



UNIVERSIDADE FEDERAL DE SANTA CATARINA

CAMPUS TRINDADE CENTRO DE CIÊNCIAS FÍSICAS E MATEMÁTICA

PROGRAMA DE PÓS-GRADUAÇÃO EM OCEANOGRAFIA

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**Variação temporal de copépodes e *Coscinodiscus* spp. na Reserva Biológica
Marinha do Arvoredo (SC) associada a variabilidade meteoceanográfica**

Florianópolis

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Marinha do Arvoredo (SC) associada a variabilidade meteoceanográfica**

Dissertação submetida ao Programa de Pós-graduação de Oceanografia do Centro de Ciências Físicas e Matemática da Universidade Federal de Santa Catarina como requisito para a obtenção do título de Mestra em Oceanografia

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Florianópolis

2025

Simões de Oliveira, Maria Luiza

Variação temporal de copépodes e *Coscinodiscus* spp. na Reserva Biológica Marinha do Arvoredo (SC) associada a variabilidade meteoceanográfica / Maria Luiza Simões de Oliveira ; orientadora, Andrea Freire, coorientador, Eduardo Gentil, 2025.

110 p.

Dissertação (mestrado) - Universidade Federal de Santa Catarina, Centro de Ciências Físicas e Matemáticas, Programa de Pós-Graduação em Oceanografia, Florianópolis, 2025.

Inclui referências.

1. Oceanografia. 2. Mesoplâncton. 3. *Coscinodiscus wailesii*. 4. Espécies invasora. 5. REBIO Arvoredo. I. Freire, Andrea. II. Gentil, Eduardo. III. Universidade Federal de Santa Catarina. Programa de Pós-Graduação em Oceanografia. IV. Título.

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Variação temporal de copépodes e *Coscinodiscus* spp. na Reserva Biológica Marinha do Arvoredo (SC) associada a variabilidade meteoceanográfica.

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CPF: ***.565.237-**
Verifique as assinaturas em <https://v.ufsc.br>

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Florianópolis, 2025.

AGRADECIMENTOS

Agradeço à toda a minha família, em especial meus pais, Simone e Fábio, por todo o apoio e educação que me foi dado, possibilitando a minha formação acadêmica.

Agradeço as orientações e instruções da minha orientadora Andrea Santarosa Freire e meu coorientador Eduardo Gentil. Ao Prof. Leonardo R. Rörig pela valiosa colaboração neste trabalho, e a toda a equipe do Laboratório de Ficologia da UFSC (LAFIC), pelo apoio e dedicação para o meu treinamento na identificação fitoplanctônica. Também estendo meus agradecimentos à Prof. Alessandra L. Fonseca e ao Laboratório de Biogeoquímica Marinha e Educação Ambiental, pelo fornecimento dos dados de clorofila, e ao Dr. Luis Carlos P. de Macedo-Soares, pela contribuição no trabalho e na construção dos dbRDA e GLMs.

Além disso, agradeço às mulheres maravilhosas, do Laboratório de Crustáceos e Plâncton, meu muito obrigada por toda parceria e ajuda. Principalmente às Dr. Érica Becker, responsável pelo meu treinamento para o escaneamento e processamento das amostras de plâncton no Zooscan, e a Dr. Andrea Green, pela orientação e análise estatística dos outros grupos taxonômicos representantes do mesoplâncton presentes nas amostras utilizadas neste trabalho.

À equipe do o projeto MAARE e do Projeto SIMCosta, por cederem os dados para que este trabalho fosse possível; à PETROBRÁS, pelo financiamento dos projetos; e ao projeto AtlantECO/ EU/ H2020/ Blue Growth, pelo apoio eventual durante as campanhas de amostragem de primavera realizadas como parte do Ocean Sampling Day (OSD).

Sou imensamente grata ao Roberto Bruno Fabiano, capitão do veleiro Pangeia, à toda equipe do ICMBio, à Prof. Bárbara Segal coordenadora do Plano de Ação para prevenção e Controle do Coral-sol na Rebio Arvoredo e Entorno (PACS Arvoredo), além de toda a sua equipe e ao Veleiro ECO pelo apoio no transporte e coleta para que a continuidade do monitoramento da comunidade planctônica da REBIO Arvoredo em 2023 e 2024 fosse possível.

Aos meus amigos Miriã, Júlio, Giulia, Natasha, Marina, Tainá, Ísis, Bea, Lisa, Ju, Lise, Cami, Gabi, Henrique, Bianca, Samuel e Kalina, que escutaram meus desabafos e me orientaram em momentos difíceis. Obrigada por estarem sempre comigo, nos momentos mais divertidos e nos difíceis também.

Agradeço ao Programa de Pós-graduação da Oceanografia UFSC (PPGOceano) pelo suporte institucional e pela oportunidade de formação acadêmica; a CAPES/CNPq pela bolsa, que foi essencial para minha permanência em Florianópolis.

Por fim, agradeço aos integrantes da banca, pela disponibilidade e pelas valiosas contribuições para o trabalho.

RESUMO

O plâncton constitui a base das cadeias alimentares marinhas, variando do picoplâncton ao macroplâncton. Os copépodes, são componentes dominantes do mesozooplâncton, e suas funções ecológicas são diretamente influenciadas pelas condições ambientais e tróficas. Em contrapartida, ainda são escassas as informações sobre os efeitos da diatomácea invasora *Coscinodiscus wailesii* (>200 µm) no Atlântico Sul. Este estudo utilizou dados coletados entre 2014 e 2024 para compreender como diferentes condições meteoceanográficas influenciam a variabilidade sazonal e interanual da composição e abundância de copépodes e *Coscinodiscus* spp. na Reserva Biológica Marinha do Arvoredo (~27°S-48°W) Santa Catarina, Brasil. As amostras de plâncton foram coletadas com redes de superfície de 200 µm na superfície. O Zooscan/EcoTaxa foi utilizado para identificar e quantificar o mesozooplâncton, enquanto a microscopia óptica, pelo método Utermöhl, foi usada para identificar as espécies de *Coscinodiscus*. Os dados de temperatura da superfície do mar (adquiridos com termômetro e MODIS/Aqua) e componentes de vento e deriva das ondas da superfície do mar (Global Ocean Daily Gridded Sea Surface Winds from Scatterometer and Copernicus Marine Service and Global Ocean Waves Reanalysis | Copernicus Marine Service) foram analisados juntamente com MFA e GLMs para explorar a influência da dinâmica meteoceanográfica sobre os grupos. Foi observada uma alternância de dominância entre *Coscinodiscus* spp. e copépodes influenciada pela dinâmica sazonal das massas de água na região. Os copépodes prosperaram, com maior abundância de Temoridae, em condições mais quentes e com maior estratificação na coluna d'água, associada à influência da intrusão da Água Central do Atlântico Sul durante os verões. *Coscinodiscus* spp., principalmente a invasora *C. wailesii*, apresentaram dominância sazonal recorrente de durante o outono, associada positivamente com a salinidade e negativamente com a temperatura. A influência da Água da Pluma do Prata no inverno resultou na redução da abundância de *Coscinodiscus* spp., contrastando com o predomínio de pequenos onívoros como Oithonidae. A adoção de técnicas de alta resolução, como análise de plâncton por imagem, aliada ao sensoriamento remoto e monitoramento contínuo, é essencial para revelar processos ecológicos complexos e orientar estratégias de conservação e manejo para reservas biológicas marinhas, principalmente em um cenário de mudanças climáticas.

Palavras-chave: Mesoplâncton, Espécies invasoras, Plataforma Continental Brasileira, REBIO Arvoredo, *Coscinodiscus wailesii*, Água da Pluma do Prata (APP), Água Central do Atlântico Sul (ACAS)

ABSTRACT

Plankton form the basis of marine food chains, ranging from picoplankton to macroplankton. Copepods are the dominant components of mesozooplankton, and their ecological functions are directly influenced by environmental and trophic conditions. However, information on the effects of the invasive diatom *Coscinodiscus wailesii* (>200 µm) in the South Atlantic is still scarce. This study used plankton sampled throughout 10-year (2014-2024) to understand how different meteoceanographic conditions influence the seasonal and interannual variability of the composition and abundance of copepods and *Coscinodiscus* spp. in the Arvoredo Marine Biological Reserve (~27°S-48°W) Santa Catarina, Brazil. Plankton samples were collected with 200 µm surface nets. Zooscan/EcoTaxa was used to identify and quantify mesozooplankton, while optical microscopy, using the Utermöhl method, was used to identify *Coscinodiscus* species. Sea surface temperature data (acquired with a thermometer and MODIS/Aqua) and wind and drift components of sea surface waves (Global Ocean Daily Gridded Sea Surface Winds from Scatterometer and Copernicus Marine Service and Global Ocean Waves Reanalysis | Copernicus Marine Service) were analyzed together with MFA and GLMs to explore the influence of meteoceanographic dynamics on the groups. An alternation of dominance between *Coscinodiscus* spp. and copepods was observed, influenced by the seasonal dynamics of the water masses in the region. Copepods thrived, with greater abundance of Temoridae, in warmer conditions and with greater stratification in the water column, associated with the influence of the intrusion of the South Atlantic Central Water during the summers. *Coscinodiscus* spp., especially the invasive *C. wailesii*, showed recurrent seasonal dominance during the fall, positively associated with salinity and negatively associated with temperature. The influence of the Plata Plume Water in winter resulted in a reduction in the abundance of *Coscinodiscus* spp., in contrast to the predominance of small omnivores such as Oithonidae. The adoption of high-resolution techniques, such as image analysis of plankton, combined with remote sensing and continuous monitoring, is essential to reveal complex ecological processes and guide conservation and management strategies for marine biological reserves, especially in a climate change scenario.

Keywords: Mesoplankton, Invasive species, *Coscinodiscus wailesii*, Southern Brazilian Bight, no-take REBIO Arvoredo, Plata Plume Water (PPW), South Atlantic Central Water (SACW).

LISTA DE FIGURAS

Figura 1. Representação esquemática do campo de fluxo numa onda gravitacional de superfície adaptada de Röhrs (2014). A superfície do mar (linha sólida azul) descreve uma onda transversal que se propaga para a direita. As velocidades de corrente eulerianas em posições fixas (representadas por vetores pretos) realizam movimentos orbitais com círculos fechados, tornando-se zero quando a média é calculada em um ciclo de onda. As partículas lagrangianas que seguem o fluxo descrevem cicloides de propagação (linhas vermelhas) com um movimento para frente, que corresponde à deriva de Stokes.	20
Figure 1. Study area. The black polygon represents the REBIO Arvoredo and the red triangle indicates the monitoring site.	34
Figure 2. Relative abundance (%) of <i>Coscinodiscus</i> spp., Copepoda and other mesoplankton taxa at the REBIO Arvoredo MPA between 2014 and 2024.	39
Figure 3. Abundance (ind.m ⁻³) of <i>Coscinodiscus</i> spp. and Copepoda at the REBIO Arvoredo no-take between 2014 and 2024.	40
Figure 4. Abundance (ind.m ⁻³) of the copepods Temoridae and Calanoida at the REBIO Arvoredo between 2014 and 2024.	41
Figure 5. Abundance (ind.m ⁻³) of Copepoda families, except for Temoridae and Calanoida, at the REBIO Arvoredo between 2014 and 2024.	42
Figure 6. Relative abundance of <i>C. asteromphalus</i> and <i>C. wailesii</i> at the REBIO Arvoredo between 2014 and 2024. Quantitative analysis in the microscope (cell/L) was a proxy of the occurrence in the net hauls.	43
Figure 7. Time series of sea surface temperature (SST) in °C obtained with the MODIS/Aqua sensor, running through January 2014 to 2024.	45
Figure 8. Sea surface temperature (SST) in °C from the MODIS/Aqua sensor in February 2015, 2016, 2018 and 2019 from the Santa Catarina continental shelf. The green dot indicates the sampling station.	46
Figure 9. Horizontal distribution of monthly sea surface temperature (SST) in °C from the MODIS/Aqua sensor in August of 2016, July of 2018, July of 2019 and July 2024 from the Santa Catarina continental shelf. The green dot indicates the sampling station.	46
Figure 10. Wind intensity and direction in summer (2015, 2016, 2018 2019 February, 2014, 2018, 2023 March and 2024 January). Each graph shows the relative frequency (%) of wind direction and intensity (m/s).	47
Figure 11. Wind intensity and direction in autumn (2014, 2018, 2019 June). Each graph shows the relative frequency (%) of wind direction and intensity (m/s).	48
Figure 13. Wind intensity and direction in spring (2018, 2019, 2022, 2023 September) and early summer (2018 December). Each graph shows the relative frequency (%) of wind direction and intensity (m/s).	49
Figure 14. Seasonal variation of Stokes drift direction and intensity from 2014 to 2024. Each panel represents the directional distribution of Stokes drift for a specific year and season. Each graph shows the relative frequency (%) of Stokes drift direction and intensity (m/s).	50
Figure 15. Distance-based Redundancy Analysis (dbRDA) obtained with <i>Coscinodiscus</i> spp. (ind.m ⁻³) and the most abundant copepoda families analyzed in the image system Zooscan/EcoTaxa. Biological components represented by abbreviations (Cosc_spp. =	

Coscinodiscus spp. (ind.m ⁻³), Cala = Calanidae (ind.m ⁻³), Onca = Oncaiedae (ind.m ⁻³), Cory = Corycaeidae (ind.m ⁻³), Temo = Temoridae (ind.m ⁻³), Cent = Centropagidae (ind.m ⁻³), Oith = Oithonidae (ind.m ⁻³) and Harp = Harpacticoida (ind.m ⁻³). Environmental vectors were represented by Temp = in situ temperature (°C), EUZ = in situ euphotic zone (m), Chla = in situ chlorophyll-a (ugL) and remote sensing data Eastward_wave_drift = Eastward Stokes drift component (m/s) and Northward_wave_drift = Northward Stokes drift component (m/s). Seasons were represented by symbols. Colorbar encompasses sampling in each year.	52
Figure 16. Generalized linear mixed models (GLMs) results from the relationship between in situ temperature (°C), salinity, chlorophyll-a (ugL), euphotic zone depth (EUZ, m) and the remote sensing northward strokes wave drift (m/s) with Coscinodiscus spp. (ind), Copepoda (ind) raw abundance. Linear regressions (lines); confidence intervals (shaded area); statistical significance (***) p < 0.001; ** p < 0.01; * p < 0.05).	53
Figure S1. Relative abundance (%) of the other mesozooplanktonic taxa at the REBIO Arvoredo MPA during the months when Copepoda were dominant. * represents the less frequent and abundant groups.	87
Figure S2. Relative abundance (%) of the other mesozooplanktonic taxa at the REBIO Arvoredo MPA during the months when Coscinodiscus spp. were dominant. * represents the less frequent and abundant groups.	88
Figure S3. Relative abundance (%) of the other mesozooplanktonic taxa at the REBIO Arvoredo MPA during the months when Others were dominant or had the same dominance of Copepoda. * represents the less frequent and abundant groups.	88
Figure S4. Equivalent spherical diameter (ESD mm) of Coscinodiscus spp. and Copepoda in REBIO Arvoredo between 2014 and 2024. Upper and lower limits (vertical lines), first and third quartile (box), median (horizontal line) and outliers (dots). Boxplots in light green represent Coscinodiscus spp. and in dark blue, Copepoda.	89
Figure S5. Horizontal distribution of monthly sea surface temperature (SST) in °C from the MODIS/Aqua sensor from January to June 2014 for the Santa Catarina continental shelf.	90
Figure S6. Horizontal distribution of monthly sea surface temperature (SST) in °C from the MODIS/Aqua sensor from July to December 2014 for the Santa Catarina continental shelf.	91
Figure S7. Horizontal distribution of monthly sea surface temperature (SST) in °C from the MODIS/Aqua sensor from January to June 2015 for the Santa Catarina continental shelf.	91
Figure S8. Horizontal distribution of monthly sea surface temperature (SST) in °C from the MODIS/Aqua sensor from July to December 2015 for the Santa Catarina continental shelf.	92
Figure S9. Horizontal distribution of monthly sea surface temperature (SST) in °C from the MODIS/Aqua sensor from January to June 2016 for the Santa Catarina continental shelf.	93
Figure S10. Horizontal distribution of monthly sea surface temperature (SST) in °C from the MODIS/Aqua sensor from July to December 2016 for the Santa Catarina continental shelf.	93
Figure S11. Horizontal distribution of monthly sea surface temperature (SST) in °C from the MODIS/Aqua sensor from January to June 2017 for the Santa Catarina continental shelf.	94
Figure S12. Horizontal distribution of monthly sea surface temperature (SST) in °C from the MODIS/Aqua sensor from July to December 2017 for the Santa Catarina continental shelf.	94
Figure S13. Horizontal distribution of monthly sea surface temperature (SST) in °C from the MODIS/Aqua sensor from January to June 2018 for the Santa Catarina continental shelf.	95
Figure S14. Horizontal distribution of monthly sea surface temperature (SST) in °C from the MODIS/Aqua sensor from July to December 2018 for the Santa Catarina continental shelf.	96
Figure S15. Horizontal distribution of monthly sea surface temperature (SST) in °C from the MODIS/Aqua sensor from January to June 2019 for the Santa Catarina continental shelf.	97

Figure S16. Horizontal distribution of monthly sea surface temperature (SST) in °C from the MODIS/Aqua sensor from July to December 2019 for the Santa Catarina continental shelf.	98
Figure S17. Horizontal distribution of monthly sea surface temperature (SST) in °C from the MODIS/Aqua sensor from January to June 2020 for the Santa Catarina continental shelf.	98
Figure S18. Horizontal distribution of monthly sea surface temperature (SST) in °C from the MODIS/Aqua sensor from July to December 2020 for the Santa Catarina continental shelf.	99
Figure S19. Horizontal distribution of monthly sea surface temperature (SST) in °C from the MODIS/Aqua sensor from January to June 2021 for the Santa Catarina continental shelf.	99
Figure S20. Horizontal distribution of monthly sea surface temperature (SST) in °C from the MODIS/Aqua sensor from July to December 2021 for the Santa Catarina continental shelf. ...	100
Figure S21. Horizontal distribution of monthly sea surface temperature (SST) in °C from the MODIS/Aqua sensor from January to June 2022 for the Santa Catarina continental shelf.	100
Figure S22. Horizontal distribution of monthly sea surface temperature (SST) in °C from the MODIS/Aqua sensor from July to December 2022 for the Santa Catarina continental shelf. ...	101
Figure S23. Horizontal distribution of monthly sea surface temperature (SST) in °C from the MODIS/Aqua sensor from January to June 2023 for the Santa Catarina continental shelf.	101
Figure S24. Horizontal distribution of monthly sea surface temperature (SST) in °C from the MODIS/Aqua sensor from July to December 2023 for the Santa Catarina continental shelf. ...	102
Figure S25. Horizontal distribution of monthly sea surface temperature (SST) in °C from the MODIS/Aqua sensor from January to June 2024 for the Santa Catarina continental shelf.	102
Figure S26. Horizontal distribution of monthly sea surface temperature (SST) in °C from the MODIS/Aqua sensor from July of 2024 for the Santa Catarina continental shelf.	103
Figure S27. Wind intensity and direction of March and August of 2014. Each graph shows the relative frequency (%) of wind direction and intensity (m/s).	104
Figure S28. Wind intensity and direction of February and July of 2015. Each graph shows the relative frequency (%) of wind direction and intensity (m/s).	104
Figure S29. Wind intensity and direction of February and August of 2016. Each graph shows the relative frequency (%) of wind direction and intensity (m/s).	104
Figure S30. Wind intensity and direction of December and February of 2018. Each graph shows the relative frequency (%) of wind direction and intensity (m/s).	105
Figure S31. Wind intensity and direction of March and April of 2018. Each graph shows the relative frequency (%) of wind direction and intensity (m/s).	106
Figure S32. Wind intensity and direction of May and June of 2018. Each graph shows the relative frequency (%) of wind direction and intensity (m/s).	106
Figure S33. Wind intensity and direction of September 2018 and November of 2019. Each graph shows the relative frequency (%) of wind direction and intensity (m/s).	106
Figure S34. Wind intensity and direction of February and April of 2019. Each graph shows the relative frequency (%) of wind direction and intensity (m/s).	107
Figure S35. Wind intensity and direction of June and July of 2019. Each graph shows the relative frequency (%) of wind direction and intensity (m/s).	107
Figure S36. Wind intensity and direction of August and September of 2019. Each graph shows the relative frequency (%) of wind direction and intensity (m/s).	108
Figure S37. Wind intensity and direction of September of 2022 and March of 2023. Each graph shows the relative frequency (%) of wind direction and intensity (m/s).	108
Figure S38. Wind intensity and direction of August and September of 2023. Each graph shows the relative frequency (%) of wind direction and intensity (m/s).	109

Figure S39. Wind intensity and direction of January and June of 2024. Each graph shows the relative frequency (%) of wind direction and intensity (m/s).	109
Figure S40. Wind intensity and direction of July of 2024. Each graph shows the relative frequency (%) of wind direction and intensity (m/s).	109

LISTA DE TABELAS

Tabela 1. Índices termoahalinos propostos por Möller et al. (2008) das massas d'água ACAS= Água Central Do Atlântico Sul, APP = Água Da Pluma Do Prata, ASTP= Água Subtropical De Plataforma, AT = Água Tropical, T = Temperatura, S = Salinidade.	18
Table S1a. Species and morphotypes list of phytoplankton processed through optical microscopy (OLYMPUS - 20x) using identification keys (TOMAS,1997) that occurred from 2014 to 2024 at the REBIO Arvoredo monitoring site.	80
Table S1b. Species and morphotypes list of phytoplankton processed through optical microscopy (OLYMPUS - 20x) using identification keys (TOMAS,1997) that occurred from 2014 to 2024 at the REBIO Arvoredo monitoring site.	81
Table S1c. Species and morphotypes list of phytoplankton processed through optical microscopy (OLYMPUS - 20x) using identification keys (TOMAS,1997) that occurred from 2014 to 2024 at the REBIO Arvoredo monitoring site.	82
Table S1d. Species and morphotypes list of phytoplankton processed through optical microscopy (OLYMPUS - 20x) using identification keys (TOMAS,1997) that occurred from 2014 to 2024 at the REBIO Arvoredo monitoring site.	83
Table S1e. Species and morphotypes list of phytoplankton processed through optical microscopy (OLYMPUS - 20x) using identification keys (TOMAS,1997) that occurred from 2014 to 2024 at the REBIO Arvoredo monitoring site.	84
Table S2. Complementary information from the Generalized Linear Models (GLMs) used to evaluate the effects of environmental variables on Copepoda and Coscinodiscus spp. For each predictor, the table shows the estimated coefficient and its standard error (Estimate ± SE), the associated z-value (test statistic), and the p-value, which indicates the level of statistical significance (values < 0.05 were considered significant). AIC represents Akaike Information Criterion and log-likelihood (logLik). Dispersion values are reported to assess the degree of overdispersion in the models, which were fitted using a negative binomial distribution (nbinom2) to account for non-normal, overdispersed count data.	85

LISTA DE ABREVIATURAS E SIGLAS

ACAS – Água Central do Atlântico Sul

APP – Água da Pluma do Prata

AT – Água Tropical

ASTP – Água Subtropical do Atlântico Sul

BC – Brazilian Current

CB – Corrente do Brasil

ENSO – El Niño Southern Oscillation

ENOS – El Niño Oscilação Sul

EUZ – Euphotic zone

MPA – Marine Protected Area

PCB – Plataforma Continental Brasil

PPW – Plata Plume Water

REBIO Arvoredo – Arvoredo Marine Biological Reserve

REBIO Arvoredo – Reserva Biológica Marinha do Arvoredo

SACW – South Atlantic Central Water

SBB – Southern Brazilian Bight

SST – Sea Surface Water

TSM – Temperatura superficial do mar

TW – Tropical Water

SUMÁRIO

INTRODUÇÃO GERAL	14
OBJETIVOS	18
OBJETIVO GERAL	18
OBJETIVOS ESPECÍFICOS	19
FUNDAMENTOS FÍSICOS - DERIVA DE STOKES	19
REFERÊNCIAS	20
ARTIGO CIENTÍFICO	27
INTRODUCTION.....	30
MATERIALS AND METHOD	33
STUDY AREA	33
SAMPLING.....	34
PLANKTON SAMPLES PROCESSING	35
REMOTE SENSING	36
STATISTICS.....	37
RESULTS	38
PLANKTON IMAGING.....	38
PLANKTON OPTICAL MICROSCOPY	42
REMOTE SENSING	44
SEA SURFACE TEMPERATURE (SST)	44
WIND.....	47
STOKES DRIFT	50
RELATIONSHIPS WITH ENVIRONMENTAL DESCRIPTORS	51
DISCUSSION.....	53
CONCLUSION	59
ACKNOWLEDGEMENTS.....	60
CONCLUSÃO GERAL	61
REFERENCES	62
SUPPLEMENTARY MATERIAL (SM)	81
APPENDIX A.....	90
APPENDIX B.....	103

ESTRUTURA DA DISSERTAÇÃO

A dissertação foi organizada seguindo as normas do PPG Oceanografia/ UFSC em:

- Introdução geral, objetivos e fundamentos físicos do estudo (em português)
- Referências.
- Artigo científico referente a dissertação de mestrado, submetido ao periódico *Continental Shelf Research*, como requisito necessário pelas normas do PPG Oceanografia/ UFSC para a defesa da dissertação.
- Conclusão do trabalho (em português)
- Referências bibliográficas.

INTRODUÇÃO GERAL

O plâncton é um componente fundamental na dinâmica do ecossistema marinho, representando os primeiros consumidores da cadeia trófica no oceano (TANG, *et al.*, 1998). A comunidade planctônica é altamente diversificada, abrange organismos de várias ordens de magnitude de tamanho, desde 0,02 μm até vários metros (SIEBURTH; SMETACEK; LENZ, 1978). Além de estarem presentes em todos os domínios da vida, incluindo bactérias, protistas, metazoários, fitoplâncton, zooplâncton e ictioplâncton (LOMBARD *et al.*, 2019; SILVA *et al.*, 2014). Podendo compor apenas uma fase da vida dos organismos, como no caso do meroplâncton (ex. larvas de organismos bentônicos, como no caso de alguns crustáceos, ou de peixes que representam o nécton na fase de vida adulta). Estes organismos, se distribuem ao longo de todos os níveis tróficos, auto, mixo e heterotrófico. Organismos mixotróficos são capazes tanto de autotrofia quanto de heterotrofia, foram observados tanto no zooplâncton quanto no fitoplâncton (MILTRA *et al.*, 2016).

O picoplâncton (0,2-2 μm) representa a menor fração de tamanho do fitoplâncton e é composto principalmente por bactérias autotróficas e heterotróficas, incluindo cianobactérias fotossintetizantes, (JOHNSON; SIEBURTH, 1979; AZAM *et al.*, 1983; CHISHOLM *et al.*, 1988; GUENTHER *et al.*, 2008). O nanoplâncton (2–20 μm) inclui

organismos autotróficos, heterotróficos ou mixotróficos, como algas flageladas fotossintetizantes (parte do fitoplâncton) e flagelados heterotróficos, que se alimentam do picoplâncton (SIEBURTH; SMETACEK; LENZ, 1978). Já o microplâncton (20–200 µm) abriga tanto organismos autotróficos representantes do fitoplâncton, quanto heterotróficos, como os ciliados que predam flagelados e outros organismos menores. O mesoplâncton (0,2–20 mm) é majoritariamente composto pelo zooplâncton, mas também inclui grandes diatomáceas e ciliados (SIEBURTH; SMETACEK; LENZ, 1978; POMEROY *et al.*, 2007).

A diatomácea cêntrica *Coscinodiscus wailesii*, Gran and Angst (1931), se destaca pelo grande tamanho (>200 µm) (BOYD; GRADMAN, 1999). *C. wailesii*, aparentemente originada dos Oceanos Pacífico e Índico (BOALCH; HARBOUR 1977), é geralmente observada em temperaturas amenas de estações intermediárias como outono e primavera, atingindo os máximos de crescimento com temperatura e a salinidade entre 20-25°C e 20-30 (NISHIKAWA *et al.*, 2000; TADA *et al.*, 2000). A espécie invasora no Atlântico Sul, provavelmente foi inserida na Plataforma de Santa Catarina por meio de água de lastro no Porto de Itajaí-SC (STRAMOSK, 2022). Ainda são escassas as informações sobre os efeitos, especialmente para as espécies invasoras de fitoplâncton, na biodiversidade marinha (OLENINA *et al.*, 2010).

Outro grupo de grande destaque, é a subclasse Copepoda de crustáceos, a qual representa entre 70% e 97% da biomassa do mesozooplâncton encontrado nas plataformas continentais (LOPES *et al.*, 2006). Os copépodes apresentam ampla variação de tamanho, com espécies de tamanho médio de 1 mm, e outras que podem atingir até 15 mm (BOLTOVSKOY *et al.*, 1999). Neste trabalho, serão abordados copépodes entre 0,4 mm e 1 mm. As funções ecológicas dos copépodes são diretamente moduladas pelas condições ambientais e tróficas (BECKER *et al.*, 2018). Mudanças na composição de espécies e diversidade funcional da subclasse ajudam a manter funções e processos ecológicos essenciais do ecossistema (MENEZES *et al.*, 2024).

Em um ecossistema marinho, a condição trófica é definida por fatores abióticos, como a disponibilidade de luz, concentração de nutrientes e clorofila (MARINOV; DONEY; LIMA, 2010), além das forçantes hidrodinâmicas de deriva de ondas e vento, especialmente fenômenos oceanográficos de mesoescala sazonais e interanuais

associados a ressurgência e variações nas massas de água (NYBAKKEN; BERTNESS, 2005). A condição trófica modula a composição, a dominância e a dinâmica das comunidades planctônicas, incluindo os traços funcionais dominantes nas assembleias de copépodes e fitoplâncton, além da distribuição espaço-temporal e abundância desses grupos (MENEZES *et al.*, 2024).

Em ambientes eutróficos, ricos em nutrientes, predominam grandes células do fitoplâncton que se beneficiam da alta disponibilidade de nutrientes na zona eufótica (DUGDALE; GOERING, 1967; PRICE; COCHLAN; HARRISON, 1985), sendo majoritariamente consumidas por copépodes herbívoros. Cadeias alimentares dispostas desta maneira, são consideradas clássicas e baseadas na herbivoria (RYTHER, 1969; AZAM *et al.*, 1983; BENEDETTI *et al.*, 2018). Por outro lado, em águas oligotróficas, onde a concentração de nutrientes é limitada, a produção primária é dominada por pico e nanoplâncton (KIØRBOE, 1993; GUENTHER *et al.*, 2008). Nestas situações, ocorre uma teia trófica mais longa e complexa, a cadeia microbiana, envolvendo flagelados, ciliados e, por fim, copépodes carnívoros e detritívoros (AZAM *et al.*, 1983; POMEROY *et al.*, 2007; MENEZES, DE MACEDO-SOARES; FREIRE, 2019).

Além disso, forçantes hidrodinâmicas, como a deriva induzida pelas ondas exerce forte influência sobre a composição e a distribuição das comunidades planctônicas (GAWARKIEWICZ *et al.*, 2007; SULLIVAN E MCWILLIAMS, 2010) atuando sobre as partículas na superfície do oceano (RÖHRS *et al.*, 2014). Partículas expostas às ondas gravitacionais sofrem um movimento na direção da propagação da onda, denominado de deriva de Stokes (STOKES, 1847). Desta forma, a deriva de Stokes está associada ao transporte físico tanto do fitoplâncton (OMAND *et al.*, 2011; SHANKS *et al.*, 2014) quanto das larvas meroplânctônicas (SHANKS; WRIGHT 1987; PINEDA 1999).

Investigações de longo prazo das comunidades planctônicas são essenciais para a compreensão da saúde do oceano, da segurança alimentar e dos impactos das mudanças climáticas neste ambiente (CHIBA *et al.*, 2018). Investigações de longo prazo sobre plâncton são raras no Brasil, tendo sido realizadas na ressurgência de Cabo Frio, e dentro de Programas Ecológicos de Longa Duração (PELD/ CNPq), na Lagoa dos Patos (RS), Baía de Guanabara (RJ) e Tamandaré (PE), limitando a associação com as mudanças globais (VALENTIN *et al.*, 2020; RESGALLA, 2022). Em geral, nestes

trabalhos, amostras mensais/ semanais são consideradas representativas do mês/semana em questão. As mudanças climáticas estão associadas a um aumento da duração e intensidade dos eventos climáticos, como o El Niño Oscilação Sul (ENOS) (RIPPLE *et al.*, 2022; IPCC, 2019b).

O El Niño é um fenômeno climático de aquecimento anômalo da temperatura da superfície do mar (TSM) no Pacífico tropical. Ele está associado a um distúrbio nos padrões de circulação atmosférica conhecido como Oscilação Sul em um determinado intervalo de meses e a ocorrência de águas anormalmente quentes na Corrente do Brasil (CB) (SEVEROV *et al.*, 2004; MCPHADEN *et al.*, 2006; CAI *et al.*, 2015). Esse distúrbio não só tem sérias consequências para o plâncton (MOORE, FOLT; STEMBERGER, 1996; MAROCHI *et al.*, 2022), mas também está associado a um aumento da precipitação na América do Sul, principalmente na Bacia do Rio da Prata (ACEITUNO, 1988; CERA *et al.*, 2015; CAI *et al.*, 2020), intensificando os fluxos dos rios para as áreas costeiras com maior aporte de nutrientes (MECHOSO; IRIBARREN, 1992).

A Reserva Biológica Marinha do Arvoredo (REBIO Arvoredo), localizada na plataforma de Santa Catarina (26-29°S e 48°W) é conhecida como um *hotspot* de biodiversidade (FLOETER *et al.*, 2008) e foi criada para proteger a biodiversidade e esse importante ecossistema marinho (BOELTER *et al.*, 2024). A região encontra-se ao sul da Plataforma Continental Brasileira e é caracterizada por uma dinâmica interação de distintas massas de água que influenciam a comunidade de plâncton. A costa está sob a influência da CB, que transporta a quente e oligotrófica Água Tropical (AT) na direção norte-sul (MÖLLER *et al.*, 2008; CASTRO *et al.*, 1990) na quebra da plataforma. Nos meses de verão, os ventos de nordeste são frequentes e intensos, gerando o transporte de Ekman das águas superficiais para o oceano aberto, induzindo afloramentos costeiros da Água Central do Atlântico Sul (ACAS) podendo resultar em eventos de ressurgência desta água fria e rica em nutrientes (CASTRO; MIRANDA, 1998; CAMPOS *et al.*, 2000). As altas temperaturas na superfície, somadas à intrusão da fria ACAS no fundo e a presença da Água Subtropical de Plataforma (ASTP) criam uma termoclina sazonal (BORDIN *et al.*, 2019; MATSUURA, 1986; CASTRO *et al.*, 2006), que aumenta a profundidade da zona eufótica (BRANDINI *et al.*, 2014). No inverno, a região apresenta forte instabilidade de ventos, com a frequente passagem de frentes frias de sul e sudeste

(CASTRO *et al.*, 2006). Os ventos sul-sudeste promovem a mistura da coluna de água e a advecção da ASTP de inverno. A Água da Pluma do Prata (APP) de baixa salinidade atinge a região (MÖLLER *et al.*, 2008) devido à ação do vento de sul e aumento da precipitação na Bacia do Rio da Prata (EVANS *et al.*, 1983; ACEITUNO, 1988). A identificação das massas d'água é realizada de acordo com os índices termohalinos propostos por Moller *et al.* (2008) (Tabela 1).

Tabela 1. Índices termoahalinos propostos por Möller *et al.* (2008) das massas d'água ACAS= Água Central Do Atlântico Sul, APP = Água Da Pluma Do Prata, ASTP= Água Subtropical De Plataforma, AT = Água Tropical, T = Temperatura, S = Salinidade.

Massas d'água	Inverno	Verão
Intervalo termohalino		
ACAS	$T \leq 18,5^{\circ}\text{C}$, $S \geq 35,3$	$T \leq 18,5^{\circ}\text{C}$, $S \geq 35,3$
APP	$T > 10^{\circ}\text{C}$, $S \leq 33,5$	$T > 10^{\circ}\text{C}$, $S \leq 33,5$
ASTP	$T > 14^{\circ}\text{C}$, $33,5 \leq S < 36$	$T > 18,5^{\circ}\text{C}$, $35,3 < S < 36$
AT	$T \geq 18,5^{\circ}\text{C}$, $S \geq 36$	$T \geq 18,5^{\circ}\text{C}$, $S \geq 36$

Apesar da grande importância biológica desta área, ainda são escassas as informações de longo prazo sobre a influência dos processos meteoceanográficos na variação temporal de copépodes e *Coscinodiscus* spp. na REBIO Arvoredo.

OBJETIVOS

OBJETIVO GERAL

Investigar a variabilidade na composição e abundância de Copepoda e *Coscinodiscus* spp. no mesoplâncton ($> \sim 200 \mu\text{m}$) da REBIO do Arvoredo ao longo de 10 anos, visando compreender a sua relação com diferentes condições meteoceanográficas.

OBJETIVOS ESPECÍFICOS

- Avaliar a composição, dominância e abundância de copépodes e *Coscinodiscus* spp. presentes na REBIO Arvoredo entre 2014 e 2024.

- Descrever a variabilidade meteoceanográfica na região entre 2014 e 2024;
- Associar a sazonalidade na composição e abundância de copépodes e *Coscinodiscus* spp. aos processos meteoceanográficos.

FUNDAMENTOS FÍSICOS - DERIVA DE STOKES

A deriva de Stokes constitui um fenômeno físico associado ao movimento de partículas na superfície do oceano sob a influência de ondas gravitacionais (PHILLIPS, 1977). Ainda que o movimento das partículas gerado por tais ondas aparente ser oscilatório, este induz um transporte na direção de propagação das ondas, denominado de deriva de Stokes (STOKES, 1847). Em termos de descrição do fluxo, a abordagem Euleriana, observando as propriedades do fluido a partir de um referencial fixo (EULER, 1757), representa as velocidades oscilatórias das ondas como trajetórias aproximadamente circulares. A abordagem Lagrangiana, identificando o movimento de partículas acompanhando sua trajetória (LAGRANGE, 1788), revela que as trajetórias reais das partículas formam cicloides abertos, evidenciando deslocamento líquido para a frente (FIGURA 1) (RÖHRS *et al.*, 2014; BREMER; BREIVIK, 2018). A intensidade da deriva de Stokes está relacionada com a energia das ondas e pode ser estimada por meio de modelos numéricos, como Marine Service and Global Ocean Waves Reanalysis | Copernicus Marine Service, de previsão de ondas e direções considerando as componentes zonal (direção leste-oeste) e meridional (norte-sul) da deriva de onda (KOMEN *et al.*, 1994).

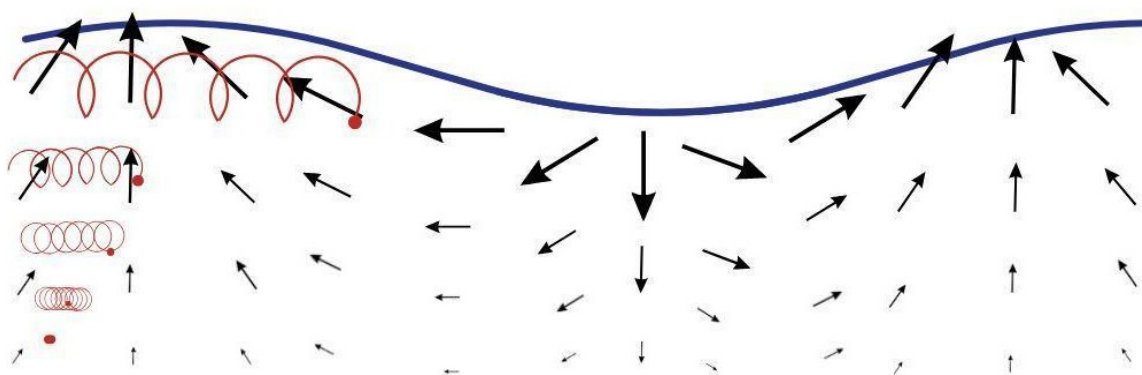


Figura 1. Representação esquemática do campo de fluxo numa onda gravitacional de superfície adaptada de Röhrs (2014). A superfície do mar (linha sólida azul) descreve uma onda transversal que se propaga para a direita. As velocidades de corrente eulerianas em posições fixas (representadas por vetores pretos) realizam movimentos orbitais com círculos fechados, tornando-se zero quando a média é calculada em um ciclo de onda. As partículas lagrangianas que seguem o fluxo descrevem cicloides de propagação (linhas vermelhas) com um movimento para frente, que corresponde à deriva de Stokes.

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ARTIGO CIENTÍFICO

Copepods and *Coscinodiscus* spp. temporal dynamics in the shallow subtropical Southern Brazilian Bight: associations with oceanographic variability.

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Manuscript submitted in Continental Shelf Research (2025)

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Highlights

- This is the first long-term (2014-2024) investigation focused on mesoplankton dynamics within the no-take Arvoredo Marine Biological Reserve (REBIO Arvoredo/Brazil).
- A multimethod approach using advanced imaging (Zooscan/EcoTaxa) and detailed phytoplankton taxonomy (Utermöhl) was crucial to accurately assess the role of large *Coscinodiscus* spp. in the ecosystem.
- The plankton imaging results uncovered the non precedent quantification of *Coscinodiscus* spp. at REBIO Arvoredo waters among organisms larger than 200 μm .
- Results showed a pronounced dominance of *Coscinodiscus* spp., in austral autumn (up to 92% relative abundance), contrasting with lower copepod presence.
- A recurrent seasonal dominance of the invasive *Coscinodiscus wailesii* was observed on austral autumns.

ABSTRACT

Plankton forms the foundation of marine food webs, ranging from picoplankton to macroplankton. A plankton monitoring study (2014–2024) was conducted at the no-take Arvoredo Marine Biological Reserve (REBIO Arvoredo). This area is located within the Southern Brazilian Bight, presenting a dynamic interaction of distinct water masses that drives the plankton community. This study aims to investigate the temporal dynamics of copepods and *Coscinodiscus* spp. abundance and dominance, associated with the oceanographic variabilities. Surface tow nets of 200 µm were used to collect 27 samples. Zooscan/EcoTaxa quantified the major groups of mesozooplankton, while optical microscopy by the Utermöhl method was used to identify *Coscinodiscus* species. Sea Surface Temperature (acquired with thermometer and MODIS/Aqua), wind and sea surface wave Stokes drift and velocity components (Global Ocean Daily Gridded Sea Surface Winds from Scatterometer and Copernicus Marine Service and Global Ocean Waves Reanalysis | Copernicus Marine Service) data were analyzed alongside MFA and GLMs to explore plankton-environment relationships. Results showed a pronounced dominance of *Coscinodiscus* spp., particularly the invasive *Coscinodiscus wailesii*, in autumn (up to 92% relative abundance), contrasting with lower copepod presence. Over time, *Coscinodiscus* spp. dominance increased, peaking in June 2024, correlating positively with salinity and negatively with temperature, while Temoridae copepods thrived in summer, with warmer, stratified conditions associated with South Atlantic Central Water. The influence of the Plata Plume Water in winter resulted in a reduction in the abundance of *Coscinodiscus* spp., in contrast to the predominance of small omnivores such as Oithonidae. These shifts highlights the meteoceanographic influence on mesoplankton dynamics, emphasizing the need for long-term monitoring in this ecologically sensitive marine protected area.

Keywords: Temoridae, *Coscinodiscus wailesii*, Invasive species, Southern Brazilian Bight, MPA, ENSO, PPW, SACW.

INTRODUCTION

Plankton community, a highly diverse group encompassing organisms from picoplankton to macroplankton (LOMBARD *et al.*, 2019), forms the energetic base of marine food webs and plays a crucial role in the overall dynamics of ocean ecosystems (TANG *et al.*, 1998). Composed of primary producers (phytoplankton), consumers (zooplankton) and decomposers (bacterioplankton), these organisms are fundamental to the cycling of organic carbon in pelagic environments, ultimately supporting all higher trophic levels, including commercially significant fish stocks and endangered species as marine mammals (BONECKER, BASSANI, 2009; CALBET, SAIZ, 2005). The structure and primary productivity of these communities are intrinsically linked to abiotic factors such as light availability and the concentration of essential nutrients (MARINOV; DONEY; LIMA, 2010). Zooplankton, on the other hand, typically encompasses heterotrophic organisms, particularly those belonging to the mesoplankton size fraction (0.2-20 mm) (SIEBURTH, SMETACEK; LENZ, 1978).

Among the mesozooplankton, copepods are a dominant component of biomass on continental shelves (BOLTOVSKOY *et al.*, 1999; LOPES *et al.*, 2006). The size of copepods varies significantly, with species exhibiting an average length of 1 mm and others reaching up to 15 mm (BOLTOVSKOY *et al.*, 1999). The present study will concentrate on copepods measuring between 0.4 mm and 1 mm. This diverse group exhibits ecological roles that are directly modulated by the prevailing environmental conditions (BECKER *et al.*, 2018). Indeed, the composition and dynamics of planktonic communities, including the interactions between copepods and phytoplankton, are strongly influenced by light and chlorophyll availability, which is, in turn, regulated by seasonal hydrodynamic forcings, particularly in tropical and subtropical regions (NYBAKKEN; BERTNESS, 2005).

Mesoscale oceanographic phenomena, such as upwelling events, wind and waves regimes, seasonal and interannual shifts in water masses, induce significant variations in water abundance and nutrient availability, consequently exerting a substantial impact on the overall structure of plankton communities (OLMEDO *et al.*, 2022; PIERI *et al.*, 2023).

Wave-induced drift and turbulence have been demonstrated to influence the transport and dispersion of particles on the ocean surface (RÖHRS *et al.*, 2014). In this manner, Stokes drift exerts a significant influence on the composition and distribution of planktonic communities (GAWARKIEWICZ *et al.*, 2007; SULLIVAN; MCWILLIAMS, 2010). Especially for understanding the dispersal of planktonic forms, including the physical transport of both phytoplankton (OMAND *et al.*, 2011; SHANKS *et al.*, 2014) and meroplankton larvae (SHANKS; WRIGHT, 1987; PINEDA, 1999).

Arvoredo Marine Biological Reserve (REBIO Arvoredo) is located at the Santa Catarina shelf (26-29°S and 48°W), south of the Southern Brazilian Bight (SBB). The Marine Protected Area (MPA) was established to safeguard substantial marine biodiversity and habitats because of its ecological significance as a biodiversity hotspot (BOELTER *et al.*, 2024). The area is characterized by a dynamic interaction of distinct water masses that drives the plankton community. The coast is under the influence of the Brazilian Current (BC), which transports the warm Tropical Water (TW) in a north-south direction (MÖLLER *et al.*, 2008; CASTRO *et al.*, 1990). In summer months, northeast winds are frequent and intense leading to Ekman transport of surface waters offshore and balancing it by onshore bottom intrusions of the South Atlantic Central Water (SACW) (CASTRO; MIRANDA, 1998; CAMPOS *et al.*, 2000). High temperatures at the surface, added to the intrusion of cold SACW in the bottom create a seasonal thermocline (MATSUURA, 1986; CASTRO *et al.*, 2006), which also enhance the depth of the euphotic zone (BRANDINI *et al.*, 2014). In winter, the region has a strong wind instability, with the frequent passage of south and southeast cold fronts (CASTRO *et al.*, 2006). South-southeasterly winds promote the water column mixing and the advection of subantarctic waters, alongside the northward expansion of the low-salinity Plata Plume Water (PPW) (EVANS *et al.*, 1983; MÖLLER *et al.*, 2008).

Furthermore, temporal plankton abundance knowledge is essential for understanding ecosystem dynamics, ocean health, food security and climate change effects on the marine system (CHIBA *et al.*, 2018). Climate changes are associated with a long-term increase in global surface temperature (STOCKER *et al.*, 2013) and has increased the duration and intensity of climate events, such as the El Niño Southern Oscillation (ENSO) (RIPPLE *et al.*, 2022; IPCC, 2019b). ENSO is a climatic phenomenon

of anomalous warming of sea surface temperature (SST) in the tropical Pacific. It is associated with a disturbance in atmospheric circulation patterns known as the Southern Oscillation with a time interval of months (MCPHADEN *et al.*, 2006; CAI *et al.*, 2015). Not only does this disturbance have serious consequences for plankton (MOORE; FOLT ; STEMBERGER, 1996; MAROCHI *et al.*, 2022), but it also results in an increase in rainfall in the southern part of Brazil (CERA *et al.*, 2015; CAI *et al.*, 2020), intensifying river flows to coastal areas with higher nutrient inputs.

Adding a significant layer of ecological complexity to the REBIO Arvoredo MPA is the introduction of the Pacific and Indian Oceans centric diatom *Coscinodiscus wailesii* Gran and Angst (1931). This invasive species was likely introduced via ballast water discharge in the Itajaí-SC Port (STRAMOSK, 2022). These large cells pose a potential threat not only for the native phytoplankton community by replacing the native phytoplankton by competition, decreasing biodiversity (EDWARDS *et al.*, 2001), but to the ecosystem.

There has been a long history of scientific study of these waters and of their resident biota, but the majority has consisted of intensive but relatively brief (1–3 year duration). However, a long-term investigation of copepods and *Coscinodiscus* spp., especially the invasive *C. wailesii*, within the REBIO Arvoredo MPA, is essential for a comprehensive understanding of the identities and seasonal cycles of the dominance between these two taxa. ecosystem dynamics, development of effective conservation strategies, as well as ecosystems predictions in a changing ocean (RATNARAJAH *et al.*, 2023). This study aims to analyze the temporal variations of copepods and *Coscinodiscus* spp. (200 µm - 1 mm), abundance and composition, associated to the oceanographic variabilities within the REBIO Arvoredo no-take using a 10-year time series data from 2014 to 2024.

MATERIALS AND METHOD

STUDY AREA

The Santa Catarina shelf is located in the transition zone between subtropical and temperate climates, according to updated in Köppen Brazilian climate map. The annual rainfall average is 1,600-1,900 mm and the ocean temperature varies seasonally (28°C to 14°C) throughout the year (CAPEL, 2012; ALVARES *et al.*, 2014). Being only 11 km from the coast, the Arvoredo MPA covers 160 km² which are 98 % underwater and only 2 % in land area; the islands of Arvoredo, Calhau of São Pedro, Deserta and Galés. The area is considered a transitional system and a boundary between tropical and temperate marine fauna (FLOETER *et al.*, 2008), where more than 1,600 marine and terrestrial species have already been recorded, including 26 endangered species (MISTURINI; SEGAL, 2017). The MPA provides a foraging, resting and recruitment environment for species that are important to the national fishing stock (BOELTER *et al.*, 2024).

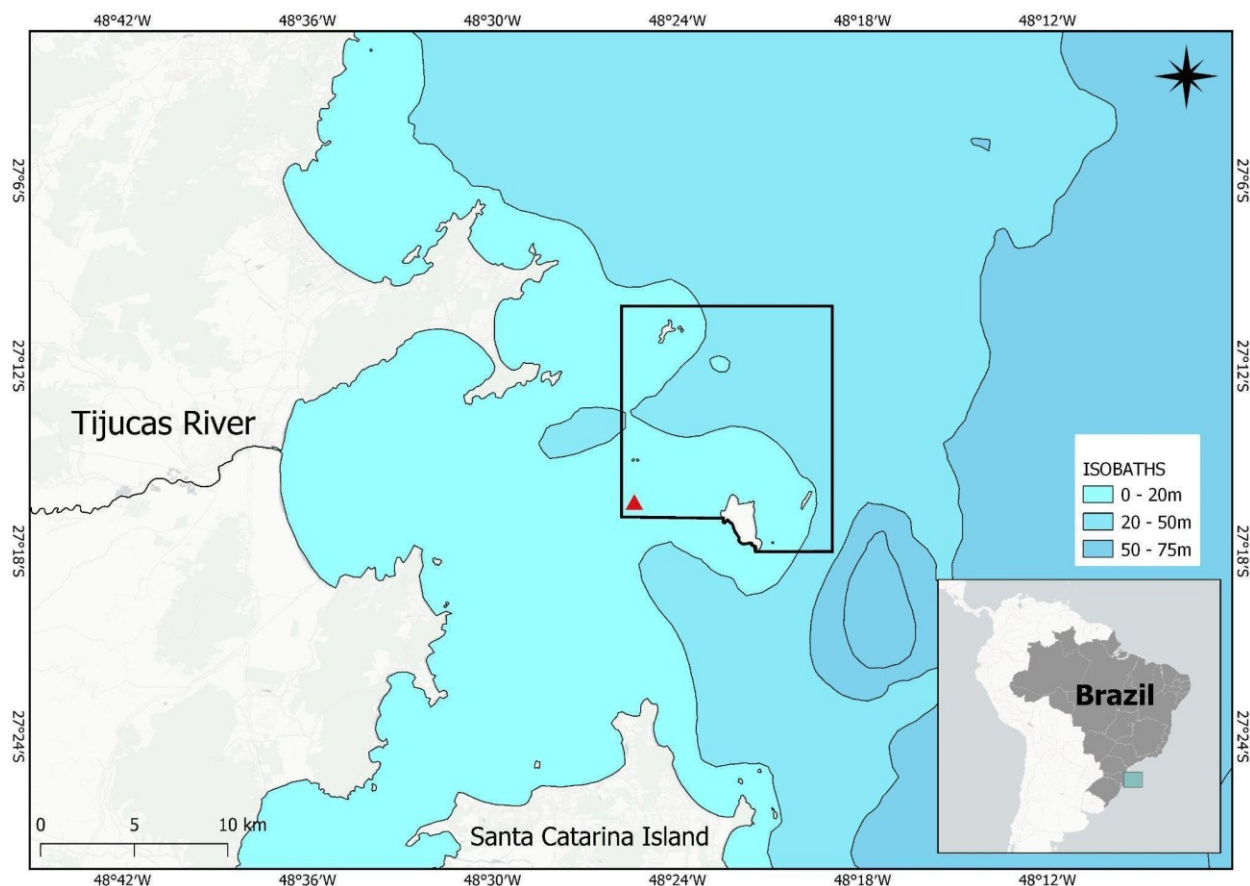


Figure 1. Study area. The black polygon represents the REBIO Arvoredo and the red triangle indicates the monitoring site.

Within the REBIO Arvoredo MPA, a monitoring sampling site was established based on the results of the Environmental Monitoring Project for the no-take Arvoredo Marine Protected Area (MAArE, <https://www.maare.ufsc.br/>) (2014-2016). It is located near Calhau of São Pedro Island in the southwestern point of the reserve (27° 16' S 48° 25' W) and has approximately 17 m of depth. Nutrient enrichment is provided by the SACW upwelling, PPW dispersal (BORDIN *et al.*, 2019), and the freshwater discharge of the Tijucas River (FREIRE *et al.*, 2017).

SAMPLING

A total of 27 plankton samples were obtained using a 200 µm net through horizontal surface tows. Six samples were acquired during the MAArE Project (MAArE,

<https://www.maare.ufsc.br/>) from 2014 to 2016, and 14 additional ones were collected as part of the Brazilian Coastal Monitoring System (SiMCosta; FRANZ *et al.*, 2021) between 2018 and 2019. Sampling was temporarily interrupted due to the COVID-19 pandemic and resumed with seven additional samples from 2022 to 2024.

Sea surface temperature and salinity was determined with a thermometer and refractometer. The depth of the euphotic zone (EUZ) was determined by the Secchi disk record depth multiplied by 2.7 (LUHTALA; TOLVANEN, 2013).

Seawater samples were collected using a Van Dorn bottle and processed through a controlled filtration system for subsequent analysis. Chlorophyll-a determination was performed using an AP-40 Millipore glass fiber filter (47 mm diameter, 0.45 µm pore size). The filtrates were then stored in a freezer for the analysis using the spectrophotometric method (GRASSHOFF *et al.*, 1999). The chlorophyll-a data was calculated by the samples acquired between 2014 to 2019 and provided by UFSC's partners from Marine Biogeochemical and Environment Education Laboratory.

PLANKTON SAMPLES PROCESSING

The plankton was sub-sampled using a Motoda splitter and the aliquots obtained from the fraction were scanned using the ZooScan Protocol (JALABERT *et al.*, 2022). Zooscan is designed to image plankton from 200 µm size. It includes a scanner and image processing software (Zooprocess). These images were uploaded in the EcoTaxa (ecotaxa.obs.vlfr.fr), which performs a semi-automatic classification by artificial intelligence that is further human-validated. This allows a quantitative analysis to determine abundance of each taxon, as well as size calculation of every particle (PICHERAL *et al.*, 2017). Copepods named as Calanoida in this study represent families that could not be identified by damaged or bad focus. All the scanned samples were submitted to a quality control where more than 70% met the criteria. The samples that didn't fit this criterion were plankton patches or had a low amount of organisms available for the fraction. The scanned samples are available on EcoTaxa (ecotaxa.obs.vlfr.fr) registered as "ZooScan_SWAtlantic_ArvoredomPA_siteBoia_SIMCosta_wp2 - Subset".

Exploratory analysis of images showed that besides the usual dominance of copepods, there was a remarkable presence of large cell diatoms of the genus *Coscinodiscus* in most of the samples. Zooscan resolution was not enough to distinguish the invasive *Coscinodiscus wailesii* (280s-500 μm) from the native *Coscinodiscus asteromphalus* Ehrenberg (1844) (80-400 μm) (TOMAS, 1997), which potentially were both captured by the 200 μm net. Therefore, the same samples were further processed through optical microscopy (OLYMPUS - 20x) using Tomas (1997) identification keys to identify the *Coscinodiscus* species. The quantification (cell/l) of the microphytoplankton followed Utermöhl (1958), with sedimentation chambers (2.973 ml), using an inverted microscope (OLYMPUSBX53) with an attached camera. It is noteworthy to say that the counting on the microscope was used as a proxy for the proportion of *C. wailesii* in the mesoplankton sampled by the net haul.

REMOTE SENSING

Satellite-derived oceanographic products were used to describe de meteo oceanographic regional features from January 2014 to December 2024. Monthly sea surface temperature (SST) data was acquired from the MODIS/Aqua sensor from January 2014 to December 2024 s at the sampling area. Daily wind components (northward and eastward) and sea surface wave Stokes drift and velocity components (northward and eastward) data have been conducted using E.U. Copernicus Marine Service Information; Global Ocean Daily Gridded Sea Surface Winds from Scatterometer and Copernicus Marine Service and Global Ocean Waves Reanalysis with a resolution of 12 km. A three-day moving average of the wind components and of sea surface wave Stokes drift and velocity components were calculated for short-term variability, considering the day before and the day after of each plankton sampling date.

Water masses were identified according to the thermohaline index of Möller (2008).

STATISTICS

The exploratory analysis of abundance, dominance (ind/m³, cell/L and percentage) and composition of copepods, *Coscinodiscus* spp., *C. wailesii* and *C. asteromphalus* using R (R Core TEAM 2021) was depicted in graphs. Abundance and composition (total and relative) of other mesozooplanktonic groups were graphically analyzed and are available as supplementary materials.

To access the relation of the *Coscinodiscus* species, copepods families and water/ air properties, Variance Inflation Factor (VIF), distance-based Redundancy Analysis (dbRDA) and Generalized linear models (GLMs) were performed.

The collinearity of the physical variables sampled *in situ* were tested using the Variance Inflation Factor (VIF) analysis. Variables with greater collinearity were removed from the analysis (BORCARD *et al.*, 2018). *In situ* Temperature, salinity, depth of euphotic zone, chlorophyll-a concentration and remote sensing Eastward Stokes drift component (m/s) and Northward Stokes drift component (m/s) displayed low collinearity (VIF < 10) and were chosen for further analyses.

The distance-based Redundancy Analysis (dbRDA) (BORCARD *et al.*, 2018) for plankton processed on Zooscan, was used to associate seasonal variation of *Coscinodiscus* spp. abundance and copepod (composition and abundance) with the meteoceanography properties. The analysis included the variables that had statistical significance with abundance of *Coscinodiscus* spp. (ind.m⁻³) and the abundance of the most abundant Copepoda families selected previously in the VIF criteria.

A F test with 9999 permutations was used to assess the relationship between the explanatory and response matrices. The abundance variables were logarithmically transformed ($\log(x+1)$), and the physical variables were standardized to remove the scale effect. The samples were associated by Bray-Curtis metrics and Lingoes were applied to correct negative eigenvalues.

Generalized linear models (GLMs) (ZUUR *et al.*, 2009) were applied using the glmTMB function (MAGNUSSON *et al.*, 2017) to predict *Coscinodiscus* spp. and Copepoda response to the environmental variables and seasonality.

The quantified number (raw data) of Copepoda and *Coscinodiscus* spp. was modeled as response variables, using a negative binomial distribution with quadratic parameterization and logarithmic link function (HARDIN; HILBE, 2018). The filtered volume of each sample was included as an offset to control for variation in sampling effort. Environmental variables were used as fixed predictors. The model selection considered only the predictors to the final models that had statistical significance with the response of Copepoda and *Coscinodiscus* spp. quantity (in *situ* temperature (°C), salinity, chlorophyll-a concentration, depth of the euphotic zone (m) and remote sensing Northward Stokes drift component (m/s). The suitability of the models were assessed by simulating the residuals using the DHARMA package (HARTIG; HARTIG 2017). Diagnostic graphics were also created to detect deviations from the expected (uniform) distribution (QQ-plot), to test normality (Kolmogorov-Smirnov), dispersion, and outliers. All the analyses were conducted using R (R Core TEAM 2021).

RESULTS

PLANKTON IMAGING

The plankton imaging results uncovered the non precedent quantification of *Coscinodiscus* spp. at REBIO Arvoredo waters among organisms larger than 200 µm.

Coscinodiscus spp. was the dominant plankton in 44% of the samples, with greater dominance in the autumns. It reached the maximum relative abundance in June 2018 with 92%, contrasting to the low contribution (3 %) of Copepoda (Figure 2). From 2014 to 2016, *Coscinodiscus* spp. exhibited contributions lower than 25%, while Copepoda had always the greatest contribution. In 2018 and 2019, all the seasons were sampled, *Coscinodiscus* spp. and Copepoda alternated the relative abundance, with similar figures in months sampled in both years. In both these years, February and April to July were dominated by the diatom (up to ~90 %) while March, September and December by the copepods (up to ~ 65%). In 2024, *Coscinodiscus* spp. exhibited a dominance of 84% in June, as higher percentages in 2018 and 2019. In 2022 and 2023 the pattern of dominance of September and August shifted to *Coscinodiscus* spp. It is

noteworthy that *Coscinodiscus* was absent in December 2018, when copepods and other zooplankton taxa composed the mesoplankton (Fig S1, S2, S3).

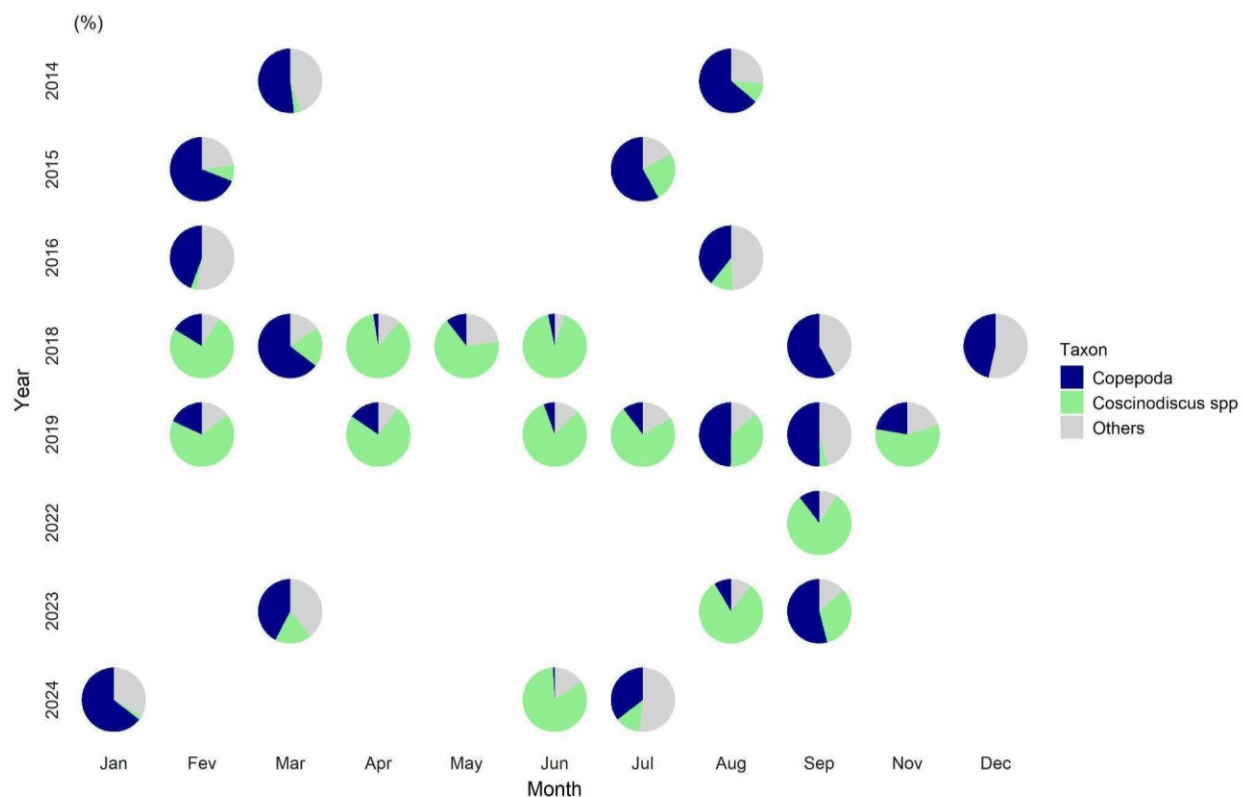


Figure 2. Relative abundance (%) of *Coscinodiscus* spp., Copepoda and other mesoplankton taxa at the REBIO Arvoredo MPA between 2014 and 2024.

Abundance heat map indicated high values of *Coscinodiscus* spp. in 2018 and 2019, with a huge value recorded in June 2024, reaching 123,292.2 ind.m⁻³. In general, *Coscinodiscus* spp. highest abundance was synchronized with the dominance of the diatom at the samples. As registered in February 2018 (13,270.1 ind.m⁻³), April 2018 (19,395.5 ind m⁻³) and June 2019 (25,724.2 ind.m⁻³), i.e. summer and autumn (Figure 3).

Copepoda higher abundance were registered in the initial years of the time series, in August 2014 (3,674 ind.m⁻³), and February 2015, 2016 and 2018 (5,055.7 ind.m⁻³, 3,5345.4 ind.m⁻³ and 2,888.7 ind.m⁻³) i.e. summer and winter.

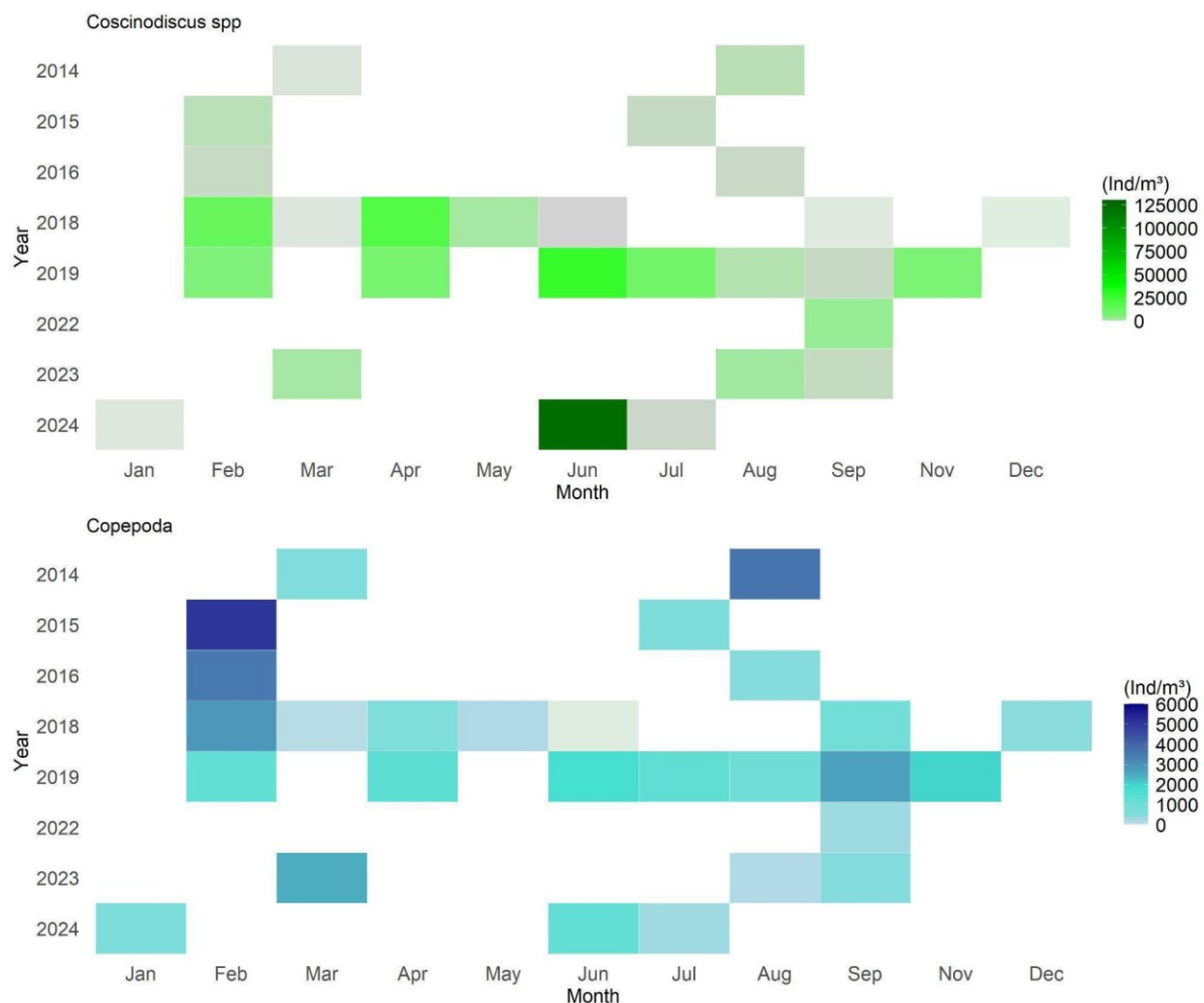


Figure 3. Abundance (ind.m^{-3}) of *Coscinodiscus* spp. and Copepoda at the REBIO Arvoredo no-take between 2014 and 2024.

Temoridae presented high values in 2015 and 2016 summers ($2,240 \text{ ind.m}^{-3}$ and $1,735 \text{ ind.m}^{-3}$) when it was dominating the plankton (Figure 4). However, the high Temoridae abundance in 2018 February ($2,238.8 \text{ ind.m}^{-3}$), was reached under the *Coscinodiscus* spp. dominance (75 %). Afterwards no family reached this range, even Temoridae that returned to be dominant after 2023, had low values.

Either way, Calanoida dominated in winter 2014 to 2016 (from 923.8 ind.m^{-3} to 98.7 ind.m^{-3}) in all 2019, and at 2023 spring with values lower than 200 ind.m^{-3} (Figure 4). There were peaks of other copepods families, Oithonidae in winter 2014 (138 ind.m^{-3}) and 2016 (77.2 ind.m^{-3}), Coricaeidae in summer 2015 and 2016, in autumn and winter

of 2019 and in June of 2024, Oncaeidae in 2014 winter (435.3 ind.m⁻³) and Calanidae in autumn of 2019 (301.2 ind.m⁻³) (Figure 5).

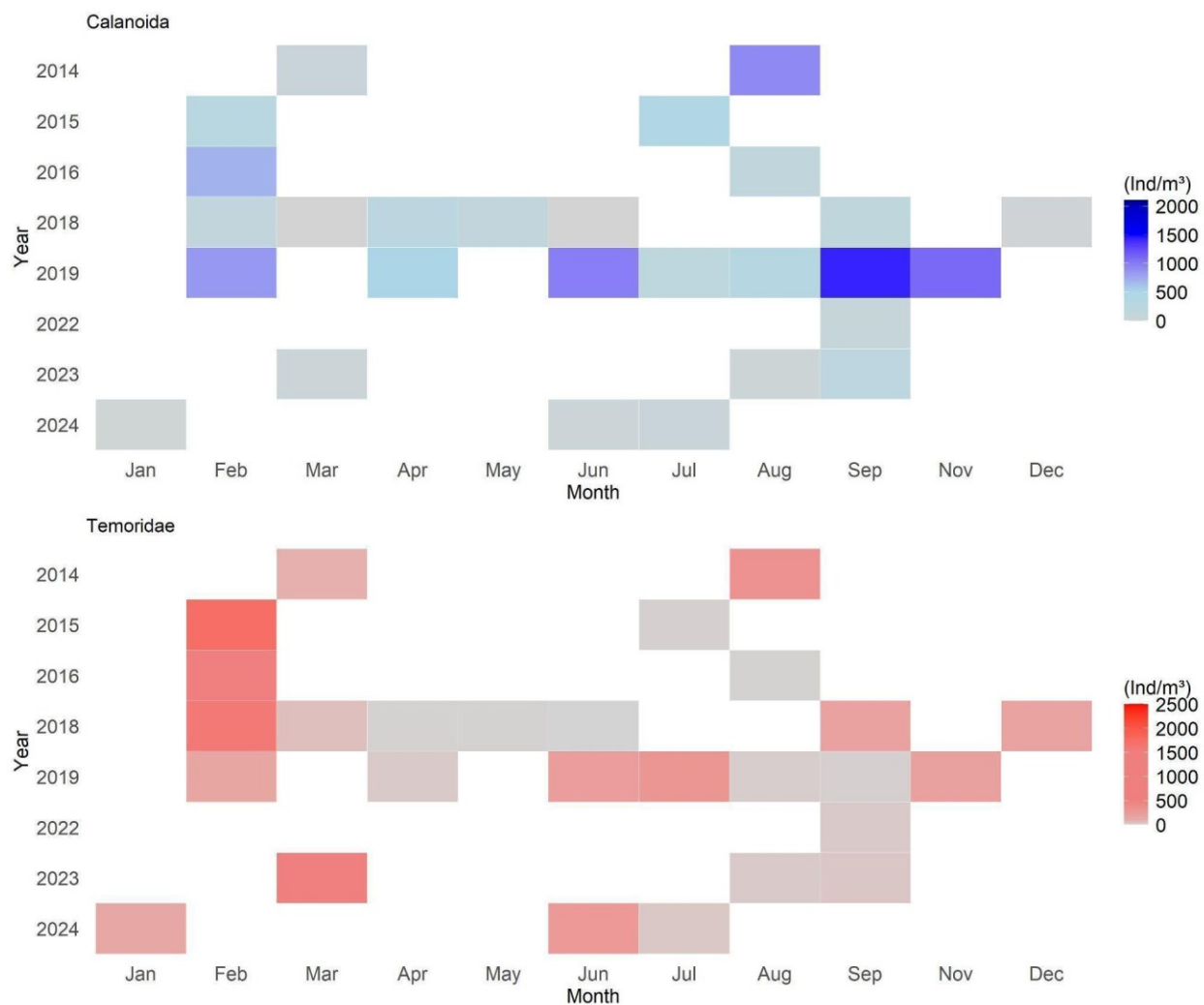


Figure 4. Abundance (ind.m⁻³) of the copepods Temoridae and Calanoida at the REBIO Arvoredo between 2014 and 2024.

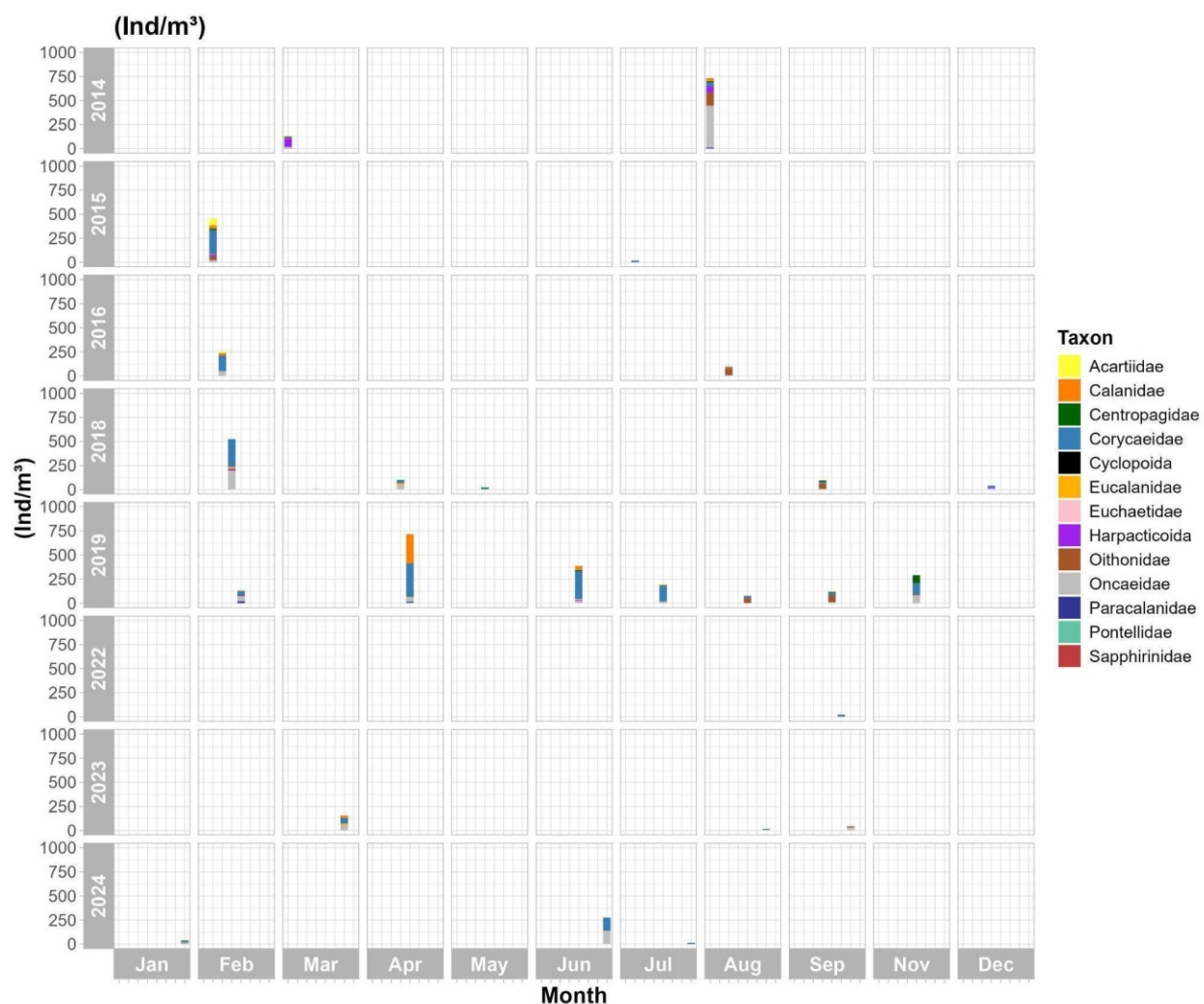


Figure 5. Abundance (ind.m^{-3}) of Copepoda families, except for Temoridae and Calanoida, at the REBIO Arvoredo between 2014 and 2024.

PLANKTON OPTICAL MICROSCOPY

Coscinodiscus asteromphalus was dominant in June to November from 2014 until 2019 (early winter to late spring) while the invasive *C. wailesii* dominated from February to May (late summer to autumn) from 2018 to 2023. Both species were equally present from June to October in 2023 and 2024. *Coscinodiscus* spp. was not registered in December 2018 and according to the taxonomic table (Tab. S1a to S1e) the

cyanobacteria *Trichodesmium erythraeum* appeared in the area.

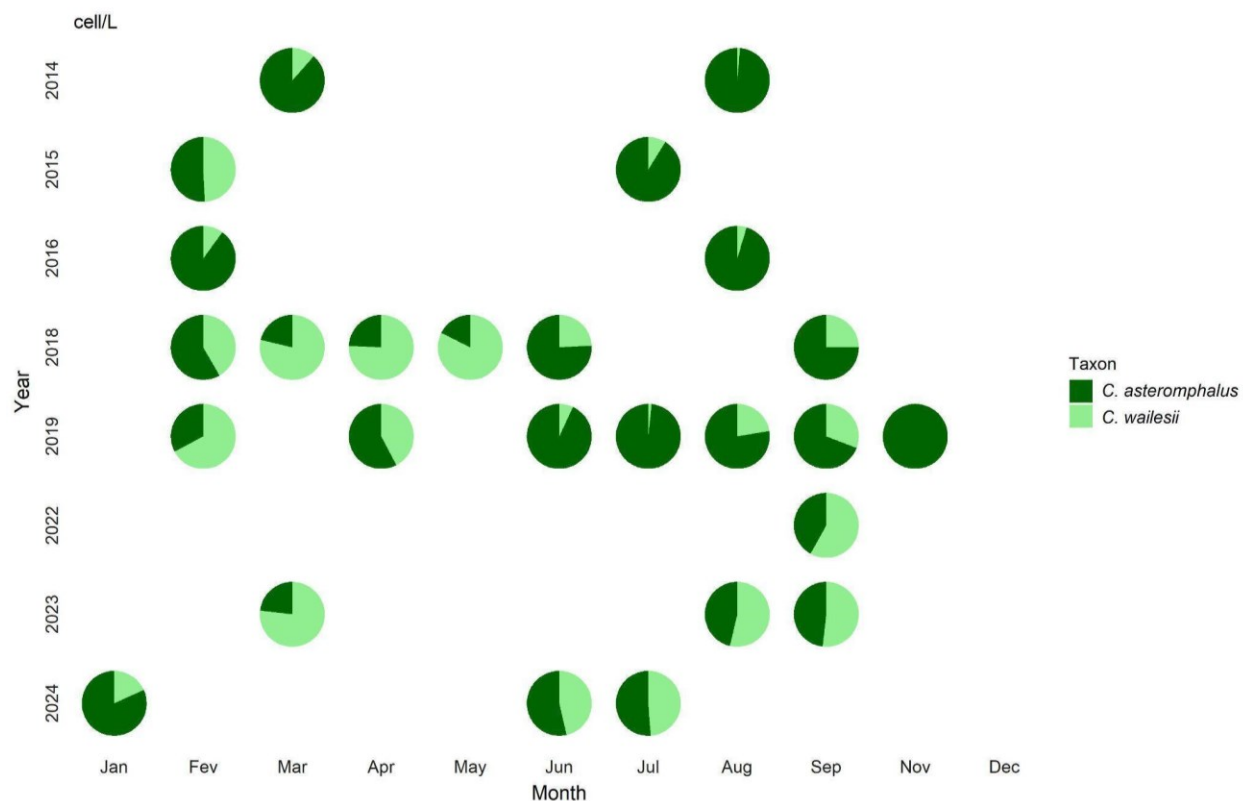


Figure 6. Relative abundance of *C. asteromphalus* and *C. waillesii* at the REBIO Arvoredo between 2014 and 2024. Quantitative analysis in the microscope (cell/L) was a proxy of the occurrence in the net hauls.

Coscinodiscus median ranged from 0.30 to 0.45 mm while copepods median ranged from 0.45 to 0.75 mm. Larger cells were registered in months with *C. waillesi* dominance. From 2018 to 2019 a trend of larger cells was observed from February to May, accompanied by a decrease in size from June to September, alongside an increase in the contribution of *C. asteromphalus*. In general, there was a decrease in size of *Coscinodiscus* spp. after a month of high abundance, as June/ July in 2019 and 2024, April/May of 2018. The largest copepods were registered together with their dominance, i.e. under lower presence of *Coscinodiscus*, with the exception of July 2024 Fig. S1.

REMOTE SENSING

SEA SURFACE TEMPERATURE (SST)

The SST monthly average dataset from 2014 to 2024, exhibited minimum values of 17°C in June 2016, 19 °C in June 2018 and 17 °C in 2024 July (Figure 7). Temperatures peaked reaching 28°C in 2016 and 2017 Januarys and 27°C in 2015, 2016 and 2019, 28°C in 2024 during Februarys (Figure 8). Interannual variability was evident in both summer and winter months throughout the study. For instance, the SSTs recorded in January and June of 2016, January (26 °C) and July (17°C) of 2018, and January (27°C) and July of 2024 (17°C) demonstrate yearly changes that occur independently of the typical seasonal cycle.

These SST time series also revealed the lowest temperatures recorded through summer and autumn months. In February and March (26°C), April (25°C) and May (23°C) 2018. The same year when the abundance of *C. wailesii* started to be noticed, contributing more than 40% to the plankton. Considering the February months sampled in this study, in February 2018, the abundance of Copepoda showed a great value (2,888.7 ind.m⁻³), considering the *Coscinodiscus* spp. dominance (75%) (Figure 3).

The huge *Coscinodiscus* spp. abundance (123,292.2 ind.m⁻³) in June 2024 occurred at 20°C, whereas the second higher abundance occurred in June 2019 at 22°C.

The average monthly temperatures throughout the spring season exhibited the coldest value in September of 2019, with 19°C, and the highest Copepoda abundance of these season (868 ind.m⁻³). In the spring of 2018 (September and December) 20°C and 24°C, in that scenario *Coscinodiscus* spp. hardly appeared, representing less than 5% of the samples, when cyanobacteria *Trichodesmium erythraeum* appeared in the area.

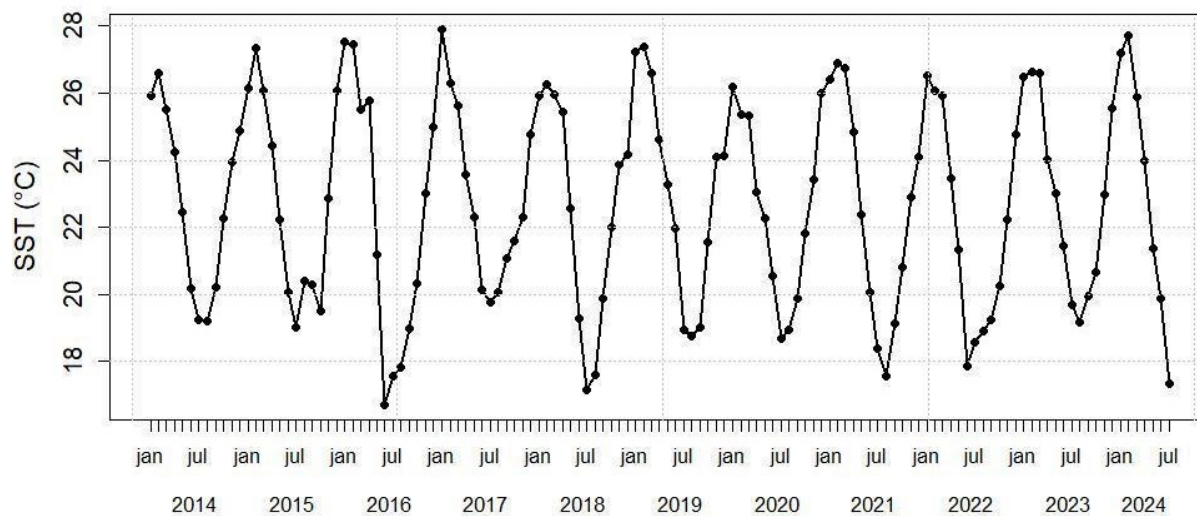


Figure 7. Time series of sea surface temperature (SST) in °C obtained with the MODIS/Aqua sensor, running through January 2014 to 2024.

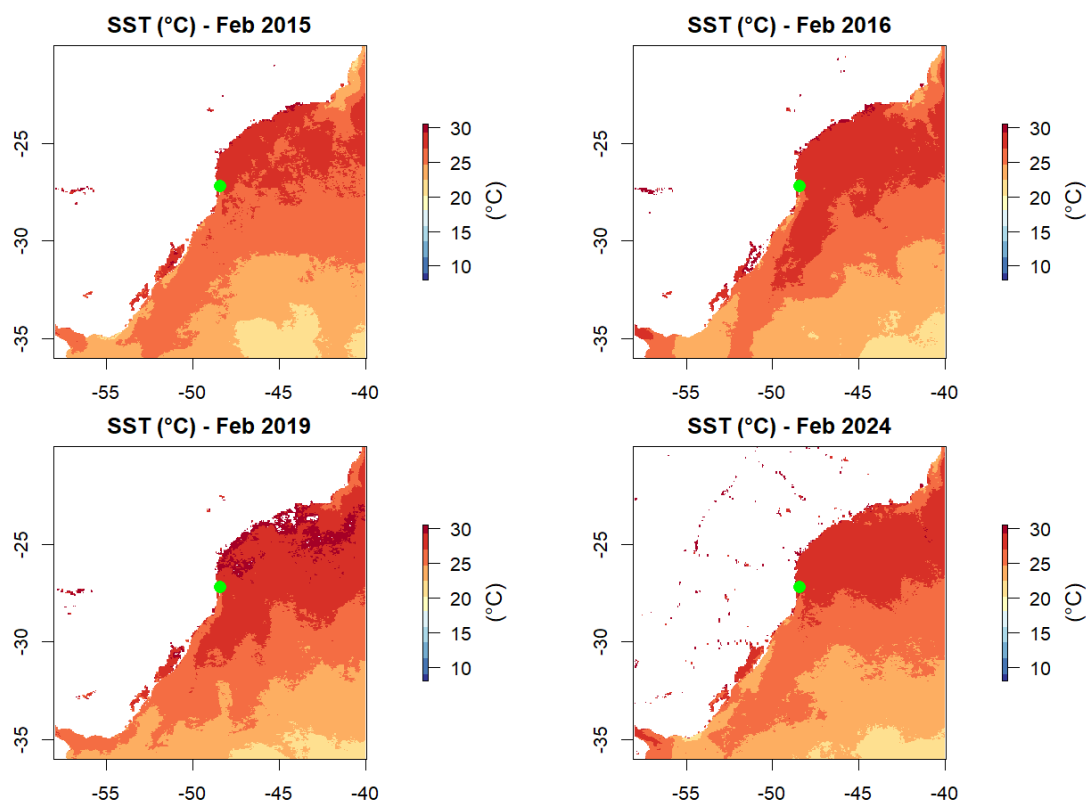


Figure 8. Sea surface temperature (SST) in °C from the MODIS/Aqua sensor in February 2015, 2016, 2018 and 2019 from the Santa Catarina continental shelf. The green dot indicates the sampling station.

The remote sensing images of the monthly SST data indicated the influence of the PPW plume in the region in 2016, 2018, 2019 and 2024 winters (Figure 9). However, the images do not provide direct evidence of the upwelling of the SACW on the surface. The complete set of images for each month in the time series is available in Appendix A.

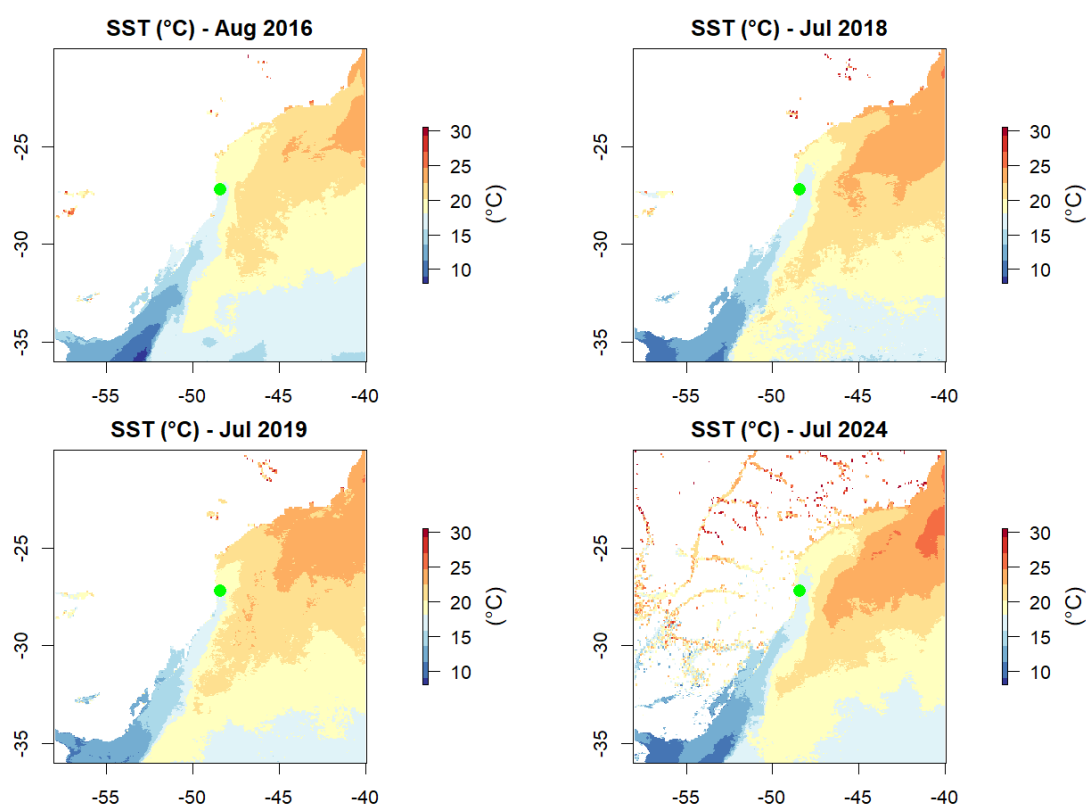


Figure 9. Horizontal distribution of monthly sea surface temperature (SST) in °C from the MODIS/Aqua sensor in August of 2016, July of 2018, July of 2019 and July 2024 from the Santa Catarina continental shelf. The green dot indicates the sampling station.

WIND

Eastward winds were the most consistent feature in the dataset. Copepod low abundance, but still dominant, occurred under intermediate W/SW winds of March 2014 and 2019, while high abundances occurred in February 2016 and March 2023 under frequent and contrasting winds of NE and SW (Figure 10).

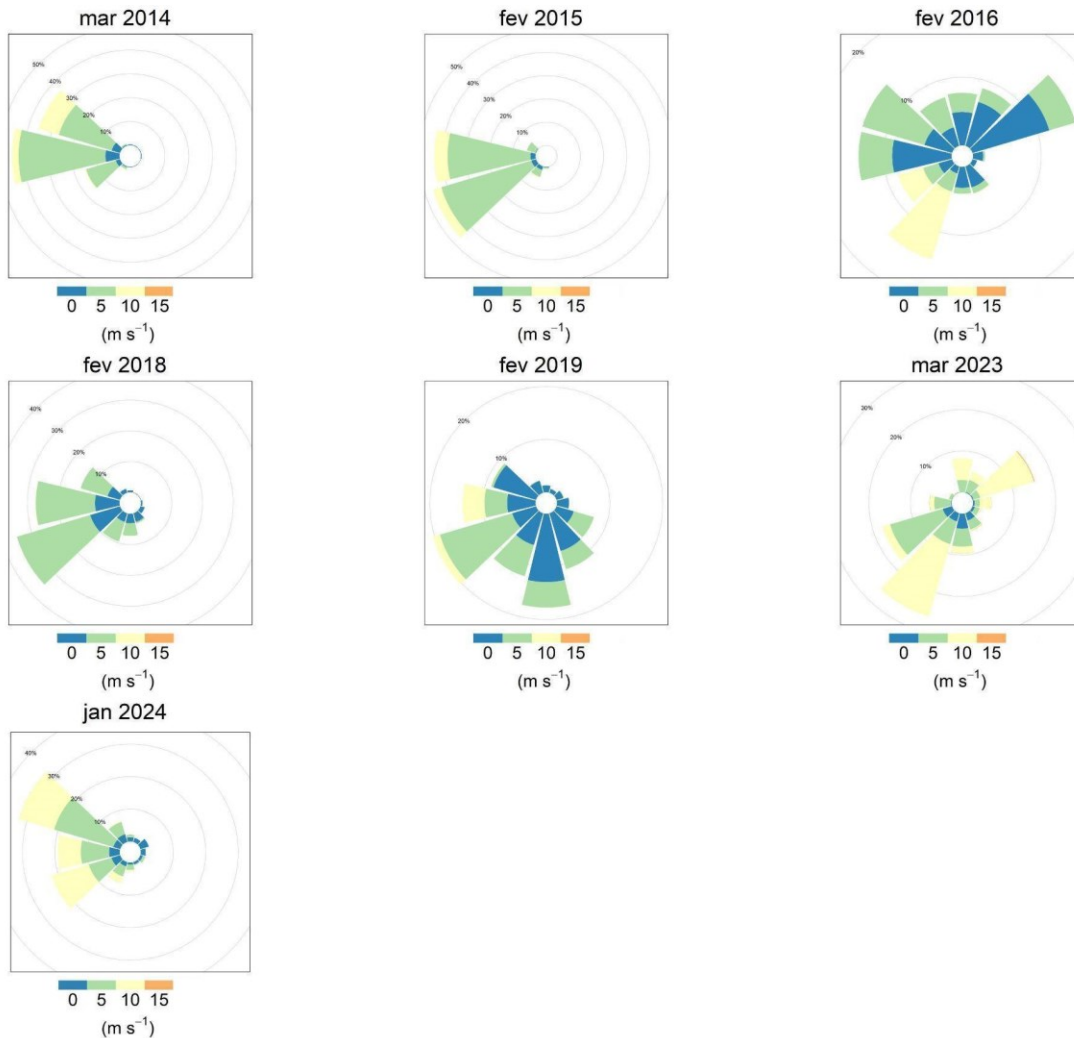


Figure 10. Wind intensity and direction in summer (2015, 2016, 2018 2019 February, 2014, 2018, 2023 March and 2024 January). Each graph shows the relative frequency (%) of wind direction and intensity (m/s).

Wind was unstable in June 2018 with strong and frequent S winds, when the lowest *Coscinodiscus* spp. abundance was recorded (97.1 ind.m⁻³). Under strong WE/NE wind of June 2019 and constant S/NE wind of June 2024, there were the highest *Coscinodiscus* spp. abundance (31,421.6 ind.m⁻³ and 147,473.5 ind.m⁻³) (Figure 11).

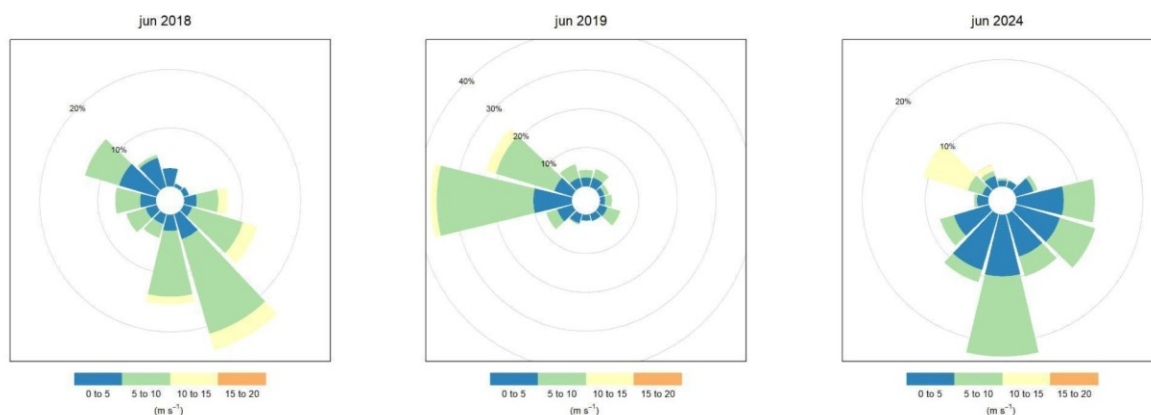


Figure 11. Wind intensity and direction in autumn (2014, 2018, 2019 June). Each graph shows the relative frequency (%) of wind direction and intensity (m/s).

During July (Figure 12), the S/SW winds were intermediate and frequent, occurring together with the huge decrease of *Coscinodiscus* spp. dominance.

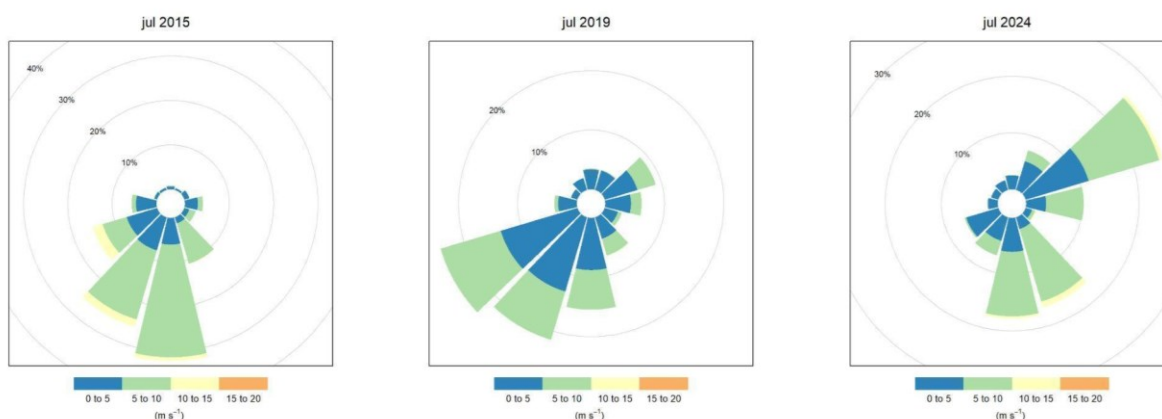


Figure 12. Wind intensity and direction in winter (2015, 2019, 2024 July). Each graph shows the relative frequency (%) of wind direction and intensity (m/s).

Spring had similar W/NE/S winds, when Copepods were dominant. December 2018 S/NW winds predominated alongside the *Trichodesmium erythraeum* presence (Figure 13).

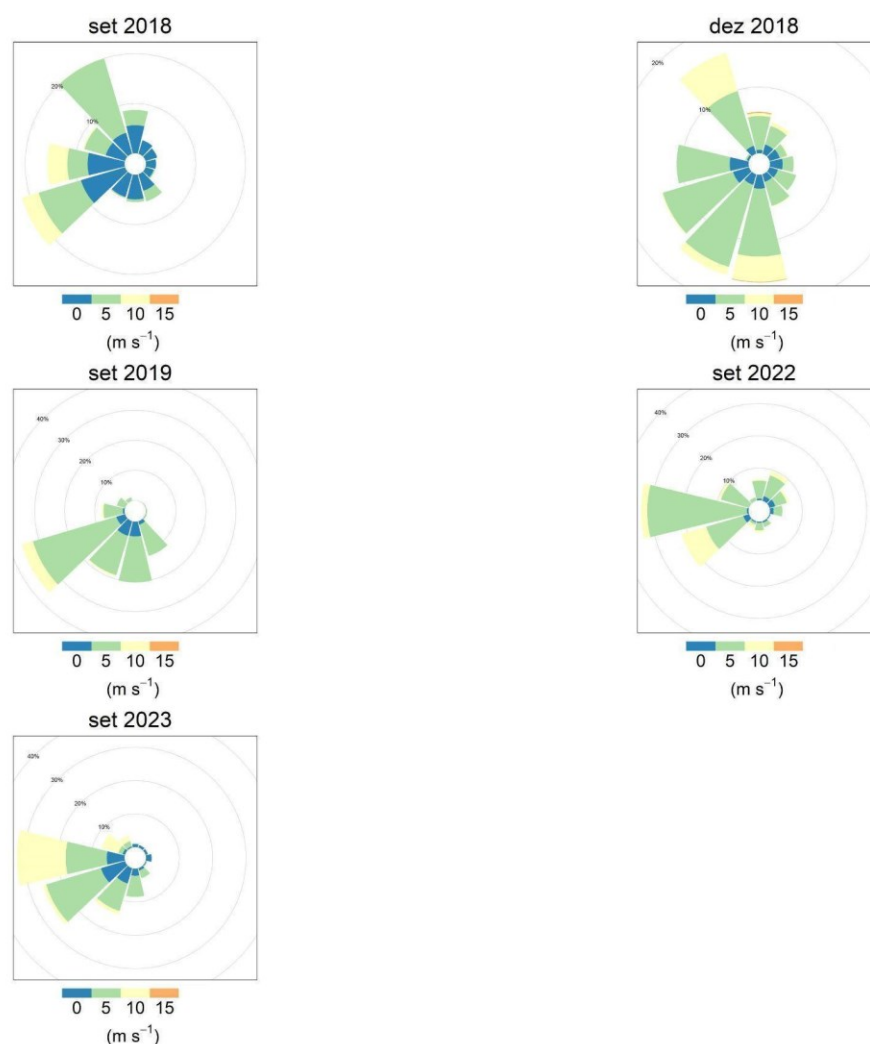


Figure 13. Wind intensity and direction in spring (2018, 2019, 2022, 2023 September) and early summer (2018 December). Each graph shows the relative frequency (%) of wind direction and intensity (m/s).

The wind intensity and direction monthly graphs from 2014 to 2014 are available in the Appendix B.

STOKES DRIFT

Stokes drift presented seasonal and interannual variability of Stokes drift direction and magnitude from 2014 to 2024. Overall, a consistent predominance of eastward-directed drift was observed across most seasons and years. Northward directed drift

events, though less frequent, were notable during winter 2019 and springs of 2018 and 2019 coupled with the decrease of *Coscinodiscus* spp. (Figure 14).

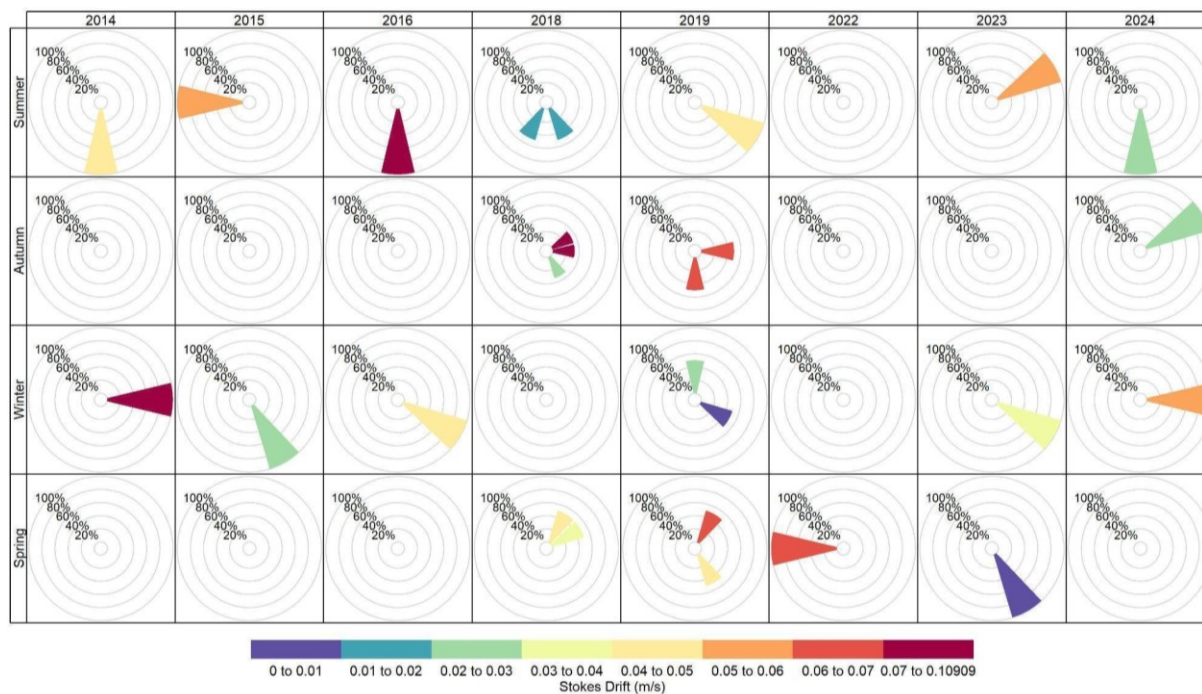


Figure 14. Seasonal variation of Stokes drift direction and intensity from 2014 to 2024. Each panel represents the directional distribution of Stokes drift for a specific year and season. Each graph shows the relative frequency (%) of Stokes drift direction and intensity (m/s).

RELATIONSHIPS WITH ENVIRONMENTAL DESCRIPTORS

The distance-based Redundancy Analysis (dbRDA) (Figure 15) described the distribution of *Coscinodiscus* spp. (ind.m⁻³) and the most abundant Copepoda families according to the environmental variables. The environment variables explained 33.2% of the abundance of *Coscinodiscus* spp. (ind.m⁻³) and the most abundant Copepoda families ($F = 1.4055$, $p = 0.03824$).

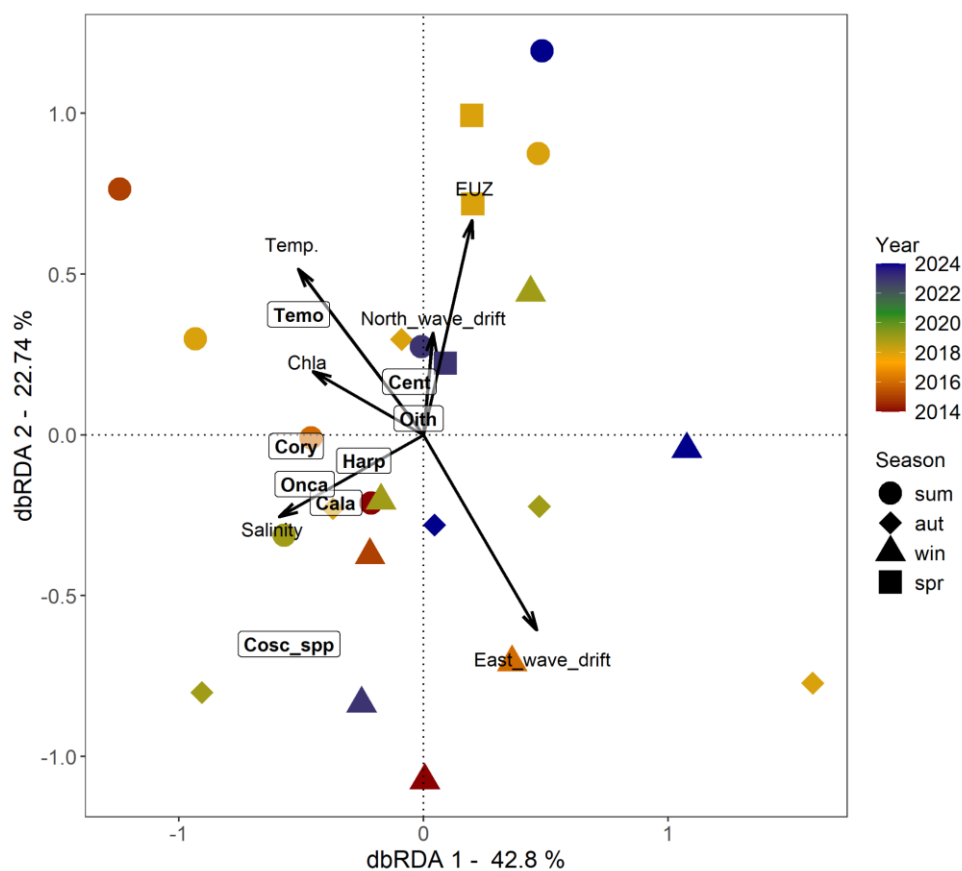


Figure 15. Distance-based Redundancy Analysis (dbRDA) obtained with *Coscinodiscus* spp. (ind.m⁻³) and the most abundant copepoda families analyzed in the image system Zooscan/EcoTaxa. Biological components represented by abbreviations (Cosc_spp. = *Coscinodiscus* spp. (ind.m⁻³), Cala = Calanidae (ind.m⁻³), Onca = Oncaiedae (ind.m⁻³), Cory = Corycaeidae (ind.m⁻³), Temo = Temoridae (ind.m⁻³), Cent = Centropagidae (ind.m⁻³), Oith = Oithonidae (ind.m⁻³) and Harp = Harpacticoida (ind.m⁻³). Environmental vectors were represented by Temp = *in situ* temperature (°C), EUZ = *in situ* euphotic zone (m), Chla = *in situ* chlorophyll-a (ugL) and remote sensing data Eastward_wave_drift = Eastward Stokes drift component (m/s) and Northward_wave_drift = Northward Stokes drift component (m/s). Seasons were represented by symbols. Colorbar encompasses sampling in each year.

The first canonical axes (dbRDA 1, 42.8% of the explained variance) had a positive association with the eastward Stokes drift component, in opposition to high temperature, chlorophyll-a and salinity associated mainly with summer samples. The second canonical axis (dbRDA 2, 22.74% of the explained variance) mostly described by the high temperature in summer, deeper euphotic zone, northward Stokes drift component, in opposition to the eastward Stokes drift component, higher salinities and lower temperature of winter and autumn. In contrast to northward Stokes drift component, influenced by lower salinities during spring and winter. While Temoridae was related to high temperature and summer, the occurrence of Oncaiedae, Calanidae, Harpacticoida and Corycaeidae in higher salinity circumstances. Moreover, the abundance of Oithonidae and Centropagidae is linked with northward strokes wave drift, whereas *Coscinodiscus* spp. is to autumn and winter.

The Generalized linear mixed models (GLMs) showed *Coscinodiscus* spp. exhibited a significant positive relationship with salinity levels (GLM: $p < 0.05$) (Figure 16a). Conversely, *Coscinodiscus* spp. quantity decreased under high temperature, northward Stokes wave and Chlorophyll-a concentration (GLM: $p < 0.05$) (Figure 16b, c and d).

A positive and significant relationship (GLM: $p < 0.05$) was disclosed with Copepoda, temperature and the depth of the EUZ (Figures 16e and f). Complementary information from GLM analysis are in Supplementary Material (Table S2).

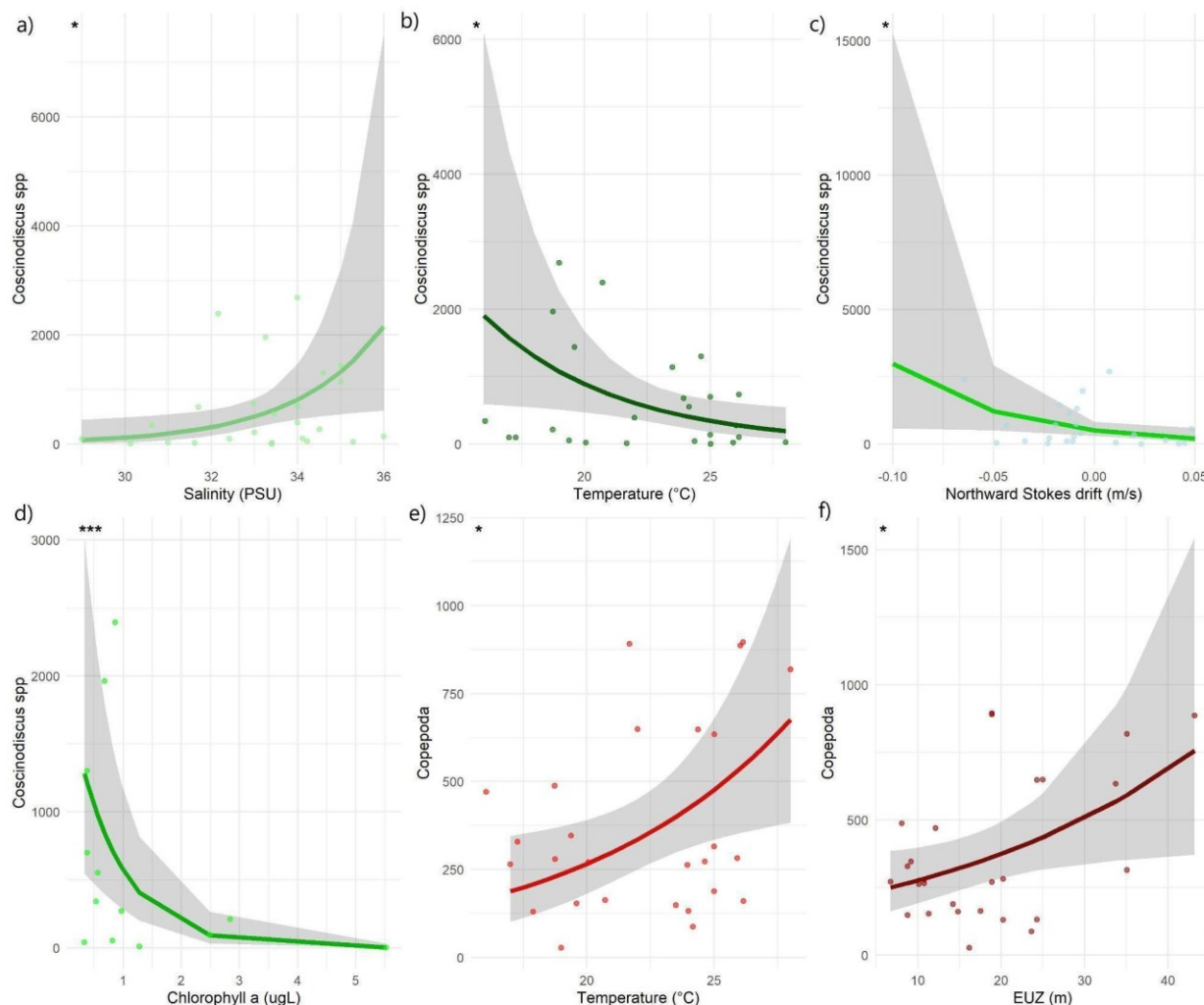


Figure 16. Generalized linear mixed models (GLMs) results from the relationship between *in situ* temperature (°C), salinity, chlorophyll-a (ugL), euphotic zone depth (EUZ, m) and the remote sensing northward strokes wave drift (m/s) with *Coscinodiscus* spp. (ind), Copepoda (ind) raw abundance. Linear regressions (lines); confidence intervals (shaded area); statistical significance (***) $p < 0.001$; ** $p < 0.01$; * $p < 0.05$).

DISCUSSION

The assessment of *Coscinodiscus* spp. in larger quantities than copepods, sampled in 200 μ m nets in the upper layer of the inner shelf waters, was possible due to the new technology approach of imaging plankton. This finding, suggests a complementary scenery to the role of huge diatoms in the ecosystem. Copepods and *Coscinodiscus* alternated their dominance with a strong seasonal trace suggesting

different ecosystems functioning in very complex and dynamic environmental conditions. The occurrence of the invasive *Coscinodiscus wailesii* in the no-take Arvoredo Marine Protected Area was indeed underestimated by the traditional phytoplankton previous analysis methods.

Over the last decade (2014–2024), the planktonic community of the REBIO Arvoredo has been subjected to marked seasonal and interannual variability, driven by fluctuations in water mass distribution, associated with nutrient dynamics. Higher average SST registered in 2015, 2016, 2019 and 2024 in summer indicating the presence of the warm TW in the surface layer may be associated occasional intrusions of nitrate-rich SACW into the intermediate/bottom layers influencing nutrient fluxes (MENEZES *et al.*, 2019; BORDIN *et al.*, 2019). The interannual yearly changes in SST are consistent with the 2015–2016, 2018–2019, and 2023–2024 ENSO events (NOAA, 2015, 2025; BATISTELA, 2023; MENEZES *et al.*, 2024), introducing broader climatic anomalies, increasing rainfall during austral winter over the Plata basin (HIRATA; GRIMM, 2016), particularly in 2016, 2018, 2019, and 2024 winters, the registered influence of PPW at the MPA (SILVA; GARCIA, 2021).

Within the copepod community, a clear seasonal pattern emerged. The Temoridae, characterized by an omnivorous-herbivorous diet (BENEDETTI *et al.*, 2016) and high tolerance to elevated temperatures (BOLTOVSKOY, 1981; TSENG *et al.*, 2011), dominated the assemblage during summer months strongly associated with SACW intrusions periods. In particular, *Temora turbinata* Dana (1849-1852), an invasive species described as one of the dominant copepods in REBIO Arvoredo that relies on phytoplankton as an important food resource (MENEZES *et al.*, 2019), had a seasonal dominance reported among the few species in shallow areas of the MPA when the SACW intrusion was registered to 50 m isobath in 2015 and ~30 m in 2016 (MENEZES *et al.*, 2024).

A notable decline in overall copepod abundance through autumn months were coupled to the presence of omnivorous-herbivorous Calanidae, omnivorous-detritivorous Oncaeidae, carnivorous Corycaidae and the late return of Temoridae at the ending of this season. Carnivores tend to be more dominant in nutrient-poor conditions, while herbivores and omnivores tend to be dominant in productive environments (BENEDETTI

et al., 2018) indicating a functional diversity at this community to reinforce a resilient copepod response in the face of environmental transitions (ZHANG *et al.*, 2022; MENEZES *et al.*, 2024).

The cold PPW influence around Arvoredo MPA favored Oithonidae (omnivorous) and Oncaeidae. This plume is characterized by low temperature and salinity, high silicate concentration and both dissolved and particulate organic material (CIOTTI *et al.*, 1995; FONTES *et al.*, 2018). Its trophic structure is associated with dinoflagellates (heterotrophic and mixotrophic), with high chlorophyll-a concentrations at the Arvoredo MPA, indicating eutrophic conditions (BATISTELA, 2023). Dissolved organic carbon converted into particulate organic carbon by nano and picoplankton (AZAM *et al.*, 1983) suggests the occurrence of the microbial trophic structure (FONTES *et al.*, 2018; SILVEIRA 2022; POMEROY *et al.*, 2007; PORTER *et al.*, 1985). The dominance of small-size omnivores in the subtropical coastal areas with estuarine influences is a well-established pattern due to their ability to exploit smaller particles like nanoplankton, contributing to transfer microbial-derived energy through the classical food web (TURNER, 2004).

A seasonal pattern observed in the *Coscinodiscus* community as well, represented by the recurring autumn dominance of *Coscinodiscus* spp. coupled with these diatoms patches in June of 2019 and 2024. These observations are consistent with prior observations of *C. wailesii*, in the SBB at this season (FERNANDES and BRANDINI, 2004; TALGATTI *et al.*, 2010). The diatoms abundance peaks coincided with intense WE/NW winds (10-15 m/s) and intermediate temperatures, (20°C and 22°C) contributing to water column mixing (MATSUURA, 1986; CASTRO *et al.*, 2006), which causes the resuspension of *Coscinodiscus* spp. that survived in the shelf sediments (SMETACEK, 1985; LEWIS *et al.*, 1999). Moreover, the large size and heavily silicified frustules of these big diatoms pose grazing limitations for most mesozooplankton species (RÖRIG *et al.*, 2018) favoring their proliferation.

Despite these limitations, certain species are capable of exploiting *Coscinodiscus* spp. through selective feeding strategies. The copepod *Temora longicornis* Müller, 1785, found in Northern Hemisphere waters, can pierce the frustule and ingest only the internal cellular content of *C. wailesii* (JANSEN, 2008). Similarly, brachyuran zoeae, including

Aratus pisonii Milne Edwards, 1837, and shrimp species such as *Artemesia longinaris* Bate, 1888, and *Trachypenaeus constrictus* Stimpson, 1871 have been reported feeding on *Coscinodiscus* spp. and the invasive diatom along the Brazilian coast (DE SOUZA-MOSIMANN *et al.*, 1993; SCHWAMBORN *et al.*, 2006). Additionally, the anchovy *Engraulis anchoita* (HUBBS; MARINI, 1935), a typically zooplanktivorous species, has been shown to shift its diet toward *Coscinodiscus* spp. depending on local availability (MAZZETTI, 1984; ESPINOZA, 2014; DO SOUTO *et al.*, 2025). These observations suggest that multiple trophic pathways mediate the transfer of these diatoms nutritional content (C:N:P ratio ~106:15:1.3; TADA *et al.*, 2000), although the role of these pathways within this MPA remains unclear.

The decline in *Coscinodiscus* spp. abundance with PPW expansion into REBIO Arvoredo, alongside northward Stokes drift and S/SW winds, suggests possible dispersion of *E. anchoita*, other predators, and the diatoms themselves. *E. anchoita* larvae and eggs have been associated with PPW in South Brazil, influenced by interannual variation driven by ENSO events (DE MACEDO-SOARES *et al.*, 2014). ENSO can influence plankton, particularly fish larvae, spawning patterns, food availability, and transport (FRANCO-GORDO *et al.*, 2008), especially when coupled with continental output. Additionally, Stokes drift has been demonstrated to enhance the physical transport of meroplanktonic and fish larvae, along with phytoplankton (SHANKS, 1988; OMAND *et al.*, 2011; SHANKS *et al.*, 2014; FRANKS *et al.*, 2020). However, how the organic matter produced by the large *Coscinodiscus* spp. cells are transferred to higher trophic levels, and the ecological role they have on the food web of the MPA still remains unclear. Further research is required to comprehensively understand the *Coscinodiscus* spp. effect in this ecosystem. Moreover, previous studies registered the dominance of *Thalassiosira* spp. and dinoflagellates during PPW influence at the REBIO Arvoredo MPA (TRANKER, 2021) suggesting microbial trophic conditions (AZAM *et al.*, 1983). Ambient conditions such as trophic structure, wind-induced water turnover and average SST < 20°C may boost sinking rate of the large *Coscinodiscus* spp. (BIENFANG and HARRISON., 1984) towards a benthic regeneration (BRANDINI *et al.*, 2014).

Traditional phytoplankton investigations within the REBIO Arvoredo have also consistently documented the presence of *Coscinodiscus* species. Tranker (2021)

reported *Coscinodiscus* spp. frequencies of 59 % in summer and 54 % in winter between 2014 and 2016. And revealed an increase in surface water phytoplankton densities within PPW influence. Summer and winter 2014 and 2015 registered $\sim 20 \times 10^3$ cells/L, while there was an increase to 40×10^3 cells/L and 60×10^3 cells/L in summer and winter 2016.

However, direct quantitative comparisons of absolute abundances between water samples collected with bottles (SOURNIA, 1978) and net sampling methods are not viable due to their inherent methodological differences. Investigations involving discrete water bottles samples, and analyzed via inverted microscopy, provided valuable insights into this phytoplankton community composition (UTERMÖHL, 1958). Bottle samplers are effective in capturing the overall phytoplankton assemblage from a limited, discrete volume (VERLECAR; DESAI, 2004). While 200 μ m tow nets, filter larger volumes over a determined trajectory, velocity and sampling effort (BOLTOVSKOY, 1981), increasing the probability of capturing rare or patchily distributed large cells. In the present study, the imaging plankton approach, using 200 μ m net surface horizontal tows, sampling around 50 m³ in three minutes, revealed *Coscinodiscus* spp. abundances comparable to, or even exceeding, those of copepods. This finding aligns with observations from imaging plankton researches that utilized 200 μ m net surface horizontal tows sampling methodology throughout three Atlantic transects (U.K. – Malvinas 1997, Malvinas – U.K. 1997, and South Africa – U.K. 1998) (e.g., WOODD-WALKER, 2001) and a recent work in the nearby shelf (SILVEIRA, 2025), suggesting that integrating a multi-methodological approaches can complement traditional methodology to expand the understanding of the ecological role of large diatoms like *C. waillesii*. within plankton communities.

Alongside imaging-based methodologies, remote sensing offers crucial insights into the environmental conditions shaping plankton distribution in the REBIO Arvoredo MPA. Remote sensing processing mesoscale oceanographic data, such as SST, wind and Stokes drifts, enlightened the environmental context (PIERI *et al.*, 2023), with the seasonal and interannual patterns and the specific plankton patches, such as *Coscinodiscus* spp. and *Trichodesmium erythraeum* under warmer, wind-influenced conditions, occurrences.

Considering the case of *Trichodesmium erythraeum*, it patched in a nitrogen-fixing state in December 2018 coinciding with a intense N/NW winds (10-20 m/s) period

transporting nutrient-rich freshwater from the Tijucas River. These conditions, coupled with higher temperatures, 24.2°C, created an optimal scenario that likely triggered the *T. erythraeum* patch (BOATMAN *et al.*, 2017; RÖRIG *et al.*, 2018).

Zooplankton monitoring sites are well established in the North Sea and North America shelf waters and Mediterranean (e.g. MAZZOCCHI *et al.*, 2011), with continuous sampling for more than 20 years. Associations that persisted over the long term provide evidence of resilience in communities in highly variable coastal conditions (MAZZOCCHI *et al.*, 2011). In the South Atlantic, such efforts are still limited, but long-term plankton monitoring studies in Brazilian waters are emerging and gaining recognition (e.g. VALENTIN *et al.*, 2020; RESGALLA, 2022). Our study adds information about Brazilian shallow shelf highlighting the replacement of copepod families in intermediate seasons and revealed the important role of big diatoms and invasive species in the ecosystem function.

CONCLUSION

This long term monitoring study complements previous short datasets investigations conducted at the REBIO Arvoredo MPA, offering a more comprehensive and integrative view of copepods and *Coscinodiscus* spp. dynamics in the region. By employing a multi-methodological approach, this study not only fills existing temporal gaps but also provides a valuable foundation for future research efforts, particularly those focusing on ecosystem dynamics within this MPA.

Our findings reveal clear patterns of alternating dominance between copepods and *Coscinodiscus* spp., shaped by a combination of water masses dynamics and climate anomalies, most notably the ENSO events of 2015–2016, 2018–2019, and 2023–2024. Seasonal and interannual variations in water masses were found to influence both the abundance and composition of these key planktonic groups, thereby affecting trophic interactions across the food web. These shifts underscore the complexity of energy transfer within the ecosystem and highlight how changes in planktonic community structure can lead to distinct trophic pathways throughout the year.

Continuous, long-term monitoring, with complimentary sampling and analysis methods, is therefore essential to fully understand the intricate mesoplankton dynamics, including the adaptive responses of copepods and *Coscinodiscus* spp. composition and abundance, to the oceanographic variability under the current global changes.

Contributor Roles

Maria Luiza Simões de Oliveira: Conceptualization, Data curation Formal analysis, Methodology, Writing – original draft, Writing – review & editing

Andréa Green Koettker: Conceptualization, Methodology (Plankton image systems and plankton identification), Funding acquisition, Writing – review & editing

Érica Caroline Becker: Conceptualization, Formal analysis, Methodology (Plankton image systems and copepods identification), Writing – review & editing

Luis Carlos Pinto de Macedo-Soares: Formal analysis (GLM and RDA), Methodology, Writing – review & editing

Leonardo Rubi Rörig: Methodology (Phytoplankton ID and microscope counting), Writing – review & editing

Eduardo Gentil: Conceptualization, Data curation, Methodology, Supervision, Writing – review & editing

Andrea Santarosa Freire: Conceptualization, Data curation, Funding acquisition, Methodology, Project administration, Supervision, Writing – review & editing

ACKNOWLEDGEMENTS

This research was conducted in the context of the Graduate Program in Oceanography (PPGOceano - UFSC) with support from CAPES (M. L. S. de Oliveira). We would like to thank the MAArE project team, including Prof. Alessandra L. Fonseca from the Marine Biogeochemical and Environment Education Laboratory for providing chlorophyll. We also thank the Chico Mendes Institute of Biodiversity Conservation (ICMBio), and PETROBRAS. The implementation of the project MAArE - Monitoramento Ambiental da Reserva Biológica Marinha do Arvoredo e Entorno - and a condition set by the ICMBio in the context of IBAMA's environmental licensing process. This work received support from the Brazilian Coastal Monitoring System (SiMCosta) team and their support is gratefully acknowledged. SiMCosta is funded by Fundo Clima, the Ministry of Environment and the Ministry of Science, Technology and Innovation. A number of field assistants were involved in the deployment of the buoy SiMCosta SC01. We would like to thank Roberto Bruno Fabiano, Captain of the sailboat *Pangeia*, the ICMBio team and Plano de Ação para prevenção e Controle do Coral-sol na Rebio Arvoredo e Entorno (PACS Arvoredo) team for their support in the continuous monitoring of the site throughout 2023 and 2024. We also acknowledge the AtlantECO/ EU/ H2020/ Blue Growth project for their occasional support during the spring sampling campaigns conducted as part of the Ocean Sampling Day (OSD).

CONCLUSÃO GERAL

Este estudo destacou a importância do uso de múltiplas metodologias para compreender a dinâmica de abundância de copépodes e *Coscinodiscus* spp. na REBIO Arvoredo, revelando padrões sazonais e interanuais marcantes influenciados por variabilidade oceanográfica e eventos climáticos de larga escala, como a dinâmica sazonal de massas de água e o ENSO. A aplicação de tecnologias avançadas de imageamento planctônico, aliada ao uso de redes de 200 µm, permitiu a detecção de *Coscinodiscus* spp. em abundâncias comparáveis ou superiores às dos copépodes. O que evidencia uma demanda por ampliação do uso de mais de uma metodologia de coleta e análise de plâncton para monitorar e compreender a composição e abundância de copépodes e da espécie invasora *Coscinodiscus wailesii* na REBIO do Arvoredo.

A alternância de dominância entre *Coscinodiscus* spp. e copépodes reflete modos distintos de funcionamento ecossistêmico, modulados por intensas variações hidrodinâmica, como intrusões da ACAS e influência da APP associada ao ENSO.

A comunidade de copépodes demonstrou variação sazonal, com destaque para a dominância de Temoridae no verão, associado a influência da intrusão da ACAS e o predomínio de pequenos onívoros como Oithonidae sob influência da pluma continental do Rio da Prata. *Coscinodiscus* spp. apresentaram frequente ocorrência e dominância no outono, representando as diatomáceas remanescentes em decorrência da limitação de seu consumo para a maioria das espécies de mesozooplâncton. A influência da Pluma do Rio da Prata no inverno resultou na redução da abundância de *Coscinodiscus* spp.

A análise conjunta de dados de sensoriamento remoto e imageamento planctônico revelou a forte influência de padrões sazonais e interanuais na composição e abundância dos copépodes e *Coscinodiscus* spp., destacando a relevância de ferramentas complementares para avaliar a resposta biológica frente à variabilidade ambiental.

Este trabalho reforça a necessidade de programas de monitoramento de longo prazo e de múltiplas metodologias para uma avaliação abrangente do funcionamento

ecológico em áreas marinhas protegidas. A adoção de técnicas de alta resolução, como análise de plâncton por imagem, aliada ao sensoriamento remoto e monitoramento contínuo, é essencial para revelar processos ecológicos complexos e orientar estratégias de conservação e manejo para reservas biológicas marinhas, principalmente em um cenário de mudanças climáticas.

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SUPPLEMENTARY MATERIAL (SM)

Table S1a. Species and morphotypes list of phytoplankton processed through optical microscopy (OLYMPUS - 20x) using identification keys (TOMAS,1997) that occurred from 2014 to 2024 at the REBIO Arvoredo monitoring site.

	2014		2015		2016		2018							2019							2022	2023			2024		
	03	08	02	07	02	08	02	03	04	05	06	09	12	02	04	06	07	08	09	11	09	03	08	09	01	06	07
O. OSCILLATORIALES																											
F. MICROCOLEACEAE																											
<i>Trichodesmium erythraeum</i>													X														
CLASS BACILLARIOPHYCEAE																											
O. BACILLARIALES																											
F.BACILLARIACEAE																											
<i>Pseudo-nitzschia sp</i>										X																	
O. COSCINODISCALES																											
F. COSCINODISCACEAE																											
<i>Coscinodiscus asteromphalus</i> Ehrenberg. 1844	X	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Coscinodiscus concinnus</i> W.Smith, 1856													X										X	X			
<i>Coscinodiscus spp. Ehrenberg</i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Coscinodiscus granii</i> Gough, 1905											X									X							X

[illegible]

[illegible]

<i>Tripes gibberus</i> (Gourret) F. Gómez, 1883																		X									
<i>Tripes hircus</i> (Schröder) F. Gómez, 2013					X					X								X									
<i>Tripes macroceros</i> (Ehrenberg) Hallegraeff and Huisman, 2020			X																								

Table S1d. Species and morphotypes list of phytoplankton processed through optical microscopy (OLYMPUS - 20x) using identification keys (TOMAS,1997) that occurred from 2014 to 2024 at the REBIO Arvoredo monitoring site.

	2014		2015		2016		2018							2019							2022	2023			2024		
	03	08	02	07	02	08	02	03	04	05	06	09	12	02	04	06	07	08	09	11	09	03	08	09	01	06	07
<i>Tripes massiliensis</i> (Gourret) F. Gómez, 2013				X																X				X	X		
<i>Tripes muelleri</i> Bory de Saint-Vincent, 1826			X		X			X		X			X									X					
<i>Tripes trichoceros</i> (Ehrenberg) Gómez, 2013		X				X				X	X		X					X									X
<i>Tripes pentagonus</i> (Gourret) F. Gómez, 2013		X																									
O. GONYAULACALES		X																									
F. PYROCYSTACEAE																											
<i>Pyrocystis fusiformis</i> C.W. Thomson, 1876									X																		
<i>Pyrocystis pseudonociluca</i> Wyville-Thompson, 1876									X																		
<i>Tripes massiliensis</i> (Gourret) F. Gómez, 2013				X																X				X	X		
<i>Tripes muelleri</i> Bory de Saint-Vincent, 1826			X		X			X		X			X									X					

[illegible]

Table S2. Complementary information from the Generalized Linear Models (GLMs) used to evaluate the effects of environmental variables on Copepoda and *Coscinodiscus* spp. For each predictor, the table shows the estimated coefficient and its standard error (Estimate $\pm$ SE), the associated z-value (test statistic), and the p-value, which indicates the level of statistical significance (values < 0.05 were considered significant). AIC represents Akaike Information Criterion and log-likelihood (logLik). Dispersion values are reported to assess the degree of overdispersion in the models, which were fitted using a negative binomial distribution (nbinom2) to account for non-normal, overdispersed count data.

Model	Predictor	Estimate ($\pm$ SE)	z-value	p-value	AIC	logLik	Dispersion
Copepoda ~ offset(Lvol) + ZEU	Intercept	1.461 ($\pm$ 0.297)	4.921	<0.001 ***	330.4	-162.2	2.15
	ZEU	0.030 ($\pm$ 0.014)	2.191	0.028 *			
Copepoda ~ offset(Lvol) + Temperature + Northward drift	Intercept	-0.601 ($\pm$ 1.125)	-0.534	0.593	291.7	-141.8	2.26
	Temperature	0.117 ($\pm$ 0.048)	2.434	0.015 *			
	Northward drift	0.015 ($\pm$ 0.112)	0.130	0.897			
<i>Coscinodiscus</i> spp ~ offset(Lvol) + Temperature + Salinity + Northward Stokes drift	Intercept	-9.473 ($\pm$ 6.794)	-1.394	0.163	330.7	-160.3	0.717
	Temperature	-0.190 ($\pm$ 0.084)	-2.274	0.023 *			
	Salinity	0.485 ($\pm$ 0.211)	2.292	0.022 *			
	Northward Stokes drift	-17.838 ($\pm$ 8.491)	-2.101	0.036 *			
<i>Coscinodiscus</i> spp ~ offset(Lvol) + Chlorophyll-a	Intercept	3.734 ($\pm$ 0.500)	7.473	<0.001 ***	174.3	-84.2	0.666
	Chlorophyll-a	-1.216 ($\pm$ 0.299)	-4.073	<0.001 ***			

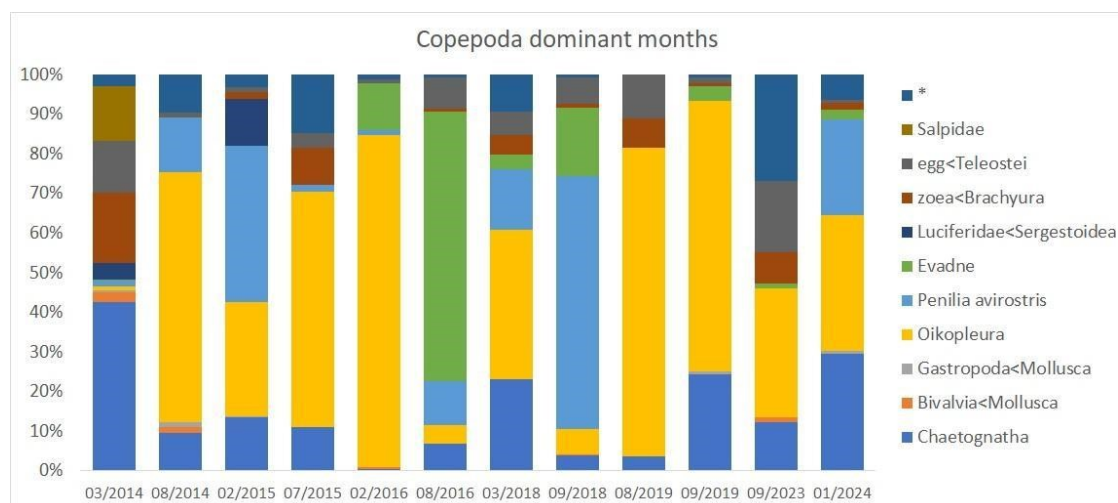


Figure S1. Relative abundance (%) of the other mesozooplanktonic taxa at the REBIO Arvoredo MPA during the months when Copepoda were dominant. * represents the less frequent and abundant groups.

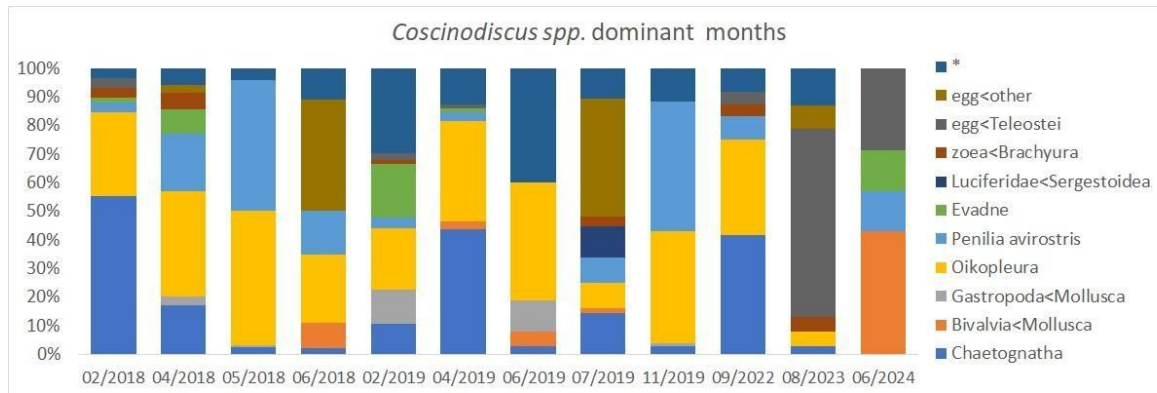


Figure S2. Relative abundance (%) of the other mesozooplanktonic taxa at the REBIO Arvoredo MPA during the months when *Coscinodiscus* spp. were dominant. * represents the less frequent and abundant groups.

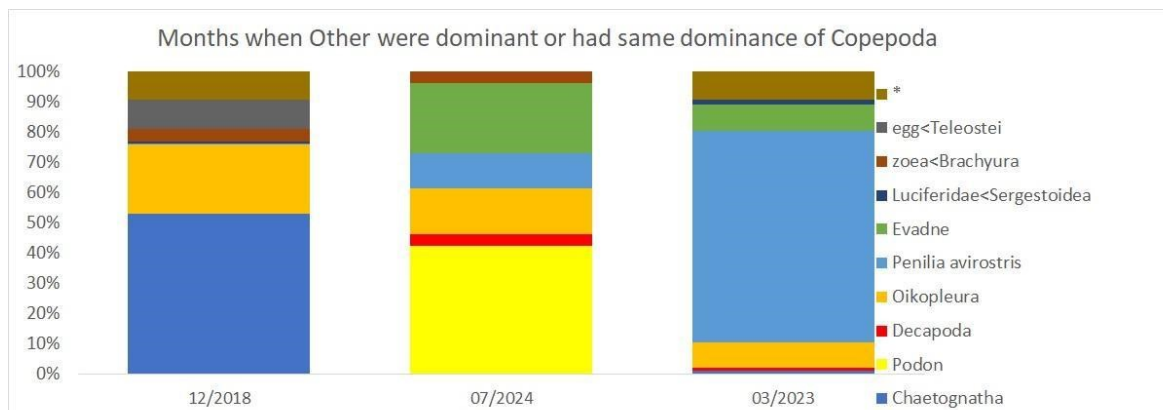


Figure S3. Relative abundance (%) of the other mesozooplanktonic taxa at the REBIO Arvoredo MPA during the months when Others were dominant or had the same dominance of Copepoda. * represents the less frequent and abundant groups.

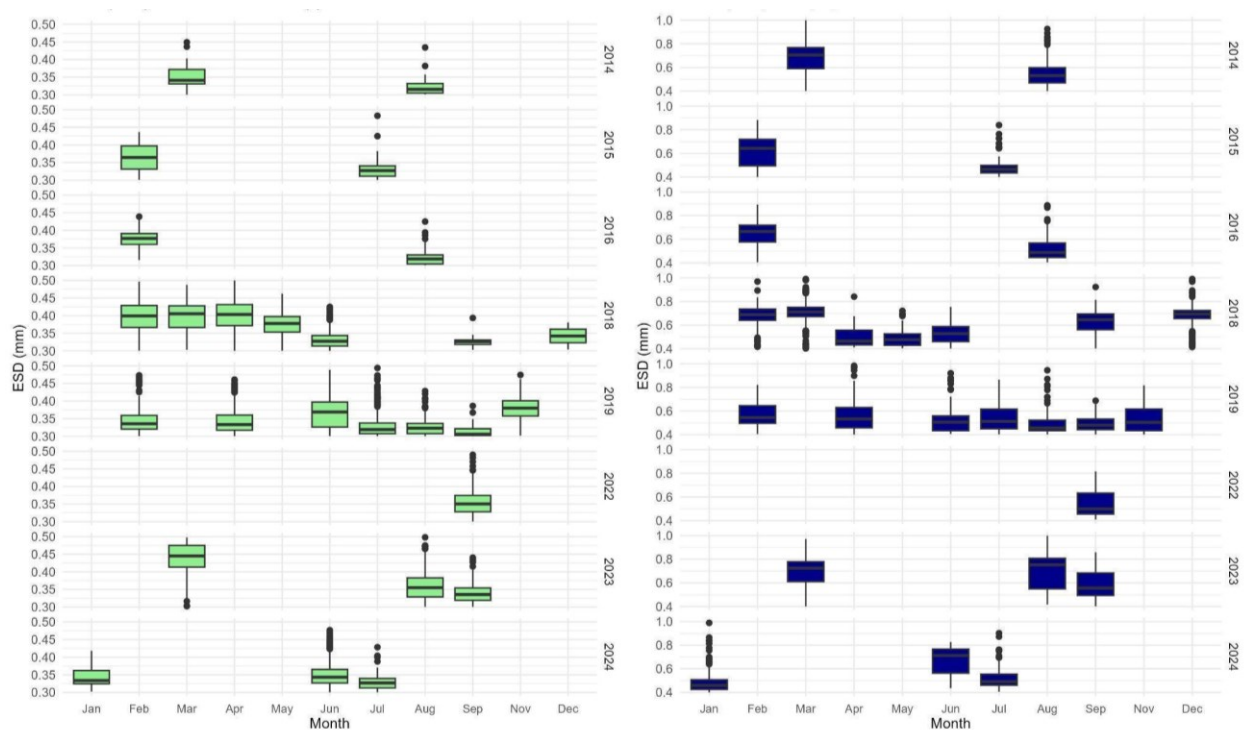


Figure S4. Equivalent spherical diameter (ESD mm) of *Coscinodiscus* spp. and Copepoda in REBIO Arvoredo between 2014 and 2024. Upper and lower limits (vertical lines), first and third quartile (box), median (horizontal line) and outliers (dots). Boxplots in light green represent *Coscinodiscus* spp. and in dark blue, Copepoda.

APPENDIX A

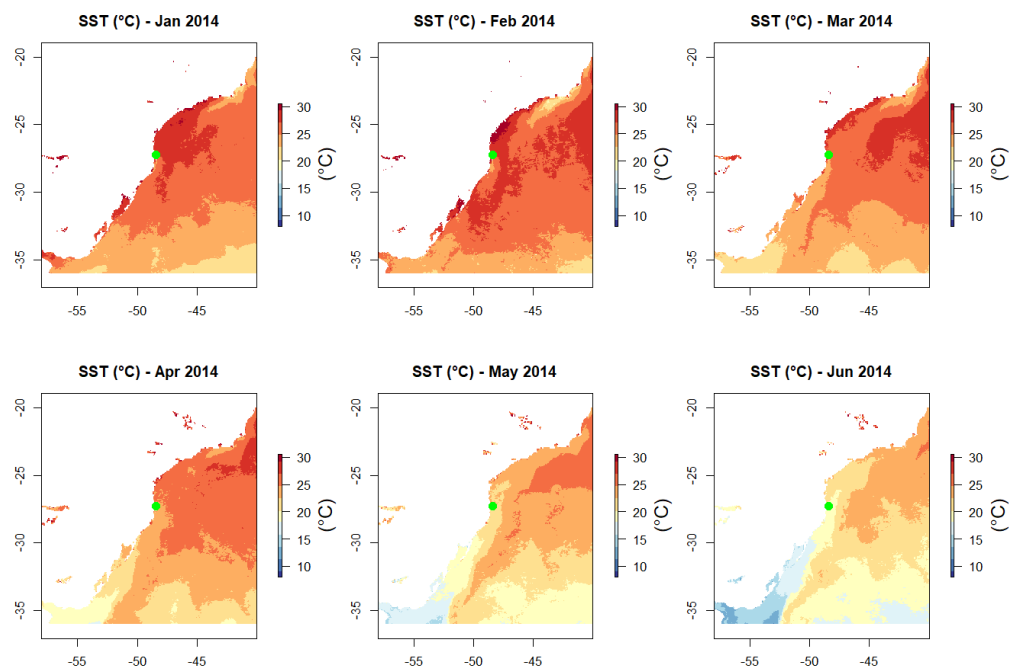


Figure S5. Horizontal distribution of monthly sea surface temperature (SST) in °C from the MODIS/Aqua sensor from January to June 2014 for the Santa Catarina continental shelf.

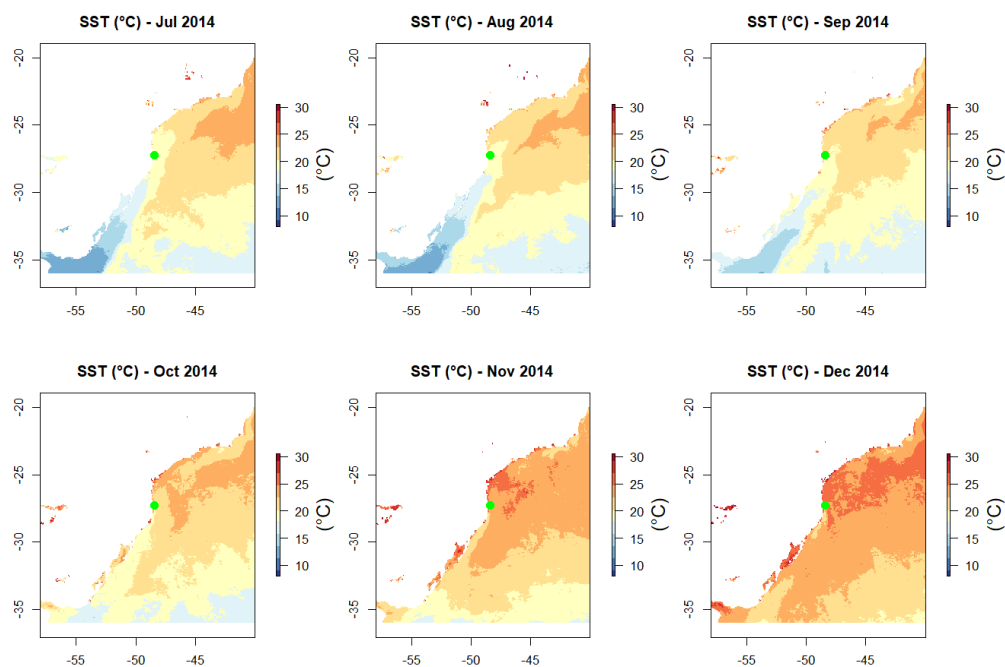


Figure S6. Horizontal distribution of monthly sea surface temperature (SST) in $^{\circ}\text{C}$ from the MODIS/Aqua sensor from July to December 2014 for the Santa Catarina continental shelf.

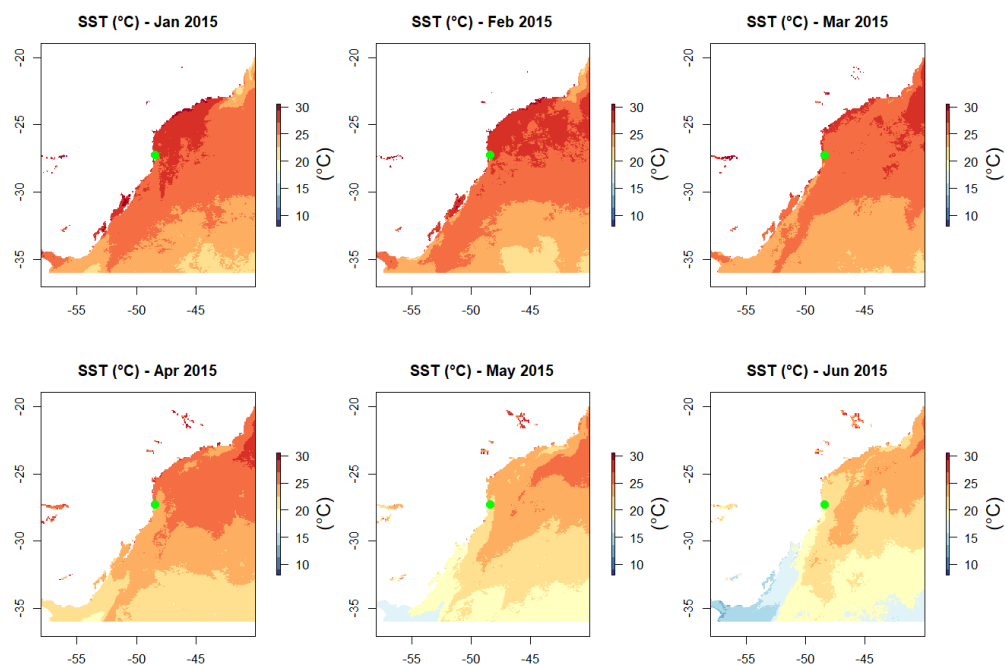


Figure S7. Horizontal distribution of monthly sea surface temperature (SST) in $^{\circ}\text{C}$ from the MODIS/Aqua sensor from January to June 2015 for the Santa Catarina continental shelf.

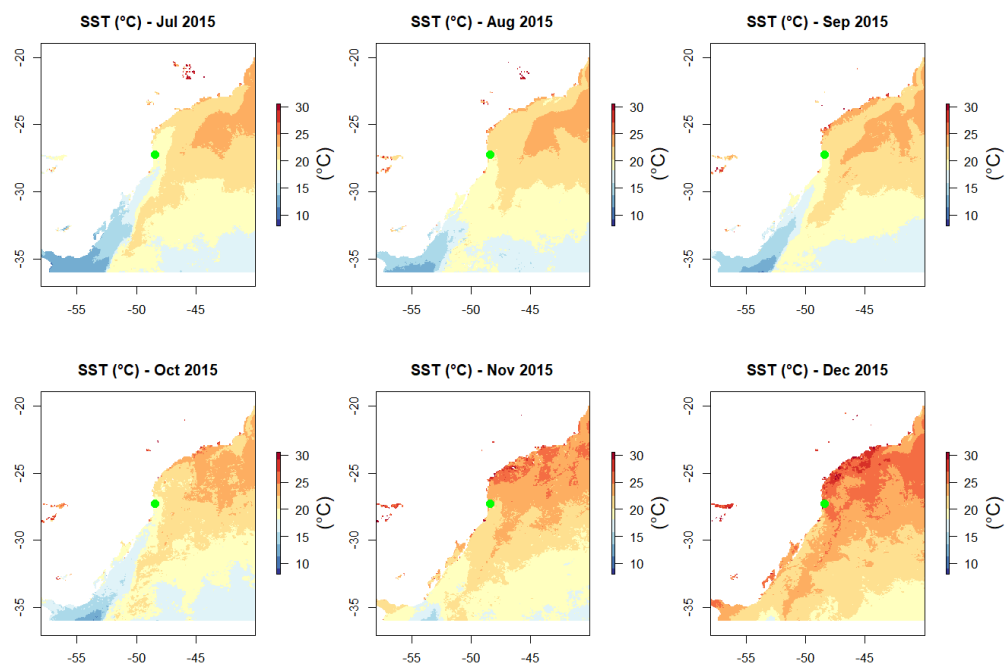


Figure S8. Horizontal distribution of monthly sea surface temperature (SST) in °C from the MODIS/Aqua sensor from July to December 2015 for the Santa Catarina continental shelf.

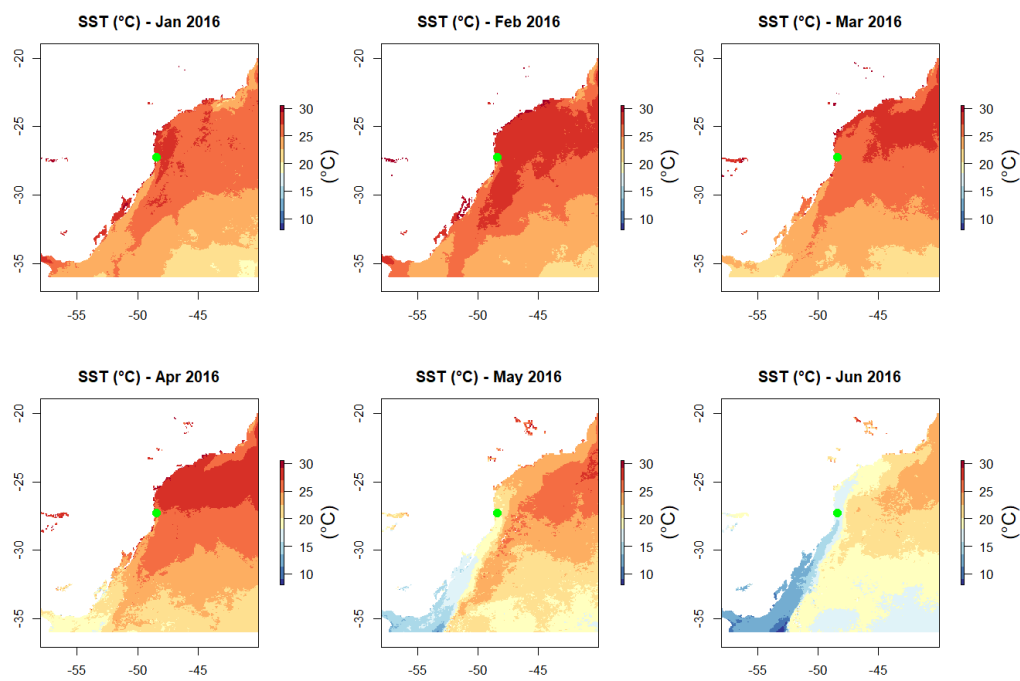


Figure S9. Horizontal distribution of monthly sea surface temperature (SST) in °C from the MODIS/Aqua sensor from January to June 2016 for the Santa Catarina continental shelf.

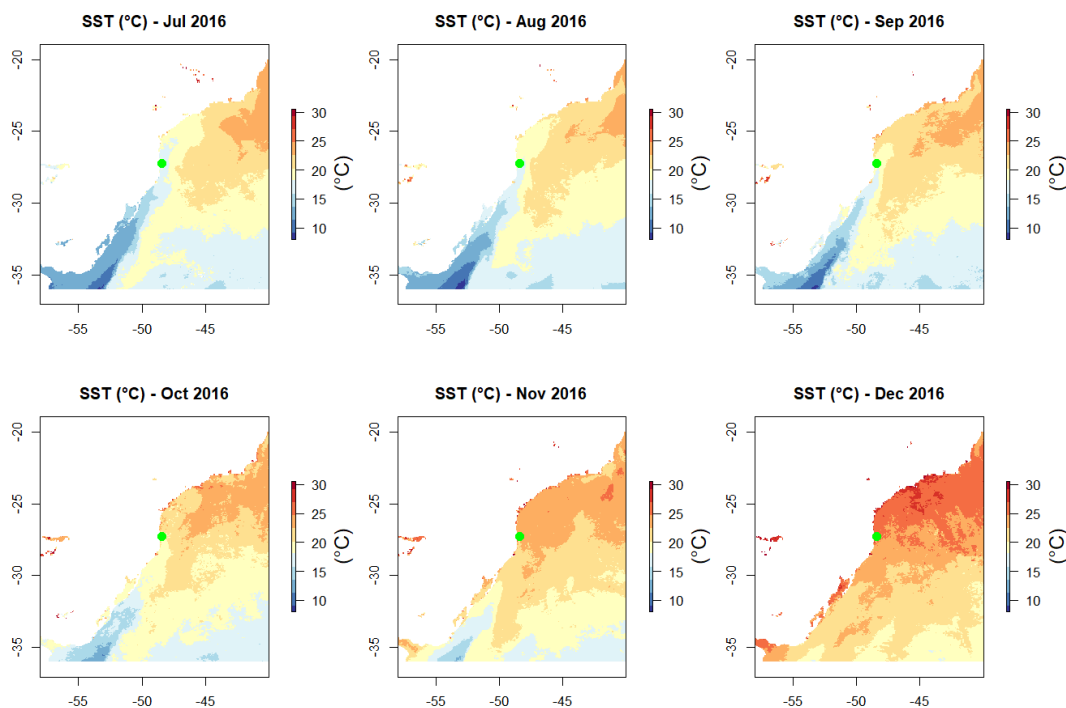


Figure S10. Horizontal distribution of monthly sea surface temperature (SST) in °C from the MODIS/Aqua sensor from July to December 2016 for the Santa Catarina continental shelf.

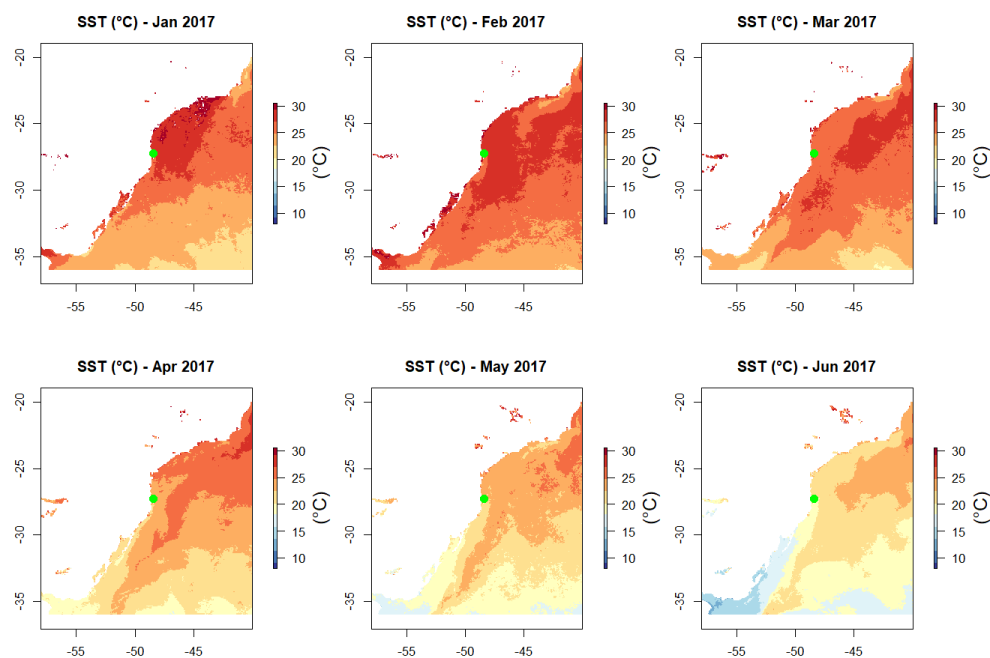


Figure S11. Horizontal distribution of monthly sea surface temperature (SST) in $^{\circ}\text{C}$ from the MODIS/Aqua sensor from January to June 2017 for the Santa Catarina continental shelf.

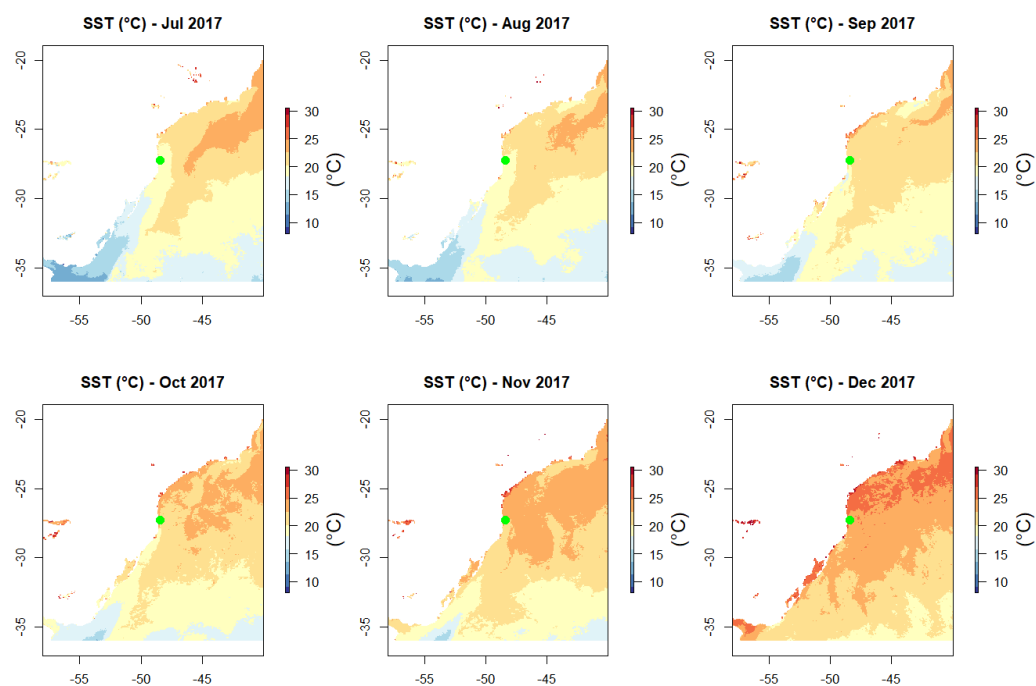


Figure S12. Horizontal distribution of monthly sea surface temperature (SST) in $^{\circ}\text{C}$ from the MODIS/Aqua sensor from July to December 2017 for the Santa Catarina continental shelf.

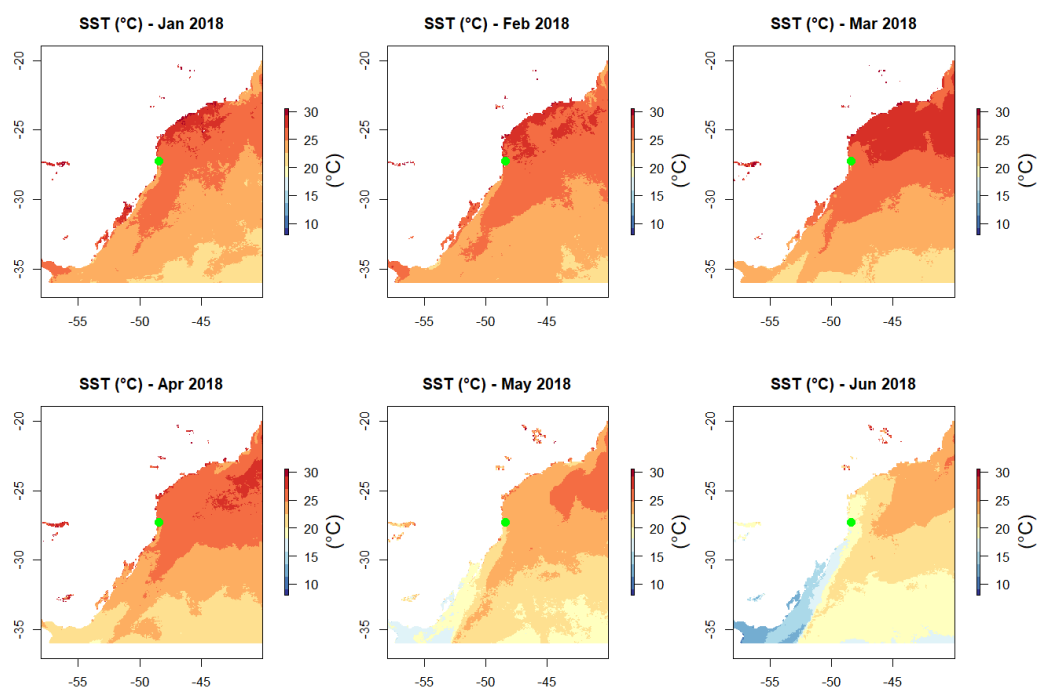


Figure S13. Horizontal distribution of monthly sea surface temperature (SST) in °C from the MODIS/Aqua sensor from January to June 2018 for the Santa Catarina continental shelf.

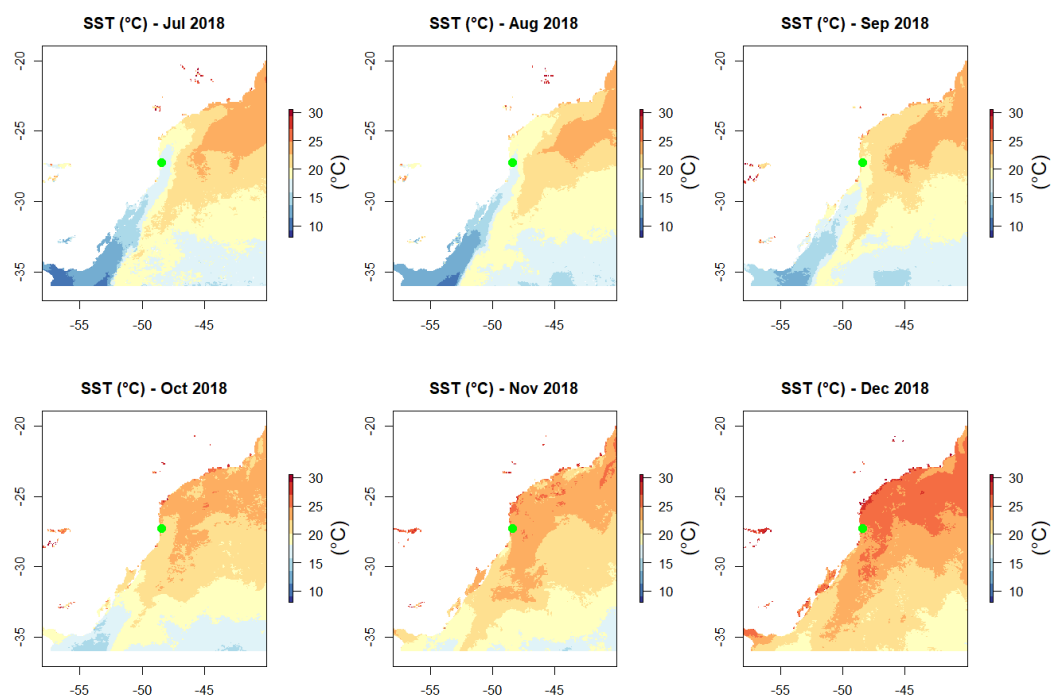


Figure S14. Horizontal distribution of monthly sea surface temperature (SST) in °C from the MODIS/Aqua sensor from July to December 2018 for the Santa Catarina continental shelf.

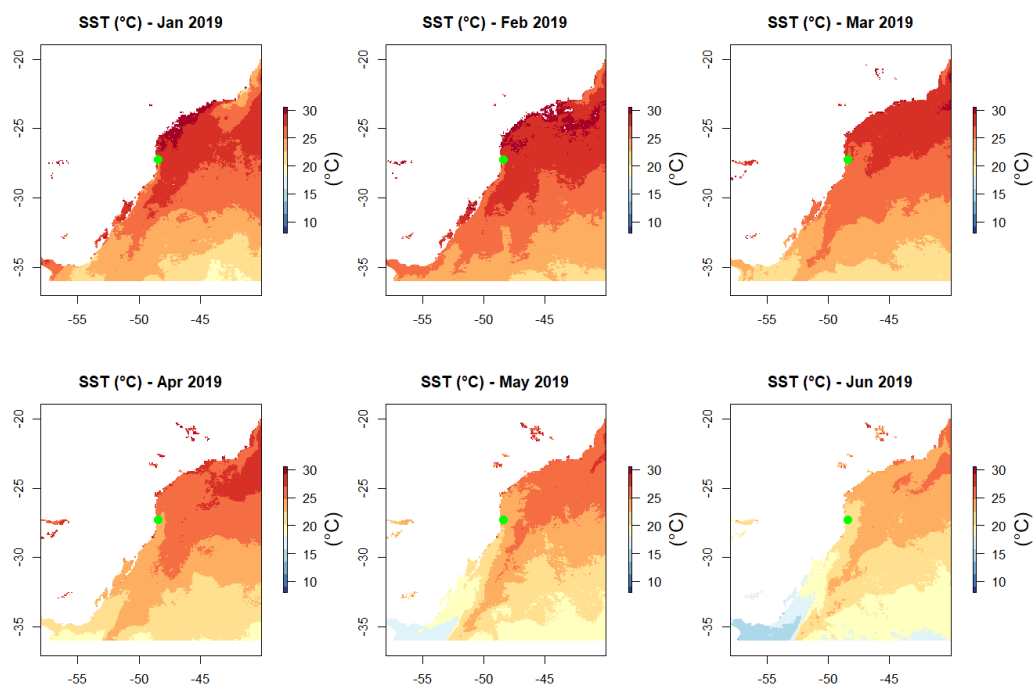


Figure S15. Horizontal distribution of monthly sea surface temperature (SST) in °C from the MODIS/Aqua sensor from January to June 2019 for the Santa Catarina continental shelf.

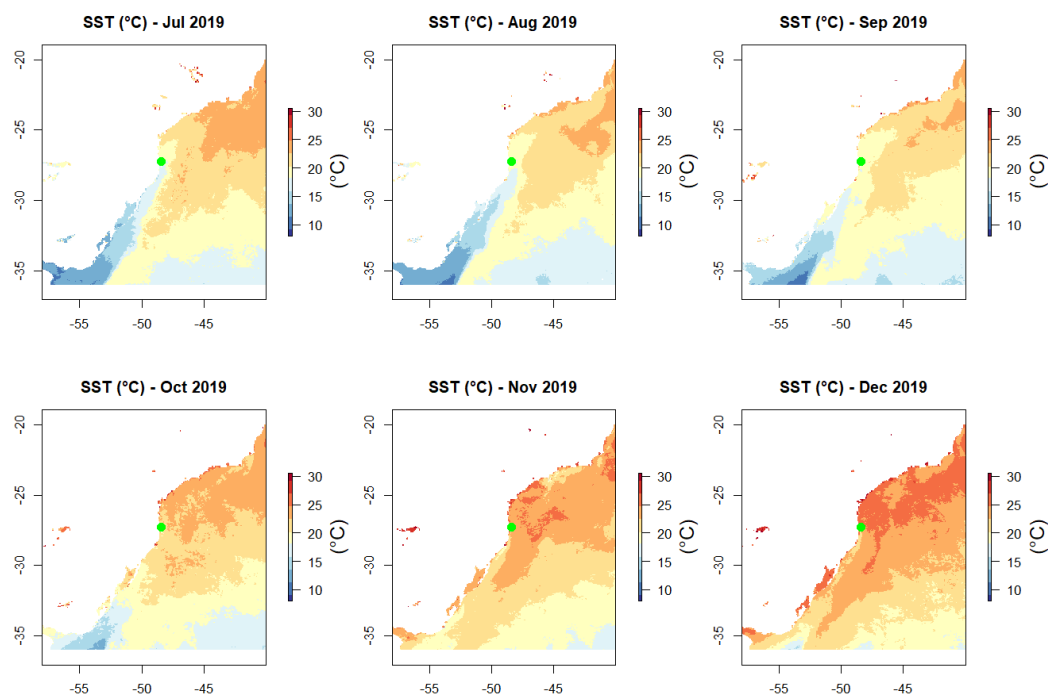


Figure S16. Horizontal distribution of monthly sea surface temperature (SST) in °C from the MODIS/Aqua sensor from July to December 2019 for the Santa Catarina continental shelf.

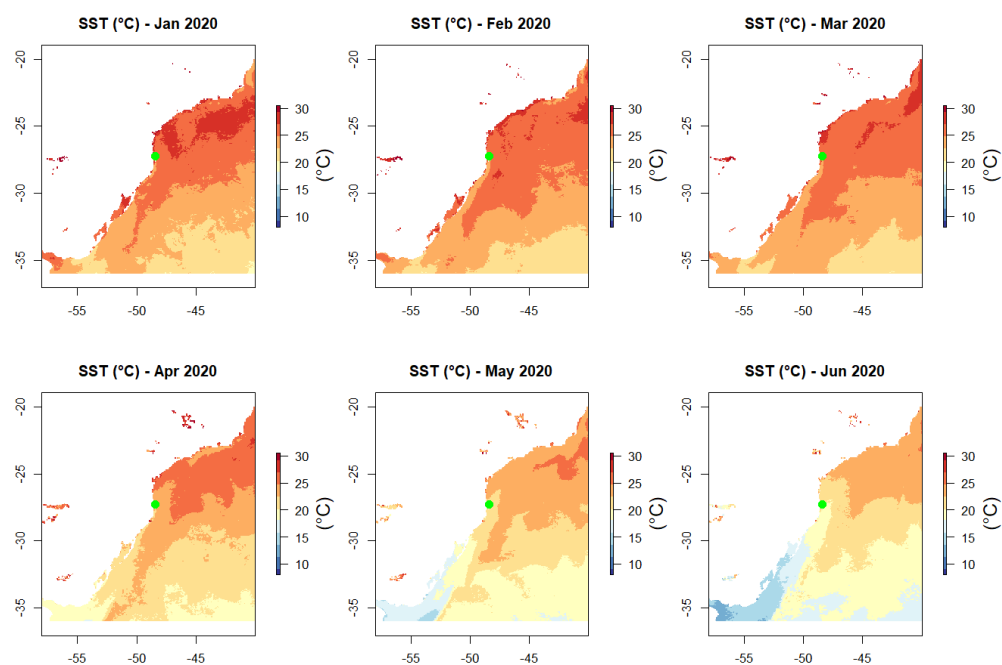


Figure S17. Horizontal distribution of monthly sea surface temperature (SST) in °C from the MODIS/Aqua sensor from January to June 2020 for the Santa Catarina continental shelf.

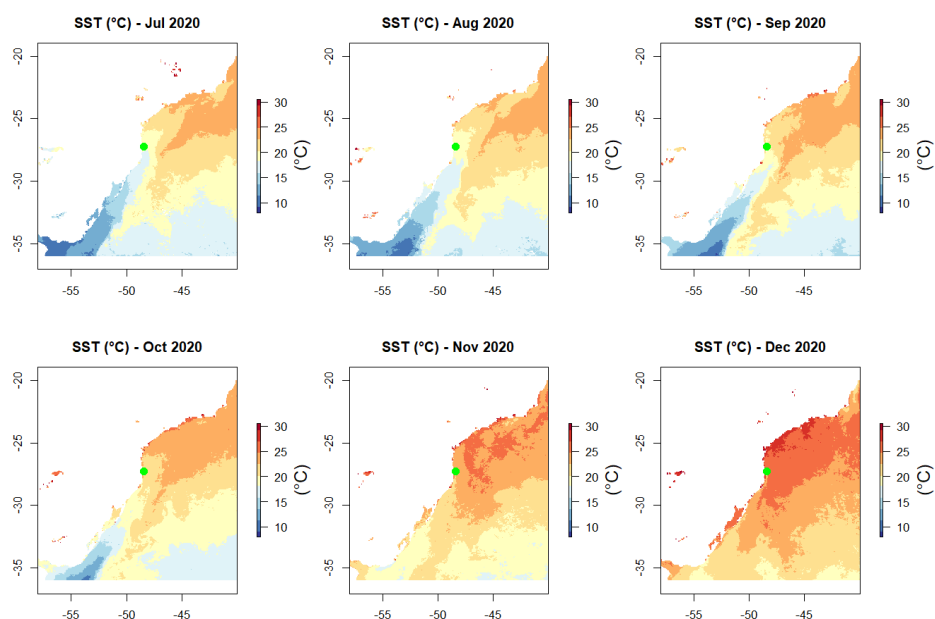


Figure S18. Horizontal distribution of monthly sea surface temperature (SST) in $^{\circ}\text{C}$ from the MODIS/Aqua sensor from July to December 2020 for the Santa Catarina continental shelf.

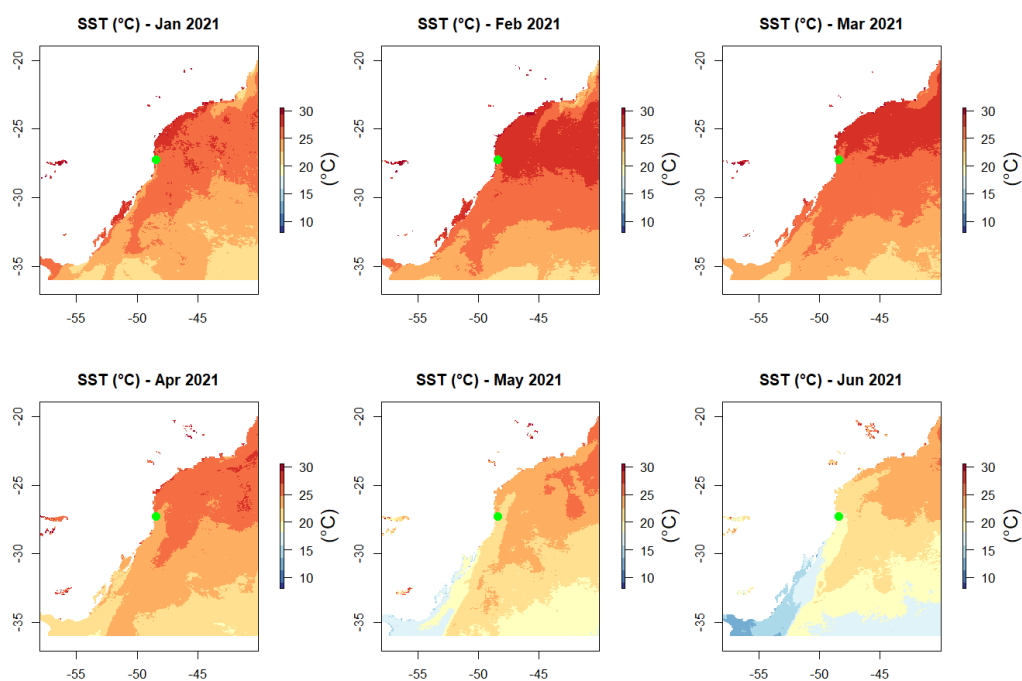


Figure S19. Horizontal distribution of monthly sea surface temperature (SST) in $^{\circ}\text{C}$ from the MODIS/Aqua sensor from January to June 2021 for the Santa Catarina continental shelf.

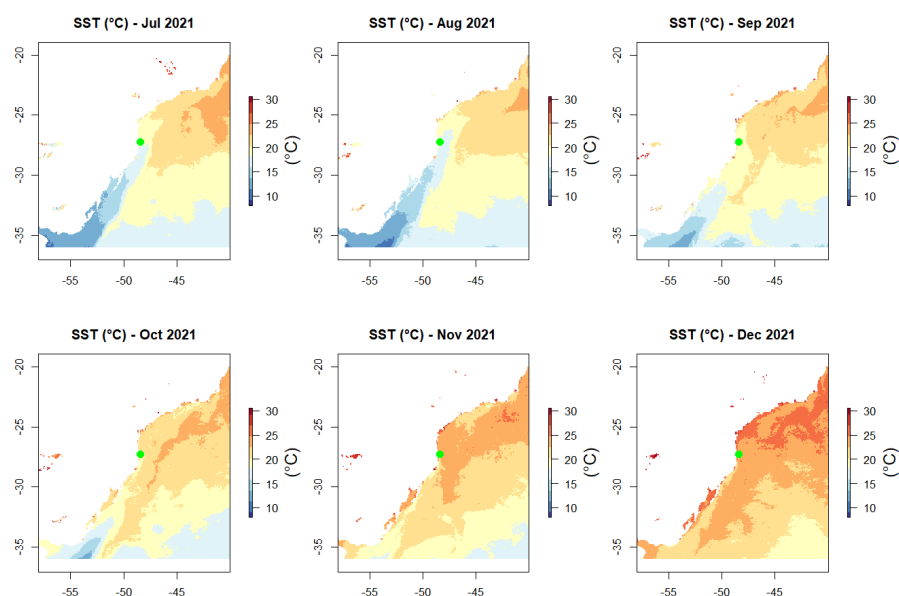


Figure S20. Horizontal distribution of monthly sea surface temperature (SST) in °C from the MODIS/Aqua sensor from July to December 2021 for the Santa Catarina continental shelf.

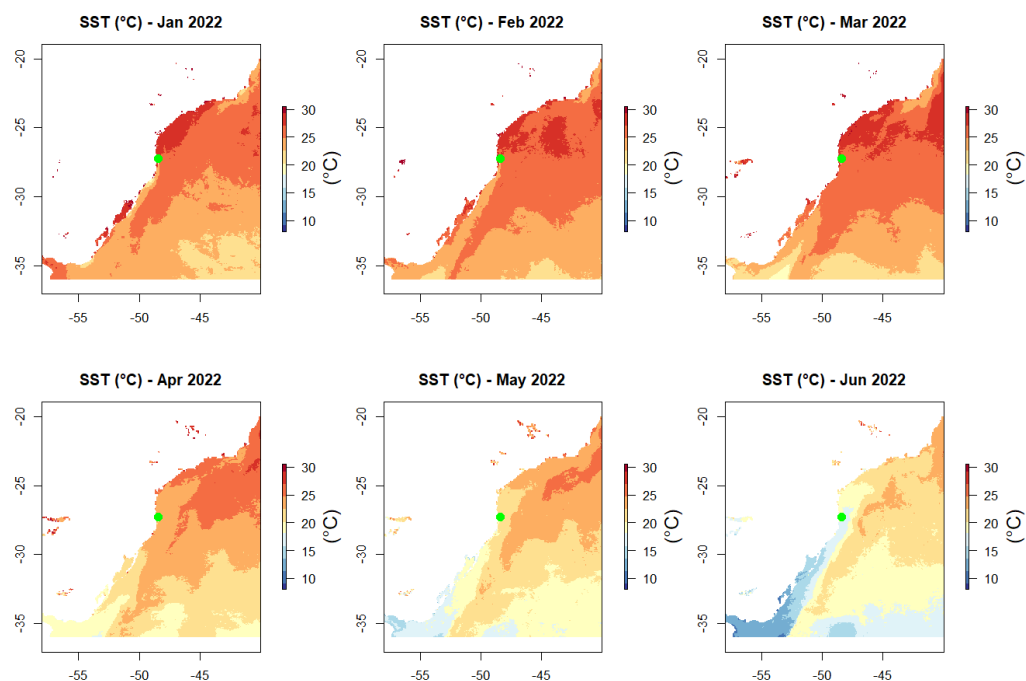


Figure S21. Horizontal distribution of monthly sea surface temperature (SST) in °C from the MODIS/Aqua sensor from January to June 2022 for the Santa Catarina continental shelf.

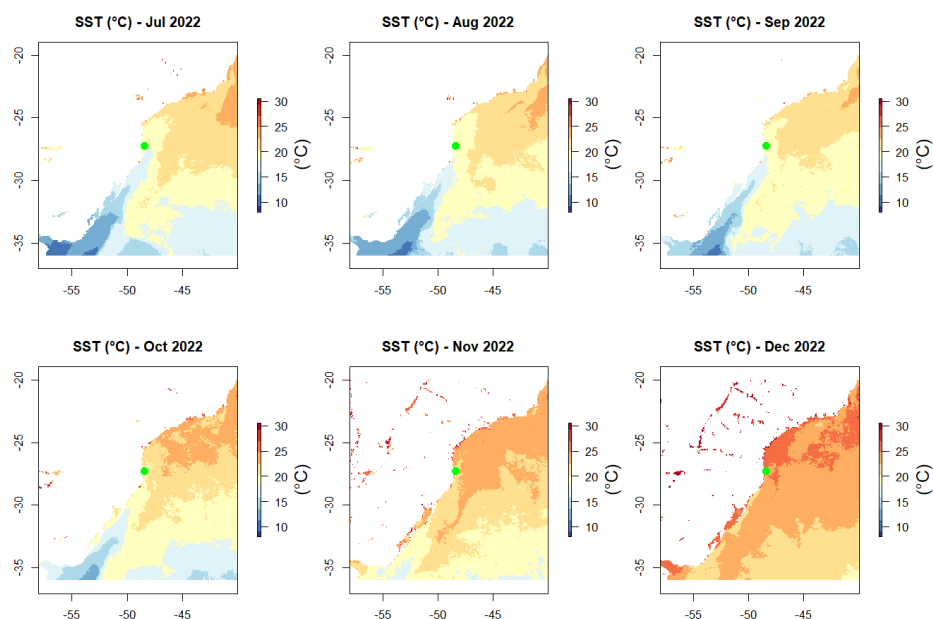


Figure S22. Horizontal distribution of monthly sea surface temperature (SST) in $^{\circ}\text{C}$ from the MODIS/Aqua sensor from July to December 2022 for the Santa Catarina continental shelf.

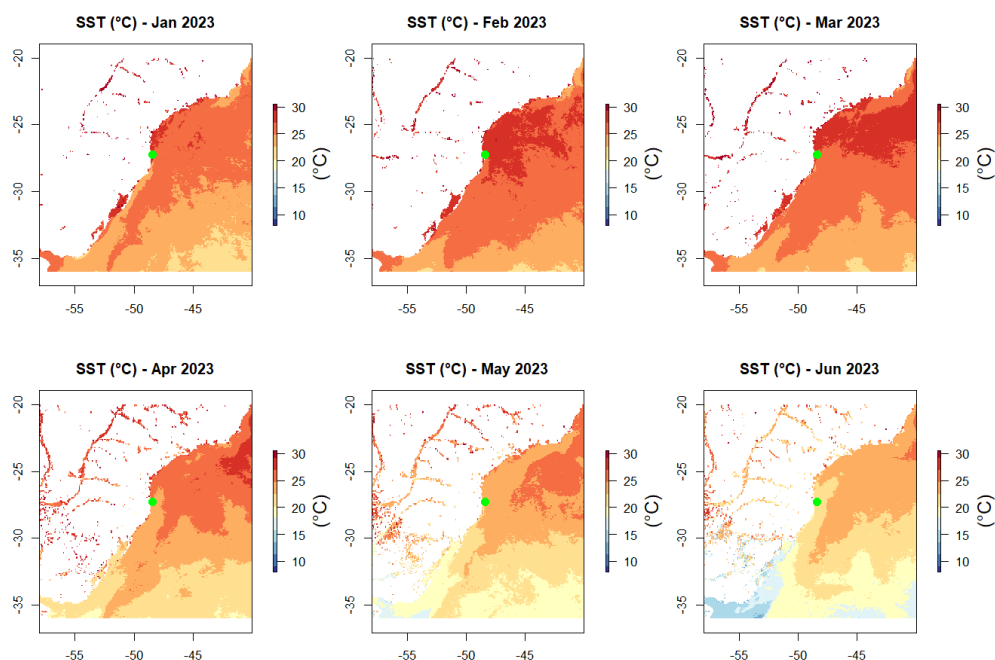


Figure S23. Horizontal distribution of monthly sea surface temperature (SST) in $^{\circ}\text{C}$ from the MODIS/Aqua sensor from January to June 2023 for the Santa Catarina continental shelf.

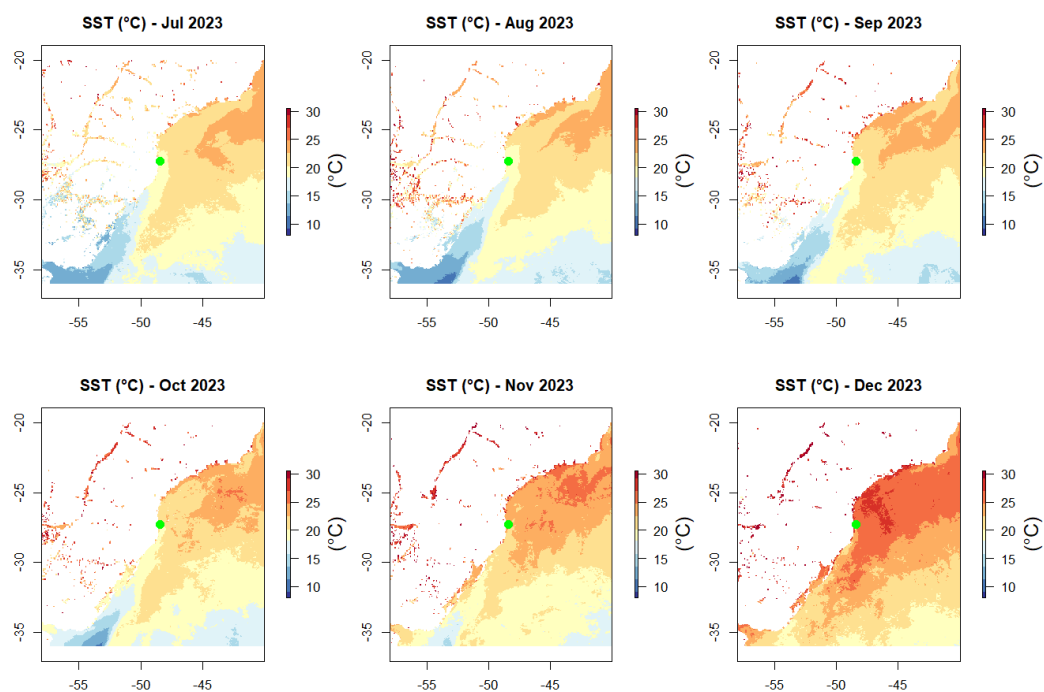


Figure S24. Horizontal distribution of monthly sea surface temperature (SST) in °C from the MODIS/Aqua sensor from July to December 2023 for the Santa Catarina continental shelf.

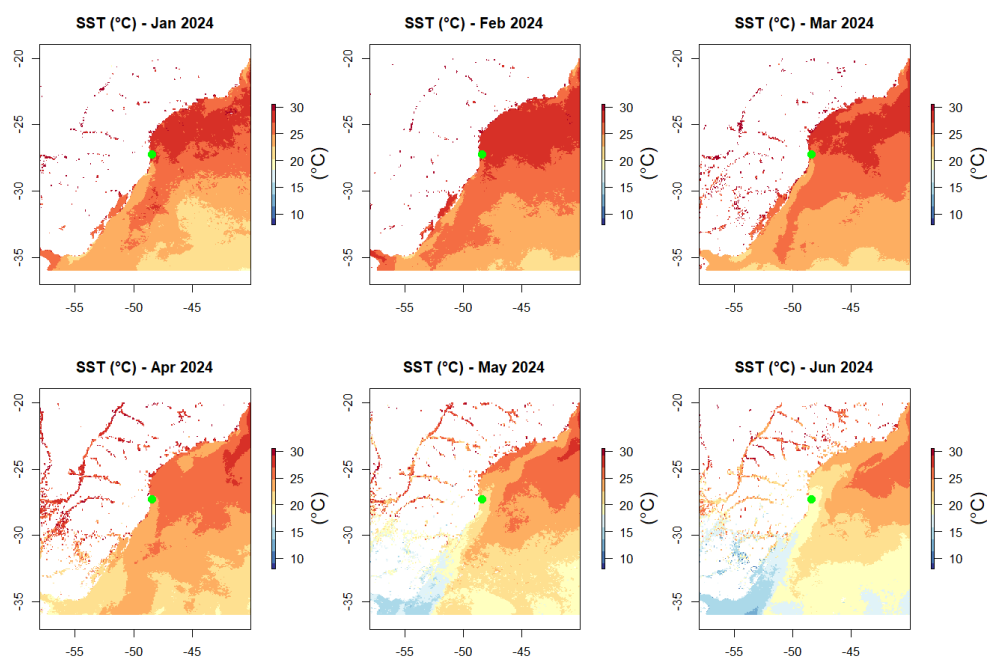


Figure S25. Horizontal distribution of monthly sea surface temperature (SST) in °C from the MODIS/Aqua sensor from January to June 2024 for the Santa Catarina continental shelf.

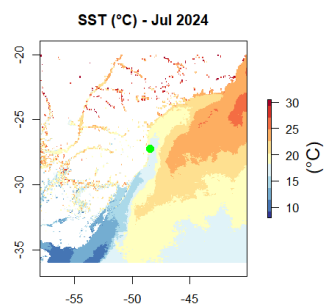


Figure S26. Horizontal distribution of monthly sea surface temperature (SST) in °C from the MODIS/Aqua sensor from July of 2024 for the Santa Catarina continental shelf.

APPENDIX B

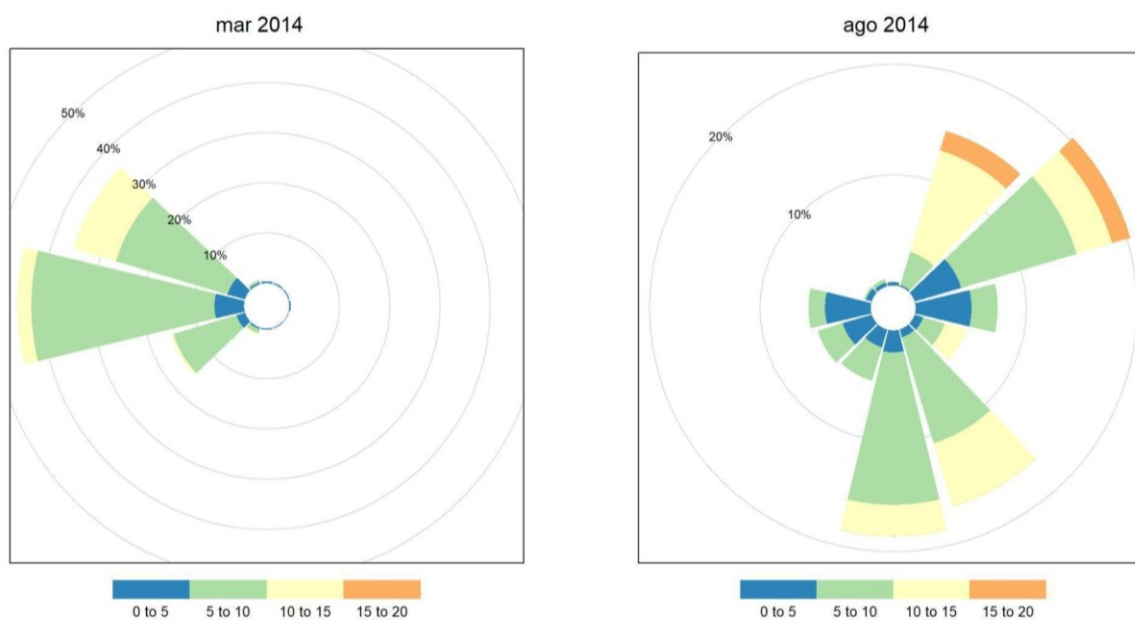


Figure S27. Wind intensity and direction of March and August of 2014. Each graph shows the relative frequency (%) of wind direction and intensity (m/s).

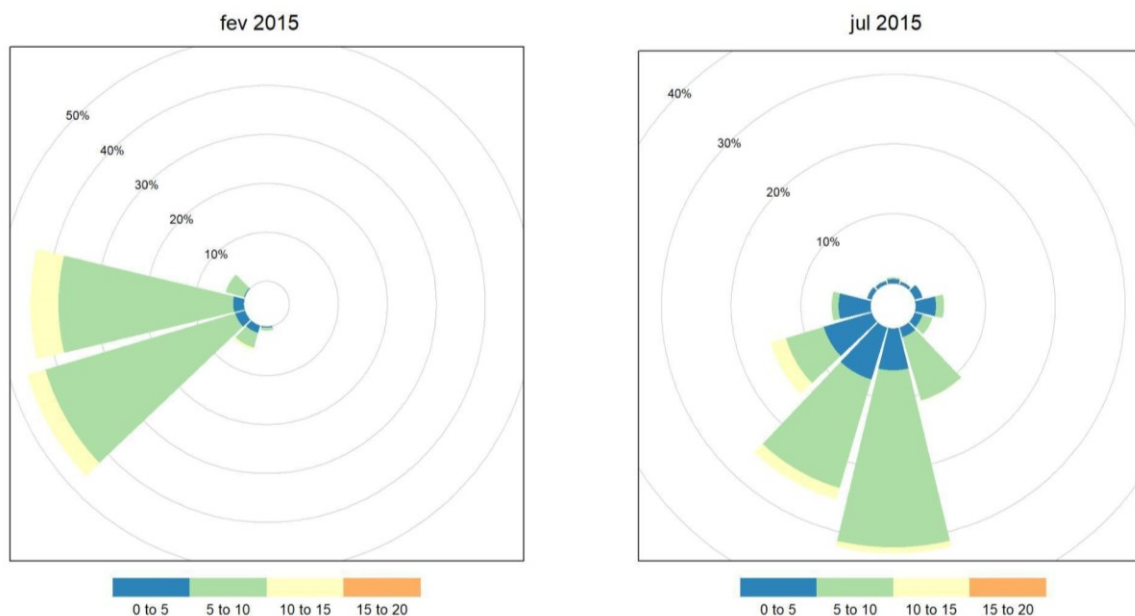


Figure S28. Wind intensity and direction of February and July of 2015. Each graph shows the relative frequency (%) of wind direction and intensity (m/s).

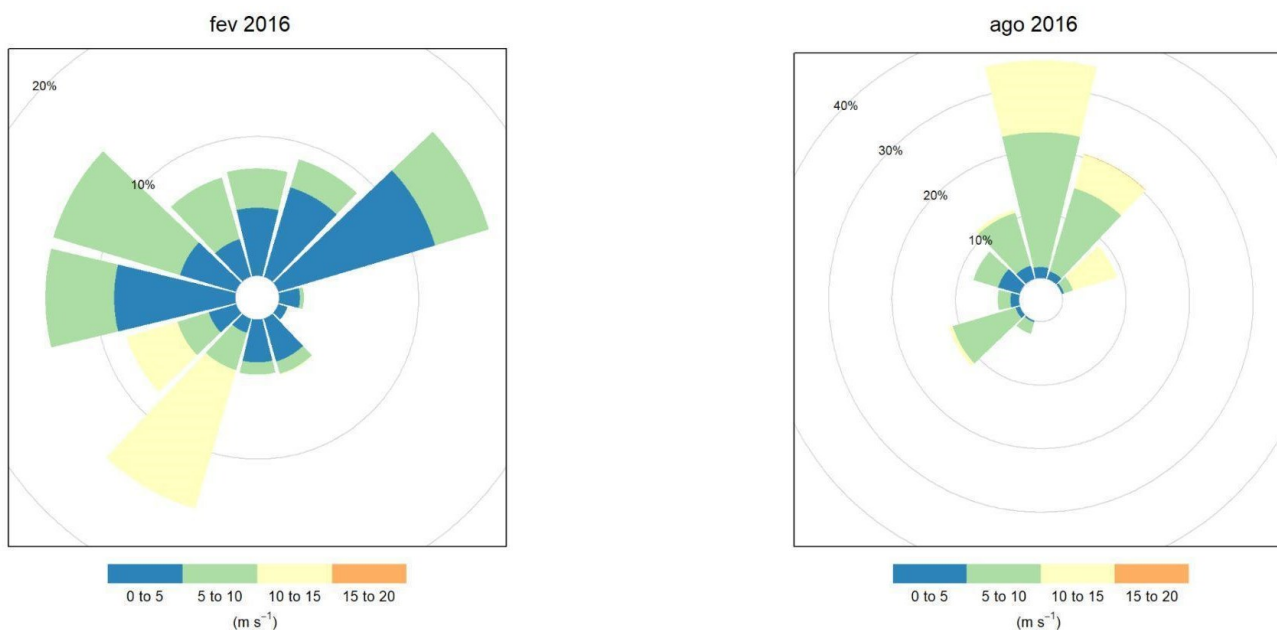


Figure S29. Wind intensity and direction of February and August of 2016. Each graph shows the relative frequency (%) of wind direction and intensity (m/s).

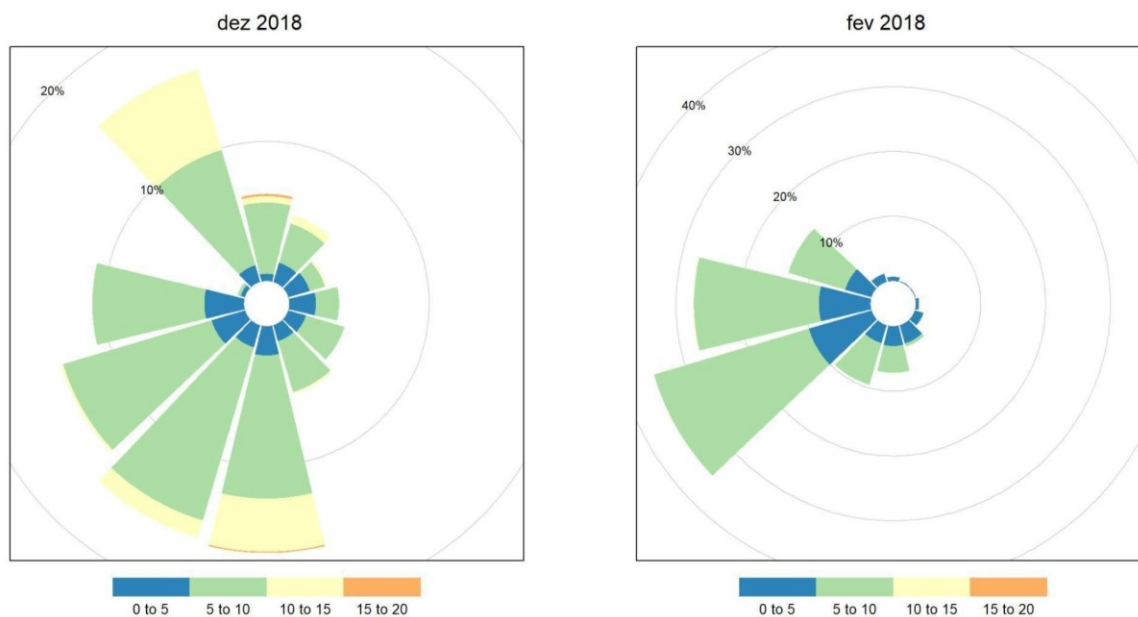


Figure S30. Wind intensity and direction of December and February of 2018. Each graph shows the relative frequency (%) of wind direction and intensity (m/s).

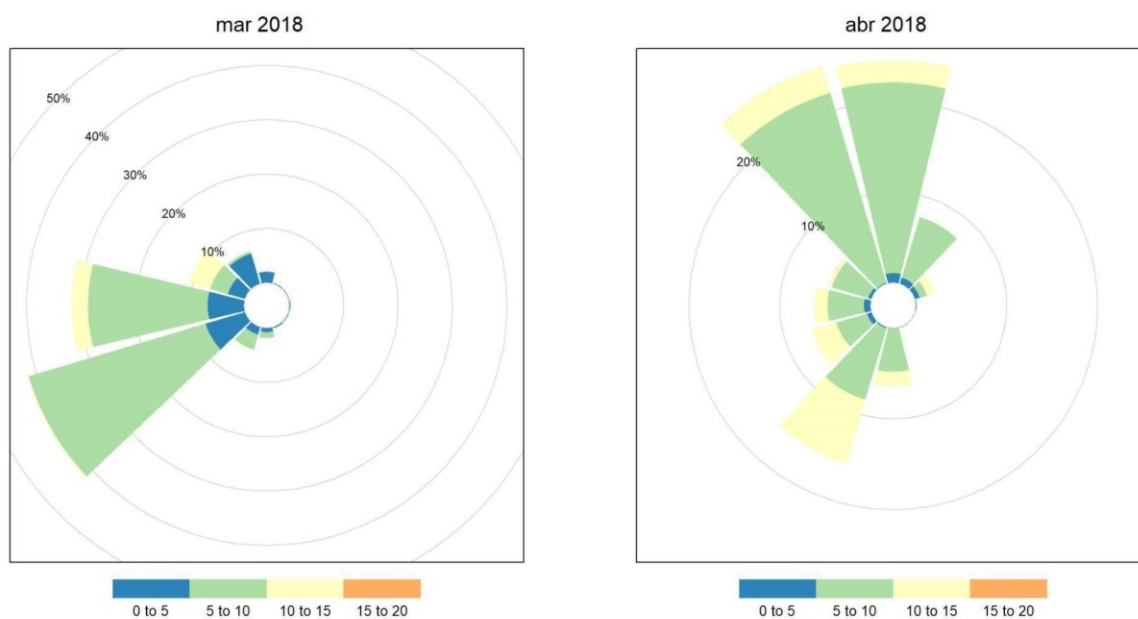


Figure S31. Wind intensity and direction of March and April of 2018. Each graph shows the relative frequency (%) of wind direction and intensity (m/s).

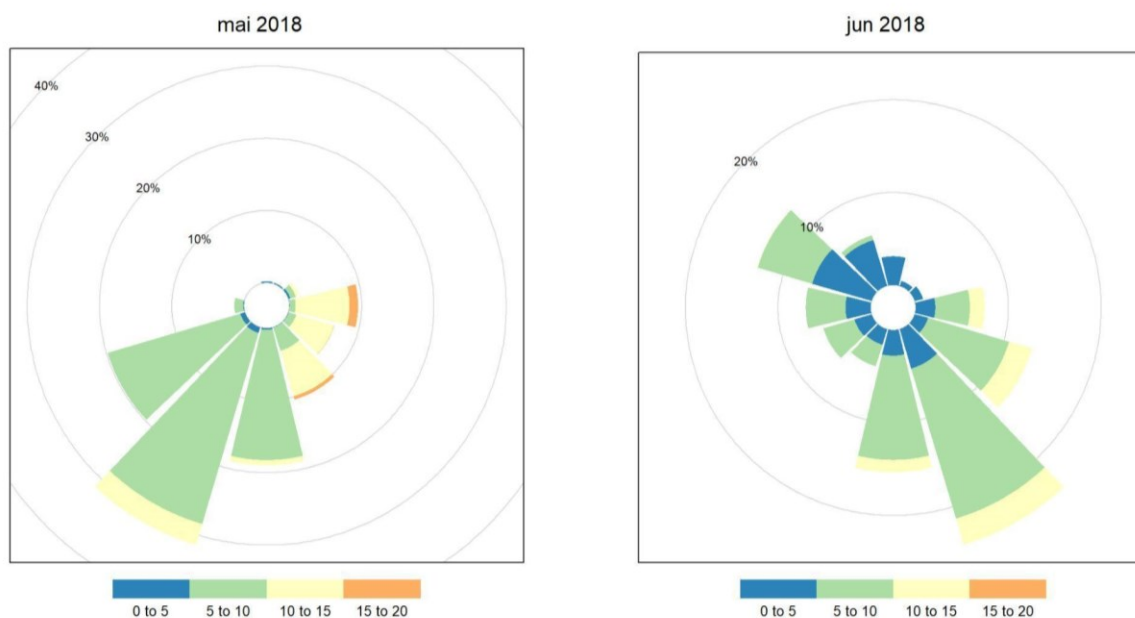


Figure S32. Wind intensity and direction of May and June of 2018. Each graph shows the relative frequency (%) of wind direction and intensity (m/s).

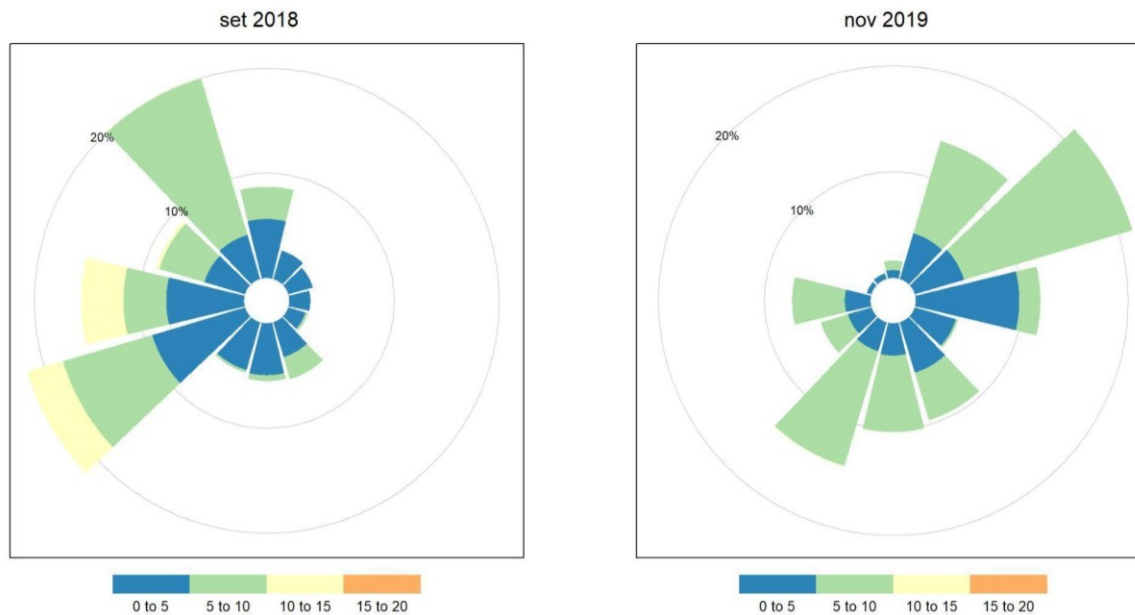


Figure S33. Wind intensity and direction of September 2018 and November of 2019. Each graph shows the relative frequency (%) of wind direction and intensity (m/s).

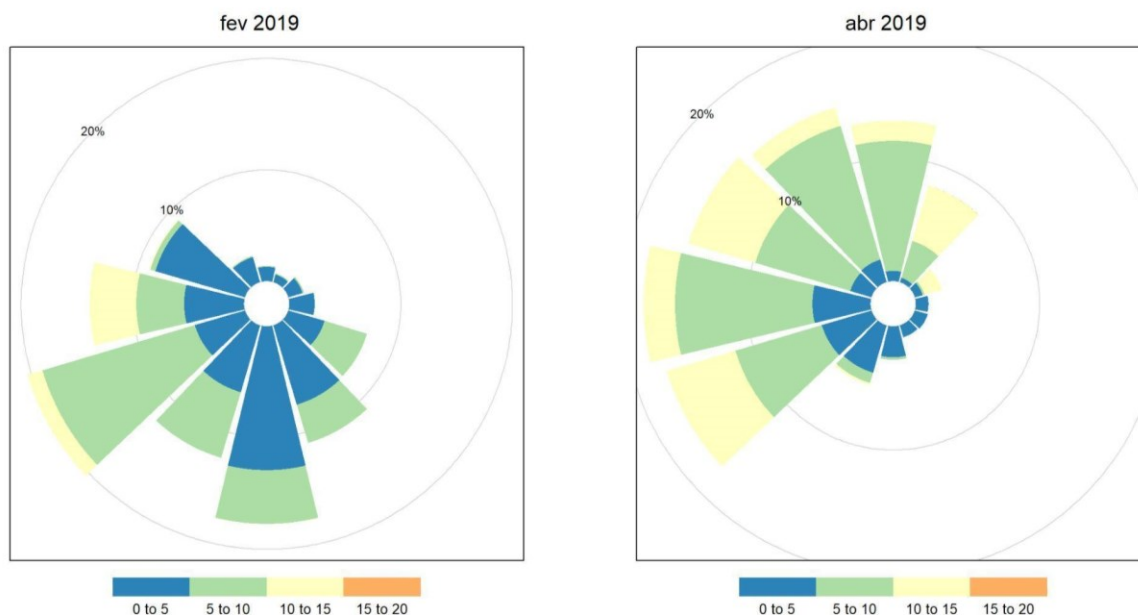


Figure S34. Wind intensity and direction of February and April of 2019. Each graph shows the relative frequency (%) of wind direction and intensity (m/s).

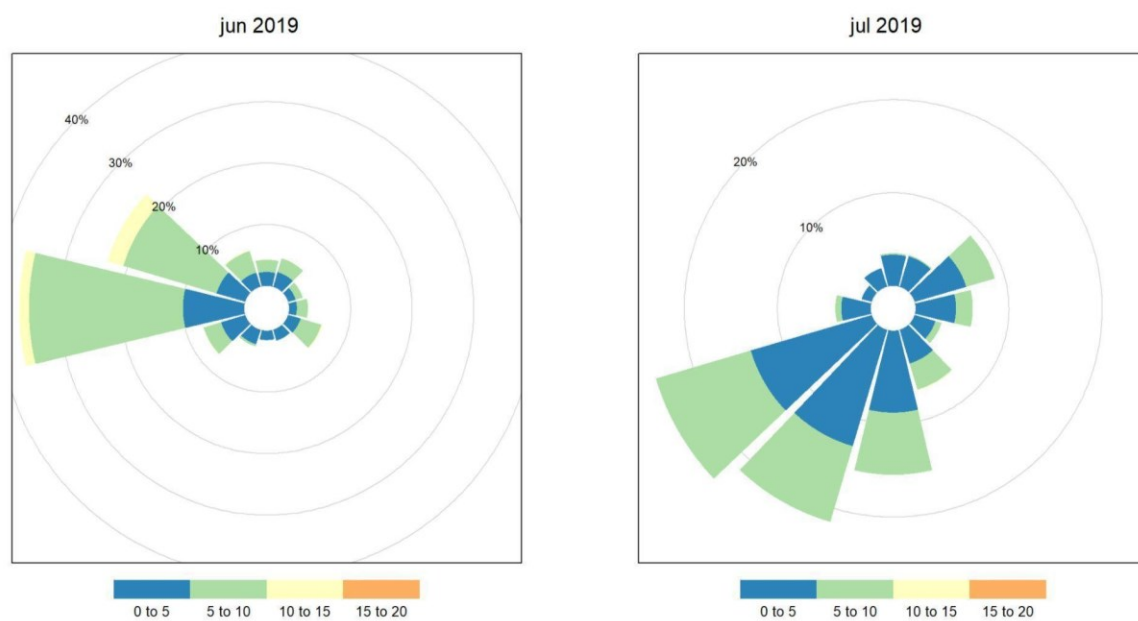


Figure S35. Wind intensity and direction of June and July of 2019. Each graph shows the relative frequency (%) of wind direction and intensity (m/s).

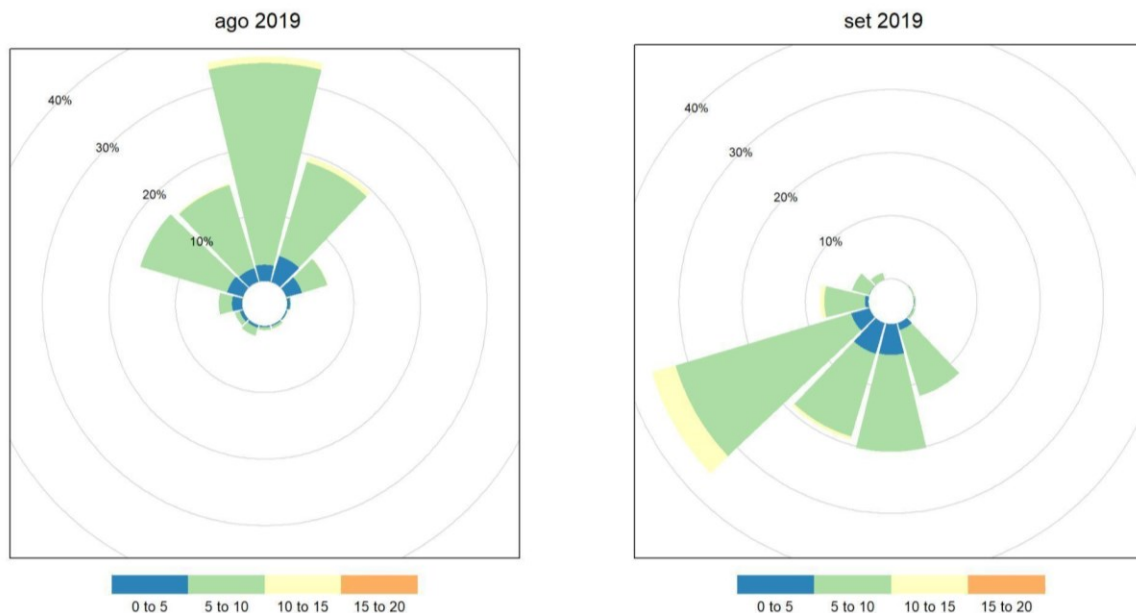


Figure S36. Wind intensity and direction of August and September of 2019. Each graph shows the relative frequency (%) of wind direction and intensity (m/s).

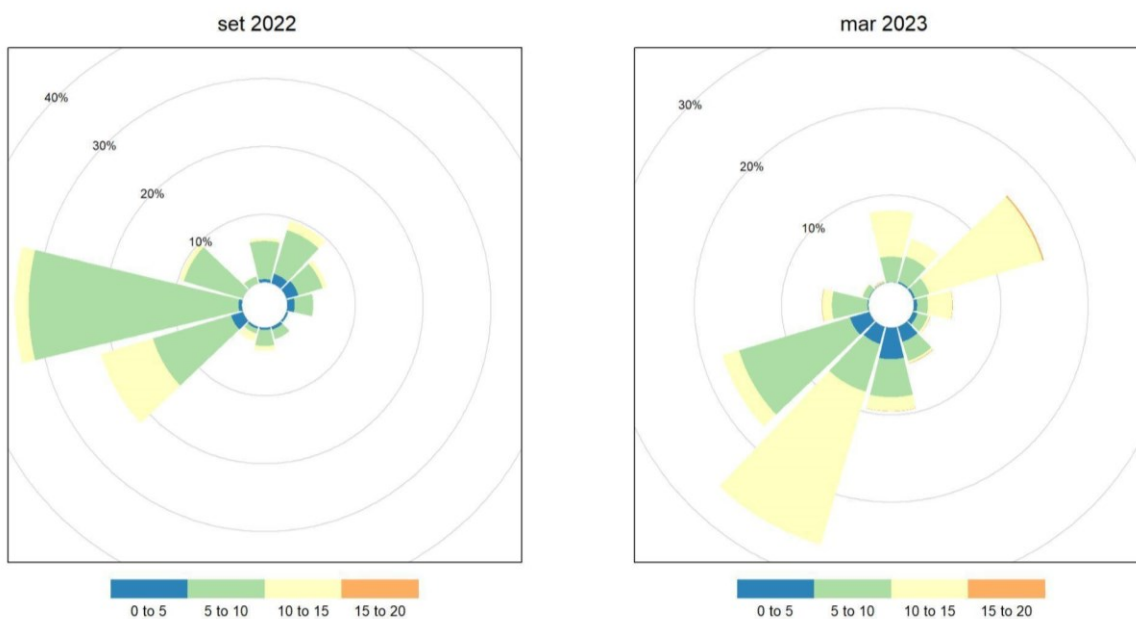


Figure S37. Wind intensity and direction of September of 2022 and March of 2023. Each graph shows the relative frequency (%) of wind direction and intensity (m/s).

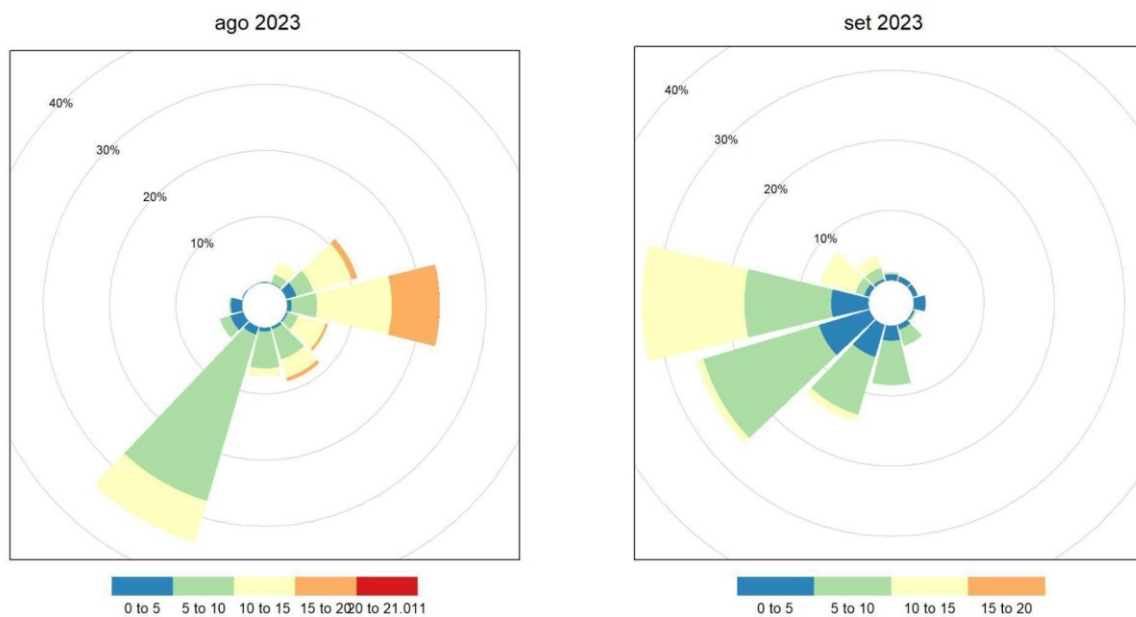


Figure S38. Wind intensity and direction of August and September of 2023. Each graph shows the relative frequency (%) of wind direction and intensity (m/s).

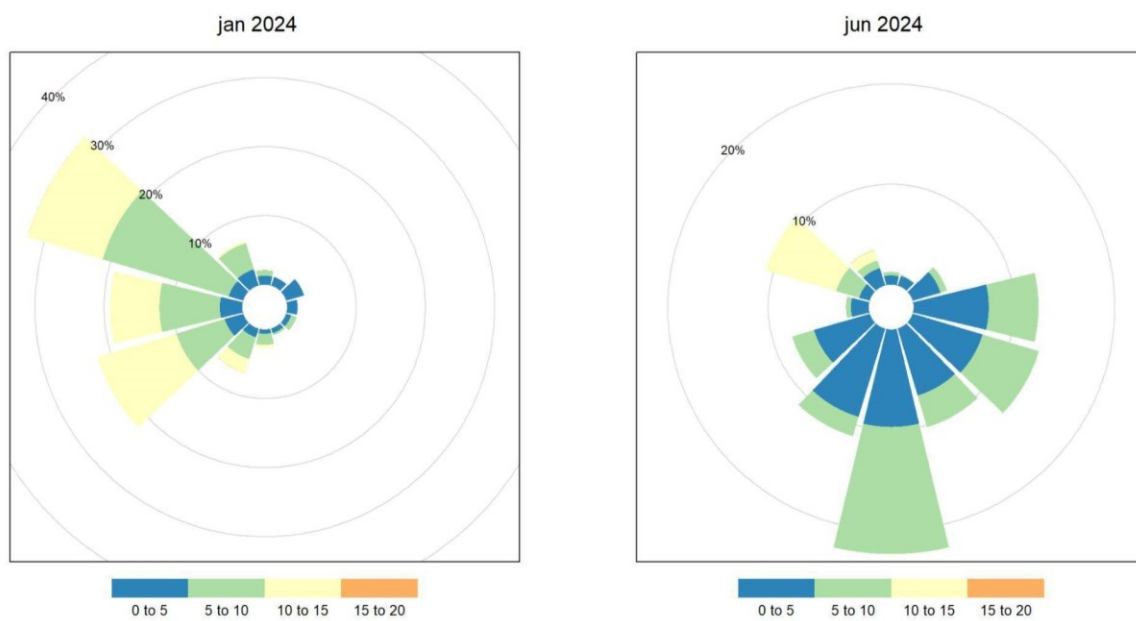


Figure S39. Wind intensity and direction of January and June of 2024. Each graph shows the relative frequency (%) of wind direction and intensity (m/s).

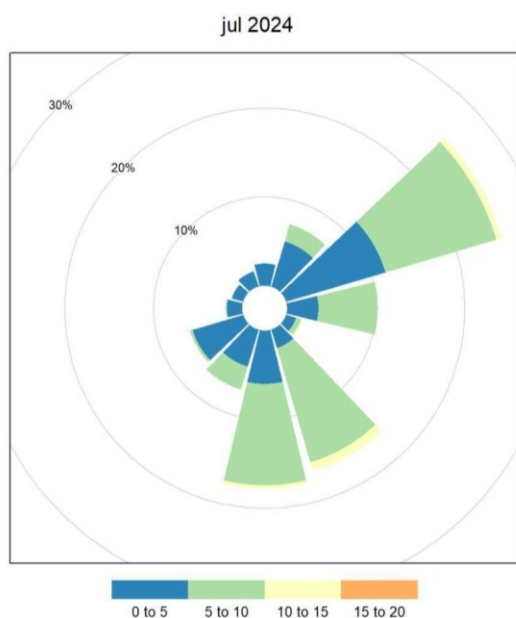


Figure S40. Wind intensity and direction of July of 2024. Each graph shows the relative frequency (%) of wind direction and intensity (m/s).