving complementarity use of resource (equatorward) and niche partitioning (poleward) among the copepod species. Future studies should consider whether species richness influences ecosystem stability and resilience, and which facet of functional diversity has the strongest influence on these ecosystem processes along environmental gradients.

Acknowledgments

We thank the Brazilian Navy, the crew and the scientific team of the MCT-II and TARA *Oceans* expeditions for their technical assistance and support during the fieldwork. We thank A. Ciotti and R. Pollery, who provided chlorophyll-a and nutrient data, respectively. EC Becker acknowledges PhD fellowships from the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), Ministry of Education of Brazil to study in SZN (88881.199266/2018-01 PE–19/2011) and to follow the Ecology Graduate Program at UFSC (Financial Code 001). The research leading to these results has received funding from the European Union’s Horizon 2020 research and innovation

programme under grant agreement No. 730984. We thank the EMBRC platform PIQv for image analysis and the CCPv collection for the access to the Tara samples. This work was supported by EMBRC-France, whose French state funds are managed by the ANR within the Investments of the Future program under reference ANR-10-INBS-02. LCPMS was supported by a post-doctoral grant awarded by CAPES. AS Freire benefited from CNPq grants (312644/2013-2 and 311994/2016-4). EC Becker would like to thank Iole di Capua for helping during taxonomic identification, Amanda Elineau for supporting in the Tara samples processing, and Maria Lorena Romero-Martinez for suggestions and intense discussions during the manuscript writing.

Supplementary material

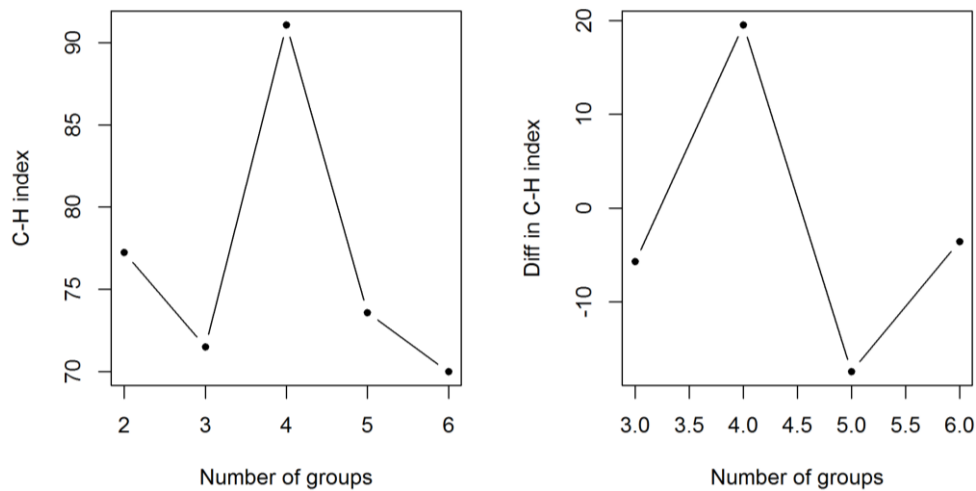


Figure S1. The optimal number of clustering groups determined via Calinski and Harabasz's index in the functional dendrogram of the relation between five functional traits and five environmental variables using average linkage clustering of 94 copepod species.

Table S1

Main features of the sampling design in the different expeditions.

Latitudinal range	Biogeographic zone	Ship	Expedition	Month/Year	No. samples
12°-20°S	Tropical gyre	<i>Tara</i> schooner	<i>Tara</i> Oceans	Oct/10	5
20°-25°S	Tropical RJ	R.V. <i>Cruzeiro do Sul</i>	MCTII	Jan/11	8
25°-30°S	Tropical SC	R.V. <i>Cruzeiro do Sul</i>	MCTII	Dec/10	5
30°-40°S	Subtropical	R.V. <i>Cruzeiro do Sul</i>	MCTII	Dec/10	6
40°-60°S	Temperate	<i>Tara</i> schooner	<i>Tara</i> Oceans	Dec/10	7
60-64°S	Polar (Antarctic)	<i>Tara</i> schooner	<i>Tara</i> Oceans	Jan/11	5

Table S2

Functional traits of the 94 selected copepod species from the South Atlantic and Southern Ocean. References are listed in the supplemental table S7. Body size represents the average adult female body length.

Species	Trophic group	Foraging behavior	Body size	Reproduction mode	Myelination	Vertical distribution
<i>Calanoides acutus</i>	Omnivorous-Herbivorous	Current feeding	4.6	Broadcasting	Myelinated	Epi-mesopelagic
<i>Calanus simillimus</i>	Omnivorous-Herbivorous	Current feeding	3.1	Broadcasting	Myelinated	Epi-mesopelagic
<i>Mesocalanus tenuicornis</i>	Omnivorous-Herbivorous	Current feeding	2.1	Broadcasting	Myelinated	Epi-bathypelagic
<i>Nannocalanus minor</i>	Omnivorous-Herbivorous	Current feeding	1.69	Broadcasting	Myelinated	Epi-mesopelagic
<i>Neocalanus gracilis</i>	Omnivorous-Herbivorous	Current feeding	2.4	Broadcasting	Myelinated	Epi-mesopelagic
<i>Neocalanus robustior</i>	Omnivorous-Herbivorous	Current feeding	3.17	Broadcasting	Myelinated	Epi-mesopelagic
<i>Undinula vulgaris</i>	Carnivorous	Cruise	2.5	Broadcasting	Myelinated	Epipelagic
<i>Eucalanus hyalinus</i>	Omnivorous	Current feeding	5.4	Broadcasting	Myelinated	Epi-mesopelagic
<i>Pareucalanus sewelli</i>	Omnivorous-Herbivorous	Current feeding	4.27	Broadcasting	Myelinated	Epipelagic
<i>Subeucalanus longiceps</i>	Herbivorous	Current feeding	3.86	Broadcasting	Myelinated	Epipelagic
<i>Rhincalanus gigas</i>	Omnivorous-Herbivorous	Current feeding	6.83	Broadcasting	Myelinated	Epi-mesopelagic
<i>Rhincalanus nasutus</i>	Omnivorous-Herbivorous	Current feeding	4.07	Broadcasting	Myelinated	Epi-bathypelagic
<i>Acrocalanus longicornis</i>	Omnivorous-Herbivorous	Current feeding	1.14	Broadcasting	Myelinated	Epipelagic
<i>Calocalanus contractus</i>	Omnivorous-Herbivorous	Current feeding	0.72	Broadcasting	Myelinated	Epipelagic
<i>Calocalanus equalicauda</i>	Omnivorous-Herbivorous	Current feeding	1.15	Broadcasting	Myelinated	Epipelagic
<i>Calocalanus pavo</i>	Omnivorous-Herbivorous	Current feeding	1	Broadcasting	Myelinated	Epipelagic
<i>Calocalanus pavoninus</i>	Omnivorous-Herbivorous	Current feeding	0.94	Broadcasting	Myelinated	Epipelagic
<i>Calocalanus plumatus</i>	Omnivorous-Herbivorous	Current feeding	0.57	Broadcasting	Myelinated	Epipelagic

<i>Calocalanus plumulosus</i>	Omnivorous-Herbivorous	Current feeding	1.07	Broadcasting	Myelinated	Epipelagic
<i>Calocalanus styliremis</i>	Omnivorous-Herbivorous	Current feeding	0.63	Broadcasting	Myelinated	Epipelagic
<i>Calocalanus tenuis</i>	Omnivorous-Herbivorous	Current feeding	1.2	Broadcasting	Myelinated	Epipelagic
<i>Mecynocera clausi</i>	Omnivorous-Herbivorous	Current feeding	1.02	Broadcasting	Myelinated	Epipelagic
<i>Paracalanus aculeatus</i>	Omnivorous-Herbivorous	Current feeding	1.08	Broadcasting	Myelinated	Epipelagic
<i>Paracalanus campaneri</i>	Omnivorous-Herbivorous	Current feeding	1.04	Broadcasting	Myelinated	Epipelagic
<i>Paracalanus denudatus</i>	Omnivorous-Herbivorous	Current feeding	0.76	Broadcasting	Myelinated	Epipelagic
<i>Paracalanus parvus</i>	Omnivorous-Herbivorous	Current feeding	0.95	Broadcasting	Myelinated	Epipelagic
<i>Paracalanus quasimodo</i>	Omnivorous-Herbivorous	Current feeding	0.85	Broadcasting	Myelinated	Epipelagic
<i>Clausocalanus arcuicornis</i>	Omnivorous-Herbivorous	Cruise	1.38	Sac-spawner	Myelinated	Epipelagic
<i>Clausocalanus brevipes</i>	Herbivorous	Cruise	1.62	Broadcasting	Myelinated	Epipelagic
<i>Clausocalanus furcatus</i>	Omnivorous-Herbivorous	Cruise	1.04	Sac-spawner	Myelinated	Epipelagic
<i>Clausocalanus ingens</i>	Omnivorous-Herbivorous	Cruise	1.67	Broadcasting	Myelinated	Epipelagic
<i>Clausocalanus laticeps</i>	Omnivorous-Herbivorous	Cruise	1.15	Broadcasting	Myelinated	Epipelagic
<i>Clausocalanus mastigophorus</i>	Omnivorous-Herbivorous	Cruise	1.55	Broadcasting	Myelinated	Epipelagic
<i>Clausocalanus parapergens</i>	Omnivorous-Herbivorous	Cruise	1.3	Sac-spawner	Myelinated	Epipelagic
<i>Clausocalanus paululus</i>	Omnivorous-Herbivorous	Cruise	0.79	Sac-spawner	Myelinated	Epipelagic
<i>Clausocalanus pergens</i>	Omnivorous-Herbivorous	Cruise	0.98	Sac-spawner	Myelinated	Epipelagic
<i>Ctenocalanus citer</i>	Omnivorous-Herbivorous	Current feeding	1.13	Broadcasting	Myelinated	Epipelagic
<i>Ctenocalanus vanus</i>	Omnivorous-Herbivorous	Current feeding	1.16	Broadcasting	Myelinated	Epipelagic
<i>Microcalanus pygmaus</i>	Omnivorous	Current feeding	0.86	Broadcasting	Myelinated	Epipelagic
<i>Euchaeta acuta</i>	Carnivorous	Current feeding	2.94	Sac-spawner	Myelinated	Epi-mesopelagic
<i>Euchaeta marina</i>	Carnivorous	Current feeding	3.19	Sac-spawner	Myelinated	Epi-mesopelagic
<i>Scolecithrix danae</i>	Detritivorous-Omnivorous	Current feeding	2.2	Broadcasting	Myelinated	Epi-mesopelagic
<i>Scolecithricella dentata</i>	Carnivorous	Current feeding	1.6	Broadcasting	Myelinated	Epi-mesopelagic
<i>Scolecithricella minor</i>	Detritivorous-Omnivorous	Current feeding	1.4	Broadcasting	Myelinated	Epi-mesopelagic
<i>Scaphocalanus curtus</i>	Carnivorous	Current feeding	1.35	Broadcasting	Myelinated	Epi-bathypelagic
<i>Scaphocalanus medius</i>	Carnivorous	Current feeding	2.4	Broadcasting	Myelinated	Epi-bathypelagic
<i>Lucicutia flavicornis</i>	Omnivorous-Herbivorous	Current feeding	1.58	Broadcasting	Amyelinated	Epi-bathypelagic
<i>Lucicutia longicornis</i>	Omnivorous-Herbivorous	Current feeding	1.9	Broadcasting	Amyelinated	Epi-bathypelagic
<i>Metridia lucens</i>	Omnivorous	Current feeding	2.01	Broadcasting	Amyelinated	Epi-bathypelagic
<i>Pleuromamma abdominalis</i>	Omnivorous	Current feeding	3.45	Broadcasting	Amyelinated	Epi-mesopelagic
<i>Pleuromamma borealis</i>	Omnivorous	Current feeding	1.78	Broadcasting	Amyelinated	Epi-mesopelagic
<i>Pleuromamma gracilis</i>	Omnivorous	Current feeding	2	Broadcasting	Amyelinated	Epi-mesopelagic

<i>Heterorhabdus papilliger</i>	Carnivorous	Current feeding	2.66	Broadcasting	Amyelinated	Epi-bathypelagic
<i>Heterorhabdus spinifrons</i>	Carnivorous	Current feeding	3.1	Broadcasting	Amyelinated	Epi-bathypelagic
<i>Centropages brachiatus</i>	Omnivorous	Mixed	2.02	Broadcasting	Amyelinated	Epipelagic
<i>Centropages violaceus</i>	Omnivorous	Mixed	1.92	Broadcasting	Amyelinated	Epipelagic
<i>Temora stylifera</i>	Omnivorous-Herbivorous	Current feeding	1.59	Broadcasting	Amyelinated	Epipelagic
<i>Temora turbinata</i>	Omnivorous-Herbivorous	Current feeding	1.29	Broadcasting	Amyelinated	Epipelagic
<i>Candacia bispinosa</i>	Carnivorous	NA	2.16	Broadcasting	Amyelinated	Epipelagic
<i>Candacia pachydactyla</i>	Carnivorous	NA	2.53	Broadcasting	Amyelinated	Epi-mesopelagic
<i>Candacia simplex</i>	Carnivorous	NA	2.32	Broadcasting	Amyelinated	Epipelagic
<i>Acartia tonsa</i>	Omnivorous-Herbivorous	Mixed	1.06	Broadcasting	Amyelinated	Epipelagic
<i>Acartia danae</i>	Omnivorous-Herbivorous	Mixed	1.05	Broadcasting	Amyelinated	Epipelagic
<i>Acartia negligens</i>	Omnivorous-Herbivorous	Mixed	1.16	Broadcasting	Amyelinated	Epipelagic
<i>Acartia longiremis</i>	Omnivorous-Herbivorous	Mixed	0.98	Broadcasting	Amyelinated	Epipelagic
<i>Labidocera acutifrons</i>	Omnivorous	Current feeding	3.87	Broadcasting	Amyelinated	Epipelagic
<i>Pontellina plumata</i>	Carnivorous	Ambush	1.69	Broadcasting	Amyelinated	Epi-mesopelagic
<i>Oithona atlantica</i>	Omnivorous	Ambush	1.22	Sac-spawner	Amyelinated	Epi-mesopelagic
<i>Oithona longispina</i>	Omnivorous	Ambush	1.24	Sac-spawner	Amyelinated	Epipelagic
<i>Oithona nana</i>	Omnivorous	Ambush	0.53	Sac-spawner	Amyelinated	Epipelagic
<i>Oithona plumifera</i>	Omnivorous	Ambush	1.01	Sac-spawner	Amyelinated	Epi-mesopelagic
<i>Oithona robusta</i>	Omnivorous	Ambush	1.51	Sac-spawner	Amyelinated	Epipelagic
<i>Oithona setigera</i>	Omnivorous	Ambush	1.25	Sac-spawner	Amyelinated	Epi-mesopelagic
<i>Oithona similis</i>	Omnivorous	Ambush	0.73	Sac-spawner	Amyelinated	Epi-bathypelagic
<i>Oithona tenuis</i>	Omnivorous	Ambush	1.15	Sac-spawner	Amyelinated	Epipelagic
<i>Oncaea media</i>	Detritivorous-Omnivorous	Cruise	0.74	Sac-spawner	Amyelinated	Epi-mesopelagic
<i>Oncaea mediterranea</i>	Detritivorous-Omnivorous	Cruise	1.2	Sac-spawner	Amyelinated	Epi-mesopelagic
<i>Oncaea venusta</i>	Detritivorous-Omnivorous	Cruise	1.04	Sac-spawner	Amyelinated	Epi-mesopelagic
<i>Oncaea waldemari</i>	Detritivorous-Omnivorous	Cruise	0.59	Sac-spawner	Amyelinated	Epipelagic
<i>Corycaeus flaccus</i>	Carnivorous	Ambush	1.67	Sac-spawner	Amyelinated	Epipelagic
<i>Corycaeus typicus</i>	Carnivorous	Ambush	1.64	Sac-spawner	Amyelinated	Epipelagic
<i>Corycaeus speciosus</i>	Carnivorous	Ambush	1.85	Sac-spawner	Amyelinated	Epipelagic
<i>Corycaeus giesbrechti</i>	Carnivorous	Ambush	0.93	Sac-spawner	Amyelinated	Epipelagic
<i>Corycaeus lautus</i>	Carnivorous	Ambush	2.85	Sac-spawner	Amyelinated	Epipelagic
<i>Farranula curta</i>	Carnivorous	Cruise	0.72	Sac-spawner	Amyelinated	Epipelagic
<i>Farranula gracilis</i>	Carnivorous	Cruise	0.92	Sac-spawner	Amyelinated	Epipelagic
<i>Farranula rostrata</i>	Carnivorous	Cruise	0.76	Sac-spawner	Amyelinated	Epipelagic

<i>Sapphirina angusta</i>	Carnivorous	Cruise	4	Sac-spawner	Amyelinated	Epipelagic
<i>Sapphirina iris</i>	Carnivorous	Cruise	6.3	Sac-spawner	Amyelinated	Epipelagic
<i>Sapphirina nigromaculata</i>	Carnivorous	Cruise	2.18	Sac-spawner	Amyelinated	Epipelagic
<i>Sapphirina opalina</i>	Carnivorous	Cruise	3.15	Sac-spawner	Amyelinated	Epipelagic
<i>Clytemnestra scutellata</i>	Detritivorous-Omnivorous	Cruise	1.14	Sac-spawner	Amyelinated	Epi-mesopelagic
<i>Macrosetella gracilis</i>	Omnivorous-Herbivorous	Particle feeder	1.34	Sac-spawner	Amyelinated	Epi-bathypelagic
<i>Microsetella rosea</i>	Detritivorous-Omnivorous	Particle feeder	0.75	Sac-spawner	Amyelinated	Epi-bathypelagic

Table S3

Species with trait gaps not included in the statistical analysis. NA: not available. Body size: mean female size (mm).

Species	Trophic group	Foraging behavior	Body size	Reproduction mode	Myelination	Vertical distribution
<i>Copilia mirabilis</i>	Detritivorous	Active	3.96	Sac-spawning	Amyelinated	Epi-mesopelagic
<i>Delius nudus</i>	NA	Active	0.55	NA	Myelinated	Epipelagic
<i>Haloptilus longicornis</i>	Omnivorous-Carnivorous	Active	2.3	Broadcasting	Amyelinated	Epi-bathypelagic
<i>Lubbockia squillimana</i>	NA	NA	1.53	Sac-spawning	Amyelinated	Epi-mesopelagic
<i>Monothula subtilis</i>	NA	Active	0.49	Sac-spawning	Amyelinated	Epi-mesopelagic
<i>Paralabidocera antarctica</i>	Herbivorous	NA	1.8	Broadcasting	Amyelinated	Epipelagic
<i>Stephos longipes</i>	Herbivorous	NA	0.84	Broadcasting	Myelinated	Epi-hyperbenthic
<i>Temoropia mayumbaensis</i>	NA	NA	0.87	NA	Myelinated	Epi-bathypelagic
<i>Triconia conifera</i>	Detritivorous-Omnivorous	Active	1	Sac-spawning	Amyelinated	Epi-bathypelagic
<i>Vetтория parva</i>	NA	NA	0.86	Sac-spawning	Amyelinated	Epi-mesopelagic

Table S4

Copepod species mean (\pm standard deviation) abundances and presence (1) or absence (0) in the different biogeographic zones. TGY: Tropical gyre; TRJ: Tropical Rio de Janeiro; TSC: Tropical Santa Catarina; SUB: Subtropical; TEM: Temperate; POL: Polar. Abundant species are highlighted in bold.

Biogeographic zone	TGY	TRJ	TSC	SUB	TEM	POL
Mean abundance (ind.m⁻³)	119.7	64.9	496.9	1054.9	1729.6	518.3
No. of species	41	46	56	55	43	17
Calanoida						
<i>Calanoides acutus</i> (Giesbrecht, 1902)	0	0	0	0	0	4.4 \pm 3.3
<i>Calanus simillimus</i> Giesbrecht, 1902**	0	0	0	0	284.7 \pm 172.9	0
<i>Mesocalanus tenuicornis</i> (Dana, 1849)	1.2 \pm 1.2	0	0	0	0.5 \pm 0.5	0
<i>Nannocalanus minor</i> (Claus, 1863)*	1.2 \pm 0.6	1.1 \pm 0.6	8.6 \pm 4.3	8.4 \pm 5.8	2.7 \pm 2.0	0
<i>Neocalanus gracilis</i> (Dana, 1849)	0	0.7 \pm 0.3	2.3 \pm 2.3	0.6 \pm 0.4	0	0
<i>Neocalanus robustior</i> (Giesbrecht, 1888)	2.4 \pm 1.7	0	0	0	0	0
<i>Undinula vulgaris</i> (Dana, 1849)	0.1 \pm 0.1	0	0	0	0	0
<i>Eucalanus hyalinus</i> (Claus, 1866)	0	0	0	0	0.7 \pm 0.7	0
<i>Pareucalanus sewelli</i> (Fleminger, 1973)	0	0.1 \pm 0.1	1.7 \pm 1.1	0	0	0
<i>Subeucalanus longiceps</i> (Matthews, 1925)	0	0	0	0	4.8 \pm 3.5	0
<i>Rhincalanus gigas</i> Brady, 1883	0	0	0	0	0	1.8 \pm 1.8
<i>Rhincalanus nasutus</i> Giesbrecht, 1888	0	0	0	0	0.1 \pm 0.1	0
<i>Acrocalanus longicornis</i> Giesbrecht, 1888	0	0.3 \pm 0.2	1.7 \pm 0.8	1.5 \pm 1.5	0	0
<i>Calocalanus contractus</i> Farran, 1926	0	0	1.5 \pm 1.5	0	0	0
<i>Calocalanus equalicauda</i> (Bernard, 1958)	0	0	3.1 \pm 3.1	4.6 \pm 4.6	0	0
<i>Calocalanus pavo</i> (Dana, 1849)	0.3 \pm 0.3	0.4 \pm 0.3	0.8 \pm 0.6	2.0 \pm 1.5	1.6 \pm 1.2	0
<i>Calocalanus pavoninus</i> Farran, 1936*	2.4 \pm 0.7	0.5 \pm 0.4	4.6 \pm 2.3	67.4 \pm 67.4	0	0
<i>Calocalanus plumatus</i> Shmeleva, 1965	0	0	0.8 \pm 0.8	0	0	0
<i>Calocalanus plumulosus</i> (Claus, 1863)	0	0.1 \pm 0.1	0	0	0	0
<i>Calocalanus styliremis</i> Giesbrecht, 1888	0.1 \pm 0.1	0.3 \pm 0.2	3.6 \pm 1.8	2.0 \pm 0.7	1.4 \pm 1.4	0
<i>Calocalanus tenuis</i> Farran, 1926	0	0	0	0	0.3 \pm 0.3	0
<i>Delibus nudus</i> (Sewell, 1929)	0	0.1 \pm 0.1	0	0	0	0
<i>Mecynocera clausi</i> Thompson, 1888*	3.4 \pm 1.8	0.8 \pm 0.4	9.9 \pm 2.6	20.1 \pm 7.5	11.1 \pm 7.2	0.003 \pm 0.003
<i>Paracalanus aculeatus</i> Giesbrecht, 1888	0.3 \pm 0.3	0.5 \pm 0.3	1.3 \pm 0.9	7.7 \pm 7.7	1.1 \pm 1.1	0
<i>Paracalanus campaneri</i> Björnberg, 1980	0	0	6.0 \pm 3.5	3.1 \pm 3.1	0	0
<i>Paracalanus denudatus</i> Sewell, 1929	1.0 \pm 0.9	0	0.3 \pm 0.3	0	0	0

<i>Paracalanus parvus</i>-Group (Claus, 1863)**	0	0.4 ± 0.2	1.0 ± 0.6	7.9 ± 4.9	30.0 ± 25.6	0.003 ± 0.003
<i>Paracalanus quasimodo</i> Bowman, 1971	0	1.7 ± 0.7	0.8 ± 0.8	1.5 ± 1.5	4.4 ± 4.4	0
<i>Clausocalanus arcuicornis</i> (Dana, 1849)	0.4 ± 0.4	0.2 ± 0.1	7.1 ± 2.5	0.2 ± 0.2	0	0
<i>Clausocalanus brevipes</i> Frost & Fleminger, 1968**	0	0	0.4 ± 0.4	1.5 ± 1.5	224.0 ± 211.7	0.03 ± 0.03
<i>Clausocalanus furcatus</i> (Brady, 1883)*	11.5 ± 5.3	6.4 ± 2.5	56.8 ± 33.7	227.1 ± 224.9	0.1 ± 0.1	0
<i>Clausocalanus ingens</i> Frost & Fleminger, 1968	0	0	0	2.3 ± 2.3	0	0.003 ± 0.003
<i>Clausocalanus laticeps</i> Farran, 1929	0	0	0	0	9.5 ± 6.0	0
<i>Clausocalanus mastigophorus</i> (Claus, 1863)	0.1 ± 0.1	0	0	0	0	0
<i>Clausocalanus parapergens</i> Frost & Fleminger, 1968	0	0	0.3 ± 0.3	0.6 ± 0.5	0.5 ± 0.3	0
<i>Clausocalanus paululus</i> Farran, 1926	2.4 ± 1.7	0.8 ± 0.8	8.2 ± 4.6	1.4 ± 0.8	21.8 ± 21.8	0
<i>Clausocalanus pergens</i> Farran, 1926	0	0	0	11.5 ± 10.6	4.5 ± 4.5	0
<i>Ctenocalanus citer</i> Heron & Bowman, 1971**	0	0	0	1.5 ± 1.5	9.6 ± 7.7	37.6 ± 22.9
<i>Ctenocalanus vanus</i> Giesbrecht, 1888	0	0	9.0 ± 5.9	14.5 ± 13.7	23.0 ± 21.6	0
<i>Microcalanus pygmaeus</i> (Sars, 1900)	0	0	0	0	0	0.1 ± 0.1
<i>Euchaeta acuta</i> Giesbrecht, 1892	0	0	0	0	0.2 ± 0.2	0
<i>Euchaeta marina</i> (Prestandrea, 1833)	3.7 ± 1.0	0.1 ± 0.1	0	1.5 ± 1.5	0	0
<i>Scolecithrix danae</i> (Lubbock, 1856)	1.5 ± 0.4	0.1 ± 0.1	3.1 ± 1.7	1.5 ± 1.5	0	0
<i>Scolecithricella dentata</i> (Giesbrecht, 1892)	0.4 ± 0.4	0	0.3 ± 0.3	0	0	0
<i>Scolecithricella minor</i> (Brady, 1883)**	0	0	0.0	0	30.5 ± 21.1	0
<i>Stephos longipes</i> Giesbrecht, 1902	0	0	0	0	0	0.03 ± 0.03
<i>Scaphocalanus curtus</i> (Farran, 1926)	0	0	0	0.1 ± 0.1	0	0
<i>Scaphocalanus medius</i> (Sars, 1907)	0	0	0	1.5 ± 1.5	0	0
<i>Lucicutia flavicornis</i> (Claus, 1863)	0.3 ± 0.3	0.4 ± 0.3	0.8 ± 0.8	0	0	0
<i>Lucicutia longicornis</i> (Giesbrecht, 1889)	0	0	2.0 ± 1.3	0	0	0
<i>Haloptilus longicornis</i> (Claus, 1863)	0.1 ± 0.1	0	0.4 ± 0.4	0	0	0
<i>Metridia lucens</i> Boeck, 1864	0	0	0	0	17.4 ± 17.4	0
<i>Pleuromamma abdominalis</i> (Lubbock, 1856)	0.1 ± 0.1	0	0	0	0.5 ± 0.5	0
<i>Pleuromamma borealis</i> (F. Dahl, 1893)	0	0	0	0	0.9 ± 0.9	0
<i>Pleuromamma gracilis</i> (Claus, 1863)	0.4 ± 0.4	0.1 ± 0.1	0	1.5 ± 1.0	9.7 ± 8.6	0
<i>Heterorhabdus papilliger</i> Claus, 1863	0	0	0.8 ± 0.8	0.4 ± 0.4	0.5 ± 0.5	0
<i>Heterorhabdus spinifrons</i> (Claus, 1863)	0.1 ± 0.1	0	0	0	0	0
<i>Centropages brachiatus</i> (Dana, 1849)	0	0	0	0	28.8 ± 28.8	0
<i>Centropages violaceus</i> (Claus, 1863)	0	0	0.8 ± 0.8	0	0	0
<i>Temora stylifera</i> Dana, 1849*	0	3.4 ± 2.0	11.3 ± 6.0	17.5 ± 16.7	0	0

<i>Temora turbinata</i> (Dana, 1849)	0	0.3 ± 0.2	3.4 ± 2.4	3.1 ± 3.1	0	0
<i>Temoropia mayumbaensis</i> T. Scott, 1894	0.1 ± 0.1	0	0	0.3 ± 0.3	0	0
<i>Candacia bispinosa</i> (Claus, 1863)	0	0	0.3 ± 0.3	0.3 ± 0.3	0	0
<i>Candacia pachydactyla</i> (Dana, 1849)	0.1 ± 0.1	0	0	0	0	0
<i>Candacia simplex</i> (Giesbrecht, 1889)	0.3 ± 0.2	0.1 ± 0.1	0.8 ± 0.8	0	0	0
<i>Acartia (Acartia) danae</i> Giesbrecht, 1889	0.3 ± 0.3	0	0.8 ± 0.8	2.2 ± 0.7	1.6 ± 1.1	0
<i>Acartia (Acartiura) longiremis</i> (Lilljeborg, 1853)	0	0.1 ± 0.1	4.0 ± 1.7	1.9 ± 1.2	0	0
<i>Acartia (Acartia) negligens</i> Dana, 1849	1.6 ± 0.8	0	5.3 ± 4.5	13.1 ± 4.9	0.6 ± 0.4	0.03 ± 0.03
<i>Acartia (Acanthacartia) tonsa</i> Dana, 1849	0	0	0	1.5 ± 1.5	2.3 ± 2.3	0
<i>Paralabidocera antarctica</i> (I.C. Thompson, 1898)	0	0	0	0	0	0.1 ± 0.1
<i>Labidocera acutifrons</i> (Dana, 1849)	0	0	0.8 ± 0.8	0	0	0
<i>Pontellina plumata</i> (Dana, 1849)	0.1 ± 0.1	0	0.3 ± 0.3	0	0	0
Cyclopoida						
<i>Oithona atlantica</i> Farran, 1908**	0	0	0	0	83.7 ± 52.3	0.01 ± 0.01
<i>Oithona longispina</i> Nishida, 1977	0	0	0	1.2 ± 0.8	3.8 ± 2.6	0
<i>Oithona nana</i> Giesbrecht, 1892	0	0	0	0.2 ± 0.2	0	0
<i>Oithona plumifera</i> Baird, 1843*	11.2 ± 2.8	0.7 ± 0.3	12.4 ± 4.8	47.1 ± 44.0	0.2 ± 0.2	0
<i>Oithona robusta</i> Giesbrecht, 1891	0	0.1 ± 0.1	1.5 ± 1.1	1.5 ± 1.5	0	0
<i>Oithona setigera</i> (Dana, 1849)	0.8 ± 0.4	0.3 ± 0.1	4.0 ± 1.7	4.6 ± 4.6	0	0
<i>Oithona similis</i>-Group Claus, 1866**	0	0	1.7 ± 1.7	2.3 ± 2.3	180.7 ± 86.4	395.5 ± 241.6
<i>Oithona tenuis</i> Rosendorn, 1917*	6.7 ± 1.1	0.5 ± 0.3	10.6 ± 1.7	6.0 ± 3.3	2.2 ± 1.7	0
<i>Monothula subtilis</i> (Giesbrecht, 1892)	0	0	0	0	0	1.5 ± 1.1
<i>Oncaea media</i> Giesbrecht, 1891*	1.1 ± 0.7	0.4 ± 0.2	14.7 ± 5.8	11.3 ± 8.9	4.6 ± 4.3	0
<i>Oncaea mediterranea</i> (Claus, 1863)	1.0 ± 0.8	1.3 ± 0.5	1.4 ± 0.9	0.1 ± 0.1	0	0
<i>Oncaea venusta</i> Philippi, 1843*	3.9 ± 1.7	3.8 ± 1.6	43.3 ± 11.1	92.4 ± 90.0	4.5 ± 4.3	0
<i>Oncaea waldemari</i> Bersano & Boxshall, 1994	0	0	0	0	0	0.003 ± 0.003
<i>Triconia conifera</i> (Giesbrecht, 1891)	0	0	1.5 ± 1.5	0.2 ± 0.2	0.2 ± 0.2	0
<i>Lubbockia squillimana</i> Claus, 1863	0	0.7 ± 0.3	0	0.3 ± 0.3	0	0
<i>Corycaeus (Corycaeus) speciosus</i> Dana, 1849*	1.4 ± 0.5	0.5 ± 0.3	3.4 ± 2.1	19.9 ± 19.9	0	0
<i>Corycaeus (Agetus) flaccus</i> Giesbrecht, 1891	1.5 ± 0.2	0.2 ± 0.1	0	0	0	0.1 ± 0.1
<i>Corycaeus (Agetus) typicus</i> (Krøyer, 1849)	0	0	0.4 ± 0.4	0	0	0
<i>Corycaeus (Onychocorycaeus) giesbrechti</i> F. Dahl, 1894*	0	1.0 ± 0.7	10.8 ± 8.1	23.0 ± 23.0	0.1 ± 0.1	0
<i>Corycaeus (Urocorycaeus) lautus</i> Dana, 1849	0.3 ± 0.3	0	0	0	0	0
<i>Farranula curta</i> (Farran, 1911)	0	0	0	1.6 ± 1.2	0.1 ± 0.1	0
<i>Farranula gracilis</i> (Dana, 1849)*	22.0 ± 4.3	4.2 ± 1.3	41.4 ± 10.2	31.5 ± 30.5	0	0

<i>Farranula rostrata</i> (Claus, 1863)	0.1 ± 0.1	0.1 ± 0.1	1.2 ± 0.8	11.6 ± 7.2	2.5 ± 1.6	0
<i>Copilia mirabilis</i> Dana, 1849	0.1 ± 0.1	2.2 ± 2.1	0.3 ± 0.3	0	0	0
<i>Sapphirina angusta</i> Dana, 1849	0	0	0	0.1 ± 0.1	0	0
<i>Sapphirina iris</i> Dana, 1849	0	0.1 ± 0.1	0	0	0	0
<i>Sapphirina nigromaculata</i> Claus, 1863	0	0.1 ± 0.1	0.3 ± 0.3	0	0	0
<i>Sapphirina opalina</i> Dana, 1849	0	0.3 ± 0.3	0	0	0	0
Harpacticoida						
<i>Clytemnestra scutellata</i> Dana, 1848	0	0	0	0.1 ± 0.1	0	0
<i>Macrosetella gracilis</i> (Dana, 1848)	0.4 ± 0.2	0.8 ± 0.3	0.8 ± 0.8	2.9 ± 1.6	0	0
<i>Microsetella rosea</i> (Dana, 1848)	0	0.1 ± 0.1	0	0	0	0
<i>Vetтория parva</i> (Farran, 1936)	0	0	0.3 ± 0.3	0	0	0

*abundant species in tropical and subtropical zones.

**abundant species in temperate and polar zones.

Table S5

Species and functional indices in the different biogeographic zones – mean (± standard deviation).

Biogeographic zones	Species Richness	Functional Richness	Functional Evenness	Functional Divergence	Functional Dispersion
Tropical GY	19 ± 6	0.75 ± 0.08	0.53 ± 0.03	0.93 ± 0.04	0.26 ± 0.02
Tropical RJ	16 ± 3	0.61 ± 0.10	0.63 ± 0.04	0.88 ± 0.04	0.26 ± 0.03
Tropical SC	22 ± 7	0.70 ± 0.17	0.52 ± 0.03	0.93 ± 0.04	0.26 ± 0.02
Subtropical	20 ± 7	0.73 ± 0.16	0.43 ± 0.07	0.91 ± 0.09	0.23 ± 0.05
Temperate	11 ± 7	0.75 ± 0.27	0.44 ± 0.15	0.79 ± 0.16	0.22 ± 0.05
Polar	5 ± 3	0.16 ± 0.14	0.30 ± 0.19	0.97 ± 0.03	0.08 ± 0.08

Table S6

RLQ axes correlations with each environmental variable. DCM: depth chlorophyll-a maximum. NID: dissolved inorganic nitrogen.

Environmental variables	Axis 1	Axis 2
Temperature	0.92	0.57
Chlorophyll-a DCM	-0.18	0.39
Oxygen	-0.89	-0.64
Silicate	-0.92	0.11
NID	-0.95	0.00

Table S7

Results of standard effect sizes (SES) based on the null model for functional richness. ns.: non significant; ***: $P < 0.05$.

Station	Zones	Latitude	SESFRic	sigFRic
TARA_73	TGY	-12.51	17.75	***
TARA_74	TGY	-16.07	15.64	***
TARA_75	TGY	-18.03	14.57	***
TARA_76d	TGY	-20.99	22.44	***
TARA_76n	TGY	-20.99	24.19	***
CZSUL_74	TRJ	-21.45	17.12	***
CZSUL_75	TRJ	-21.83	17.97	***
CZSUL_84	TRJ	-22.3	11.07	***
CZSUL_86	TRJ	-22.73	12.48	***
CZSUL_98	TRJ	-23.23	12.96	***
CZSUL_99	TRJ	-23.65	10.13	***
CZSUL_107	TRJ	-23.99	7.13	***
CZSUL_108	TRJ	-24.01	12.56	***
TARA_77	TSC	-24.59	29.77	***
CZSUL_65	TSC	-25.05	15.25	***
CZSUL_64	TSC	-25.82	14.10	***
CZSUL_63	TSC	-26.58	24.08	***

CZSUL_51	TSC	-27.34	8.29	***
CZSUL_50	TSC	-28.25	13.85	***
CZSUL_40	SUB	-29.53	26.68	***
CZSUL_27	SUB	-30.86	15.02	***
CZSUL_26	SUB	-32.08	17.66	***
CZSUL_9	SUB	-33.66	8.97	***
TARA_79	SUB	-34.43	8.77	***
CZSUL_8	SUB	-34.86	9.17	***
TARA_80d	TEM	-40.64	13.74	***
TARA_80n	TEM	-40.64	19.43	***
TARA_81	TEM	-44.54	6.02	***
TARA_82d	TEM	-47.17	3.54	***
TARA_82n	TEM	-47.17	0.67	ns.
TARA_83	TEM	-54.74	2.05	***
TARA_89	TEM	-57.73	1.73	ns.
TARA_84d	POL	-60.32	-0.27	ns.
TARA_85	POL	-62.14	4.53	***
TARA_87	POL	-63.85	3.97	***
TARA_86	POL	-64.35	0.52	ns.

Table S8

Copepod trait references.

Australian Marine Zooplankton: A taxonomic guide and atlas. Available from: http://www.imas.utas.edu.au/zooplankton/ .
Atkinson, A. (1998) Life cycle strategies of epipelagic copepods in the Southern Ocean. <i>Journal of Marine Systems</i> , 15 , 289-311.
Barton, A.D., Pershing, A.J., Litchman, E., Record, N.R., Edwards, K.F., Finkel, Z.V., Kjørboe, T. & Ward, B.A. (2013) The biogeography of marine plankton traits. <i>Ecology Letters</i> , 16 , 522–534.
Benedetti, F., Gasparini, S., Ayata, S.D. (2016) Identifying copepod functional groups from species functional traits. <i>Journal of Plankton Research</i> , 38 ,159–166.
Benedetti, F., Vogt, M., Righetti, D., Guilhaumon. F. & Ayata, S.D. (2018) Do functional groups of planktonic copepods differ in their ecological niches? <i>Journal of Biogeography</i> , 45 , 604–616.
Björnberg. T.K.S. (1981) Copepoda, p. 587-679. In: Boltovskoy D. (Ed.) Atlas del zooplancton del Atlántico sudoccidental y metodos de trabajos com el zooplancton mariño. Mar del Plata, INIDEP, 330 936p.
Böttger-Schnack, R. (1990) Community structure and vertical distribution of cyclopoid copepods in the Red Sea. <i>Marine Biology</i> , 106 , 473-85.

Böttger-Schnack, R. (1996) Vertical structure of small metazoan plankton, especially non calanoid copepods. I. Deep Arabian Sea. <i>Journal of Plankton Research</i> , 18 , 1073-101.
Böttger-Schnack, R. & Schnack, D. (1989) Vertical distribution and population structure of <i>Macrosetella gracilis</i> (Copepoda: Harpacticoida) in the Red Sea in relation to the occurrence of <i>Oscillatoria (Trichodesmium)</i> spp. (Cyanobacteria). <i>Marine Ecology Progress Series</i> , 52 , 17-31.
Boxshall, G.A. & Halsey, S.H. (2004) An introduction to copepod diversity: Ray Society.
Bradford-Grieve, J.M., Markhaseva, E.L., Rocha, C.E.F. & Abiahy, B. (1999) Copepoda. In: Boltovskoy D. (Ed.). South Atlantic Zooplankton. Leiden, Backhuys Publishers, 2 , 869-1098.
Brun, P., Payne, M.R. & Kiørboe, T. (2017) A trait database for marine copepods. <i>Earth System Science Data</i> , 9 , 99–113.
Brun, P., Payne, M.R. & Kiørboe, T. (2016) Trait biogeography of marine copepods – an analysis across scales. <i>Ecology Letters</i> , 19 , 1403–1413.
Di Carlo, B.S., Ianora, A., Fresi, E. & Hure, J. (1984) Vertical zonation patterns for Mediterranean copepods from the surface to 3000 m at a fixed station in the Tyrrhenian Sea. <i>Journal of Plankton Research</i> , 6 , 1031-1056.
Eberl, R. & Carpenter, E.J. (2007) Association of the copepod <i>Macrosetella gracilis</i> with the cyanobacterium <i>Trichodesmium</i> spp. in the North Pacific Gyre. <i>Marine Ecology Progress Series</i> , 333 , 205-212.
Go Y-B, Oh B-C, Terazaki M. (1998) Feeding behavior of the poecilostomatoid copepods <i>Oncaea</i> spp. on chaetognaths. <i>Journal of marine systems</i> , 15 , 475-82.
Kiørboe, T. (2011) How zooplankton feed: Mechanisms, traits and trade-offs. <i>Biological Reviews</i> , 86 , 311–339.
Kuriyama, M. & Nishida, S. (2006) Species diversity and niche-partitioning in the pelagic copepods of the family Scolecitrichidae (Calanoida). <i>Crustaceana</i> , 293-317.
Lenz, P. H. (2012) The biogeography and ecology of myelin in marine copepods. <i>Journal of plankton research</i> , 34 , 575-589.
Litchman E, Ohman MD, Kiørboe T (2013) Trait-based approaches to zooplankton communities. <i>Journal of Plankton Research</i> , 35 , 473–484.
Maar, M., Visser, A. W., Nielsen, T. G., Stips, A., & Saito, H. (2006) Turbulence and feeding behaviour affect the vertical distributions of <i>Oithona similis</i> and <i>Microsetella norwegica</i> . <i>Marine Ecology Progress Series</i> , 313 , 157-172.
Mazzocchi MG, Paffenhöfer GA (1999) Swimming and feeding behaviour of the planktonic copepod <i>Clausocalanus furcatus</i> . <i>Journal of Plankton Research</i> , 21 , 1501–1518.
Mauchline, J. (1998) The Biology of Calanoid Copepods, <i>Advances in Marine Biology</i> , 33.
McGinty N, Barton AD, Record NR, Finkel Z V., Irwin AJ (2018) Traits structure copepod niches in the North Atlantic and Southern Ocean. <i>Marine Ecology Progress Series</i> , 601 , 109–126.
Minoda, T. (1971) Pelagic Copepoda in the Bering Sea and the northwestern North Pacific with special reference to their vertical distribution. Memoirs of the Faculty of Fisheries Hokkaido University, 18 , 1-74.
Nishida, S. (1985) Taxonomy and distribution of the family Oithonidae (Copepoda, Cyclopoida) in the Pacific and Indian Oceans. Bulletin of the Ocean Research Institute of the University of Tokyo, 20 , 1-167.
Ohtsuka, S., Soh, H. Y. & Nishida, S. (1997) Evolutionary switching from suspension feeding to carnivory in the calanoid family Heterorhabdidae (Copepoda). <i>Journal of Crustacean Biology</i> , 17 , 577-595.
Peralba, À., Mazzocchi, M.G. & Harris, R.P. (2017) Niche separation and reproduction of <i>Clausocalanus</i> species (Copepoda, Calanoida) in the Atlantic Ocean. <i>Progress in Oceanography</i> , 158 , 185–202.
Pomerleau, C., Sastri, A. R. & Beisner, B. E. (2015) Evaluation of functional trait diversity for marine zooplankton communities in the Northeast subarctic Pacific Ocean. <i>Journal of Plankton Research</i> , 37 , 712-726.

Razouls, C., Bovée, F. de, Kouwenberg, J. & Desreumaux, N. (2005-2020) Diversity and Geographic Distribution of Marine Planktonic Copepods. Available from: http://copepodes.obs-banyuls.fr/en/ .
Saiz, E. & Kiørboe, T. (1995) Predatory and suspension feeding of the copepod <i>Acartia tonsa</i> in turbulent environments. <i>Marine Ecology Progress Series</i> , 122 , 147-158.
Schnack-Schiel, S.B. (2010) <i>Stephos longipes</i> – ein Eiscopepode.
Scripps Institution of Oceanography: Zooplankton Guide, [online] Available from: https://scripps.ucsd.edu/zooplanktonguide/ .
Steinberg, D.K., Silver, M.W., Pilskaln, C.H., Coale, S.L. & Paduan, J.B. (1994) Midwater zooplankton communities on pelagic detritus (giant larvacean houses) in Monterey Bay, California. <i>Limnology and Oceanography</i> , 39 , 1606-1620.
Timonin, A.G., (1971) The structure of plankton communities of the Indian Ocean. <i>Marine Biology</i> , 9 (4), 281-289.
Venello, T.A., Sastri, A.R., Galbraith, M.D. & Dower, J.F. (2021) Zooplankton functional group responses to environmental drivers off the west coast of Vancouver Island, Canada. <i>Progress in Oceanography</i> , 190 , 102482.
Walter, T.C. & Boxshall, G. (2019) World of Copepods database. Available from: http://www.marinespecies.org/copepoda/ .
Yamaguchi, A., Ikeda, T. & Hirakawa, K. (1999) Diel vertical migration, population structure and life cycle of the copepod <i>Scolecithricella minor</i> (Calanoida: Scolecitrichidae) in Toyama Bay, southern Japan Sea. <i>Plankton biology and ecology</i> , 46 , 54-61.
* Personal communication: Iole Di Capua, Claudia Castellani.

References

- Acha, E.M., Mianzan, H.W., Guerrero, R.A., Favero, M. & Bava, J. (2004) Marine fronts at the continental shelves of austral South America. *Journal of Marine Systems*, **44**, 83–105.
- Acha, E.M., Viñas, M.D., Derisio, C., Alemany, D., Piola, A.R. (2020) Large-scale geographic patterns of pelagic copepods in the southwestern South Atlantic. *Journal of Marine Systems*, **204**, 103281.
- Atkinson, A. (1998) Life cycle strategies of epipelagic copepods in the Southern Ocean. *Journal of Marine Systems*, **15**(1-4), 289-311.
- Atkinson, A., Ward, P., Hunt, B., Pakhomov, E. & Hosie, G. (2012) An overview of Southern Ocean zooplankton data: abundance, biomass, feeding and functional relationships. *CCAMLR Science*, **19**, 171–218.
- Barton, A.D., Pershing, A.J., Litchman, E., Record, N.R., Edwards, K.F., Finkel, Z. V., Kiørboe, T. & Ward, B.A. (2013) The biogeography of marine plankton traits. *Ecology Letters*, **16**, 522–534.
- Beaugrand, G., Edwards, M. & Legendre, L. (2010) Marine biodiversity, ecosystem functioning, and carbon cycles. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 10120–10124.

- Becker, É.C., Eiras Garcia, C.A. & Freire, A.S. (2018) Mesozooplankton distribution, especially copepods, according to water masses dynamics in the upper layer of the Southwestern Atlantic shelf (26°S to 29°S). *Continental Shelf Research*, **166**, 10–21.
- Benedetti, F., Ayata, S., Irisson, J., Adloff, F. & Guilhaumon, F. (2018a) Climate change may have minor impact on zooplankton functional diversity in the Mediterranean Sea. *Diversity and Distributions*, **25**, 568–581.
- Benedetti, F., Gasparini, S. & Ayata, S.-D. (2015) Identifying copepod functional groups from species functional traits. *Journal of Plankton Research*, **38**, 159–166.
- Benedetti, F., Vogt, M., Righetti, D., Guilhaumon, F. & Ayata, S.-D. (2018b) Do functional groups of planktonic copepods differ in their ecological niches? *Journal of Biogeography*, **45**, 604–616.
- Björnberg, T.K.S. (1981) Copepoda, p. 587-679. In: Boltovskoy D. (Ed.) Atlas del zooplancton del Atlántico sudoccidental y metodos de trabajos com el zooplancton mariño. Mar del Plata, *INIDEP*, 330-936.
- Borcard, D., Gillet, F. & Legendre, P. (2011) *Numerical Ecology with R*, Springer New York, New York, NY.
- Bordin, L.H., Machado, E. da C., Carvalho, M., Freire, A.S. & Fonseca, A.L.D.O. (2019) Nutrient and carbon dynamics under the water mass seasonality on the continental shelf at the South Brazil Bight. *Journal of Marine Systems*, **189**, 22–35.
- Bradford-Grieve, J.M., Markhaseva, E.L., Rocha, C.E.F., Abiahy, B. (1999) Copepoda. In: Boltovskoy D. (Ed.). South Atlantic Zooplankton. *Leiden, Backhuys Publishers*, **2**: 869- 1098.
- Brandão, M.C., Garcia, C.A.E. & Freire, A.S. (2015) Large-scale spatial variability of decapod and stomatopod larvae along the South Brazil Shelf. *Continental Shelf Research*, **107**, 11–23.
- Brandão, M.C., Benedetti, F., Martini, S., Soviadan, Y.D., Irisson, J.-O., Romagnan, J.-B., Elineau, A., Desnos, C., Jalabert, L., Freire, A.S., Picheral, M., Guidi, L., Gorsky, G., Bowler, C., Karp-Boss, L., Henry, N., de Vargas, C., Sullivan, M.B., Tara Oceans Consortium Coordinators, Stemmann, L. & Lombard, F. (2021) Macroscale patterns of oceanic zooplankton composition and size structure. *Scientific Reports*, **11**, 15714.
- Brandini, F.P., Tura, P.M. & Santos, P.P.G.M. (2018) Ecosystem responses to biogeochemical fronts in the South Brazil Bight. *Progress in Oceanography*, **164**,

52–62.

- Brun, P., Payne, M.R. & Kjørboe, T. (2017) A trait database for marine copepods. *Earth System Science Data*, **9**, 99–113.
- Brun, P., Payne, M.R. & Kjørboe, T. (2016) Trait biogeography of marine copepods - an analysis across scales. *Ecology Letters*, **19**, 1403–1413.
- Calbet, A. & Agustí, S. (1999) Latitudinal changes of copepod egg production rates in Atlantic waters: Temperature and food availability as the main driving factors. *Marine Ecology Progress Series*, **181**, 155–162.
- Campos, P.C., Möller, O.O., Piola, A.R. & Palma, E.D. (2013) Seasonal variability and coastal upwelling near Cape Santa Marta (Brazil). *Journal of Geophysical Research: Oceans*, **118**, 1420–1433.
- Cardinale, B.J., Palmer, M.A. & Collins, S.L. (2002) Species diversity enhances ecosystem functioning through interspecific facilitation. *Nature*, **415**, 426–429.
- Cepeda, G.D., Viñas, M.D., Molinari, G.N., Hozbor, M.C., Silva, R.I., Martínez, A. & Acha, E.M. (2020) The impact of Río de la Plata plume favors the small-sized copepods during summer. *Estuarine, Coastal and Shelf Science*, **245**, 107000.
- Chaudhary, C., Saeedi, H., & Costello, M. J. (2016) Bimodality of latitudinal gradients in marine species richness. *Trends in Ecology & Evolution*, **31**(9), 670-676.
- Combes, V. & Matano, R.P. (2014) A two-way nested simulation of the oceanic circulation in the Southwestern Atlantic. *Journal of Geophysical Research: Oceans*, **119**, 731–756.
- Cornils, A., Sieger, R., Mizdalski, E., Schumacher, S., Grobe, H. & Schnack-Schiel, S.B. (2018) Copepod species abundance from the Southern Ocean and other regions (1980-2005) - A legacy. *Earth System Science Data*, **10**, 1457–1471.
- Cornils, A., Wend-Heckmann, B. & Held, C. (2017) Global phylogeography of *Oithona similis* s.l. (Crustacea, Copepoda, Oithonidae) – A cosmopolitan plankton species or a complex of cryptic lineages? *Molecular Phylogenetics and Evolution*, **107**, 473–485.
- Cornwell, L.E., Fileman, E.S., Bruun, J.T., Hirst, A.G., Tarran, G.A., Findlay, H.S., Lewis, C., Smyth, T.J., McEvoy, A.J. & Atkinson, A. (2020) Resilience of the Copepod *Oithona similis* to Climatic Variability: Egg Production, Mortality, and Vertical Habitat Partitioning. *Frontiers in Marine Science*, **7**, 1–15.
- Da Rosa, J. da C.L., Monteiro-Ribas, W.M. & Fernandes, L.D. de A. (2016) Herbivorous copepods with emphasis on dynamic *Paracalanus quasimodo* in an upwelling

- region. *Brazilian Journal of Oceanography*, **64**, 67–74.
- De Bello, F. (2012) The quest for trait convergence and divergence in community assembly: are null-models the magic wand? *Global Ecology and Biogeography*, **21**, 312–317.
- De Macedo-Soares, L.C.P., Garcia, C.A.E., Freire, A.S. & Muelbert, J.H. (2014) Large-scale ichthyoplankton and water mass distribution along the South Brazil shelf. *PLoS ONE*, **9**, 1–14.
- Dolan, J. R., Pierce, R. W., Yang, E. J., & Kim, S. Y. (2012) Southern Ocean Biogeography of Tintinnid Ciliates of the Marine Plankton. *Journal of Eukaryotic Microbiology*, **59**(6), 511-519.
- Dolédec, S., Chessel, D., ter Braak, C.J.F. & Champely, S. (1996) Matching species traits to environmental variables: a new three-table ordination method. *Environmental and Ecological Statistics*, **3**, 143–166.
- Dubischar, C.D., Lopes, R.M. & Bathmann, U.V. (2002) High summer abundances of small pelagic copepods at the Antarctic Polar Front—implications for ecosystem dynamics. *Deep Sea Research Part II: Topical Studies in Oceanography*, **49**(18), 3871-3887.
- Edwards, M., Atkinson, A., Bresnan, E., Helaouet, P., McQuatters-Gollup, A., Ostle, C., Pitois, S. & Widdicombe, C. (2020) Plankton, jellyfish and climate in the North-East Atlantic. *MCCIP Science Review 2020*, 322-353.
- Gotelli, N.J.; Entsminger, G.L. Swap and fill algorithms in null model analysis: Rethinking the knight’s tour. *Oecologia* 2001, 129, 281–291.
- Gower, J.C. (1971) A General Coefficient of Similarity and Some of Its Properties. *Society*, **27**, 857–871.
- Götzenberger, L., de Bello, F., Bråthen, K. A., Davison, J., Dubuis, A., Guisan, A., ... Zobel, M. (2012). Ecological assembly rules in plant communities—Approaches, patterns and prospects. *Biological Reviews*, **87**(1), 111–127.
- Guidi, L., Chaffron, S., Bittner, L., Eveillard, D., Larhlimi, A., Roux, S., Darzi, Y., Audic, S., Berline, L., Brum, J.R., Coelho, L.P., Espinoza, J.C.I., Malviya, S., Sunagawa, S., Dimier, C., Kandels-Lewis, S., Picheral, M., Poulain, J., Searson, S., Stemmann, L., Not, F., Hingamp, P., Speich, S., Follows, M., Karp-Boss, L., Boss, E., Ogata, H., Pesant, S., Weissenbach, J., Wincker, P., Acinas, S.G., Bork, P., De Vargas, C., Iudicone, D., Sullivan, M.B., Raes, J., Karsenti, E., Bowler, C. & Gorsky, G. (2016) Plankton networks driving carbon export in the oligotrophic ocean. *Nature*, **532**,

465–470.

- Hébert, M., Beisner, B.E. & Maranger, R. (2016) Linking zooplankton communities to ecosystem functioning: toward an effect-trait framework. *Journal of Plankton Research*, **39**, 3–12.
- Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J. & Wardle, D.A. (2005) Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs*, **75**, 3–35.
- Hutchinson, G.E. (1959) Homage to Santa Rosalia or Why Are There So Many Kinds of Animals? *The American of Naturalists*, **93(870)**, 145–159.
- Ibarbalz, F.M., Henry, N., Brandão, M.C., Martini, S., Busseni, G., Byrne, H., Coelho, L.P., Endo, H., Gasol, J.M., Gregory, A.C., Mahé, F., Rigonato, J., Royo-Llonch, M., Salazar, G., Sanz-Sáez, I., Scalco, E., Soviadan, D., Zayed, A.A., Zingone, A., Labadie, K., Ferland, J., Marec, C., Kandels, S., Picheral, M., Dimier, C., Poulain, J., Pisarev, S., Carmichael, M., Pesant, S., Babin, M., Boss, E., Iudicone, D., Jaillon, O., Acinas, S.G., Ogata, H., Pelletier, E., Stemmann, L., Sullivan, M.B., Sunagawa, S., Bopp, L., de Vargas, C., Karp-Boss, L., Wincker, P., Lombard, F., Bowler, C., Zinger, L., Acinas, S.G., Babin, M., Bork, P., Boss, E., Bowler, C., Cochrane, G., de Vargas, C., Follows, M., Gorsky, G., Grimsley, N., Guidi, L., Hingamp, P., Iudicone, D., Jaillon, O., Kandels, S., Karp-Boss, L., Karsenti, E., Not, F., Ogata, H., Pesant, S., Poulton, N., Raes, J., Sardet, C., Speich, S., Stemmann, L., Sullivan, M.B., Sunagawa, S. & Wincker, P. (2019) Global Trends in Marine Plankton Diversity across Kingdoms of Life. *Cell*, **179**, 1084-1097.e21.
- Jelihovschi E.G., Faria J.C., Allaman, I.B. (2014). ScottKnott: A Package for Performing the Scott-Knott Clustering Algorithm in R. *Trends in Applied and Computational Mathematics*, 15(1), 3-17.
- Kembel, S.W., Cowan, P.D., Helmus, M.R., Cornwell, W.K., Morlon, H., Ackerly, D.D., et al. (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, **26**, 1463–1464.
- Kenitz, K.M., Visser, A.W., Mariani, P. & Andersen, K.H. (2017) Seasonal succession in zooplankton feeding traits reveals trophic trait coupling. *Limnology and Oceanography*, **62**, 1184–1197.
- Kjørboe, T. (2011) How zooplankton feed: Mechanisms, traits and trade-offs. *Biological Reviews*, **86**, 311–339.

- Kleyer, M., Dray, S., Bello, F., Lepš, J., Pakeman, R.J., Strauss, B., Thuiller, W. & Lavorel, S. (2012) Assessing species and community functional responses to environmental gradients: which multivariate methods? *Journal of Vegetation Science*, **23**, 805–821.
- Lakkis, S. (1994) Coexistence and competition within *Acartia* (Copepoda, Calanoida) congeners from Lebanese coastal water: niche overlap measurements. *Hydrobiologia*, **292–293**, 481–490.
- Laliberté, E.; Legendre, P.; Shipley, B. (2015) Package ‘FD.’ *Measuring functional diversity (FD) from multiple traits, and other tools for functional ecology*, 1–28.
- Lenz, P. H. (2012) The biogeography and ecology of myelin in marine copepods. *Journal of plankton research*, **34**(7), 575–589.
- Litchman, E., Ohman, M.D. & Kiørboe, T. (2013) Trait-based approaches to zooplankton communities. *Journal of Plankton Research*, **35**, 473–484.
- Longhurst A. R. (2006) *Ecological Geography of the Sea*, 2nd ed. Academic Press, San Diego.
- Lopes, R. M., Marcolin, C. R., & Brandini, F. P. (2016) Influence of oceanic fronts on mesozooplankton abundance and grazing during spring in the south-western Atlantic. *Marine and Freshwater Research*, **67**(5), 626–635.
- Mackas, D. L. & Coyle, K. O. (2005) Shelf–offshore exchange processes, and their effects on mesozooplankton biomass and community composition patterns in the northeast Pacific. *Deep Sea Research II*, **52**, 707–725.
- Mayfield, M.M., Bonser, S.P., Morgan, J.W., Aubin, I., McNamara, S. & Vesik, P.A. (2010) What does species richness tell us about functional trait diversity? Predictions and evidence for responses of species and functional trait diversity to land-use change. *Global Ecology and Biogeography*, 423–431.
- Mazzocchi, M.G., Dubroca, L., García-Comas, C., Capua, I. Di & Ribera d’Alcalà, M. (2012) Stability and resilience in coastal copepod assemblages: The case of the Mediterranean long-term ecological research at Station MC (LTER-MC). *Progress in Oceanography*, **97–100**, 135–151.
- Mazzocchi, M.G. & Paffenhofer, G.-A. (1999) Swimming and feeding behaviour of the planktonic copepod *Clausocalanus furcatus*. *Journal of Plankton Research*, **21**, 1501–1518.
- McEwen, G.F., Johnson, M.W. & Folsom, T.R. (1954) A statistical analysis of the performance of the folsom plankton sample splitter, based upon test observations.

- Archiv für Meteorologie, Geophysik und Bioklimatologie Serie A*, **7**, 502–527.
- McGinty, N., Barton, A.D., Record, N.R., Finkel, Z. V. & Irwin, A.J. (2018) Traits structure copepod niches in the North Atlantic and Southern Ocean. *Marine Ecology Progress Series*, **601**, 109–126.
- McGinty, N., Barton, A. D., Record, N. R., Finkel, Z. V., Johns, D. G., Stock, C. A., & Irwin, A. J. (2021) Anthropogenic climate change impacts on copepod trait biogeography. *Global Change Biology*, **27**(7), 1431-1442.
- Menegotto, A. & Rangel, T.F. (2018) Mapping knowledge gaps in marine diversity reveals a latitudinal gradient of missing species richness. *Nature Communications*, **9**, 4713.
- Menezes, B.S., de Macedo-Soares, L.C.P. & Freire, A.S. (2019) Changes in the plankton community according to oceanographic variability in a shallow subtropical shelf: SW Atlantic. *Hydrobiologia*, **835**, 165–178.
- Metzler, P.M., Glibert, P.M., Gaeta, S.A. & Ludlam, J.M. (1997) New and regenerated production in the South Atlantic off Brazil. *Deep Sea Research Part I: Oceanographic Research Papers*, **44**, 363–384.
- Miller, C. B. (2009). *Biological oceanography*. John Wiley & Sons.
- Mouchet, M. A., Villéger, S., Mason, N. W., & Mouillot, D. (2010). Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology*, **24**(4), 867-876.
- Mouillot, D., Graham, N.A.J., Villéger, S., Mason, N.W.H. & Bellwood, D.R. (2013) A functional approach reveals community responses to disturbances. *Trends in Ecology and Evolution*, **28**, 167–177.
- Mouillot, D., Villéger, S., Parravicini, V., Kulbicki, M., Arias-González, J.E., Bender, M., Chabanet, P., Floeter, S.R., Friedlander, A., Vigliola, L. & Bellwood, D.R. (2014) Functional over-redundancy and high functional vulnerability in global fish faunas on tropical reefs. *Proceedings of the National Academy of Sciences of the United States of America*, **111**, 13757–13762.
- Napp, J.M., Hopcroft, R.R., Baier, C.T. & Clarke, C. (2005) Distribution and species-specific egg production of *Pseudocalanus* in the Gulf of Alaska. *Journal of Plankton Research*, **27**, 415–426.
- Neumann-Leitão, S., Melo, P.A.M.C., Schwamborn, R., Diaz, X.F.G., Figueiredo, L.G.P., Silva, A.P., Campelo, R.P.S., Júnior, M. de M., Melo, N.F.A.C., Costa, A.E.S.F., Araújo, M., Veleda, D.R.A., Moura, R.L. & Thompson, F. (2018)

- Zooplankton from a reef system under the influence of the Amazon River plume. *Frontiers in Microbiology*, **9**, 1–15.
- Neumann Leitão, S., Melo Junior, M. de, Porto Neto, F. de F., Silva, A.P., Diaz, X.F.G., Silva, T. de A. e, Nascimento Vieira, D.A. do, Figueiredo, L.G.P., Costa, A.E.S.F. da, Santana, J.R. de, Campelo, R.P. de S., Melo, P.A.M. de C., Pessoa, V.T., Lira, S.M. de A. & Schwamborn, R. (2019) Connectivity Between Coastal and Oceanic Zooplankton From Rio Grande do Norte in the Tropical Western Atlantic. *Frontiers in Marine Science*, **6**, 1–19.
- Oksanen, A.J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., Mcglinn, D., Minchin, P.R., Hara, R.B.O., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E. & Wagner, H. (2019) Vegan: Community Ecology Package. *R package version 2.4-2*, 1–296.
- Orsi, H., Whitworth, T. & Jr, W.D.N. (1995) On the meridional extent and fronts of the Antarctic Circumpolar Current Pronounced meridional gradients in surface properties separate waters of the Southern Ocean from the warmer and saltier waters of the subtropical circulations . Deacon (1933 , the S. **42**.
- Paffenhöfer, G.A. & Mazzocchi, M.G. (2002) On some aspects of the behaviour of *Oithona plumifera* (Copepoda: Cyclopoida). *Journal of Plankton Research*, **24(2)**, 129-135.
- Pelletier, M.C., Ebersole, J., Mulvaney, K., Rashleigh, B., Gutierrez, M.N., Chintala, M., Kuhn, A., Molina, M., Bagley, M. & Lane, C. (2020) Resilience of aquatic systems: Review and management implications. *Aquatic Sciences*, **82**, 44.
- Peralba, À., Mazzocchi, M.G. & Harris, R.P. (2017) Niche separation and reproduction of *Clausocalanus* species (Copepoda, Calanoida) in the Atlantic Ocean. *Progress in Oceanography*, **158**, 185–202.
- Pesant, S., Not, F., Picheral, M., Kandels-Lewis, S., Le Bescot, N., Gorsky, G., Iudicone, D., Karsenti, E., Speich, S., Trouble, R., Dimier, C. & Searson, S. (2015) Open science resources for the discovery and analysis of Tara Oceans data. *Scientific Data*, **2**, 1–16.
- Petchey, O.L., Hector, A. & Gaston, K.J. (2004) How do different measures of functional diversity perform? *Ecology*, **85**, 847–857.
- Pinckney, J., Papa, R. & Zingmark, R. (1994) Comparison of high-performance liquid chromatographic, spectrophotometric, and fluorometric methods for determining

- chlorophyll a concentrations in estuarine sediments. *Journal of Microbiological Methods*, **19**, 59-66.
- Piola, A.R., Matano, R.P., Palma, E.D., Möller, O.O. & Campos, E.J.D. (2005) The influence of the Plata River discharge on the western South Atlantic shelf. *Geophysical Research Letters*, **32**, 1–4.
- Pomerleau, C., Sastri, A.R. & Beisner, B.E. (2015) Evaluation of functional trait diversity for marine zooplankton communities in the Northeast subarctic Pacific Ocean. *Journal of Plankton Research*, **37**, 712–726.
- Prowe, A. F., Visser, A. W., Andersen, K. H., Chiba, S., & Kiørboe, T. (2019) Biogeography of zooplankton feeding strategy. *Limnology and Oceanography*, **64**(2), 661-678.
- Ras, J., Claustre, H. & Uitz, J. (2008) Spatial variability of phytoplankton pigment distributions in the Subtropical South Pacific Ocean: Comparison between in situ and predicted data. *Biogeosciences*, **5**, 353–369.
- Rombouts, I., Beaugrand, G., Ibañez, F., Gasparini, S., Chiba, S., Legendre, L. (2009) Global latitudinal variations in marine copepod diversity and environmental factors. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 3053-3062.
- Rosenfeld, J.S. (2002) Functional redundancy in ecology and conservation. *Oikos*, **98**, 156–162.
- Saba, G.K., Steinberg, D.K. & Bronk, D.A. (2011) The relative importance of sloppy feeding, excretion, and fecal pellet leaching in the release of dissolved carbon and nitrogen by *Acartia tonsa* copepods. *Journal of Experimental Marine Biology and Ecology*, **404**, 47–56.
- Scott R.J., Knott M. (1974) A cluster analysis method for grouping mans in the analysis of variance. *Biometrics*, **30**, 507-512.
- Silveira, I.C.A. da, Schmidt, A.C.K., Campos, E.J.D. & Ikeda, S.S. de G.& Y. (2000) A Corrente do Brasil ao Largo da Costa Leste Brasileira. *Rev. bras. oceanogr.*, **48**, 171–183.
- Song, Y., Wang, P., Li, G. & Zhou, D. (2014) Relationships between functional diversity and ecosystem functioning: A review. *Acta Ecologica Sinica*, **34**, 85–91.
- Spalding, M.D., Fox, H.E., Allen, G.R., Davidson, N., Ferdaña, Z.A., Finlayson, M., Halpern, B.S., Jorge, M.A., Lombana, A., Lourie, S.A., Martin, K.D., McManus, E., Molnar, J., Recchia, C.A. & Robertson, J. (2007) Marine Ecoregions of the World: A Bioregionalization of Coastal and Shelf Areas. *BioScience*, **57**, 573–583.

- Steinberg, D. K., & Landry, M. R. (2017) Zooplankton and the ocean carbon cycle. *Annual review of marine science*, **9**, 413-444.
- Stramma, L. & England, M. (1999) On the water masses and mean circulation of the South Atlantic Ocean. *Water*, **104**, 863–883.
- Swenson, N.G. Functional and Phylogenetic Diversity in R. Springer: New York, NY, USA, 2014.
- Svensen, C. & Kiørboe, T. (2000) Remote prey detection in *Oithona similis*: hydromechanical versus chemical cues. *Journal of Plankton Research*, **22(6)**, 1155-1166.
- Teuber, L., Schukat, A., Mhagen, W. & Auel, H. (2014) Trophic interactions and life strategies of epi- to bathypelagic calanoid copepods in the tropical Atlantic Ocean. *Journal of Plankton Research*, **36**, 1109–1123.
- Teuber, L., Hagen, W., Bode, M., & Auel, H. (2019) Who is who in the tropical Atlantic? Functional traits, ecophysiological adaptations and life strategies in tropical calanoid copepods. *Progress in oceanography*, **171**, 128-135.
- Van Heukelem, L. & Thomas, C.S. (2001) Computer-assisted high-performance liquid chromatography method development with applications to the isolation and analysis of phytoplankton pigments. *Journal of Chromatography A*, **910**, 31–49.
- Veríssimo, H., Patrício, J., Gonçalves, É., Moura, G.C., Barbosa, J.E.L. & Gonçalves, A.M.M. (2017) Functional diversity of zooplankton communities in two tropical estuaries (NE Brazil) with different degrees of human-induced disturbance. *Marine Environmental Research*, **129**, 46–56.
- Villar, E., Farrant, G.K., Follows, M., Garczarek, L., Speich, S., Audic, S., Bittner, L., Blanke, B., Brum, J.R., Brunet, C., Casotti, R., Chase, A., Dolan, J.R., D’Ortenzio, F., Gattuso, J.-P., Grima, N., Guidi, L., Hill, C.N., Jahn, O., Jamet, J.-L., Le Goff, H., Lepoivre, C., Malviya, S., Pelletier, E., Romagnan, J.-B., Roux, S., Santini, S., Scalco, E., Schwenck, S.M., Tanaka, A., Testor, P., Vannier, T., Vincent, F., Zingone, A., Dimier, C., Picheral, M., Searson, S., Kandels-Lewis, S., Acinas, S.G., Bork, P., Boss, E., de Vargas, C., Gorsky, G., Ogata, H., Pesant, S., Sullivan, M.B., Sunagawa, S., Wincker, P., Karsenti, E., Bowler, C., Not, F., Hingamp, P. & Iudicone, D. (2015) Environmental characteristics of Agulhas rings affect interocean plankton transport. *Science*, **348**, 1261447–1261447.
- Villéger, S., Mason, N.W.H. & Mouillot, D. (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, **89**,

2290–2301.

- Walker, B.H. (1992) Biodiversity and Ecological Redundancy. *Conservation Biology*, **6**, 18–23.
- Woodd-Walker, R., Ward, P. & Clarke, A. (2002) Large-scale patterns in diversity and community structure of surface water copepods from the Atlantic Ocean. *Marine Ecology Progress Series*, **236**, 189–203.
- Yamaguchi, A., Watanabe, Y., Ishida, H., Harimoto, T., Furusawa, K., Suzuki, S., Ishizaka, J., Ikeda, T. et al. (2002) Community and trophic structures of pelagic copepods down to greater depths in the western subarctic Pacific. *Deep Sea Research II*, **49**, 1007–1025.
- Zamora-Terol, S., Nielsen, T.G. & Saiz, E. (2013) Plankton community structure and role of *Oithona similis* on the western coast of Greenland during the winter-spring transition. *Marine Ecology Progress Series*, **483**, 85–102.
- Zar, J.H. (2010) Biostatistical Analysis. 5 ed. *Prentice Hall*, New Jersey. 944 p.
- Zuur A.F., Ieno E.N., Walker N.J., Saveliev A.A., Smith, G.M. (2009) Mixed Effects Models and Extensions in Ecology with R. Springer, New York. 574 p.

4 TRANSIÇÃO PARA O CAPÍTULO II

Os traços e grupos funcionais apresentados no primeiro capítulo podem ser usados para descrever e quantificar a biodiversidade funcional das comunidades de copépodes em diferentes escalas espaço-temporal. Além disso, a existência de diferentes grupos funcionais do mesozoplâncton incentiva o desenvolvimento de compartimentos mais diversos dentro dos modelos de ecossistema, que geralmente distinguem poucas classes de tamanho para representar o zooplâncton.

Portanto, a questão citada acima também exige que olhemos para outro tema: o tamanho corporal, o principal traço funcional da estrutura de comunidades planctônicas. No segundo capítulo estamos interessados em desvendar como os diferentes tamanhos médios das famílias copépodes respondem aos gradientes ambientais do Oceano Atlântico Sul ao Oceano Antártico (13°-64°S). Especificamente, famílias de copépodes com diferentes histórias de vida e estágios (adultos e copepoditos) responderão de forma semelhante? Testamos a tendência geral de que o tamanho do corpo dos copépodes seguirá a regra de Bergmann, no nível de família, onde espera-se que o tamanho corporal aumente em direção a altas latitudes/baixas temperaturas. Nossa hipótese é que a influência adicional de processos oceanográficos regionais no Atlântico Sul impulsiona esse padrão.

Para testar a regra de Bergmann, aplicamos modelos lineares generalizados mistos (GLMMs) que são uma extensão dos os modelos lineares tradicionais para incluir uma combinação de efeitos fixos e aleatórios como variáveis preditoras. Modelamos o tamanho corporal médio de um subconjunto das 15 famílias mais abundantes de 25 identificadas, em relação a variação de cada uma das quatro variáveis preditivas selecionadas a partir dos resultados do capítulo anterior (temperatura, salinidade, oxigênio e clorofila-a). Isso nos permitirá verificar se as famílias têm preferências ambientais distintas ao longo de gradientes ambientais.

Posteriormente, exploramos as forças oceanográficas, ecológicas e evolutivas que governam esses padrões e consequências mais amplas no contexto do aquecimento climático.

5 CAPÍTULO II

Copepod body size latitudinal patterns and their environmental drivers in the South Atlantic

Érica Caroline Becker^{a,*}, Luis Carlos Pinto Macedo-Soares^a, Catarina Marcolin^b, Manoela Costa Brandão^a, Lars Stemmann^c, Maria Grazia Mazzocchi^d, Andrea Santarosa Freire^a

a Universidade Federal de Santa Catarina, Campus Universitário, 88010-970 Florianópolis, Brazil

b Universidade Federal do Sul da Bahia, Instituto de Humanidades, Artes e Ciências, Porto Seguro, Brazil

c Sorbonne Université, Laboratoire d'Océanographie de Villefranche, Villefranche-sur-mer, France

d Stazione Zoologica Anton Dohrn, Villa Comunale, 80121 Naples, Italy

Manuscript under preparation for *Journal of Biogeography*

* Corresponding author: ericabeckker@gmail.com

Abstract

The importance of environmental drivers on copepod body size structure is poorly understood in the South Atlantic Ocean (SAO), a highly under-sampled ocean. Yet, little is known to which degree copepods body size changes can be generalized across family level. We investigated the body size distribution of the most abundant copepod families and compared their environmental responses, to test if body size follows Bergmann's rule by increasing contribution of smaller organisms in warmer localities. We hypothesize that the additional influence of particular oceanographic features boosts this pattern in the SAO. Temperature and salinity decreased from tropical to polar waters, while oxygen and the depth chlorophyll-a maximum increased. Small copepods were the most abundant families, especially along the Brazil Current (BC), presenting narrow body size range but widespread distribution. A clear shift in the community occurred southward to the Subtropical Confluence Zone (SCZ-47°S), together with the dominance of Oithonidae. Large-sized families (>1mm) had wide body size ranges, but narrower latitudinal distribution (except Calanidae), and reached higher abundances between SCZ and Antarctic Circumpolar Current. Generalized linear mixed models (GLMMs) showed that the latitudinal patterns in copepod size have a strong taxonomic signal. Although most copepods contain, to some extent, a latitudinal increasing size pattern towards high latitudes and low temperatures, not all families follow Bergmann's rule, and the relative abundance of copepodites increased poleward. Small adult copepods contributed mostly in the BC domain, while Calanidae copepodites disproportionately contributed to the copepod biomass, and Oithonidae adults were the most abundant in high latitudes. Generally, copepod abundance or biomass hotspots were in the southern limit of the warm BC (25°-30°S), at the SCZ, and in the rich subantarctic waters at the Drake passage. Our results suggest that regional oceanographic processes seem to strengthen latitudinal body size relationships during summer due to seasonal food availability, and that the responses to environmental drivers are related to the different life history strategies.

Keywords: copepods, body size, environmental drivers, temperature, Bergmann's rule, GLMM

Introduction

Decades-old ecogeographical rules postulate latitudinal gradients in body sizes, such that species in the tropics are predicted to have smaller body sizes than their counterparts at higher latitudes (Bergmann, 1847). Originally restricted to homeotherms, Bergmann's rule proposes that the pattern is thought to result from selection favoring larger sizes in colder environments, which minimizes heat loss through body surfaces by reducing surface/volume ratios and giving them an energetic advantage in cold environments (Salewski & Watt, 2017). However, it has been shown to apply widely to ectotherms but through different mechanisms. About 83.5% of ectothermic species present a negative relationship with temperature and body size (Atkinson, 1994), in which decreasing temperature is the main driver of increasing body size in marine crustaceans along both latitudinal and depth gradients (Timofeev, 2001). Global fingerprints of climate warming, however, have revitalized the interest in the relationship between body size and temperature (Sommer et al., 2017). The increase of temperature may select for smaller sizes (Daufresne et al., 2009, Beaugrand et al., 2010, Campbell et al., 2021), which will affect the influence of marine community size structure exerts on regional fisheries productivity and vertical carbon transport efficiency (Beaugrand and Kirby, 2010; Bi et al. 2011).

Zooplankton communities exhibit larger size and abundance towards the poles and tropical upwelling regions, a pattern that is largely driven by copepods (San Martin et al., 2006, Evans et al., 2020, Brandão & Benedetti et al., 2021, Campbell et al., 2021). Yet, fundamental biological differences within population life history strategies in response to environmental gradients may modify spatiotemporal responses of marine copepods. For instance, the strength of temperature-size response in copepods is density dependent on seasonal changes in dominant species, from reductions of ca. 3% to 10% of carbon mass. $^{\circ}\text{C}^{-1}$ (Corona et al., 2021). Feeding strategies also play a significant role in dictating the magnitude of seasonal temperature-size responses in copepods, which is negative in ca. 90% of the copepod species, and exhibit a four-fold greater reduction in adult body mass per $^{\circ}\text{C}$ in current-feeding calanoids compared with ambush-feeding cyclopoids (Horne et al. 2016). Consequently, the response of body size to the environmental gradient varies between and within taxonomic groups, and it is associated with different ecophysiological strategies adopted by the organisms to cope with the

environment (Ackerly & Cornwell, 2007), and ultimately, how they will respond in a context of climate change.

Since the classic explanation of Bergmann's rule based on thermoregulation principles is not applicable to most ectotherms, quite a few hypotheses have been proposed that appeal to other foundations in search of such an explanation (Vinarski et al., 2014). The resource availability hypothesis suggests that body size co-varies with the length of the season, then smaller-sized species might be prevalent both at lower latitudes due to resource competition, and at higher latitudes due to resource shortages after the short reproductive period during summer (Blackburn et al. 1999). Further, the oxygen limitation hypothesis stated that metabolism is higher at lower and warmer latitudes, increasing individual cost of growth to a large body size (Atkinson et al. 2006). Thus, other abiotic and biotic factors may constrain copepod body sizes, and most studies look for an adaptive sense of the increase in the body size of ectotherms at high latitudes and/or low temperatures. It appears that a single universal explanation of all the cases of Bergmann's variation in ectotherms cannot be formulated. Most likely, the observed patterns arise as a result of synergetic interactions between several factors covarying with latitude (Vinarski et al., 2014).

The dominance of small copepods in food-web dynamics is a prominent feature in the South Atlantic Ocean. In relatively warmer conditions, primary production is typically low and dominated by pico- and nano-size primary producers as occurs under the Brazil Current (Brandini et al., 2018), the Rio de la Plata plume influence (Cepeda et al., 2020) down to the frontal areas in the subantarctic waters in the South Atlantic Ocean (Lopes et al., 2016). There is an ecological advantage of specializing on food sources other than phytoplankton, becoming the microzooplankton an important component of copepods diet (Barton et al., 2013). They typically colonize the nutrient-rich marine snow, suspended organic matter and floating substrates, thus contributing to recycling the organic matter (Uye et al., 2002), and support a well-developed microbial-based production (Cepeda et al., 2020). Therefore, high biomass of small-sized copepods during summer is food source for different developmental stages of pelagic fishes, the Brazilian sardine *Sardinella brasiliensis* and the anchovy *Engraulis anchoita* (Kurtz & Matsuura, 2001, Miyashita et al., 2009, Padovani et al., 2011), and justify the role of the regional oceanographic processes as feeding grounds for fisheries production. The prevalence of small-sized copepods in the community-level of global marine ecosystems is mainly represented by small calanoids that comprises more than 50% of community abundance

in all the latitudinal bands from tropical, temperate and polar (Brandão & Benedetti et al., 2021). While the level of taxonomic identification of the non-automated methods (e.g. ZooScan imaging system) remains suitable for a size-based community-level study, it does not enable to depict small size fraction composition, remaining mostly unidentified Calanoida (Brandão & Benedetti et al., 2021, Soviadan et al., 2022). Consequently, macroecological studies usually better represent only large copepods, which greatly oversimplifies the contribution of the small ones to the functioning of ecosystems and biogeochemical cycles. Therefore, it could have underestimated the strength of some latitudinal abundance and size structure patterns, and their relationships to environmental gradients.

The volume and type of evidence associated with copepod body size and responses to environmental gradients is variable across ocean regions and taxonomic groups. We face major gaps and challenges in the South Atlantic Ocean in comparison to the heavily-studied North Atlantic Ocean (Poloczanska et al., 2016). Most of our current knowledge of copepod body size variation relies on high-resolution temporal series from temperate and polar oceans in the community level but low tropical sampling (Campbell et al., 2021), single location monitoring sites (Persson et al., 2012, Corona et al., 2021), and considering mainly the influence of life history strategy of large bodied copepods (e.g., *Calanus* species) (Evans et al., 2020). The implications of body size changes partitioning within the copepod community is not fully understood, especially the role of small body size families in the South Atlantic Ocean. Thus, considering the spatial variability of life history strategies might clarify whether the response of body size to the environment can be generalized among the different copepod families or whether each of these populations responds to it independently. In this study, we are interested in unraveling how the copepod families with different size ranges respond to the environmental gradients from the Southwestern Atlantic Ocean to Southern Ocean (13°-64°S). In this regard, will different life stages (adult and copepodite) of copepod families respond similarly? We test the general trend that copepod body size will follow Bergmann's rule at the family level by increasing contribution of smaller organisms in warmer localities. Subsequently, we explore if the relationship between copepod families body size and environmental drivers can be explained by other latitude-related effects acting additively or synergistically with those of temperature.

Material and Methods

Study area

In the South Atlantic, the circulation near the surface is dominated by a wind driven, anticyclonic subtropical gyre, which is formed by the Benguela Current, the southernmost branch of the South Equatorial Current, the Brazil Current (BC) and the South Atlantic Current (Campos et al., 2017). Along the western side, the upper water column is depicted by the southward flowing BC, and the Malvinas Current flows equatorward carrying water from the Antarctic Circumpolar Current (ACC).

At approximately 36-38°S, the Malvinas Current encounters the BC, forming the Subtropical Confluence Zone – SCZ (Garzoli & Matano, 2011). The connections of the three major oceans are in the South Atlantic Ocean (SAO). The meridional gaps between the continents of the southern hemisphere and Antarctica allow for a free exchange of water among the basins. The SAO receives considerable inflows from the Pacific, through the Drake Passage (Campos et al., 2017), and on the eastern side, the Agulhas current contributes with Indian Ocean water through the rings shed from its retroflexion (Villar et al., 2015).

Field sampling

A total of 37 stations were established during two cruises conducted in the South Atlantic and Southern Ocean from October 2010 to January 2011 (Fig. 1). These stations covered a wide latitudinal range and a large variety of ecosystems, from tropical to polar oceanic waters (see table S1). The MCT-II *Cruzeiro do Sul* expedition was conducted in the Brazilian tropical and subtropical shelves (06/12/2010-11/01/2011). Then, to enlarge the latitudinal gradient as part of the *Tara* Oceans expedition, the stations here considered as representative of the main basins are TARA_073 to TARA_080 for the South Atlantic Ocean, and TARA_082 to TARA_089 for the Southern Ocean.

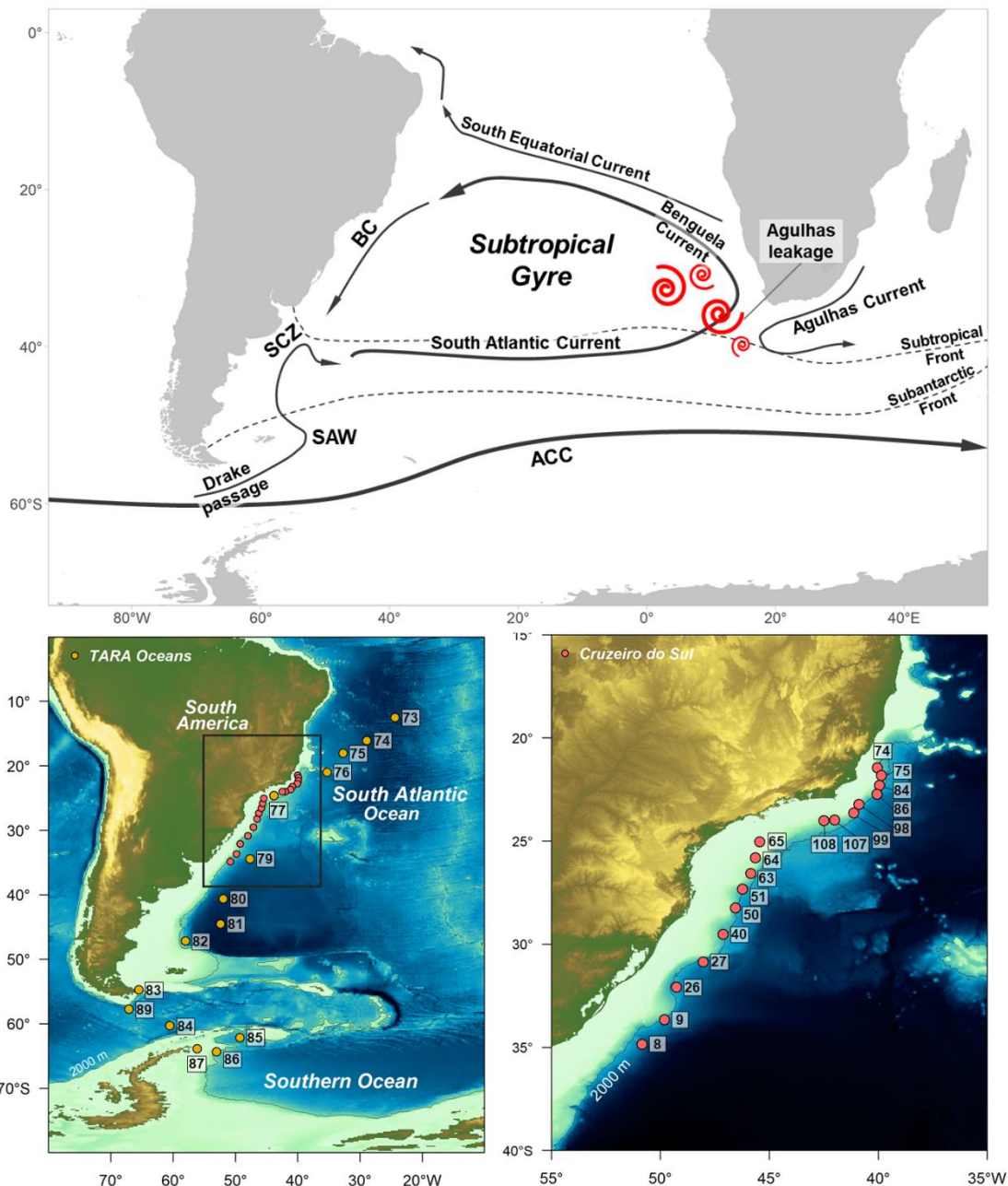


Figure 1. South Atlantic and Southern Ocean circulation, including some of the key oceanographic features and its connection to the neighboring basins (adapted from Peterson & Stramma, 1991; Stramma & England, 1999; Garzoli & Matano, 2011; Villar et al., 2015; Campos et al., 2017). A map of the South Atlantic bathymetry and the sampling stations from *TARA Oceans* and *Cruzeiro do Sul* expeditions is detailed. BC: Brazil Current; SCZ: Subtropical Confluence Zone; SAW: Subantarctic Water; ACC: Antarctic Circumpolar Current.

Vertical profiles of temperature, salinity, fluorescence and dissolved oxygen were obtained with a SeaBird CTD (conductivity, temperature and depth) profiler, coupled with sensors. In the MCT-II expedition, water samples were collected with 5-L Niskin

bottles to determine nutrients (ammonium, nitrite, nitrate, phosphate and silicate) and chlorophyll-a (chl-a) at selected depths (at 3 m or 5 m, the chlorophyll maximum depth and at the base of the mixture layer). Nutrients were determined using the methods described by Grasshoff et al. (1983) and Strickland and Parsons (1968), and chlorophyll-a determination followed Welschmeyer (1994). In the *Tara* Oceans sampling, chlorophyll concentrations were measured using high-performance liquid chromatography (Van Heukelem & Thomas, 2001, Ras et al., 2008). Nutrient concentrations (ammonium, nitrite, nitrate, phosphate and silicate) were determined using segmented flow analysis (Aminot et al. 2009).

Zooplankton samples were collected using a WP-2 net of 200 μm mesh size, therefore, our sampling is representative of epipelagic mesozooplankton size fraction, which highly underestimate the abundance of small-sized copepod taxa and their copepodites. The net was towed vertically from 100 m depth to the surface and the samples were preserved on-board with buffered formaldehyde for later analyses. The net was equipped with a flowmeter for filtered volume determination.

Copepod data quality

Both cruises use similar methods to collect and sort copepods. Precisely, sampling was consistent with the same period during austral summer of the same year (2010/2011), followed similar field protocols (De Macedo-Soares et al. 2014, Brandão et al. 2015, and Pesant et al. 2015 for more details), use the same mesh size (200 μm), towed at the similar depth layers (depth chlorophyll-a maximum, or ~ 100 m) and have the same sorting process at laboratory. Yet, the preserved zooplankton samples were fractionated, in each fraction a subsample was taken (between 10 to 30mL), and at least 100 copepod individuals were sorted (Frontier 1981).

Copepod identification was divided into 2 phases. Body size is a morphological trait that has an optical signature and can be inferred from images, thus in the first step were scanned the organisms using the ZooScan imaging system. The images were processed with the *ZooProcess* software, imported and uploaded into EcoTaxa (Picheral et al., 2017) for classification into taxonomic categories (semi-automatic), and size metrics estimations (Grosjean et al. 2004; Gorsky et al. 2010). The lower particle recognition size limits were standardized to 300 μm equivalent spherical diameter (ESD). In step 2, the same scanned organisms were analyzed under stereomicroscope to observe

the morphological characters, and to validate the EcoTaxa taxonomic categories to the family level (very useful to unidentified Calanoida vignettes). Therefore, we were able to make accurate identification as to even the different life stages from the images (adult and juvenile copepodite). Besides using the taxonomic characters, the damaged morphological structures due to sample fixation also became diagnostic characters to identify the same organisms in the EcoTaxa images.

Abundance ($\log \text{ind m}^{-3}$) and biomass ($\log \mu\text{gC m}^{-3}$) of copepods were calculated using conversion equations according to specific literature relating the size, area or volume to the individual weight (Uye, 1982; Lehetto & Hernández-león, 2009). Small-sized families were considered for copepods smaller than 1 mm, covering both adult and juvenile copepodite stages. Large-sized families are greater than 1 mm but most of their copepodites lie within the 1 mm threshold.

Statistical analyses

To test Bergmann's rule, we applied Generalized linear mixed effects models (GLMMs) that extend traditional linear models to include a combination of fixed and random effects as predictor variables (Zuur et al., 2009; Bolker et al., 2009). GLMMs accounted the effects of the Temperature ($^{\circ}\text{C}$), Salinity, Oxygen (mg.l^{-1}) and Chlorophyll-a (mg.m^{-3}) on mean adult body size (ESD mm) among different copepod families along the latitudinal gradient in the South Atlantic and Southern Ocean (13° - 64°S).

Prior to the GLMMs, we tested the relationship of the environmental variables with the latitude using Pearson's correlations. Furthermore, correlation coefficients between most of the explanatory variables were high. Because correlation coefficients only show pairwise correlations, we used variance inflation factors (VIF) to assess which explanatory variables are collinear and should be dropped before starting the models. We used a cut-off value of 5 or even 3, which might remove collinear variables (Zuur et al., 2009). To find a set of explanatory variables that does not contain collinearity, we removed one variable at a time, recalculated the VIF values, and repeated this process until VIF values were lower than 5. Even selecting a small set of environmental variables, VIF values were always higher than 5 and could not be included together in the model. Thus, assessed their relative importance in four separate models: temperature, salinity, Chlo-a and oxygen.

To account for temporal and spatial correlation in the data, we used three random effects to adjust model-building approaches accordingly fitting the random effect structure. The first was a random intercept for the period of sampling (day and night). This accounts for natural and sampling differences among the regions, which minimizes bias associated with dial differences in sampling regions. The second was a random intercept associated with differences among cruises, which accounts for the use of different vessels and large-scale regional effects. The third was a random intercept for life stage (adult and copepodite) within families, which adjusts for both temperature differences among life stages (i.e., Temperature | life stage), or if not significant, just the life stage differences among families (i.e., 1 | life stage).

From preliminary analysis testing the three random effects described above, the final model set up included the mean body size of each family as response variable, the environmental variables as fixed effects, and accounted for the different life stages as random effect. Family was included as an interactive factor with each environmental variable and contributed significantly to model performance ($p < 0.05$). Accordingly, latitudinal gradients select different ranges of the environmental variables for each copepod family (i.e. changing both the intercepts and slopes).

Assessment of model fit and adequacy was performed with the Diagnostics for Hierarchical Regression Models (DHARMA) (Hartig, 2021). It calculates randomized quantile residuals (1000 simulations) that are standardized to values between 0 and 1. To interpret the residuals, the scaled residual value of 0.5 means that half of the simulated data are higher than the observed value, and half of them lower. DHARMA also creates diagnostic graphics to detect deviations from the expected (uniform) distribution (QQ-plot), to test normality (Kolmogorov-Smirnov), dispersion, and outliers. Finally, the model selection procedure was evaluated by ranking competing models according to Akaike's Information Criterion (AIC). Higher AIC values indicate a more parsimonious model. Additionally, log-likelihood represents the goodness of fit (higher is better), and degrees of freedom (df) represents the complexity.

These analyses were conducted in the statistical software R (R Core Team, 2021) with the packages 'glmmTMB' (Magnusson et al. 2017), and model validations were checked using the 'DHARMA' package (Hartig & Hartig, 2017).

Results

Environmental variables displayed spatial variability across a large latitudinal gradient ($\sim 52^\circ$), ranging from the South Equatorial Current to the Antarctic Circumpolar Current.

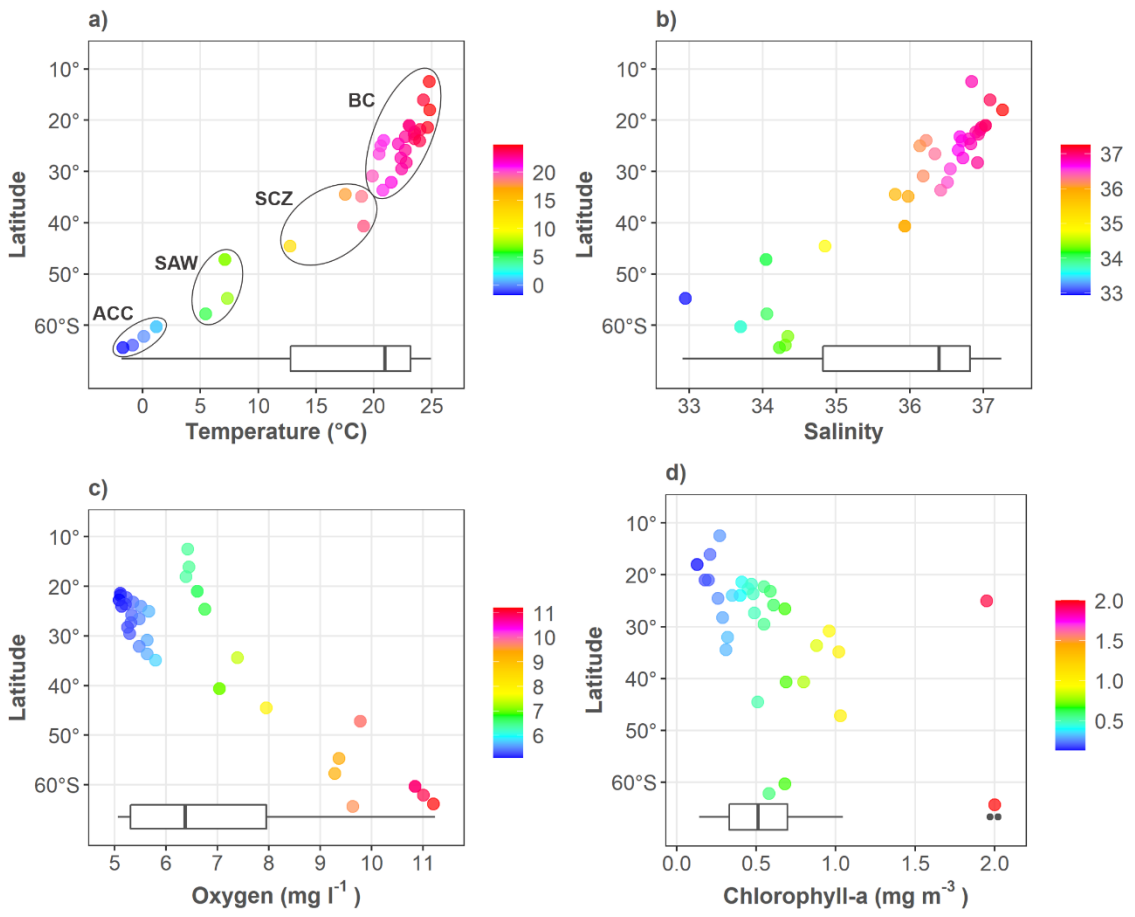


Figure 2. Temperature (a; $^\circ\text{C}$), Salinity (b), Oxygen (c; mg l^{-1}) and Deep Chlorophyll-a Maximum (d; mg m^{-3}) along the latitudinal gradient of the South Atlantic and Southern Ocean (13° - 64°S). Black ellipses in temperature values delimit the oceanographic features considered in this study. BC: Brazil Current; SCZ: Subtropical Confluence Zone; SAW: Subantarctic Water; ACC: Antarctic Circumpolar Current. The data distribution statistics are summarized in the box plots.

Both temperature and salinity decreased (Fig. 2a and b) from tropical to polar waters, while oxygen and the deep chlorophyll-a maximum (DCM) increased (Fig. 2c and d). Near the tropics, maximal temperature and salinity values were located within the tropical circulation of the salty-warm Brazil Current (BC) (T: $\sim 25^\circ\text{C}$; S: ~ 37). Along the BC, lower DCM levels ($< 0.5 \text{ mg m}^{-3}$) were recorded, as well as a peak at 25°S (1.9 mg m^{-3}). A transition area characterized by high environmental variability depicts the SCZ

(35–47°S). In this area, temperatures ranged from 12 to 19°C, salinity was below 36, while oxygen values increased between 7 to 8 mg l⁻¹, together with higher chl-a concentrations (0.5–1 mg m⁻³). Subsequently, under the influence of sub-Antarctic waters (SAW) the lowest salinity was recorded (< 33) flowing northward along the Argentinian slope down to the Drake Passage (55–58°S), temperature ranged between 5–7°C and oxygen almost reached 10 mg l⁻¹. Minimal values (T: -2 °C; S: ~34) occurred in the SO featuring the ACC frontal system. The ACC had intermediate Chl-*a* levels, with a peak at 64°S similar to oxygen (Chl-*a*: 2 mg m⁻³; O₂: 11.2 mg l⁻¹).

ZooScan recordings yielded ~11,200 image segments, including representatives of three orders, and 25 families (Fig. 3). The latitudinal gradient in copepod size spectra were also evident across the life stages showing that a greater part of the organisms were adults along the BC, while copepodites were mostly identified at the SCZ, SAW and ACC waters (Fig. S1). Except at ~27°S, where Clausocalanidae copepodites made a great contribution to the relative abundance.

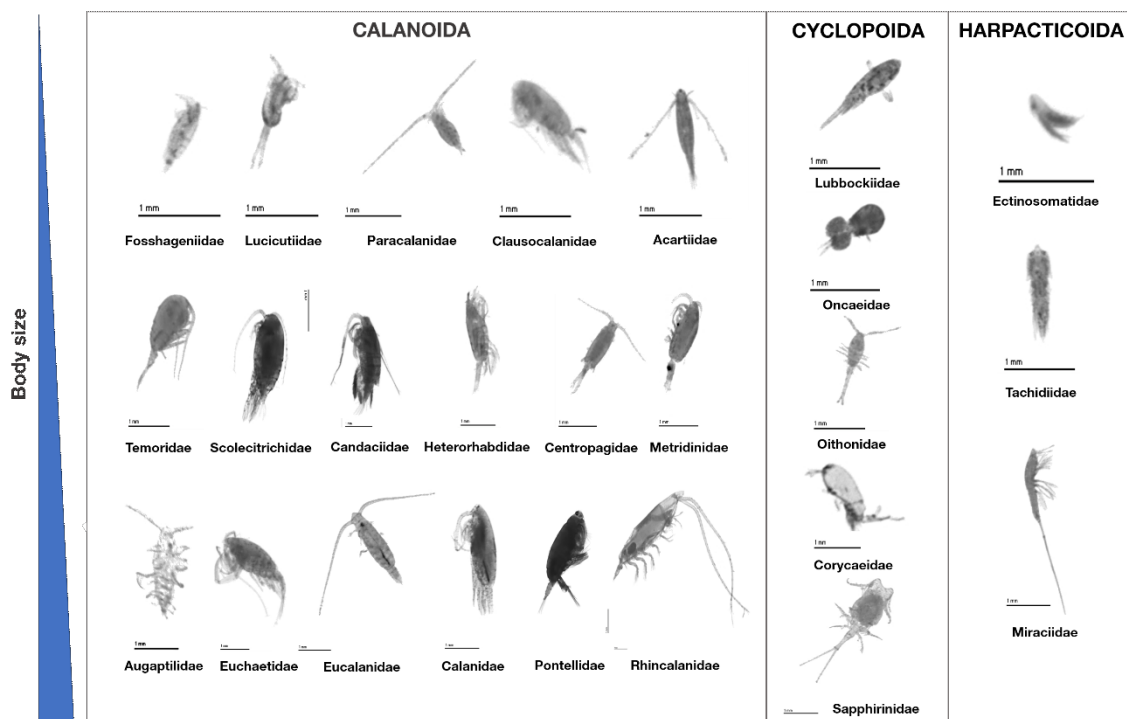


Figure 3. Copepod imaged with the ZooScan System. A representative collection of copepod families from the South Atlantic and Southern Ocean. Scale bar: 1 mm.

Small adult copepods were by far the most prominent in terms of relative abundance, especially along the BC influence (Figs. 4a and S2). The families Acartiidae, Clausocalanidae, Paracalanidae, Corycaeiidae, Oncaeiidae, and Oithonidae were

dominant. These families presented narrow body size ranges but widespread latitudinal distribution (Fig. 5 and S2), which reflected in general low biomass, except at the SCZ region (Fig. S4).

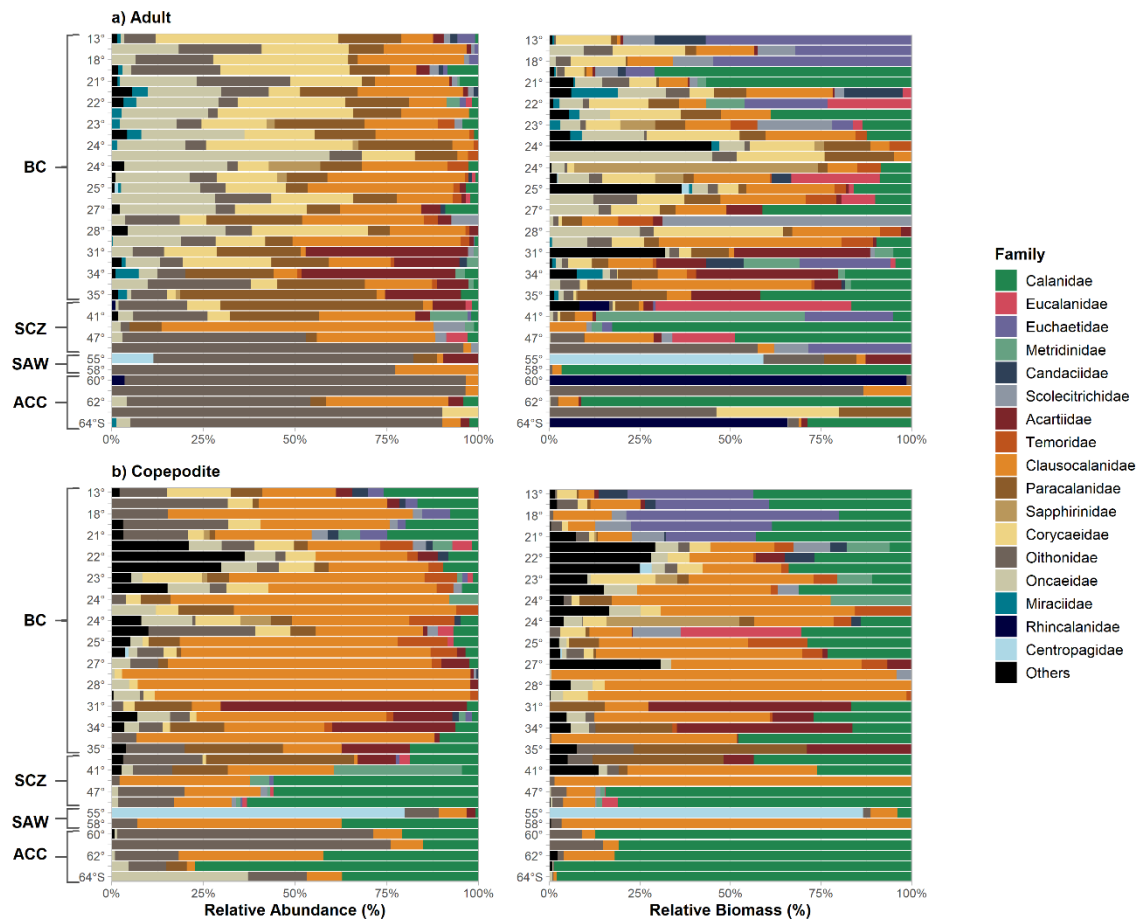


Figure 4. Relative abundance and biomass of the main copepod families and life stages along the latitudinal gradient in the South Atlantic and Southern Ocean (13°-64°S).

A clear shift in the community composition occurred down to the SCZ (47°S), along with the dominance of Oithonidae. Large-sized families (>1 mm) mainly corresponded to Calanidae, Eucalanidae, Euchaetidae, Metridinidae, Candaciidae, Scolecitrichidae, and the cyclopoid family Sapphirinidae. They had wide body size ranges (Fig. 5 and S2), a narrower latitudinal distribution (except Calanidae), and reached higher abundances between SCZ and ACC at 60°S (Fig. S3). Clausocalanidae copepodites exhibited large abundance and biomass in the BC zone, while Calanidae copepodites increased poleward, showing a great impact in biomass values (Fig. 4b).

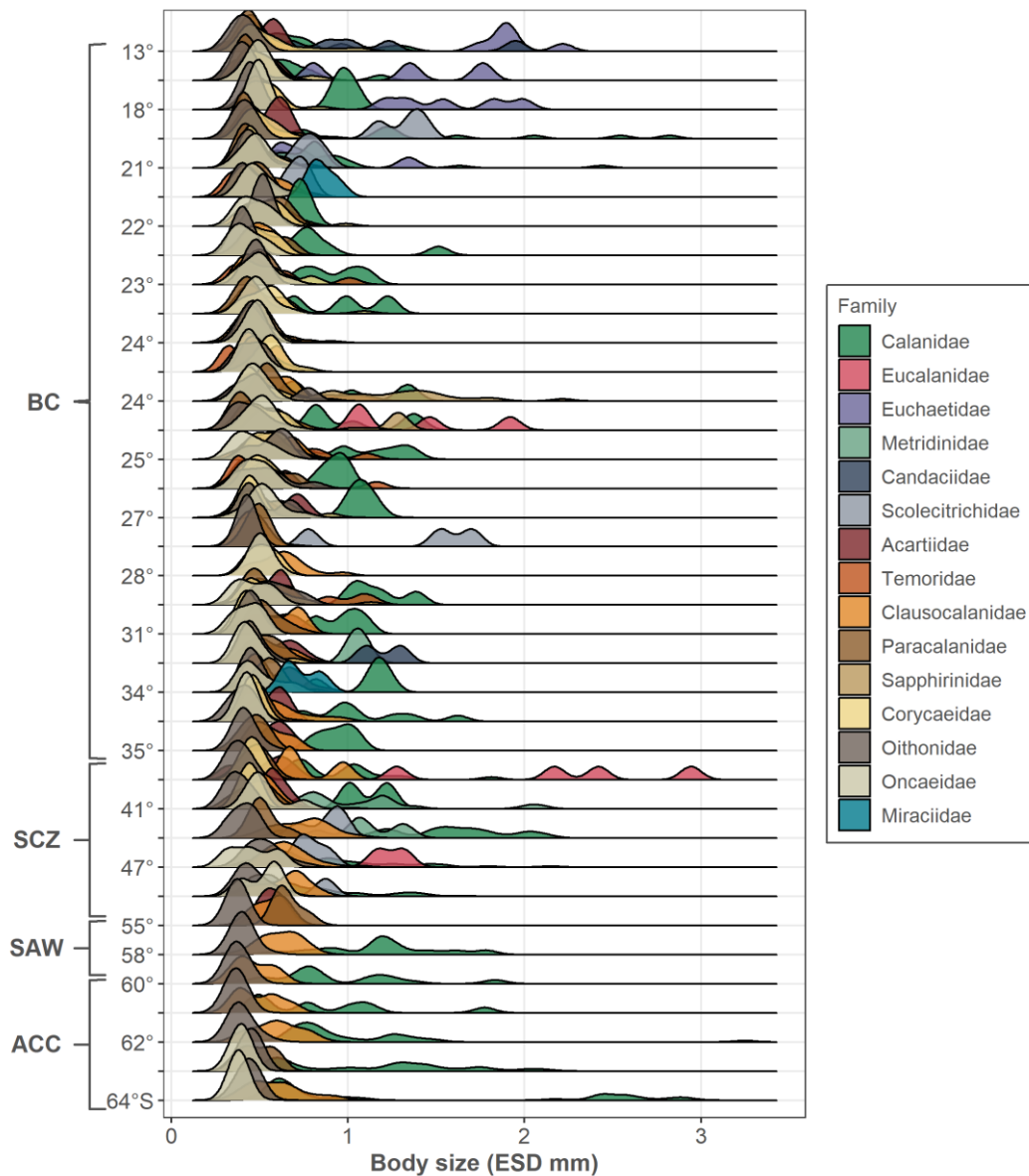


Figure 5. Body size frequency distribution estimated through equivalent spherical diameter (ESD) of copepod families, both copepodites and adults, along the latitudinal gradient of the South Atlantic and Southern Ocean (13°-64°S).

In both life stages, Euchaetidae showed low abundances but large biomass equatorward (13°-21°S), and increased populations of Acartiidae were found in the southern limit of BC (31°-35°S). The rarest copepod families were the calanoid Fosshageniidae, Lucicutiidae, Centropagidae, Heterorhabdidae, Pontellidae, Augaptilidae, Rhincalanidae, the cyclopoid Lubbockiidae, and the harpacticoid Ectinosomatidae and Tachidiidae. They had relatively low abundance and biomass values across the entire latitudinal gradient, forming the group Others in Fig. 4, exceptions were represented by centropagids at 55°S and adult rhincalanid biomass at 60°S and 64°S.

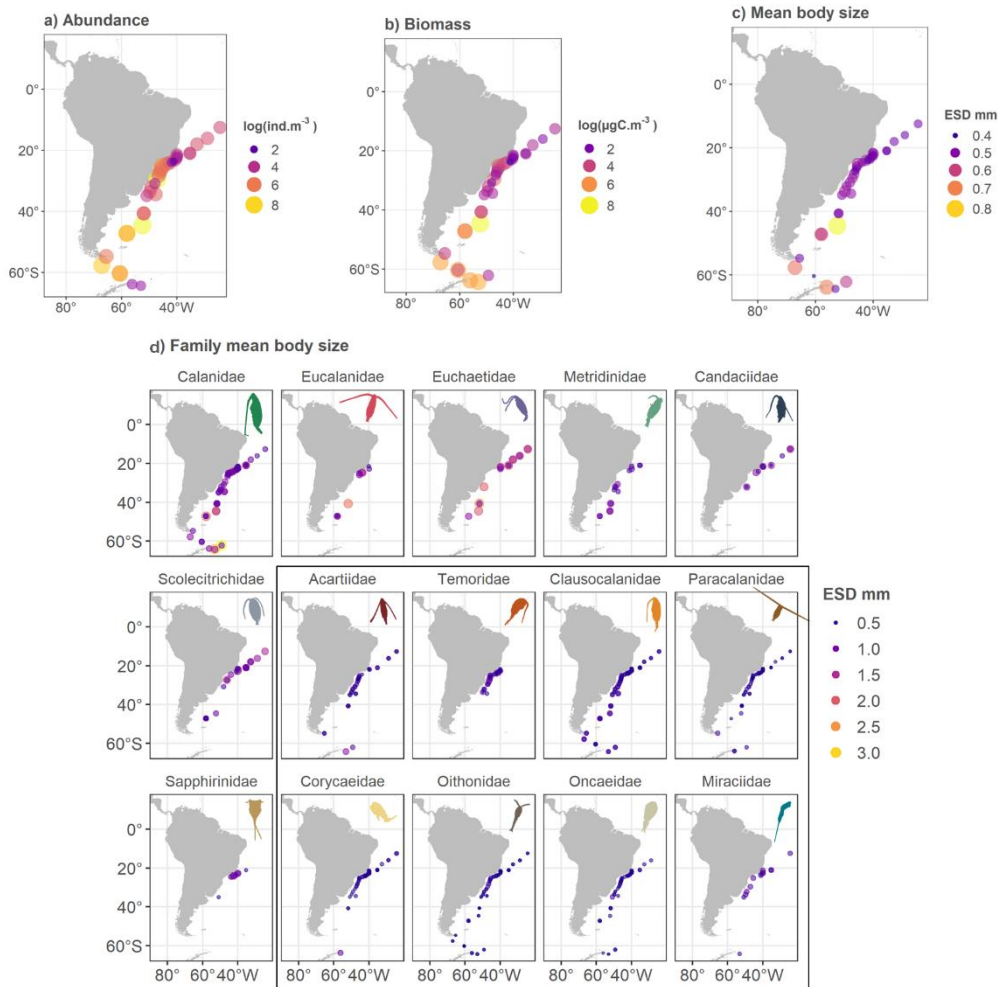


Figure 6. Total community abundance (a; ind.m⁻³), biomass (b; µgC m⁻³), community mean body size (c) and family mean body size (d) along the latitudinal gradient in the South Atlantic and Southern Ocean (13°-64°S). Body size was estimated through equivalent spherical diameter (ESD mm), and copepod families with mean body size smaller than 1 mm are highlighted (black box). Circles display a designated geographical region with the size and color proportional to its value in the sampling station.

Overall, the copepod family abundance and/or biomass mainly peaked following important oceanographic features: under the influence of the Subtropical gyre close to the southern limit of BC waters (~ 25°-30°S), southwards the SCZ (~ 45°S), and at the input area of SAW in the Drake passage (~ 60°S) (Fig. 6a and 6b). Generally, community mean body size increased towards high latitudes (Fig. 6c). However, the relationship between body size and latitude changed within the different copepod families. Mean family body size smaller than 1 mm presented a slight or no latitudinal gradient (Fig. 6d). Only the Calanidae family, among those with mean body size larger than 1 mm (Fig. 5), was distributed in the full latitudinal range. Accordingly, the relative contribution of

Calanidae seemed likely to drive the general increase in mean copepod body size (Fig. 6d), boosted by the biomass of large adult rhincalanids at ACC zone (Fig. 4a).

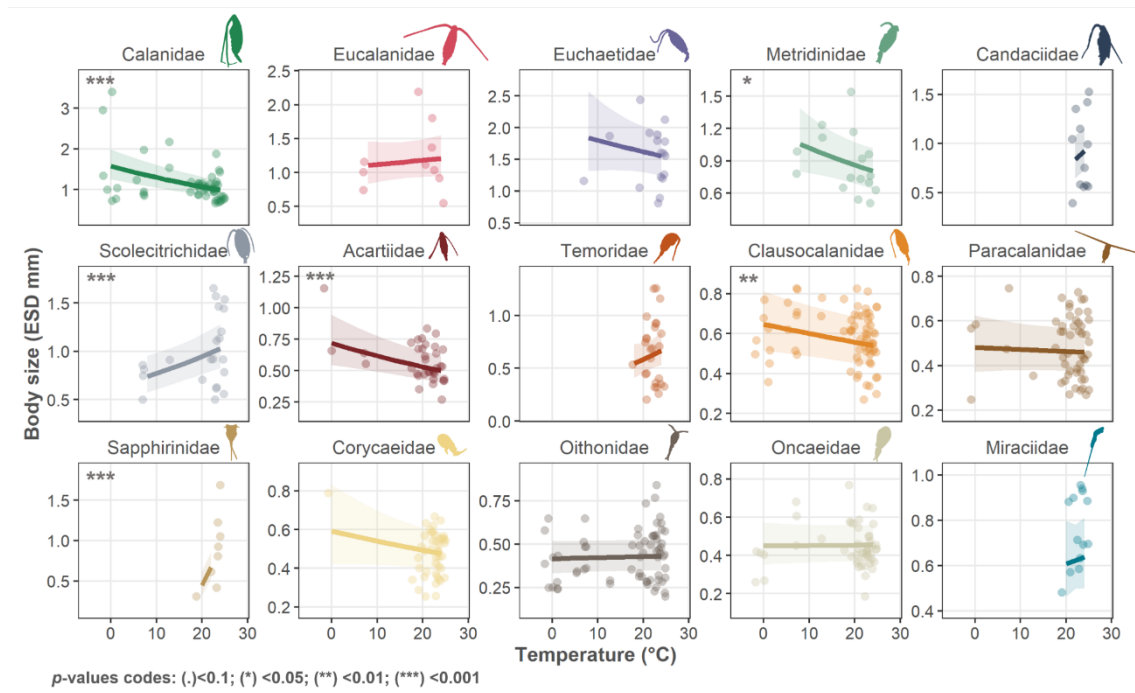


Figure 7. Mean body size (ESD mm) of copepod families along the temperature ($^{\circ}\text{C}$) gradient in the South Atlantic and Southern Ocean (13° - 64°S). Solid lines represent the fitted values (\pm 95% CI, colored shading) predicted for each family from GLMM models. Respective p values are shown in the top left corners. Note that the y-axis scale is different among the families, given the various body size ranges.

The modeled mean body size across the environmental gradients (temperature, salinity, oxygen and chl- a), shows that the contribution of some families to the latitudinal pattern was notable. As temperature decreases along the latitudinal gradient, the families Calanidae ($p < 0.000$), Euchaetidae, Metridinidae ($p < 0.035$), Acartiidae ($p < 0.001$), Clausocalanidae ($p < 0.004$) and Corycaeidae increased in body size (Fig. 7). On the other hand, the families Candaciidae, Scolecitrichidae ($p < 0.000$), Temoridae, Sapphirinidae ($p < 0.000$), Miraciidae displayed steeper positive slopes than families increasing in body size poleward (negative slopes; Table S1), presenting an inverse trend in body size. The salinity model presented a very similar pattern as temperature with the same families presenting significant either increasing or decreasing latitudinal trends (Fig. S5).

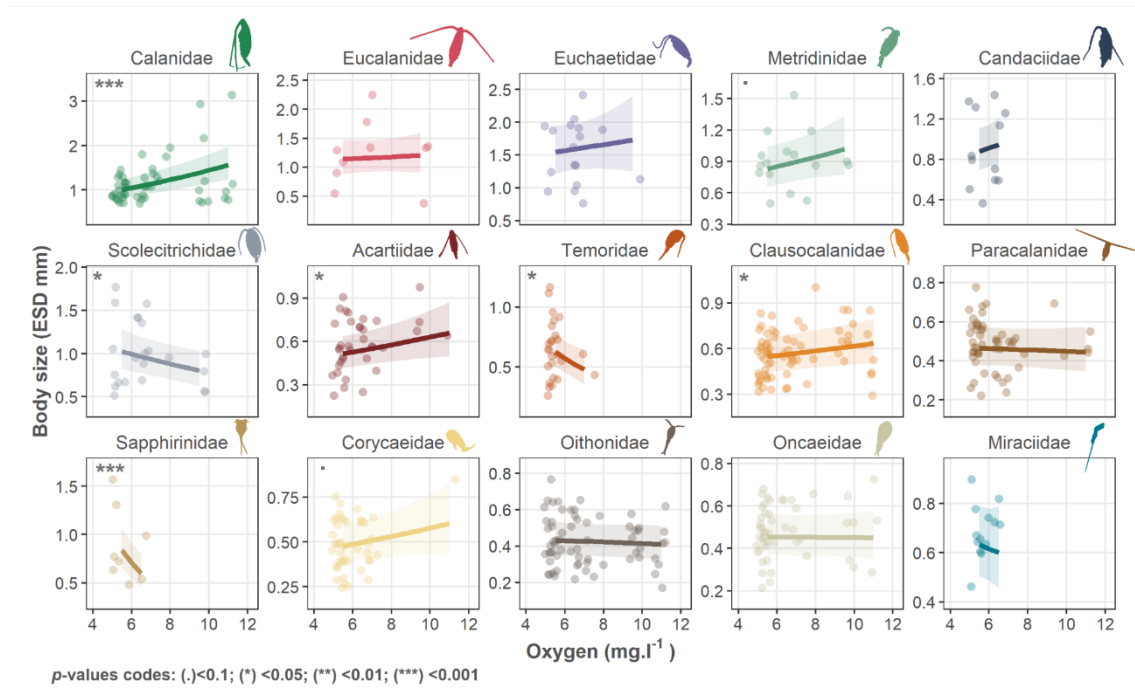


Figure 8. Mean body size (ESD mm) of copepod families along the oxygen (mg l^{-1}) gradient in the South Atlantic and Southern Ocean (13° - 64°S). Solid lines represent the fitted values ($\pm 95\%$ CI, colored shading) predicted for each family from GLMM models. Respective p values are shown in the top left corners. Note that the y-axis scale is different among the families, given the various body size ranges.

The mean body size was higher in more oxygenated waters (Fig. 8) for the families Calanidae ($p < 0.000$), Euchaetidae, Metridinidae ($p < 0.087$), Candaciidae, Acartiidae ($p < 0.032$), Clausocalanidae ($p < 0.019$), and Corycaeidae ($p < 0.082$). In contrast, body size decreased with higher oxygen levels in Scolecitrichidae ($p < 0.014$), Temoridae ($p < 0.013$), Sapphirinidae ($p < 0.000$), and Miraciidae. Finally, body size increase in enhanced concentrations of DCM (Fig. 9) for the families Calanidae ($p < 0.005$), Metridinidae ($p < 0.087$), Acartiidae ($p < 0.002$), Temoridae, Clausocalanidae, and Paracalanidae ($p < 0.071$). The body size decreased with higher DCM values in Scolecitrichidae ($p < 0.002$), Sapphirinidae ($p < 0.002$), and to a lesser extent in Eucalanidae, Candaciidae, and Corycaeidae.

Interestingly, Eucalanidae, Paracalanidae, Oithonidae and Oncaeidae seemed to maintain an even mean body size along all environmental gradients, as well as Euchaetidae and Miraciidae for DCM concentrations.

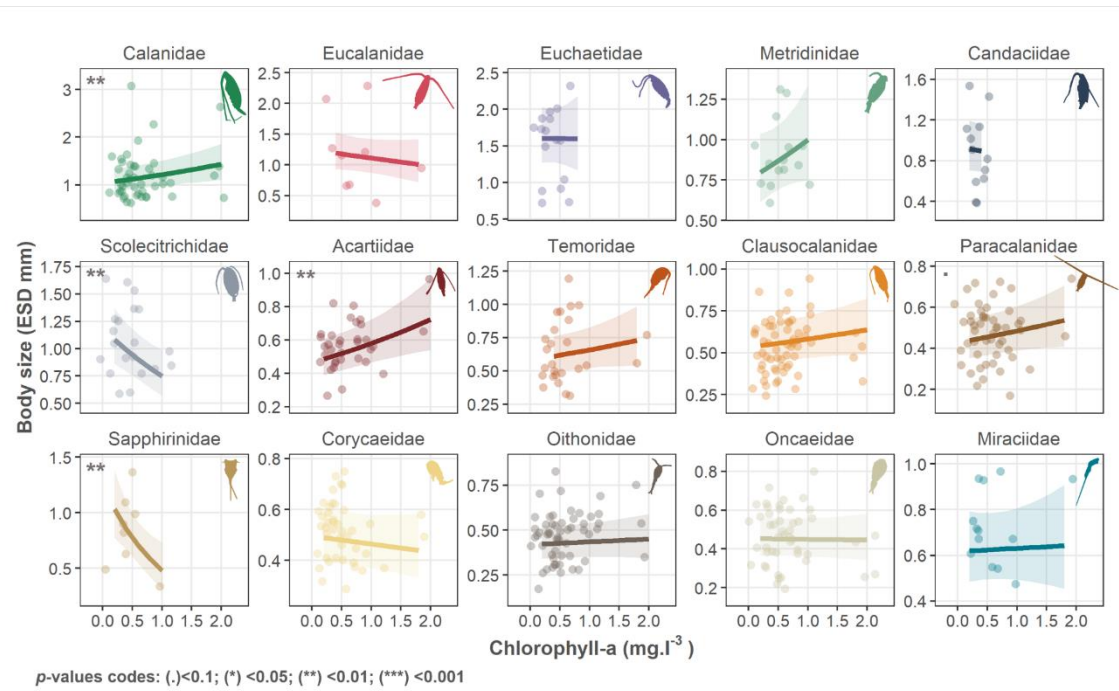


Figure 9. Mean body size (ESD mm) in copepod families along the deep chlorophyll-*a* maximum (mg l^{-3}) gradient in the South Atlantic and Southern Ocean (13° - 64°S). Solid lines represent the fitted values (\pm 95% CI, colored shading) predicted for each family from GLMM models. Respective *p* values are shown in the top left corners. Note that the y-axis scale is different among the families, given the various body size ranges.

Finally, competing models were ranked according to Akaike's Information Criterion (AIC). Temperature model with the lowest AIC was the most important predictor optimizing model fit and complexity. Oxygen was the second important predictor followed by salinity, and the latter was the deep chlorophyll-*a* maximum model (Table S2).

Discussion

Our findings suggest that the latitudinal patterns in copepod body size have a strong taxonomic signal. Although the latitudinal gradients of body size have been described for over 170 years (Bergmann, 1847), an analysis of family differences concomitantly with environmental drivers has uncovered three general patterns in a size diversified zooplankton assemblage. Our analyses revealed that, although the body size of most pelagic copepods contains, to some extent, a latitudinal decreasing body size pattern towards high latitudes, the calanoid copepods contribute more to the foundation of this pattern, while for cyclopoid copepods were less pronounced. This disproportional

contribution is consistent considering the diverse of life history strategies among copepod families, in particular Calanidae family, and environmental drivers, especially temperature variation. Additionally, the analyses provide support for the mechanism underlying the latitudinal pattern found, where regional oceanographic processes appear to booster the latitudinal pattern causing increases in biomass and/or abundance in the confluence and frontal systems of subtropical and sub-Antarctic waters, and in the connection region between the Atlantic Ocean and the Pacific Ocean, the Drake Passage. Below we argue that the explanation may lie in a combination of the oceanographic, ecological and climate drivers.

Oceanographic drivers

The latitudinal gradient in body size is perhaps the best known global biogeographic pattern and has been presumed to be stable over centuries. For instance, the temperature gradient has been consistently demonstrated to be a strong predictor of body size in pelagic copepods worldwide (Evans et al. 2020, Brandão & Benedetti et al., 2021, Campbell et al., 2021, Corona et al., 2021). However, we show that the effect of the latitudinal gradient is pronounced in some copepod families, especially the dominant-biomass Calanidae, largely because of the extremely high abundance of copepodite stages, which suggests that general size–temperature relationships provide only a partial explanation. While the latitudinal extent may, indeed, provide macroscale environmental gradients, it also promotes highly dynamic oceanographic conditions, which might help explain the latitudinal patterns of copepod body size found therein. Regional oceanographic processes appear to booster the latitudinal pattern promoting increases in biomass and/or abundance, as they alter markedly the average body size distribution in most of the copepod families along the latitudinal gradient, suggesting that body size is a function of availability of nutrients and energy during periods of growth season (Geist, 1987). These features are likely to be localities of biomass and/or abundance hotspots, confirming our working hypothesis that major oceanographic changes enhance Bergmann’s rule.

The first important element is associated with the constancy of resource availability along the latitudinal gradient. Pelagic copepods are reliant on allochthonous food sources that are brought up by complex water movements related to oceanographic currents and water masses. The South Atlantic Ocean (SAO) and the Southern Ocean

(SO) jointly are one of the most complex and dynamic oceanographic regions, where marine fronts are abundant (Acha et al., 2004), covering several scales of space and time. Hence, it is widely hypothesized that marine fronts separate different water masses, and hence different pelagic populations (Sournia, 1994) is ultimately linked to this oceanographic complexity.

The tropical and subtropical regions are characterized by relatively low phytoplankton concentrations all year round, and high concentrations of cyanobacteria, bacterioplankton and ciliates during the warm season (Cepeda et al., 2020). In turn, the interactions of forcing factors (winds, freshwater discharges, ocean currents) with geomorphological features, such as bottom topography and/or coastal orientation produce several frontal types, e.g., tidal fronts, estuarine fronts, shelf-break fronts (Acha et al., 2015). Therefore, SCZ, SAW and ACC are important resources of water making up a remarkable marine frontal system in the SAO and SO (Acha et al., 2020). Besides supporting an intense unidirectional flow of ocean currents from the Pacific to the Atlantic Ocean through the Drake Passage (Thompson et al., 2012). The SAO and SO may thus provide a constant input of cold rich waters. The broad scale oceanographic dynamics in the SAO and SO below 40°S, promotes a constant input of resources for pelagic copepods. Thus, bottom-up processes related to food size and quality allows the occurrence of large copepods in this region. Taken together, these evidences suggest that the disparities in the copepod size pattern along the latitudinal gradient, mainly from mid- to high latitudes, might be the result of successful energetic inputs of constant and abundant resources in the water column in the position of the abovementioned oceanographic processes.

Ecological drivers

We identified three general patterns of how copepod body size scales with environmental drivers on the South Atlantic basin scale during summer. These patterns are determined by how tradeoffs relate to environmental gradients. First, family variation in body size positively correlated with latitude and inversely with temperature leads to the classic Bergmann's rule. The other two latitudinal patterns either lead to an inverse scaling with environmental drivers or do not follow a power-law relationship at all. Our work highlights how copepods may deviate from the classic body size scaling pattern with latitude. A global analysis of zooplankton size structure by *Tara* Oceans (2009–

2013) found similar patterns, as the foundation of the global interspecific temperature–copepod size relationship is supported by the dominance of the large Calanidae driving the latitudinal increase in average size poleward (Brandão & Benedetti et al., 2021), as did other studies in higher temporal resolution on the North Atlantic (Evans et al., 2020). This pattern is especially clear in the northern hemisphere, where there is a sharp decline in copepod body size from the Arctic to the equator, a consistent cross-net pattern among 3 mesh sizes, which is not as clear in the southern hemisphere. Copepod median ESD sharply increased towards the Southern Ocean according to the Regent net (680 μm), whereas it showed no variations or a slight decrease according to the WP2 (200 μm) and Bongo (300 μm), respectively (Brandão & Benedetti et al., 2021).

Difference in the environmental drivers and size response strengths between Cyclopoida and Calanoida may relate to their different feeding strategies (active filtering in calanoids vs. ambush-feeding in cyclopoids) and the difference in body mass scaling of physiological rates between these different feeding types (Horne et al., 2016, Corona et al., 2021). Smaller omnivorous-carnivorous Cyclopoida follows the opposite pattern (Corycaeidae) and clearly increase in size from towards the tropics, confirming the global pattern found by *Tara* Oceans (Brandão & Benedetti et al., 2021), or even showed no variation along the latitudinal gradient (i.e. Oithonidae, Oncaeidae). Life history tradeoffs are associated with the coexistence and adaptations of several sizes and trophic behaviors (Atkinson, 1998). In the BC domain, the environment generally more stable and the microbial-based production appears to be an important feature of the food webs in the South Atlantic. The ability of small-bodied omnivorous-herbivorous copepods (i.e. Clausocalanidae, Paracalanidae, Oithonidae) to feed on particles smaller than those utilized by larger copepods, and colonize the nutrient-rich marine snow and floating substrates like Oncaeidae, emphasizes their ecological importance in channeling the energy of the microbial components into the classical food web (Turner, 2004). Greater specialization such as carnivory is also evident in warm oligotrophic conditions, represented by typical medium Corycaeidae, and large Euchaeitidae and Candaciidae carnivorous copepod species (Woodd-Walker et al., 2002, Teuber et al., 2019). Based on these characteristics, the life strategy of most epipelagic calanoid copepods in tropical oceans can be described as active converters, as they are rapidly and continuously metabolizing food for growth and reproductive processes (Teuber et al., 2019). Polar copepod communities are defined by 2 principal life history strategies that allow families to be successful: generalists, and lipid storers with diapause stages (Atkinson, 1998).

Oithonidae, being omnivorous, typifies the generalist with a wide range of feeding mechanisms, enabling an extended feeding period throughout the year. The lipid storing strategy is typified by family Calanidae, which are herbivorous in summer, have a short reproductive period and overwinter in diapause at depth (Atkinson, 1998). Thus, the seasonality and patchiness in food supply, overcome by either storing or by switching diet, that make it hard for other groups to thrive in the Southern Ocean (Woodd-Walker et al., 2002).

Since the classic explanation of Bergmann's rule based on thermoregulation principles is not applicable to most ectotherms, quite a few hypotheses have been proposed that appeal to other foundations in search of such an explanation (Vinarski et al., 2014). It appears that a single universal explanation of all the observed patterns of Bergmann's rule in ectotherms cannot be formulated, instead it arises as a result of synergetic interactions between several factors covarying with latitude (Vinarski et al., 2014). Temperature is generally explained as the main driver, either as direct effects on developmental rates or metabolism, or indirect effects via duration of the seasonal productivity or oxygen solubility (Verberk et al. 2021). But the thermoregulatory consequences of being large is not the only hypothesis responsible for larger body in colder climates. In fact, Bergmann's rule may be causally linked to the decreasing latitudinal gradient of species diversity from the equator to the poles. Lower diversity means reduced interspecific interactions, including competition. In the absence of larger competitors, smaller ones of the same assemblage often exhibit ecological relaxation, and increased size in species-poor environments at high latitudes (Iriarte et al., 1990). Carnivorous families are associated with tropical oligotrophic conditions, whereas current-feeding herbivores are associated with more productive and seasonally varying conditions in the South Atlantic (Becker et al., 2021), pointing to the potential for increased predation in low latitudes. Indeed, the dominance of larger *Calanus* species at high latitude due to reduced importance of visual predators in the Arctic (Kaartvedt, 2000). According to Corona et al., (2020), seasonal changes in copepod body size may reflect density dependence mechanisms via competition for food and/or intraguild predation in periods when the food/zooplankton biomass ratio is low. Taken together, our results points temperature as a main driver of size differences between SAO and SO copepod populations, but those trophic interactions, and indirectly oxygen concentrations (Verberk et al. 2021) and regional oceanographic processes may pose additional effects.

Climate drivers and concluding remarks

Equatorial biodiversity is threatened by decreasing species richness, suggesting that the equator is already too hot for some species to survive and indicating further low latitude declines of species are likely with continued warming (Chaudhary et al., 2021). Greater latitudinal shift in zooplankton body size over the past few decades were driven by strong size declines in copepod populations across the North Atlantic (Cornwell et al., 2020), due to the greater warming conditions in the northern hemisphere (Beaugrand et al., 2010). Although it is well-established that the global oceans are changing at an unprecedented rate, the drivers behind the observed copepod body size declines are uncertain, and some important species have maintained stable populations, such as *Oithona similis* over the last 30 years (Cornwell et al., 2020). We identified in the South Atlantic and Southern Ocean that some widely distributed small copepods (mean body size smaller than 1 mm) presented a slight or no environmental gradient (e.g. Oithonidae, Oncaeidae, Paracalanidae), which might indicate certain resilience to climatic variability. These families might arise as prime candidates to emerge as “winners” if smaller taxa replace larger ones due to warming-induced decreases in median body size (Campbell et al. 2021, Benedetti et al., 2022).

Bergmann's rule is an adaptive response (Geist, 1987), and it does suggest that phenotypic plasticity, rather than genetic differences, may account for much of the latitudinal variation. Copepods with higher thermal limits, or copepods that can survive at higher temperatures, are less able to acclimate to changes in temperature within their life spans (Sasaki & Dam, 2021). For example, carnivory is one of the main traits contributing to the functional diversity of tropical waters (Becker et al., 2021). Projected environmental changes shows an increase in carnivorous copepods species richness and significant habitat area increases due to poleward expansion at the expense of herbivorous copepods at high latitudes (McGinty et al., 2021). Hence, these warm-adapted, low-latitude populations are more vulnerable to warming as they already experience temperatures near their thermal maxima and lack the ability to respond to increases in temperature through phenotypic plasticity (Vinagre et al., 2016). Since our study is consistent of mesozooplankton mesh size (200 μ m) rather than larger size classes, it likely underestimates the contribution of common and abundant carnivorous families, such as Euchaeitidae, Candaciidae and Corycaeidae at low latitudes (Brandão & Benedetti et al., 2021). As a result, we probably underestimate their proportion in warm water latitudinal

bands. However, they displayed contrasting latitudinal patterns in mean body size that could be explained by differences in environmental niches preferences, such feeding modes and spawning strategies (Becker et al., 2021, Benedetti et al., 2022).

There is considerable opportunity to include well-tested macroecological principles such as Bergmann’s rule in future modelling efforts focused on climate change (Campbell et al., 2021). Our analysis shows that these principles are not universal laws, and groups with a wide diversity of functional traits such as copepods vary substantially in body size due to their life-history strategies that emerge from environmental conditions and biotic interactions, such as changes in food availability and predation pressure (Horne et al., 2016, Benedetti et al., 2022). Ignoring family-specific differences in body size latitudinal gradients may result in an underestimation of population-level impacts of warming. Furthermore, the patterns depicted for the most important copepod families need to be evaluated in other geographical areas, in order to fully understand the generality between copepod and/or zooplankton taxa, and whether the underlying eco-evolutionary mechanisms are the same in other regions. As our planet and ocean warm, understanding how keystone copepod life history and the body size latitudinal patterns adapt to changing temperatures will be critical.

Supplementary material

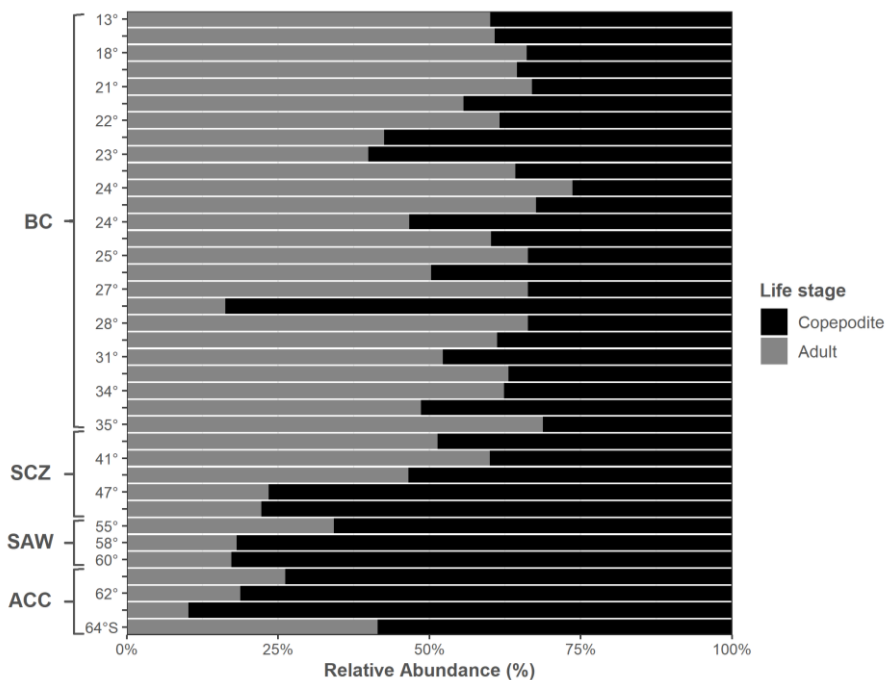


Figure S1. Relative copepod abundance according to the life stages along the latitudinal gradient of the South Atlantic and Southern Ocean (13°-64°S).

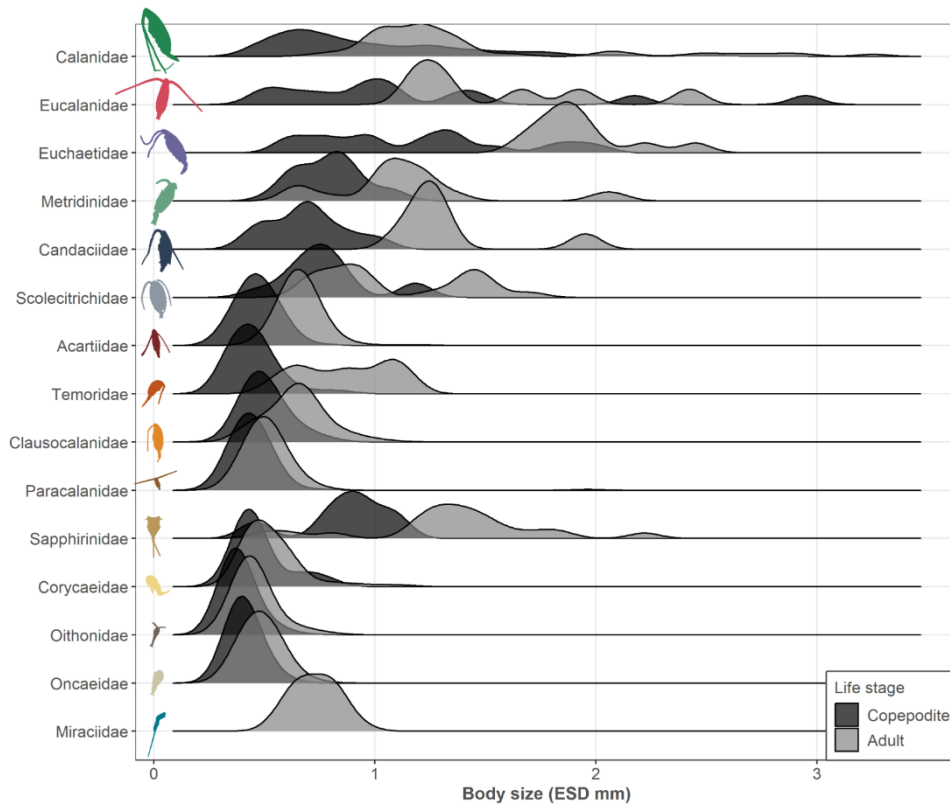


Figure S2. Body size frequency distribution estimated through equivalent spherical diameter (ESD mm) of the main copepod families and life stages along the latitudinal gradient in the South Atlantic and Southern Ocean (13°-64°S).

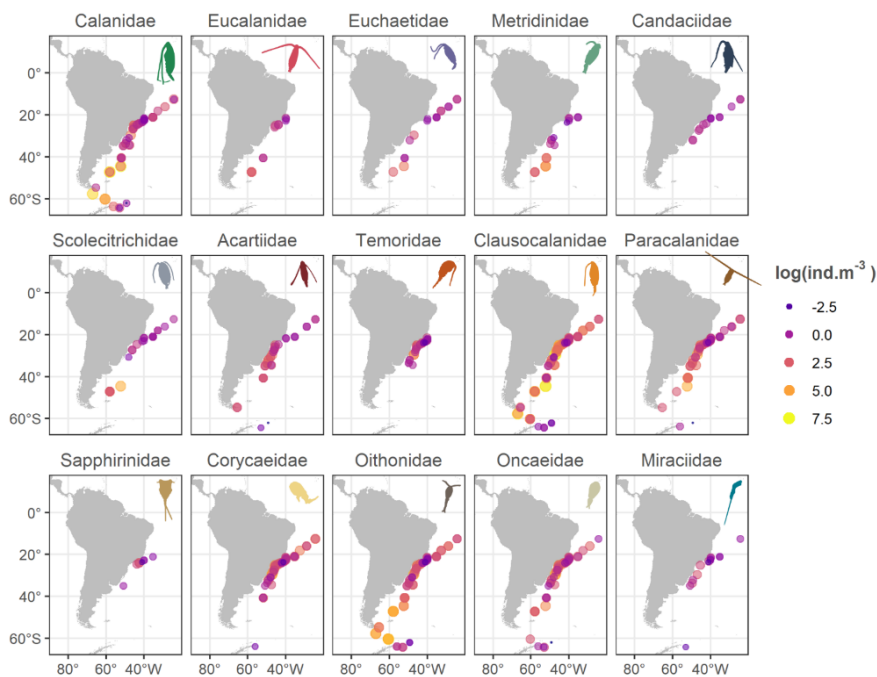


Figure S3. Abundance (ind.m^{-3}) of the main copepod families along the latitudinal gradient in the South Atlantic and Southern Ocean (13°-64°S). Circles display designated geographical region with the size and color proportional to its value in the sampling station.

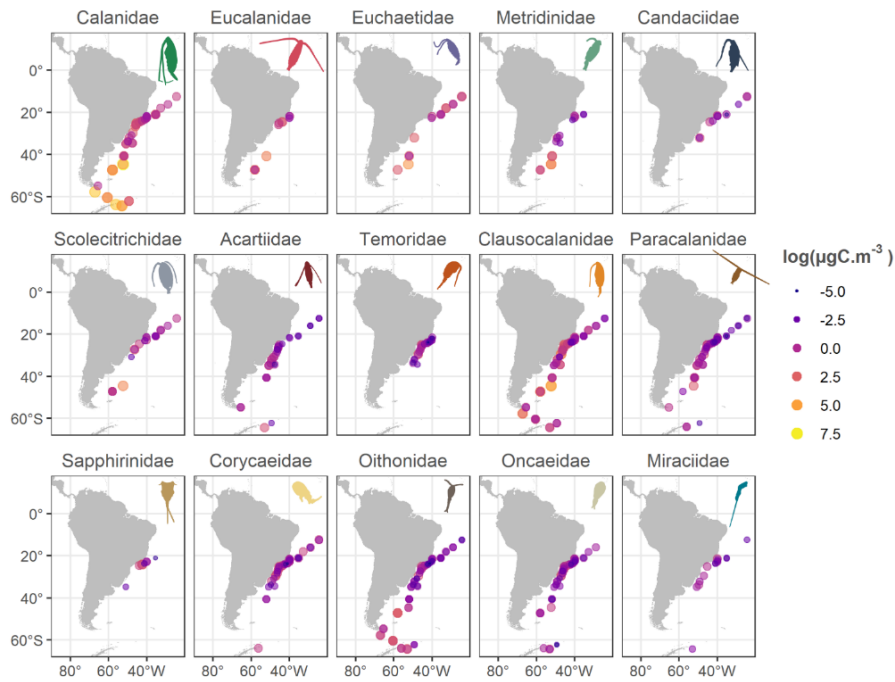


Figure S4. Biomass ($\mu\text{gC}\cdot\text{m}^{-3}$) of the main copepod families along the latitudinal gradient in the South Atlantic and Southern Ocean (13° - 64°S). Circles display designated geographical region with the size and color proportional to its value in the sampling station.

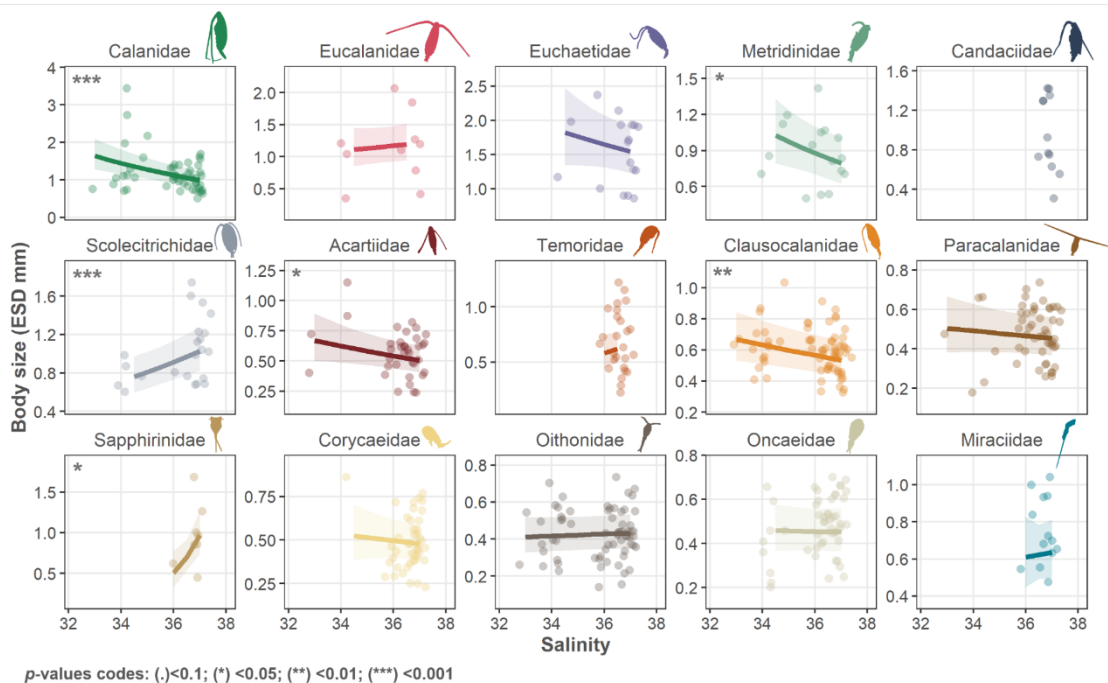


Figure S5. Mean body size (ESD mm, dots) of copepod families along the salinity gradient in the South Atlantic and Southern Ocean (13° - 64°S). Solid lines represent the fitted values (\pm 95% CI, colored shading) predicted for each family from GLMM models. Respective p values are shown in the top left corners. Note that the y-axis scale is different among the families, given the various body size ranges.

Table S1. Generalized linear mixed model (GLMM) accounting the effects of the Temperature (°C), Salinity, Oxygen (mg.l⁻¹) and Chlorophyll-a (mg.m⁻³) on mean body size (ESD mm) within different copepod families along the latitudinal gradient in the South Atlantic and Southern Ocean (13°-64°S). Models also accounted the different life stages (adult and copepodite) as random effects.

Copepod family	<i>Temperature</i>				<i>Salinity</i>				<i>Oxygen</i>				<i>Chlorophyll-a</i>			
	Estimate	Standard error	z value	p-value	Estimate	Standard error	z value	p-value	Estimate	Standard error	z value	p-value	Estimate	Standard error	z value	p-value
Calanidae	-0.019	0.003	-6.703	***	-0.125	0.022	-5.669	***	0.081	0.013	6.119	***	0.161	0.057	2.825	**
Eucalanidae	0.006	0.008	0.664	n.s.	0.035	0.049	0.712	n.s.	0.014	0.034	0.403	n.s.	-0.119	0.119	-1.000	n.s.
Euchaetidae	-0.011	0.009	-1.141	n.s.	-0.065	0.053	-1.234	n.s.	0.028	0.041	0.685	n.s.	-0.011	0.243	-0.047	n.s.
Metridinidae	-0.017	0.008	-2.114	*	-0.101	0.046	-2.193	*	0.051	0.030	1.711	.	0.282	0.194	1.452	n.s.
Candaciidae	0.049	0.041	1.195	n.s.	0.035	0.509	0.068	n.s.	0.074	0.078	0.948	n.s.	-0.122	0.629	-0.194	n.s.
Scolecitrichidae	0.020	0.006	3.606	***	0.119	0.033	3.629	***	-0.061	0.025	-2.447	*	-0.461	0.149	-3.105	**
Acartiidae	-0.015	0.005	-3.297	***	-0.071	0.030	-2.319	*	0.045	0.021	2.138	*	0.221	0.073	3.024	**
Temoridae	0.034	0.023	1.431	n.s.	0.100	0.134	0.747	n.s.	-0.176	0.071	-2.482	*	0.126	0.089	1.415	n.s.
Clausocalanidae	-0.007	0.003	-2.870	**	-0.056	0.018	-3.120	**	0.027	0.011	2.350	*	0.089	0.055	1.597	n.s.
Paracalanidae	-0.002	0.004	-0.522	n.s.	-0.026	0.028	-0.932	n.s.	-0.008	0.016	-0.525	n.s.	0.128	0.071	1.807	.
Sapphirinidae	0.203	0.038	5.339	***	0.628	0.315	1.996	*	-0.341	0.092	-3.721	***	-0.956	0.313	-3.057	**
Corycaeidae	-0.009	0.006	-1.448	n.s.	-0.035	0.051	-0.689	n.s.	0.043	0.025	1.741	n.s.	-0.066	0.072	-0.915	n.s.
Oithonidae	0.001	0.002	0.611	n.s.	0.013	0.018	0.716	n.s.	-0.009	0.011	-0.836	n.s.	0.036	0.060	0.605	n.s.
Oncaeidae	0.000	0.003	0.144	n.s.	-0.006	0.027	-0.234	n.s.	-0.002	0.014	-0.119	n.s.	-0.007	0.060	-0.118	n.s.
Miraciidae	0.011	0.030	0.376	n.s.	0.037	0.169	0.216	n.s.	-0.052	0.093	-0.565	n.s.	0.022	0.111	0.201	n.s.

p-values codes: (.) < 0.1; () < 0.05; (**) < 0.01; (***) < 0.001; n.s.: non-significant.*

Table S2. Competing models selection using the ranked Akaike's Information Criterion (AIC) in GLMM analysis. The models accounted the effects of environmental variables on mean body size (ESD mm) within different copepod families along the latitudinal gradient in the South Atlantic and Southern Ocean (13°-64°S). Models also accounted the different life stages (adult and copepodite) as random effects. *: interaction.

Model	AIC	dAIC	Log-likelihood	df
Mean body size ~ Temperature * Family	-724.1	0	394	32
Mean body size ~ Oxygen * Family	-695.9	28.2	379.9	32
Mean body size ~ Salinity * Family	-692.4	31.6	378.2	32
Mean body size ~ DCM * Family	-610.3	113.7	337.2	32

References

- Acha, E. M., Mianzan, H. W., Guerrero, R. A., Favero, M. & Bava, J. (2004). Marine fronts at the continental shelves of austral South America: physical and ecological processes. *Journal of Marine systems*, 44(1-2), 83-105.
- Acha, E. M., Piola, A., Iribarne, O. & Mianzan, H. (2015). Ecological processes at marine fronts: oases in the ocean. Springer.
- Ackerly, D. D. & Cornwell, W. K. (2007). A trait-based approach to community assembly: partitioning of species trait values into within-and among-community components. *Ecology letters*, 10(2), 135–145.
- Aminot, A., K erouel, R. & Coverly, S. C. (2009). Nutrients in seawater using segmented flow analysis. *Practical guidelines for the analysis of seawater*, 143–178.
- Atkinson, D. (1994). Temperature and organism size: a biological law for ectotherms? *Advances in Ecological Research*, 25, 1–58.
- Atkinson, A. (1998). Life cycle strategies of epipelagic copepods in the Southern Ocean. *Journal of Marine Systems*, 15(1-4), 289-311.
- Atkinson, D., Morley, S. A. & Hughes, R. N. (2006). From cells to colonies: at what levels of body organization does the 'temperature-size rule' apply? *Evolution & development*, 8(2), 202–214.
- Barton, A. D., Pershing, A. J., Litchman, E., Record, N. R., Edwards, K. F., Finkel, Z. V., K orboe, T., Ward, B. A. (2013). The biogeography of marine plankton traits. *Ecology letters*, 16(4), 522–534.
- Beaugrand, G. & Kirby, R. R. (2010). Spatial changes in the sensitivity of Atlantic cod to climate-driven effects in the plankton. *Climate research*, 41(1), 15–19.
- Beaugrand, G., Edwards, M. & Legendre, L. (2010). Marine biodiversity, ecosystem functioning, and carbon cycles. *Proceedings of the National Academy of Sciences*, 107(22), 10120–10124.

- Becker, É. C., Mazzocchi, M. G., de Macedo-Soares, L. C. P., Brandão, M. C. & Freire, A. S. (2021). Latitudinal gradient of copepod functional diversity in the South Atlantic Ocean. *Progress in Oceanography*, 199, 102710.
- Benedetti, F., Wydler, J. & Vogt, M. (2022). Copepod functional traits and groups show contrasting biogeographies in the global ocean. *bioRxiv*.
- Bergmann, C. (1847). Über die verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. *Gött. Stud.*, 1, 595–708.
- Bi, H., Peterson, W. T., Lamb, J., & Casillas, E. (2011). Copepods and salmon: characterizing the spatial distribution of juvenile salmon along the Washington and Oregon coast, USA. *Fisheries Oceanography*, 20(2), 125–138.
- Blackburn, T. M., Gaston, K. J., & Loder, N. (1999). Geographic gradients in body size: a clarification of Bergmann's rule. *Diversity and distributions*, 5(4), 165–174.
- Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H. & White, J. S. S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in ecology & evolution*, 24(3), 127–135.
- Brandão, M. C., Garcia, C. A. E. & Freire, A. S. (2015). Large-scale spatial variability of decapod and stomatopod larvae along the South Brazil Shelf. *Continental Shelf Research*, 107, 11–23.
- Brandão, M. C., Benedetti, F., Martini, S., Soviadan, Y. D., Irisson, J. O., Romagnan, J. B., Elineau, A., Desnos, C., Jalabert, L., Freire, A. S., Picheral, M., Guidi, L., Gorsky, G., Bowler, C., Karp-Boss, L., Henry, N., de Vargas, C., Sullivan, M. B., Tara Oceans Consortium Coordinators, Stemmann, L. & Lombard, F. (2021). Macroscale patterns of oceanic zooplankton composition and size structure. *Scientific Reports*, 11(1), 1–19.
- Brandini, F.P., Tura, P.M. & Santos, P.P.G.M. (2018). Ecosystem responses to biogeochemical fronts in the South Brazil Bight. *Progress in Oceanography*, 164, 52–62.
- Campbell, M. D., Schoeman, D. S., Venables, W., Abu-Alhaija, R., Batten, S. D., Chiba, S., Coman, F., Davies, C. H., Edwards, M., Eriksen, R. S., Everett, J. D., Fukai, Y., Fukuchi, M., Garrote, O. E., Hosie, G., Huggett, J. A., Johns, D. G., Kitchener, J. A., Koubbi, P., McEnnulty, F. R., Muxagata, E., Ostle, C., Robinson, K. V., Slotwinski, A., Swadling, K. M., Takahashi, K. T., Tonks, M., Uribe-Palomino, J., Verheye, H. M., Wilson, W. H., Worship, M. M., Yamaguchi, A., Zhang, W. & Richardson, A. J. (2021). Testing Bergmann's rule in marine copepods. *Ecography*, 44(9), 1283–1295.
- Cepeda, G.D., Viñas, M.D., Molinari, G.N., Hozbor, M.C., Silva, R.I., Martínez, A. & Acha, E.M. (2020) The impact of Río de la Plata plume favors the small-sized copepods during summer. *Estuarine, Coastal and Shelf Science*, 245, 107000.
- Campos, M. C., Chiessi, C. M., Voigt, I., Piola, A. R., Kuhnert, H. & Mulitza, S. (2017). $\delta^{13}\text{C}$ decreases in the upper western South Atlantic during Heinrich Stadials 3 and 2. *Climate of the Past*, 13(4), 345–358.

- Chaudhary, C., Richardson, A. J., Schoeman, D. S. & Costello, M. J. (2021). Global warming is causing a more pronounced dip in marine species richness around the equator. *Proceedings of the National Academy of Sciences*, 118(15).
- Cornwell, L. E., Fileman, E. S., Bruun, J. T., Hirst, A. G., Tarran, G. A., Findlay, H. S., Lewis, C., Smyth, T. J. & Atkinson, A. (2020). Resilience of the copepod *Oithona similis* to climatic variability: egg production, mortality, and vertical habitat partitioning. *Frontiers in Marine Science*, 7, 29.
- Corona, S., Hirst, A., Atkinson, D. & Atkinson, A. (2021). Density-dependent modulation of copepod body size and temperature–size responses in a shelf sea. *Limnology and Oceanography*, 66(11), 3916–3927.
- Daufresne, M., Lengföllner, K. & Sommer, U. (2009). Global warming benefits the small in aquatic ecosystems. *Proceedings of the National Academy of Sciences*, 106(31), 12788–12793.
- Evans, L. E., Hirst, A. G., Kratina, P. & Beaugrand, G. (2020). Temperature-mediated changes in zooplankton body size: large scale temporal and spatial analysis. *Ecography*, 43(4), 581–590.
- Frontier, S. (1981). Cálculo del error en el recuento de organismos zooplanctónicos. *Atlas del Zooplancton del Atlántico Sudoccidental y métodos de trabajo con el zooplancton marino. Mar del Plata, INIDEP*, 936p, 163–167.
- Garzoli, S. L. & Matano, R. (2011). The South Atlantic and the Atlantic meridional overturning circulation. *Deep Sea Research Part II: Topical Studies in Oceanography*, 58(17-18), 1837–1847.
- Geist, V. (1987). Bergmann's rule is invalid. *Canadian Journal of Zoology*, 65(4), 1035–1038.
- Grasshoff, K., Ehrhardt, M. & Kremling, K. (1983). *Seawater Analysis*.
- Gorsky, G., Ohman, M. D., Picheral, M., Gasparini, S., Stemmann, L., Romagnan, J. B., Cawood, A., Pesant, S., García-Comas, C. & Prejger, F. (2010). Digital zooplankton image analysis using the ZooScan integrated system. *Journal of plankton research*, 32(3), 285–303.
- Grosjean, P., Picheral, M., Warembourg, C. & Gorsky, G. (2004). Enumeration, measurement, and identification of net zooplankton samples using the ZOOSCAN digital imaging system. *ICES Journal of Marine Science*, 61(4), 518–525.
- Hartig, F., & Hartig, M. F. (2017). Package ‘DHARMa’. *R package*.
- Hartig, F. (2020). DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. *R package version 0.3*, 3.
- Horne, C. R., Hirst, A. G., Atkinson, D., Neves, A. & Kiørboe, T. (2016). A global synthesis of seasonal temperature–size responses in copepods. *Global Ecology and Biogeography*, 25(8), 988–999.

- Iriarte, J. A., Franklin, W. L., Johnson, W. E. & Redford, K. H. (1990). Biogeographic variation of food habits and body size of the America puma. *Oecologia*, 85(2), 185-190.
- Kaartvedt, S. (2000). Life history of *Calanus finmarchicus* in the Norwegian Sea in relation to planktivorous fish. *ICES Journal of Marine Science*, 57(6), 1819-1824.
- Kurtz, F. W. & Matsuura, Y. (2001). Food and feeding ecology of Brazilian sardine (*Sardinella brasiliensis*) larvae from the southeastern Brazilian Bight. *Revista Brasileira de Oceanografia*, 49, 60–74.
- Lehette, P. & Hernández-León, S. (2009). Zooplankton biomass estimation from digitized images: a comparison between subtropical and Antarctic organisms. *Limnology and Oceanography: Methods*, 7(4), 304–308.
- Lopes, R. M., Marcolin, C. R. & Brandini, F. P. (2016) Influence of oceanic fronts on mesozooplankton abundance and grazing during spring in the south-western Atlantic. *Marine and Freshwater Research*, 67(5), 626–635.
- de Macedo-Soares, L. C. P., Garcia, C. A. E., Freire, A. S. & Muelbert, J. H. (2014). Large-scale ichthyoplankton and water mass distribution along the South Brazil Shelf. *PLoS One*, 9(3), e91241.
- Magnusson, A., Skaug, H., Nielsen, A., Berg, C., Kristensen, K., Maechler, M., Koen van Bentham, K., Bolker, B., Sadat, N., Lüdecke, D., Lenth, R., O'Brien, J. & Brooks, M. M. (2017). Package ‘glmmTMB’. *R Package Version 0.2.0*.
- Marcolin, C. R., Gaeta, S., & Lopes R. M. (2015). Seasonal and interannual variability of zooplankton vertical distribution and biomass size spectra off Ubatuba, Brazil. *Journal of Plankton Research*, 37(4), 808–819.
- McGinty, N., Barton, A. D., Record, N. R., Finkel, Z. V., Johns, D. G., Stock, C. A. & Irwin, A. J. (2021). Anthropogenic climate change impacts on copepod trait biogeography. *Global Change Biology*, 27(7), 1431-1442.
- Miyashita, L. K., de Melo Junior, M. & Lopes, R. M. (2009). Estuarine and oceanic influences on copepod abundance and production of a subtropical coastal area. *Journal of Plankton Research*, 31(8), 815–826.
- Padovani, L. N., Viñas, M. D., & Pájaro, M. (2011). Importance of the Río de la Plata estuarine front (southwestern Atlantic Ocean) in the feeding ecology of Argentine anchovy, *Engraulis anchoita* (Clupeiformes, Clupeidae). *Latin American Journal of Aquatic Research*, 39(2), 205–213.
- Persson, J., Stige, L. C., Stenseth, N. C., Usov, N., & Martynova, D. (2012). Scale-dependent effects of climate on two copepod species, *Calanus glacialis* and *Pseudocalanus minutus*, in an Arctic-boreal sea. *Marine Ecology Progress Series*, 468, 71–83.
- Pesant, S., Not, F., Picheral, M., Kandels-Lewis, S., Le Bescot, N., Gorsky, G., Iudicone, D., Karsenti, E., Speich, S., Troublé, R., Dimier, C., Searson, S. & Tara Oceans

- Consortium Coordinators. (2015). Open science resources for the discovery and analysis of Tara Oceans data. *Scientific data*, 2(1), 1–16.
- Peterson, R. G. & Stramma, L. (1991). Upper-level circulation in the South Atlantic Ocean. *Progress in oceanography*, 26(1), 1–73.
- Picheral, M., Colin, S. & Irisson, J. O. (2017). EcoTaxa, a tool for the taxonomic classification of images. URL <http://ecotaxa.obs-vlfr.fr>.
- Poloczanska, E. S., Burrows, M. T., Brown, C. J., García Molinos, J., Halpern, B. S., Hoegh-Guldberg, O., Carrie V. Kappel, C. V., Moore, P. J., Richardson, A. J., Schoeman, D. S. & Sydeman, W. J. (2016). Responses of marine organisms to climate change across oceans. *Frontiers in Marine Science*, 62.
- R Core Team (2021). R: A language and environment for statistical computing. *R Foundation for Statistical Computing*, Vienna, Austria. URL <https://www.R-project.org/>.
- Ras, J., Claustre, H. & Uitz, J. (2008). Spatial variability of phytoplankton pigment distributions in the Subtropical South Pacific Ocean: comparison between in situ and predicted data. *Biogeosciences*, 5(2), 353–369.
- Salewski, V., & Watt, C. (2017). Bergmann's rule: a biophysiological rule examined in birds. *Oikos*, 126(2).
- San Martin, E., Harris, R. P. & Irigoien, X. (2006). Latitudinal variation in plankton size spectra in the Atlantic Ocean. *Deep Sea Research Part II: Topical Studies in Oceanography*, 53(14-16), 1560–1572.
- Sasaki, M. & Dam, H. G. (2021). Global patterns in copepod thermal tolerance. *Journal of Plankton Research*, 43(4), 598-609.
- Sommer, U., Peter, K. H., Genitsaris, S. & Moustaka-Gouni, M. (2017). Do marine phytoplankton follow Bergmann's rule *sensu lato*? *Biological Reviews*, 92(2), 1011–1026.
- Sournia, A. (1994). Pelagic biogeography and fronts. *Progress in Oceanography*, 34(2-3), 109–120.
- Soviadan, Y. D., Benedetti, F., Brandão, M. C., Ayata, S. D., Irisson, J. O., Jamet, J. L., Kiko, R., Lombard, F., Gnandi, K. & Stemmann, L. (2022). Patterns of mesozooplankton community composition and vertical fluxes in the global ocean. *Progress in Oceanography*, 200, 102717.
- Stramma, L., & England, M. (1999). On the water masses and mean circulation of the South Atlantic Ocean. *Journal of Geophysical Research: Oceans*, 104(C9), 20863–20883.
- Strickland, J. D. H. & Parsons, T. R. (1968). A practical handbook of seawater analysis. *Bulletin - Fisheries Research Board of Canada*, 167, 311 pp.

- Teuber, L., Hagen, W., Bode, M. & Auel, H. (2019). Who is who in the tropical Atlantic? Functional traits, ecophysiological adaptations and life strategies in tropical calanoid copepods. *Progress in oceanography*, 171, 128-135.
- Thompson, G., Dinofrio, E. O., Alder, V. A., Takahashi, K. T. & Hosie, G. W. (2012). Copepod distribution in surface waters of the Drake Passage using Continuous Plankton Recorder and a Pump-Net onboard system. *Brazilian Journal of Oceanography*, 60(3), 367-380.
- Timofeev, S. F. (2001). Bergmann's principle and deep-water gigantism in marine crustaceans. *Biology Bulletin of the Russian Academy of Sciences*, 28(6), 646–650.
- Turner, J. T. (2004). The importance of small planktonic copepods and their roles in pelagic marine food webs. *Zoological Studies*, 43(2), 255-266.
- Uye, S. I. (1982). Length-weight relationships of important zooplankton from the Inland Sea of Japan. *Journal of the Oceanographical Society of Japan*, 38(3), 149–158.
- Uye, S. I., Aoto, I., & Onbé, T. (2002). Seasonal population dynamics and production of *Microsetella norvegica*, a widely distributed but little-studied marine planktonic harpacticoid copepod. *Journal of Plankton Research*, 24(2), 143–153.
- Van Heukelem, L. & Thomas, C. S. (2001). Computer-assisted high-performance liquid chromatography method development with applications to the isolation and analysis of phytoplankton pigments. *Journal of Chromatography A*, 910(1), 31–49.
- Verberk, W. C., Atkinson, D., Hoefnagel, K. N., Hirst, A. G., Horne, C. R. & Siepel, H. (2021). Shrinking body sizes in response to warming: explanations for the temperature–size rule with special emphasis on the role of oxygen. *Biological Reviews*, 96(1), 247-268.
- Villar, E., Farrant, G.K., Follows, M., Garczarek, L., Speich, S., Audic, S., Bittner, L., Blanke, B., Brum, J.R., Brunet, C., Casotti, R., Chase, A., Dolan, J.R., D’Ortenzio, F., Gattuso, J.-P., Grima, N., Guidi, L., Hill, C.N., Jahn, O., Jamet, J.-L., Le Goff, H., Lepoivre, C., Malviya, S., Pelletier, E., Romagnan, J.-B., Roux, S., Santini, S., Scalco, E., Schwenck, S.M., Tanaka, A., Testor, P., Vannier, T., Vincent, F., Zingone, A., Dimier, C., Picheral, M., Searson, S., Kandels-Lewis, S., Acinas, S.G., Bork, P., Boss, E., de Vargas, C., Gorsky, G., Ogata, H., Pesant, S., Sullivan, M.B., Sunagawa, S., Wincker, P., Karsenti, E., Bowler, C., Not, F., Hingamp, P. & Iudicone, D. (2015) Environmental characteristics of Agulhas rings affect interocean plankton transport. *Science*, 348, 1261447–1261447.
- Vinagre, C., Leal, I., Mendonca, V., Madeira, D., Narciso, L., Diniz, M. S. & Flores, A. A. (2016). Vulnerability to climate warming and acclimation capacity of tropical and temperate coastal organisms. *Ecological indicators*, 62, 317-327.
- Vinarski, M. V. (2014). On the applicability of Bergmann’s rule to ectotherms: the state of the art. *Biology Bulletin Reviews*, 4(3), 232–242.
- Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A. & Smith, G. M. (2009). Mixed effects models and extensions in ecology with R (Vol. 574). New York: Springer.

- Welschmeyer, N. A. (1994). Fluorometric analysis of chlorophyll a in the presence of chlorophyll b and pheopigments. *Limnology and oceanography*, 39(8), 1985–1992.
- Woodd-Walker, R. S., Ward, P. & Clarke, A. (2002). Large-scale patterns in diversity and community structure of surface water copepods from the Atlantic Ocean. *Marine Ecology Progress Series*, 236, 189-203.

6 CONCLUSÃO

O Oceano Atlântico Sul é reconhecido como um dos oceanos menos estudados do mundo, e juntamente com os demais oceanos globais, está ameaçado pelos aumentos acentuados da temperatura causados pelas atividades humanas. No entanto, poucos estudos têm procurado estimar a diversidade funcional do zooplâncton, no Oceano Atlântico Sul e Oceano Antártico, e explorar os gradientes ambientais sobre este componente da biodiversidade. O Oceano Atlântico apresenta uma variedade de condições físico-químicas e regimes tróficos que o tornam um local interessante para estudar as respostas dos ecossistemas pelágicos aos gradientes latitudinais.

O trabalho realizado durante esta tese permitiu descrever pela primeira vez os grupos funcionais para os copépodes epipelágicos do Oceano Atlântico Sul. Esses grupos funcionais não apenas aprofundam nossa compreensão do funcionamento dos ecossistemas pelágicos a partir de índices de diversidade funcional (Capítulo I), mas também melhorarão a representação do zooplâncton em modelos regionais e globais, principalmente a resolução do gradiente latitudinal do tamanho corporal das principais famílias de copépodes epipelágicos (Capítulo II). A diversidade funcional de aproximadamente 100 espécies de copépodes mostrou como as condições ambientais controlam a distribuição dos diferentes grupos e, portanto, potencialmente a expressão das funções que eles fornecem, ou seja, a relação da biodiversidade e o funcionamento do ecossistema (BEF). Mecanismos ecológicos destacam o papel substancial da complementariedade funcional na estruturação da comunidade de copépodes e como a heterogeneidade ambiental mantém a estrutura funcional mínima para o funcionamento do ecossistema, apesar da diminuição da riqueza funcional em direção a região polar. Do ponto de vista da função do ecossistema, o Oceano Antártico suporta uma fauna empobrecida, com preferencialmente herbívoros desempenhando cada função, e com um efeito marcado da temperatura no padrão encontrado. Futuros aumentos de temperatura no Atlântico Sul irão potencialmente modificar a riqueza e composição das comunidades planctônicas de copépodes. Espécies de hábitos alimentares carnívoros serão potencialmente as mais afetadas pelo aumento da temperatura, ao contrário de espécies com hábitos omnívoros e herbívoros, levando a uma queda na riqueza funcional das assembleias na zona tropical.

No entanto, o tamanho médio de copépodes aumentou ao longo do gradiente latitudinal, ou seja, com a diminuição da temperatura e aumento do oxigênio. A resposta do tamanho corporal de copépodes ao longo do gradiente latitudinal tem uma forte

assinatura taxonômica. De forma geral, esse padrão é impulsionado por processos oceanográficos regionais que aumentam a produção primária no verão principalmente nas regiões frontais temperada e polar, ocasionando um aumento da abundância e biomassa de copépodes grandes, especialmente pertencentes à família Calanidae. Por outro lado, copépodes pequenos foram extremamente importantes principalmente em regiões tropicais e subtropicais, porém apresentaram pouca ou nenhuma variação de tamanho ao longo do gradiente latitudinal. Além disso, a modelagem do tamanho médio para as diferentes famílias mostrou que cada família responde diferente ao gradiente termal, e aos outros fatores ambientais projetados, demonstrando as contribuições relativas das diferentes estratégias de história de vida, inclusive algumas famílias da ordem Cyclopoida apresentam um padrão inverso a regra de Bergmann.

Ainda há muito a aprender sobre a regra de Bergmann. Por exemplo, estudos devem considerar como as intrusões de águas ricas em nutrientes (ACAS) na Corrente do Brasil controlam a diversidade e abundância de assembléias de copépodes, e permite que os copépodes atinjam sua maior produção no verão. Como consequência, muitas espécies de pequenos peixes pelágicos, incluindo a anchova do *Engraulis anchoita* e a sardinha brasileira *Sardinella brasiliensis*, reproduzem-se mais intensamente durante este período. A principal presa das larvas desses peixes de interesse comercial são copépodes pequenos (Kurtz & Matsuura, 2001). Famílias de copépodes de tamanho corporal pequeno apresentam biogeografias contrastantes em comparação a copépodes grandes preferencialmente herbívoros, e nossos resultados poderiam auxiliar na compreensão dos potenciais efeitos ecológicos da mudança global e a capacidade de adaptação às condições oceanográficas locais e/ou climáticas. A tendência latitudinal da variação do tamanho corporal dessas famílias pode indicar maior resiliência climática nas águas do Atlântico Sudoeste.

Neste contexto, a abordagem funcional baseada em traços funcionais levanta questões sobre a necessidade de incorporar a dimensão evolutiva nas projeções futuras para responder a um problema-chave colocado pela mudança climática antropogênica: as espécies terão tempo para se adaptar? O potencial adaptativo do zooplâncton ainda é muito debatido, e os estudos sobre o assunto destacam que, à medida que o nosso planeta e oceano aquecem, espécies de copépodes menores provavelmente emergirão como “vencedoras”, reduzindo potencialmente as taxas de produção pesqueira e sequestro de carbono (Campbell et al., 2021). Será fundamental entender como os traços funcionais que representam mudanças na composição de copépodes, como mielinização, estratégia

de desova, carnívoria ou outros modos de alimentação, exibem gradientes latitudinais que são correlacionados positiva ou negativamente com o gradiente de tamanho corporal, considerando as relações não lineares entre tamanho e as interações abióticas e bióticas, como a disponibilidade e qualidade de alimentos e a pressão de predação.

7 DIVULGAÇÃO CIENTÍFICA

Um mundo minúsculo de pequenos andarilhos do mar: o caso do copépode padeiro

Numa conversa de almoço de domingo, ouço meu pai comentando que quando ele trabalhava numa padaria descobriu o significado do seu sobrenome «Becker», para sua surpresa, é ‘padeiro’. Na Alemanha, para as pessoas comuns (não nobres) os sobrenomes surgiram na Baixa Idade Média e muitas vezes foram adotados para indicar a profissão do chefe da família. O sobrenome por si só já conta um pouco da história da família que o detém, ou atuação na sociedade.

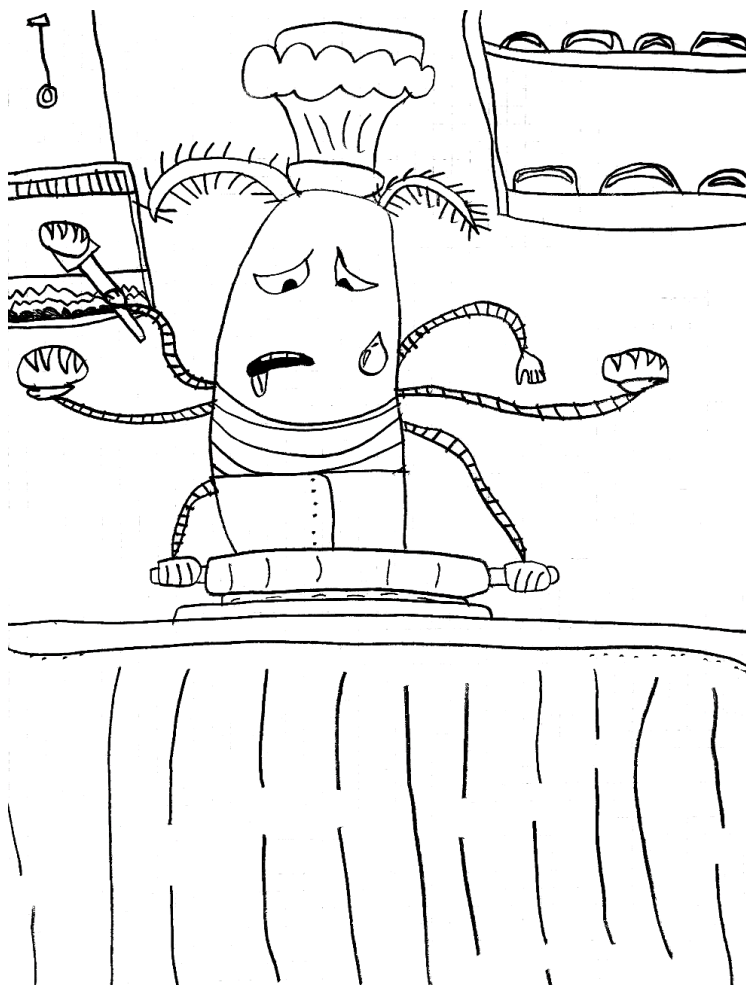
Diferente da cultura alemã, para identificar as profissões, ou melhor, as funções das diversas espécies nos ecossistemas, nos baseamos em «traços funcionais». Com essa abordagem, as espécies com os mesmos papéis funcionais são colocadas em um grupo funcional e provavelmente responderão de maneira semelhante às mudanças ambientais. Como resultado, a identificação de grupos funcionais pode encontrar relações com funções ecossistêmicas mais facilmente. A diversidade funcional refere-se à gama de traços funcionais entre as espécies de uma comunidade biológica.

Minha pesquisa se concentra no zooplâncton marinho, que considero a «microfauna carismática». Eles são animais minúsculos, do tamanho de insetos, que flutuam com as correntes oceânicas. Muitos deles são adoráveis, mas exceto pelos cientistas que os estudam, poucas pessoas sabem que eles estão entre os animais mais numerosos e importantes da Terra. Há também os «copépodes» que são pequenos crustáceos e atores-chave nas cadeias alimentares oceânicas. Os copépodes marinhos comem pequenas algas unicelulares (fitoplâncton) e são comidos por pequenos peixes, outros crustáceos e até baleias. Os copépodes também desempenham um papel crucial no envio de carbono que sustenta a vida para o oceano profundo; pelotas e carcaças fecais de copépodes, contendo carbono, descem de águas superficiais para águas mais profundas. Esse processo, parte da «bomba biológica», não apenas ajuda a alimentar os organismos do fundo do mar, mas também aprisiona o carbono da atmosfera nas profundezas do oceano. Esta é uma maneira de remover os gases de efeito estufa da atmosfera.

Os copépodes exibem uma ampla gama de traços, como características morfológicas, histórias de vida, hábitos tróficos, comportamentos, distribuições verticais e geográficas, o que resulta em variadas funções ecossistêmicas nas águas superficiais dos oceanos. No entanto, entendemos pouco sobre como essas combinações de

características e funções mudam nos diferentes ecossistemas e climas desde a região tropical do Oceano Atlântico Sul à região polar do Oceano Antártico. Copépodes do oceano Atlântico tem maior riqueza de funções em relação as águas frias do Oceano Antártico. Um dos traços definidores da diversidade funcional de copépodes é a tendência de aumento do tamanho do corpo, e o clima - particularmente a temperatura - tem sido o principal fator de mudanças no tamanho do corpo. Apesar de sustentar uma fauna mais empobrecida funcionalmente, regiões mais frias são mais oxigenadas e ricas em alimento, o que contribui para tamanhos corporais maiores. Porém, quando falamos da diversidade de copépodes, não há uma única regra geral! Existem ainda pequenos carnívoros que aumentam de tamanho em direção à climas mais quentes, sendo o grupo trófico um dos traços que mais contribuem para a maior riqueza funcional do grupo em águas quentes.

Assim como para descendentes de alemães como eu, somente o fato de se conhecer o significado de seu sobrenome já traz implícito alguma história cultural ou familiar. Traços funcionais também contam histórias de vida de organismos cruciais para a saúde e funcionamento dos ecossistemas, como os copépodes, que são fundamentais para entendermos o papel da biodiversidade marinha.



«Ilustração por: Miguel Becker da Silva, em conversa sobre traços funcionais, copépodes e a origem dos sobrenomes»

8 ANEXO I

8.1 LISTA DE MANUSCRITOS EM PREPARAÇÃO, SUBMETIDOS E PUBLICADOS

Becker, É.C., Macedo-Soares, L.C.P., Marcolin, C., Brandão, M.C., Stemmann, L., Mazzocchi, M.G., Freire, A.S. Latitudinal patterns and environmental drivers of copepod body size in the South Atlantic. Manuscrito em preparação para o *Journal of Biogeography*.

Orenstein, E. C., Ayata, S. D., Maps, F., **Becker, É. C.**, Benedetti, F., Biard, T., ... & Irisson, J. O. (2022). Machine learning techniques to characterize functional traits of plankton from image data. *Limnology and Oceanography*, 9999, 2022, 1–21. <https://aslopubs.onlinelibrary.wiley.com/doi/10.1002/lno.12101>

Orenstein, E., Ayata, S.D., Maps, F., Biard, T., **Becker, É.C.**, Benedetti, F., Garidel-Thoron, T., Ellen, J.S., Ferrario, F., Giering, S.L.C., Guy-Haim, T., Hoebeke, L., Iversen, M.H., Kiørboe, T., Lalonde, J-F., Lana, A., Laviale, M., Lombard, F., Lorimer, T., Martini, S., Meyer, A., Möller, K.O., Niehoff, B., Ohman, M.D., Pradalier, C., Romagnan, J-B., Schröder, S-M., Sonnet, V., Sosik, H.M., Stemmann, L.S., Stock, M., Terbiyik-Kurt, T., Valcárcel-Pérez, N., Vilgrain, L., Wacquet, G., Waite, A.M. & Irisson, J.O. (2021). Machine learning techniques to characterize functional traits of plankton from image data. Manuscrito submetido à *Limnology & Oceanography*, e aceito sujeito a pequenas revisões de texto. Preprint: <https://hal.univ-lorraine.fr/hal-03482282>

Becker, É.C., Mazzocchi, M.G., de Macedo-Soares, L.C.P., Brandão, M.C., Freire, A.S. (2021). Latitudinal gradient of copepod functional diversity in the South Atlantic Ocean. Marine Data Archive. <https://doi.org/10.14284/458>

Becker, É.C., Mazzocchi, M.G., de Macedo-Soares, L.C.P., Brandão, M.C., Freire, A.S. (2021). Latitudinal gradient of copepod functional diversity in the South Atlantic Ocean. *Progress in Oceanography*, 199, 102710. <https://doi.org/10.1016/j.pocean.2021.102710>

8.2 LISTA DE COMUNICAÇÕES CIENTÍFICAS

Becker, É.C., Mazzocchi, M.G., Macedo-Soares, L.C.P., Brandão, M.C., Freire, A.S. (2022). Ecological mechanisms shaping copepod functional diversity along biogeographic zones in the Southwestern Atlantic and Antarctic waters. e-ICOC 2022: International Conference on Copepoda. 25 à 30 de julho de 2022. Primeiro encontro online organizado pela World Association of Copepodologists.

Becker, É.C., Mazzocchi, M.G., Marcolin, C., Stemmann, L., Brandão, M.C., Freire, A.S. (2022). Copepod body size latitudinal patterns and their environmental drivers in the South Atlantic. Congresso Brasileiro sobre Crustáceos (CBC) The Crustacean Society (TCS) Summer Meeting. 06 à 09 de junho de 2022, Santos, Brasil.

Gonçalves, F., Silveira, G.R., Corrêa, M.S., **Becker, É.C.** & Freire, A.S. (2021). Distribuição sazonal da estrutura de tamanho da comunidade zooplânctônica na reserva biológica marinha do Arvoredo em Santa Catarina, sul do Brasil. II Simpósio Fluminense de Zoologia. 04 à 08 de outubro de 2021, de forma *on-line*.

Becker, É.C., Mazzocchi, M.G. & Freire, A.S. (2019). Imaging and Traditional Taxonomy: An integrative approach for biodiversity and biogeography of pelagic copepods. Seminario interno Stazione Zoologica Anton Dorn, SZN, Nápoles, Itália.

Becker, É.C. (2019). Artificial intelligence for characterizing plankton traits from images: Lessons learned. Seminario interno Stazione Zoologica Anton Dorn, SZN, Nápoles, Itália.

Becker, É.C., Mazzocchi, M.G., Marcolin, C., Stemmann, L., Brandão, M.C., Freire, A.S. (2019). Imaging and traditional taxonomy: an integrated approach for copepod biodiversity in the Southwestern Atlantic Ocean In: Workshop ARTIFACTZ: Artificial intelligence for characterizing plankton traits from images. 24 à 26 de abril de 2019, Villefranche-sur-mer, França.

Becker, É.C. & Freire, A.S. (2018). Latitudinal distribution of copepod size structure across the South Atlantic Ocean. 1º Advanced Zooplankton Course (AZC1): Morphological and Molecular Taxonomy of Marine Copepods. 22 de outubro à 02 de novembro de 2018, Nápoles, Itália.

Becker, É.C. & Freire, A.S. (2018). Do oceanic copepods follow Bergman's rule? Latitudinal distribution of copepod size structure across the South Atlantic Ocean. Semana de Seminários de Pesquisas de Pós-graduação em Ecologia (SAPECO). Universidade Federal de Santa Catarina, UFSC, Florianópolis, Brasil.

8.3 MÍDIAS SOCIAIS E WEBSITE

Lab. de Crustáceos e Plâncton (UFSC): [instagram.com/lab.crustaceos.plancton/](https://www.instagram.com/lab.crustaceos.plancton/)
Mediadora no encontro Infografia e Ciência: [www.youtube.com/ infografia ciencia](https://www.youtube.com/channel/UCinfografia-ciencia)
Retrato da série Mulheres do *AtlantECO*: [instagram.com/p/CasHTq0I5Jp/](https://www.instagram.com/p/CasHTq0I5Jp/)
Dia Internacional da Mulher na Ciência: [instagram.com/p/CZ1q7s6jPH2/](https://www.instagram.com/p/CZ1q7s6jPH2/)
Live escala do *Tara* no Rio de Janeiro: [instagram.com/p/CWBReSRsQbD/](https://www.instagram.com/p/CWBReSRsQbD/)
Depoimento *Assemble Plus*: twitter.com/ASSEMBLE_Plus/status/1374045960851005441
Website Lab. de Crustáceos e Plâncton (UFSC): lcpufscbio.wixsite.com/my-site

8.4 GRANTS DE PESQUISA

e-ICOC-2022: 14th International Conference on Copepoda

Concedido em: Julho de 2022

Subsídio: ZAR 6.000

Financiamento: World Association of Copepodologists (WAC)

Referência de concessão: Inscrição no evento

Instituição de pesquisa: devido a COVID-19, foi transferido para o formato online

ARTIFACTZ Workshop: Artificial Intelligence for Characterizing Plankton Traits from Images

Concedido em: Abril de 2019

Subsídio: EUR 200

Financiamento: programa Sentinelle Nord, Laboratoire d'Océanographie de Villefranche (LOV) e programa MODELIFE
Referência de concessão: subsídio de viagem
Instituição de pesquisa: Institut de la Mer de Villefranche (IMEV), França

Assemble Plus – projeto COPINTAX: “Imaging and traditional taxonomy: an integrated approach for copepod biodiversity on the Southwestern Atlantic Ocean”

Concedido em: Abril à Maio de 2019

Subsídio: Hospedagem e alimentação

Financiamento: European Union's Horizon 2020 research and innovation program

Referência de concessão: acesso as amostras da Expedição *Tara Oceans* e uso do equipamento de imagem ZOOSCAN

Instituição de pesquisa: Institut de la Mer de Villefranche (IMEV), França

9 REFERÊNCIAS

- Ackerly, D. D. & Cornwell, W. K. (2007). A trait-based approach to community assembly: partitioning of species trait values into within-and among-community components. *Ecology letters*, 10(2), 135-145.
- Atkinson, D. (1994). Temperature and organism size: a biological law for ectotherms? *Advances in Ecological Research*, 25, 1-58.
- Barange, M., Butenschön, M., Yool, A., Beaumont, N., Fernandes, J. A., Martin, A. P. & Allen, J. (2017). The cost of reducing the North Atlantic Ocean biological carbon pump. *Frontiers in Marine Science*, 3, 290.
- Barton, A. D., Pershing, A. J., Litchman, E., Record, N. R., Edwards, K. F., Finkel, Z. V., Kjørboe, T., Ward, B. A. (2013). The biogeography of marine plankton traits. *Ecology letters*, 16(4), 522–534.
- Beaugrand, G. & Kirby, R. R. (2010). Spatial changes in the sensitivity of Atlantic cod to climate-driven effects in the plankton. *Climate research*, 41(1), 15-19.
- Beaugrand, G., Edwards, M. & Legendre, L. (2010). Marine biodiversity, ecosystem functioning, and carbon cycles. *Proceedings of the National Academy of Sciences*, 107(22), 10120-10124.
- Benedetti, F., Guilhaumon, F., Adloff, F. & Ayata, S. D. (2018). Investigating uncertainties in zooplankton composition shifts under climate change scenarios in the Mediterranean Sea. *Ecography*, 41(2), 345–360.
- Benedetti, F., Vogt, M., Righetti, D., Guilhaumon, F., & Ayata, S. D. (2018b). Do functional groups of planktonic copepods differ in their ecological niches?. *Journal of Biogeography*, 45(3), 604-616.
- Benfield, M. C., P. Grosjean, P. F. Culverhouse, and others. (2007). RAPID: research on automated plankton identification. *Oceanography*, 20, 172–187.
- Bergmann, C. (1847). Über die verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. *Gött. Stud.*, 1, 595-708.
- Bi, H., Peterson, W. T., Lamb, J., & Casillas, E. (2011). Copepods and salmon: characterizing the spatial distribution of juvenile salmon along the Washington and Oregon coast, USA. *Fisheries Oceanography*, 20(2), 125-138.
- Blanchard, J. L., Heneghan, R. F., Everett, J. D., Trebilco, R. & Richardson, A. J. (2017). From bacteria to whales: using functional size spectra to model marine ecosystems. *Trends in Ecology & Evolution*, 32(3), 174-186.
- Boltovskoy, D. & Valentin, J. L. (2018). Overview of the history of biological oceanography in the southwestern Atlantic, with emphasis on plankton. In: *Plankton ecology of the Southwestern Atlantic* (pp. 3-34). Springer, Cham.
- Brandão, M. C., Benedetti, F., Martini, S., Soviadan, Y. D., Irisson, J. O., Romagnan, J. B., Elineau, A., Desnos, C., Jalabert, L., Freire, A. S., Picheral, M., Guidi, L., Gorsky, G.,

- Bowler, C., Karp-Boss, L., Henry, N., de Vargas, C., Sullivan, M. B., Tara Oceans Consortium Coordinators, Stemmann, L. & Lombard, F. (2021). Macroscale patterns of oceanic zooplankton composition and size structure. *Scientific Reports*, 11(1), 1-19.
- Brun, P., Payne, M. R. & Kiørboe, T. (2016). Trait biogeography of marine copepods—an analysis across scales. *Ecology Letters*, 19(12), 1403–1413.
- Cadotte, M. W., Carscadden, K., Mirotnick, N. (2011). Beyond species: functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology*, 48, 1079–1087.
- Campbell, M. D., Schoeman, D. S., Venables, W., Abu-Alhaija, R., Batten, S. D., Chiba, S., Coman, F., Davies, C. H., Edwards, M., Eriksen, R. S., Everett, J. D., Fukai, Y., Fukuchi, M., Garrote, O. E., Hosie, G., Huggett, J. A., Johns, D. G., Kitchener, J. A., Koubbi, P., McEnulty, F. R., Muxagata, E., Ostle, C., Robinson, K. V., Slotwinski, A., Swadling, K. M., Takahashi, K. T., Tonks, M., Uribe-Palomino, J., Verheye, H. M., Wilson, W. H., Worship, M. M., Yamaguchi, A., Zhang, W. & Richardson, A. J. (2021). Testing Bergmann's rule in marine copepods. *Ecography*, 44(9), 1283-1295.
- Campos, M. C., Chiessi, C. M., Voigt, I., Piola, A. R., Kuhnert, H. & Mulitza, S. (2017). $\delta^{13}\text{C}$ decreases in the upper western South Atlantic during Heinrich Stadials 3 and 2. *Climate of the Past*, 13(4), 345-358.
- Corona, S., Hirst, A., Atkinson, D. & Atkinson, A. (2021). Density-dependent modulation of copepod body size and temperature–size responses in a shelf sea. *Limnology and Oceanography*, 66(11), 3916-3927.
- Daufresne, M., Lengfellner, K. & Sommer, U. (2009). Global warming benefits the small in aquatic ecosystems. *Proceedings of the National Academy of Sciences*, 106(31), 12788-12793.
- Davis, C. S., S. M. Gallagher, and A. R. Solow. (1992). Microaggregations of Oceanic Plankton Observed by Towed Video Microscopy. *Science*, 257, 230–232.
- Dolédec, S. & Bonada, N. (2013). So What? Implications of loss of biodiversity for ecosystem functioning. *River Conservation Challenges and Opportunities*. Fundacion BBVA, Madrid, 169–192.
- Ecorys. (2014). Food taxes and their impact on competitiveness in the agri-food sector. Final report (No. Ref. Ares(2014)2365745—16/07/2014). Rotterdam: Client: DG Enterprise and Industry.
- Evans, L. E., Hirst, A. G., Kratina, P. & Beaugrand, G. (2020). Temperature-mediated changes in zooplankton body size: large scale temporal and spatial analysis. *Ecography*, 43(4), 581-590.
- García-Comas, C., L. Stemmann, F. Ibanez, L. Berline, M. G. Mazzocchi, S. Gasparini, M. Picheral, and G. Gorsky. 2011. Zooplankton long-term changes in the NW Mediterranean Sea: Decadal periodicity forced by winter hydrographic conditions related to large-scale atmospheric changes? *Journal of Marine Systems*, 87, 216–226.

- García-Comas, C., Sastri, A. R., Ye, L., Chang, C. Y., Lin, F. S., Su, M. S., Gong, G-C. & Hsieh, C. H. (2016). Prey size diversity hinders biomass trophic transfer and predator size diversity promotes it in planktonic communities. *Proceedings of the Royal Society B: Biological Sciences*, 283(1824), 20152129.
- Garzoli, S. L. & Matano, R. (2011). The South Atlantic and the Atlantic meridional overturning circulation. *Deep Sea Research Part II: Topical Studies in Oceanography*, 58(17-18), 1837-1847.
- Gorsky, G., Ohman, M. D., Picheral, M., Gasparini, S., Stemmann, L., Romagnan, J-B., Cawood, A., Pesant, S., García-Comas, C., Prejger, F. (2010). Digital zooplankton image analysis using the ZooScan integrated system. *Journal of Plankton Research*, 32, 285–303.
- Guidi, L., Chaffron, S., Bittner, L., Eveillard, D., Larhlimi, A., Roux, S., Darzi, Y., Audic, S., Berline, L., Brum, J. R., Coelho, L. P., Espinoza, J. C. I., Malviya, S., Sunagawa, S., Dimier, C., Kandels-Lewis, S., Picheral, M., Poulain, J., Searson, S., Tara Oceans Consortium Coordinators, Stemmann, L., Not, F., Hingamp, P., Speich, S., Follows, M., Karp-Boss, L., Boss, E., Ogata, H., Pesant, S., Weissenbach, J., Wincker, P., Acinas, S. G., Bork, P., de Vargas, C., Iudicone, D., Sullivan, M. B., Raes, J., Karsenti, E., Bowler, C. & Gorsky, G. (2016). Plankton networks driving carbon export in the oligotrophic ocean. *Nature*, 532(7600), 465-470.
- Hansen, B., Bjornsen, P. K. & Hansen, P. J. (1994). The size ratio between planktonic predators and their prey. *Limnology & Oceanography*, 39, 395–403.
- Hébert, M. P., Beisner, B. E. & Maranger, R. (2017). Linking zooplankton communities to ecosystem functioning: toward an effect-trait framework. *Journal of Plankton Research*, 39(1), 3–12.
- Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J. & Wardle, D.A. (2005) Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs*, 75, 3–35.
- Horne, C. R., Hirst, A. G., Atkinson, D., Neves, A. & Kiørboe, T. (2016). A global synthesis of seasonal temperature–size responses in copepods. *Global Ecology and Biogeography*, 25(8), 988-999.
- Hutchinson, G. E. (1961). The paradox of the plankton. *The American Naturalist*, 95(882), 137–145.
- Johnson, K. H., Vogt, K. A., Clark, H. J., Schmitz, O. J., & Vogt, D. J. (1996). Biodiversity and the productivity and stability of ecosystems. *Trends in Ecology & Evolution*, 11(9), 372–377.
- Kiørboe, T. (2011). How zooplankton feed: mechanisms, traits and trade-offs. *Biological reviews*, 86(2), 311–339.
- Kiørboe, T., A. Visser, and Andersen, K. H. (2018). A trait-based approach to ocean ecology. *ICES Journal of Marine Science*, 75, 1849–1863.

- Klépanski, L., Beaugrand, G. & Edwards, M. (2021). Plankton biogeography in the North Atlantic Ocean and its adjacent seas: Species assemblages and environmental signatures. *Ecology and evolution*, 11(10), 5135-5149.
- Laliberté, E. & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, 91(1), 299–305.
- Lawton, J. H. & Jones, C. G. (1995). Linking species and ecosystems: organisms as ecosystem engineers. In *Linking species & ecosystems*. Springer, Boston, MA, pp. 141–150.
- Lefcheck, J. S., Byrnes, J. E., Isbell, F., Gamfeldt, L., Griffin, J. N., Eisenhauer, N., Hensel, M. J. S., Hector, A., Cardinale, B. J. & Duffy, J. E. (2015). Biodiversity enhances ecosystem multifunctionality across trophic levels and habitats. *Nature communications*, 6(1), 1–7.
- Leps, J., De Bello, F., Lavorel, S., Berman, S. (2006). Quantifying and interpreting functional diversity of natural communities: practical considerations matter. *Preslia* (Prague), 78, 481–501.
- Litchman, E. & Klausmeier, C. A. (2008). Trait-based community ecology of phytoplankton. *Annual Review of Ecology, Evolution, and Systematics*, 39, 615–639.
- Litchman, E., M. D. Ohman, and T. Kiørboe. (2013). Trait-based approaches to zooplankton communities. *Journal of Plankton Research*, 35, 473–484.
- Lombard, F., Boss, E., Waite, A. M., Vogt, M., Uitz, J., Stemmann, L., Sosik, H. M., Schulz, J., Romagnan, J-B., Picheral, M., Pearlman, J., Ohman, M. D., Niehoff, B., Möller, K. O., Miloslavich, P., Lara-Lpez, A., Kudela, R., Lopes, R. M., Kiko, R., Karp-Boss, L., Jaffé, J. S., Iversen, M. H., Irisson, J-O., Fennel, K., Hauss, H., Guidi, L., Gorsky, G., Giering, S. L. C., Gaube, P., Gallager, S., Dubelaar, G., Cowen, R. K., Carlotti, F., Briseño-Avena, C., Berline, L., Benoit-Bird, K., Bax, N., Batten, S., Ayata, S-D., Artigas, L. F., Appeltans, W. (2019). Globally Consistent Quantitative Observations of Planktonic Ecosystems. *Frontier in Marine Science*, 6, 196.
- Longhurst, A.R., 1998. *Ecological Geography of the Sea*. Academic Press, San Diego, pp. xiv, 398.
- Marshall, J. & Speer, K. (2012). Closure of the meridional overturning circulation through Southern Ocean upwelling. *Nature Geoscience*, 5(3), 171-180.
- Martini, S., Larras, F., Boyé, A., Faure, E., Aberle, N., Archambault, P., Bacouillard, L., Beisner, B. E., Bittner, L., Castella, E., Danger, M., Gauthier, O., Karp-Boss, L., Lombard, F., Maps, F., Stemmann, L., Thiébaud, E., Usseglio-Polatera, P., Vogt, M., Laviale, M., Ayata, S-D. (2021). Functional trait-based approaches as a common framework for aquatic ecologists. *Limnology & Oceanography*, 66, 965–994.
- Mason, N., Mouillot, D., Lee, W., Wilson, J. (2005). Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos*, 1, 112–118.

- Mazzocchi, M. G., Dubroca, L., García-Comas, C., Di Capua, I. & d'Alcalà, M. R. (2012). Stability and resilience in coastal copepod assemblages: the case of the Mediterranean long-term ecological research at Station MC (LTER-MC). *Progress in Oceanography*, 97, 135–151.
- McGinty, N., Barton, A. D., Record, N. R., Finkel, Z. V., Johns, D. G., Stock, C. A., & Irwin, A. J. (2021). Anthropogenic climate change impacts on copepod trait biogeography. *Global Change Biology*, 27(7), 1431–1442.
- Moreno-Ostos, E., Blanco, J. M., Agustí, S., Lubián, L. M., Rodríguez, V., Palomino, R. L., Llabrés, M. & Rodríguez, J. (2015). Phytoplankton biovolume is independent from the slope of the size spectrum in the oligotrophic Atlantic Ocean. *Journal of Marine Systems*, 152, 42-50.
- Neumann-Leitão, S., Melo, P. A., Schwamborn, R., Diaz, X. F., Figueiredo, L. G., Silva, A. P., Campelo, R. P. S., Melo Júnior, M., Melo, N. F. A. C., Costa, A. E. S. F., Araújo, M., Veleda, D. R. A., Moura, R. L. & Thompson, F. (2018). Zooplankton from a reef system under the influence of the Amazon River plume. *Frontiers in Microbiology*, 9, 355.
- Neumann Leitão, S., Melo Junior, M., Porto Neto, F. D. F., Silva, A. P., Diaz, X. F. G., Silva, T. D. A., Vieira, D. A. N., Figueiredo, L. G. P., Costa, A. E. S. F., de Santana, J. R., Campelo, R. P. S., Melo, P. A. M. C., Pessoa, V. T., Lira, S. M. A. & Schwamborn, R. (2019). Connectivity between coastal and oceanic zooplankton from Rio Grande do Norte in the Tropical Western Atlantic. *Frontiers in Marine Science*, 6, 287.
- OECD (2016). Organisation for Economic Co-operation and Development. <https://www.oecd.org/>
- Ohman, M. D., R. E. Davis, J. T. Sherman, K. R. Grindley, B. M. Whitmore, C. F. Nickels, and J. S. Ellen. (2018). Zooglider: An autonomous vehicle for optical and acoustic sensing of zooplankton. *Limnology & Oceanography Methods*, 17(1), 69–86.
- Ortner, P. B., S. R. Cummings, R. P. Aftiring, and H. E. Edgerton. (1979). Silhouette photography of oceanic zooplankton. *Nature*, 277, 50–51.
- Parent, G. J., Plourde, S. & Turgeon, J. (2011). Overlapping size ranges of *Calanus* spp. off the Canadian Arctic and Atlantic Coasts: impact on species' abundances. *Journal of Plankton Research*, 33(11), 1654-1665.
- Pavoine, S. & Bonsall, M. B. (2011). Measuring biodiversity to explain community assembly: a unified approach. *Biological Reviews*, 86, 792–812.
- Peacock, E. E., R. J. Olson, and H. M. Sosik. (2014). Parasitic infection of the diatom *Guinardia delicatula*, a recurrent and ecologically important phenomenon on the New England Shelf. *Marine Ecology Progress Series*, 503, 1–10.
- Pershing, A. J. & Stamieszkin, K. (2020). The North Atlantic ecosystem, from plankton to whales. *Annual Review of Marine Science*, 12, 339-359.
- Petchey, O. L. & Gaston, K. J. (2002). Functional diversity (FD), species richness and community composition. *Ecology letters*, 5(3), 402–411.

- Picheral, M., L. Guidi, L. Stemmann, D. M. Karl, G. Iddaoud, and G. Gorsky. (2010). The Underwater Vision Profiler 5: An advanced instrument for high spatial resolution studies of particle size spectra and zooplankton. *Limnology & Oceanography Methods*, 8, 462–473.
- Piredda, R., Tomasino, M. P., D'erchia, A. M., Manzari, C., Pesole, G., Montresor, M., Kooistra, W. H. C. F., Sarno, D. & Zingone, A. (2017). Diversity and temporal patterns of planktonic protist assemblages at a Mediterranean Long Term Ecological Research site. *FEMS Microbiology Ecology*, 93(1), 1–14.
- Pla, L., Casanoves, F., Di Rienzo, J. (2012). Functional groups. Quantifying functional biodiversity. Springer, Amsterdam, pp. 9–25.
- Platt, T., & Denman, K. (1977). Organisation in the pelagic ecosystem. *Helgoländer Wissenschaftliche Meeresuntersuchungen*, 30(1), 575–581.
- Poos, M. S., Walker, S. C., Jackson, D. A. (2009). Functional-diversity indices can be driven by methodological choices and species richness. *Ecology*, 90, 341–347.
- Quesado, L. B. Padrões geográficos da diversidade taxonômica e funcional do fitoplâncton em ecossistemas aquáticos do litoral ao semiárido do Rio Grande do Norte. (2017). Rio Grande do Norte: Universidade Federal do Rio Grande do Norte (UFRN).
- Razouls C., Desreumaux N., Kouwenberg J. & de Bovée F. (2005-2022). Biodiversity of Marine Planktonic Copepods (morphology, geographical distribution and biological data). Sorbonne University, CNRS. <http://copepodes.obs-banyuls.fr/en>
- Record, N. R., Ji, R., Maps, F., Varpe, Ø., Runge, J. A., Petrik, C. M. & Johns, D. (2018). Copepod diapause and the biogeography of the marine lipidscape. *Journal of Biogeography*, 45(10), 2238–2251.
- Reid, P. C., Edwards, M., Beaugrand, G., Skogen, M. & Stevens, D. (2003). Periodic changes in the zooplankton of the North Sea during the twentieth century linked to oceanic inflow. *Fisheries Oceanography*, 12(4-5), 260–269.
- Romagnan, J.-B., L. Legendre, L. Guidi, and others. (2015). Comprehensive Model of Annual Plankton Succession Based on the Whole-Plankton Time Series Approach. *PLOS ONE*, 10, e0119219.
- Rosado, B., Dias, A., de Mattos, E. (2013). Going back to basics: importance of ecophysiology when choosing functional traits for studying communities and ecosystems. *Nature Conservation*, 11, 15–22.
- Rosenfeld, J. S. (2002). Functional redundancy in ecology and conservation. *Oikos*, 98(1), 156–162.
- Salewski, V., & Watt, C. (2017). Bergmann's rule: a biophysiological rule examined in birds. *Oikos*, 126(2).
- San Martin, E., Harris, R. P. & Irigoien, X. (2006). Latitudinal variation in plankton size spectra in the Atlantic Ocean. *Deep Sea Research Part II: Topical Studies in Oceanography*, 53(14-16), 1560–1572.

- Sheldon, R. W., Prakash, A. & Sutcliffe Jr., W. (1972). The size distribution of particles in the Ocean 1. *Limnology & Oceanography*, 17, 327–340.
- Sieracki, M. E., M. Benfield, A. Hanson, and others. (2010). Optical plankton imaging and analysis systems for ocean observation. *Proceedings of OceanObs*, 9, 21–25.
- Sommer, U., Peter, K. H., Genitsaris, S. & Moustaka-Gouni, M. (2017). Do marine phytoplankton follow Bergmann's rule *sensu lato*? *Biological Reviews*, 92(2), 1011–1026.
- Steinberg, D. K. & Landry, M. R. (2017). Zooplankton and the ocean carbon cycle. *Annual review of marine science*, 9, 413–444.
- Stemmann, L. & Boss, E. (2012). Plankton and Particle Size and Packaging: From Determining Optical Properties to Driving the Biological Pump. *Annual Review of Marine Science*, 4, 263–290.
- Tilman, D. (1977). Resource competition between plankton algae: an experimental and theoretical approach. *Ecology*, 58(2), 338–348.
- Tilman, D. (1990). Constraints and tradeoffs: toward a predictive theory of competition and succession. *Oikos*, 3–15.
- Timofeev, S. F. (2001). Bergmann's principle and deep-water gigantism in marine crustaceans. *Biology Bulletin of the Russian Academy of Sciences*, 28(6), 646–650.
- de Vargas, C., Audic, S., Henry, N., Decelle, J., Mahé, F., Logares, R., Lara, E., Berney, C., Le Bescot, N., Probert, I., Carmichael, M., Poulain, J., Romac, S., Colin, S., Aury, J-M., Bittner, L., Chaffron, S., Dunthorn, M., Engelen, S., Flegontova, O., Guidi, L., Horák, A., Jaillon, O., Lima-Mendez, G., Lukeš, J., Malviya, S., Morard, R., Mulot, M., Scalco, E., Siano, R., Vincent, F., Zingone, A., Dimier, C., Picheral, M., Searson, S., Kandels-Lewis, S., Tara Oceans Coordinators, Acinas, S., G., Bork, P., Bowler, C., Gorsky, G., Grimsley, N., Hingamp, P., Iudicone, D., Not, F., Ogata, H., Pesant, S., Raes, J., Sieracki, M. E., Speich, S., Stemmann, L., Sunagawa, S., Weissenbach, J., Wincker, P and Karsenti, E. (2015). Eukaryotic plankton diversity in the sunlit ocean. *Science*, 348.
- Veríssimo, H., Patrício, J., Gonçalves, É., Moura, G. C., Barbosa, J. E. L. & Gonçalves, A. M. (2017). Functional diversity of zooplankton communities in two tropical estuaries (NE Brazil) with different degrees of human-induced disturbance. *Marine environmental research*, 129, 46–56.
- Villar, E., Farrant, G.K., Follows, M., Garczarek, L., Speich, S., Audic, S., Bittner, L., Blanke, B., Brum, J.R., Brunet, C., Casotti, R., Chase, A., Dolan, J.R., D'Ortenzio, F., Gattuso, J.-P., Grima, N., Guidi, L., Hill, C.N., Jahn, O., Jamet, J.-L., Le Goff, H., Lepoivre, C., Malviya, S., Pelletier, E., Romagnan, J.-B., Roux, S., Santini, S., Scalco, E., Schwenck, S.M., Tanaka, A., Testor, P., Vannier, T., Vincent, F., Zingone, A., Dimier, C., Picheral, M., Searson, S., Kandels-Lewis, S., Acinas, S.G., Bork, P., Boss, E., de Vargas, C., Gorsky, G., Ogata, H., Pesant, S., Sullivan, M.B., Sunagawa, S., Wincker, P., Karsenti, E., Bowler, C., Not, F., Hingamp, P. & Iudicone, D. (2015) Environmental characteristics of Agulhas rings affect interocean plankton transport. *Science*, 348, 1261447–1261447.

Violle, C., M.-L. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel, and E. Garnier. (2007). Let the concept of trait be functional! *Oikos*, 116, 882–892.

Walker, B. H. (1992). Biodiversity and ecological redundancy. *Conservation Biology*, 6(1), 18–23.