UNIVERSIDADE FEDERAL DO ESTADO DO RIO DE JANEIRO

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Taxonomia integrada de espécies bentônicas de *Prorocentrum* e análise espaço-temporal de dinoflagelados bentônicos do Arquipélago de Fernando de Noronha

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Tese apresentada ao Programa de Pós-Graduação em Ciências Biológicas - Biodiversidade Neotropical da Universidade Federal do Estado do Rio de Janeiro como requisito para a obtenção do grau de Doutora em Ciências Biológicas.

Orientadora: Profª. Drª. Silvia Mattos Nascimento

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Resumo

Dinoflagelados bentônicos produzem biotoxinas que afetam ecossistemas e podem intoxicar humanos pelo consumo de organismos contaminados ou pela exposição a aerossóis marinhos. Fatores antrópicos, como as mudanças climáticas e a eutrofização, têm impulsionado o aumento global das florações nocivas. Esta tese está dividida em três capítulos. O capítulo 1 apresenta um estudo de taxonomia integrada e abundância das espécies bentônicas de *Prorocentrum* da costa e das ilhas oceânicas do Brasil, assim como uma revisão global da distribuição geográfica e da riqueza dessas espécies. Onze espécies bentônicas de *Prorocentrum* foram identificadas no Brasil, e a revisão da literatura indicou um gradiente latitudinal, com maior riqueza em regiões tropicais e subtropicais. No capítulo 2, a análise temporal dos gêneros de dinoflagelados bentônicos em Fernando de Noronha (FN) mostrou aumento significativo na abundância de dinoflagelados entre 2021–2023 em relação a 2017–2019, associado ao aumento da temperatura da superfície do mar e ao maior aporte de nutrientes decorrente do crescimento populacional, da expansão do turismo e da baixa eficiência do tratamento de efluentes. Os dados de abundância gerados nesta tese foram importantes para alertar a comunidade e os gestores de FN sobre a possível ocorrência da doença ciguatera, posteriormente registrada na região. No capítulo 3, a análise espacial de dinoflagelados bentônicos em 12 sítios, situados na Área de Proteção Ambiental (APA) e no Parque Nacional Marinho (PARNAMAR) de FN, revelou variações na composição, abundância e riqueza de dinoflagelados bentônicos entre as duas áreas, associadas a diferentes níveis de pressão antrópica. Sítios da APA, mais impactados por nutrientes e efluentes, apresentaram dominância e florações de *Ostreopsis* e menor riqueza de espécies. Já os sítios do PARNAMAR exibiram assembleias mais ricas e com menor abundância, indicando o potencial desses organismos como bioindicadores. A interação entre mudanças climáticas e outros estressores antrópicos influencia a assembleia de dinoflagelados bentônicos e a ocorrência de florações nocivas em FN, reforçando a urgência de gerir efluentes, controlar a poluição e implementar monitoramento ambiental para proteger a biodiversidade, os serviços ecossistêmicos, a saúde humana e as atividades econômicas de uma das áreas mais biodiversas do Oceano Atlântico Sudoeste.

Palavras-chave: Florações de algas nocivas, microalgas, *Prorocentrum*, *Ostreopsis*, *Gambierdiscus*, Ciguatera.

Abstract

Benthic dinoflagellates produce biotoxins that affect ecosystems and can intoxicate humans through the consumption of contaminated organisms or exposure to marine aerosols. Anthropogenic factors, such as climate change and eutrophication, have driven the global increase in harmful algal blooms. This thesis is divided into three chapters. Chapter 1 presents a study of integrated taxonomy and abundance of benthic *Prorocentrum* species from the Brazilian coast and oceanic islands, as well as a global review of the geographic distribution and species richness of these genus. Eleven benthic *Prorocentrum* species were identified in Brazil, and the literature review indicated a latitudinal gradient, with higher richness in tropical and subtropical regions. In Chapter 2, the temporal analysis of benthic dinoflagellate genera at Fernando de Noronha (FN) showed a significant increase in dinoflagellate abundance between 2021–2023 compared to 2017–2019, associated with rising sea surface temperature and increased nutrient inputs resulting from population growth, tourism expansion, and low efficiency of wastewater treatment. The abundance data generated in this thesis were important to alert the community and managers of FN to the possible occurrence of ciguatera disease, which was subsequently recorded in the region. In Chapter 3, the spatial analysis of benthic dinoflagellates at 12 sites located within the Environmental Protection Area (EPA) and the Marine National Park (MNP) of FN revealed variations in the composition, abundance, and richness of benthic dinoflagellates between the two areas, associated with different levels of anthropogenic pressure. Sites within the EPA, more impacted by nutrients and effluents, exhibited dominance and *Ostreopsis* blooms, and lower species richness. In contrast, sites within the MNP displayed richer assemblages with lower abundance, indicating the potential of these organisms as bioindicators. The interaction between climate change and other anthropogenic stressors influences benthic dinoflagellate assemblages and the occurrence of harmful blooms at FN, reinforcing the urgency of managing effluents, controlling pollution, and implementing environmental monitoring to protect biodiversity, ecosystem services, human health, and economic activities in one of the most biodiverse areas of the Southwestern Atlantic Ocean.

Keywords: Harmful algal blooms, microalgae, *Prorocentrum*, *Ostreopsis*, *Gambierdiscus*, Ciguatera.

Sumário

Introdução geral.....11

Estrutura da tese.....14

Capítulo 01: Taxonomy and abundance of epibenthic *Prorocentrum* (Dinophyceae) species from the tropical and subtropical Southwest Atlantic Ocean including a review of their global diversity and distribution.....16

Abstract.....17

Introduction.....17

Materials and Methods.....18

Results.....20

Discussion.....25

Conclusion.....31

Acknowledgements.....32

References.....32

Capítulo 02: Temporal dynamics of benthic dinoflagellates at the oceanic Fernando de Noronha Archipelago (Tropical South Atlantic) in a warming ocean…….....35

Abstract.....35

Introduction.....36

Materials and Methods.....38

Results.....43

Discussion.....54

Acknowledgements.....60

References.....60

Capítulo 03: Influence of marine pollution on benthic dinoflagellates assemblage of a Marine Protected Area in the Tropical South Atlantic Ocean….....73

Introduction.....73

Materials and Methods.....75

Results.....81

Discussion.....89

Conclusion.....93

Acknowledgements.....93

References.....94

Conclusões gerais.....102

Referências Bibliográficas.....104

Apêndice 1: Atividades de divulgação científica e popularização da ciência 110

Anexo: Manual do Cientista Cidadão em Noronha – Capítulo: Microalgas Nocivas e Ciguatera.....112

Apêndice 2: Materiais suplementares dos capítulos 1 e 2.....116

Introdução geral

Os oceanos cobrem cerca de 70% da superfície da Terra e são uma parte essencial do sistema hidrosférico global, desempenhando um papel crucial na manutenção da saúde planetária (Santos et al., 2020). Eles sustentam a vida e fornecem inúmeros serviços ecossistêmicos, incluindo o fornecimento de alimentos, a regulação climática, a provisão de habitat, os serviços culturais e a ciclagem biogeoquímica de nutrientes (Hattam et al., 2015). Contudo, a zona costeira e o ambiente marinho encontram-se em processo contínuo de alteração devido a impactos múltiplos e cumulativos derivados das atividades humanas (Halpern et al., 2012). Além de impactos como a poluição, a degradação de habitats, a sobrepesca e a invasão de espécies exóticas, as mudanças climáticas têm comprometido a biodiversidade e os padrões regulatórios do oceano (Talukder et al., 2022). Muitos ecossistemas marinhos vêm passando por mudanças de fase, nas quais sistemas estruturalmente complexos e biodiversos dão lugar a sistemas simplificados e de menor biodiversidade (Souter et al., 2021).

O aquecimento oceânico está influenciando e modificando a diversidade de espécies, os padrões de abundância e a composição das comunidades, impulsionando extinções e desencadeando deslocamentos em direção aos polos e em escala regional na distribuição das espécies, resultando em alterações biogeográficas (Antão et al., 2020; Talukder et al., 2022). Além do aumento da temperatura, a eutrofização constitui outro problema ambiental de escala global, afetando regiões costeiras em todo o mundo devido à entrada excessiva de nutrientes, especialmente nitrogênio (N) e fósforo (P) (Devlin e Brodie, 2023).

A poluição por nutrientes pode ter como origem fontes pontuais, como efluentes de esgoto (tratados ou não), e fontes difusas, principalmente o escoamento superficial de bacias agrícolas (Kitsiou e Karydis, 2011). N e P são considerados macronutrientes em ambientes aquáticos, e são a base de moléculas essenciais à vida, como aminoácidos, proteínas e fosfolipídios. Entretanto, a entrada excessiva de nutrientes causa uma variedade de impactos, como: altos níveis de clorofila-a, crescimento elevado de macroalgas, florações de algas nocivas (FANs), redução da biodiversidade e diminuição da transparência da água. Em estágios mais avançados, observam-se altos níveis de bactérias e fungos, formação de espuma, além de hipóxia e anóxia (Kitsiou e Karydis, 2011; Devlin e Brodie, 2023).

Em nível global, o oceano tem sido historicamente tratado como destino final de resíduos, sobretudo em razão da crença de que a diluição seria suficiente para solucionar a poluição (Knowlton, 2004). Enquanto países de alta renda tratam cerca de 70% dos efluentes municipais e industriais, nos países de baixa renda apenas 8% passam por algum tipo de tratamento, o que resulta na estimativa de que mais de 80% dos efluentes gerados no mundo são descartados sem tratamento (WWAP, 2017), podendo chegar aos oceanos.

Entre os organismos que habitam o oceano, as microalgas estão entre os primeiros a responder às mudanças nas condições oceânicas, pois apresentam tempos de geração rápidos e ciclos de vida curtos (Irwin et al., 2015), além de sua distribuição, sobrevivência e sucesso estarem estreitamente relacionadas às características físicas e químicas das águas que habitam (Trainer et al., 2020). A distribuição geográfica das espécies de microalgas é, em grande parte, determinada pela temperatura (Longhurst, 1998), uma vez que este fator influencia a motilidade celular, a germinação de cistos, a absorção de nutrientes, a fotossíntese, o crescimento celular e outros processos fisiológicos (Wells et al., 2015). A disponibilidade de nutrientes, tanto inorgânicos quanto orgânicos, desempenha um papel importante no crescimento, abundância e distribuição das microalgas, pois alteram suas taxas de crescimento, tolerâncias fisiológicas e vantagens competitivas (Wells et al., 2020; Glibert, 2020).

É amplamente reconhecido que as alterações climáticas e o aumento da disponibilidade de nutrientes têm contribuído para a intensificação da eutrofização global e para a ampliação da ocorrência de FANs (Glibert, 2020). Essas florações vêm sendo registradas com maior frequência, em novas áreas geográficas, apresentando maior duração, bem como uma ampla variedade de impactos e níveis de toxicidade (Glibert, 2020). As FANs, especialmente aquelas formadas por espécies capazes de sintetizar toxinas, são prejudiciais ao ecossistema marinho e podem afetar negativamente a fauna (Landsberg, 2002), além de impactar a saúde humana (Vila et al., 2016) e a economia, com perdas significativas nos recursos pesqueiros e no turismo (Berdalet et al., 2017).

Dentre as microalgas, os dinoflagelados constituem o grupo com o maior número de espécies tóxicas, com 118 espécies listadas na Lista de Referência de Microalgas Nocivas do IOC-UNESCO (Lundholm et al., 2026). Entre os dinoflagelados de hábito bentônico, destacam-se os gêneros *Ostreopsis*, *Gambierdiscus*, *Prorocentrum*, *Coolia* e *Amphidinium* (Holmes et al., 1995; Kobayashi e Kubota, 2007; Lee et al., 2016; Berdalet et al., 2017).

Essas toxinas incluem análogos da palitoxina (PLTX), as ovatoxinas, produzidas por espécies do gênero *Ostreopsis* (Pavaux et al., 2020). *Ostreopsis* tem sido amplamente estudado por estar associado a eventos de floração massiva, especialmente no Mar Mediterrâneo (Gladan et al., 2019), os quais podem causar impactos à saúde humana, tanto pelo consumo de frutos do mar contaminados com PLTX (Alcala et al., 1988; Randall, 2005) quanto pela exposição direta à água do mar e/ou aos aerossóis durante as florações (Vila et al., 2016), além de provocar a morte de organismos marinhos (Pavaux et al., 2020).

Espécies do gênero *Gambierdiscus* produzem ciguatoxinas (CTX) que são responsáveis pela doença ciguatera (Friedman et al., 2017). O gênero *Gambierdiscus* geralmente não forma florações, entretanto, devido à alta toxicidade de algumas espécies (Litaker et al., 2017), baixas abundâncias deste gênero já podem ser prejudiciais à saúde humana. Há cerca de 180 sintomas já descritos associados à ciguatera, incluindo sintomas gastrointestinais, neurológicos e cardiovasculares que ocorrem após o consumo de organismos marinhos, principalmente peixes, contaminados com CTX (Friedman et al., 2017). Em áreas afetadas, como o Caribe e o Pacífico, a ciguatera representa uma importante ameaça à saúde humana e gera impactos econômicos significativos, com perdas financeiras severas para o comércio de peixe local e internacional, bem como para o turismo (Chinain et al., 2021).

O gênero *Prorocentrum* constitui uma parte significativa da assembleia de dinoflagelados bentônicos em áreas tropicais (Delgado et al., 2006; Okolodkov et al., 2007; Boisnoir et al., 2019). Algumas espécies bentônicas de *Prorocentrum* produzem toxinas, como o ácido ocadáico e/ou seus derivados, dinofisistoxinas, borbotoxinas e prorocentrolídeos (Lee et al., 2016; Nascimento et al., 2017). Essas toxinas podem se acumular em moluscos e, consequentemente, causar a intoxicação diarreica por moluscos (DSP, da sigla em inglês *Diarrhetic Shellfish Poisoning*) em humanos (Lee et al., 2016). Os demais gêneros, *Coolia* e *Amphidinium*, produzem diferentes compostos tóxicos (Holmes et al., 1995; Kobayashi e Kubota, 2007), entretanto, até o momento, não foram registrados impactos ecológicos ou à saúde humana devido à presença de suas toxinas no ambiente marinho.

Portanto, uma vez que a assembleia de dinoflagelados bentônicos possui espécies produtoras de diferentes toxinas, incluindo algumas das toxinas naturais marinhas mais potentes conhecidas até o momento, produzidas por espécies de *Gambierdiscus* e *Ostreopsis*

(Fusetani e Kem, 2009), torna-se de extrema importância realizar a identificação taxonômica e a quantificação desses organismos, visto que diferentes espécies produzem diferentes toxinas e em concentrações distintas. Além disso, compreender a distribuição geográfica e abundância dessas espécies é particularmente relevante frente às mudanças climáticas, como o aumento da temperatura do oceano, e à eutrofização global, fatores que podem favorecer a intensificação das FANs e aumentar os riscos ecológicos e à saúde humana.

No Oceano Atlântico Sudoeste, a maioria das pesquisas sobre dinoflagelados bentônicos tem se concentrado na taxonomia, filogenia e/ou toxicidade dos gêneros *Ostreopsis* (Nascimento et al., 2012, 2020; Gómez et al., 2017a; Mendes et al., 2017; Tibiriçá et al., 2019; Borsato et al., 2020), *Gambierdiscus* (Nascimento et al., 2015), *Prorocentrum* (Nascimento et al., 2016, 2017; Gómez et al., 2017b; Mendes et al., 2019; Moreira-González et al., 2019a, 2019b, 2022) e *Coolia* (Gómez et al., 2016; Nascimento et al., 2019; Mendes et al., 2019; Moreira-González et al., 2019a; Tibiriçá et al., 2020), geralmente isolados da costa brasileira. Estudos ecológicos, que abordam a abundância da assembleia de dinoflagelados bentônicos em escalas espacial e temporal, são ainda escassos na região, e, até o momento, nenhum foi realizado em ilhas oceânicas brasileiras, que permanecem em grande parte inexploradas. Assim, torna-se essencial preencher essas lacunas de conhecimento e expandir os estudos para regiões geográficas ainda pouco investigadas.

Estrutura da tese

Esta tese foi dividida em três capítulos:

O primeiro capítulo, intitulado “Taxonomy and abundance of epibenthic *Prorocentrum* (Dinophyceae) species from the tropical and subtropical Southwest Atlantic Ocean including a review of their global diversity and distribution”, foi publicado em uma edição especial da revista científica Harmful Algae, em 2023. Este artigo investigou os padrões de riqueza e distribuição de espécies bentônicas do gênero *Prorocentrum* ao longo do Oceano Atlântico Sudoeste tropical e subtropical, abrangendo áreas costeiras e ilhas oceânicas. Foram integrados dados morfológicos, moleculares e de abundância das espécies encontradas ao longo de aproximadamente 2000 km de litoral. Além disso, foi apresentada uma revisão global da riqueza e distribuição geográfica das espécies bentônicas de *Prorocentrum*.

O segundo capítulo, intitulado “Temporal dynamics of benthic dinoflagellates at the oceanic Fernando de Noronha Archipelago (Tropical South Atlantic) in a warming ocean”, está em preparação para submissão à revista científica Harmful Algae. Este artigo apresenta a primeira investigação espacial e temporal da assembleia de dinoflagelados bentônicos no Arquipélago de Fernando de Noronha. A composição de espécies dessa assembleia foi caracterizada, e foram realizadas análises de tendência temporal da abundância dos gêneros de dinoflagelados no período de 2017 a 2023, bem como da temperatura da superfície do mar no arquipélago ao longo dos últimos 40 anos. Além disso, foram analisadas as diferenças na abundância de dinoflagelados em função da profundidade de amostragem.

O terceiro capítulo, intitulado “Influence of marine pollution on benthic dinoflagellates assemblage of a Marine Protected Area in the Tropical South Atlantic Ocean”, está em preparação para submissão à revista Marine Pollution Bulletin. Neste artigo, a abundância, a composição de espécies e a riqueza da assembleia de dinoflagelados bentônicos foram avaliadas em duas Unidades de Conservação do Arquipélago de Fernando de Noronha, locais inseridos no Parque Nacional Marinho (PARNAMAR) e na Área de Proteção Ambiental (APA), que apresentam diferentes níveis de proteção. Esses parâmetros foram relacionados aos impactos antropogênicos locais.

Todos os capítulos são apresentados em língua inglesa seguindo as normas das respectivas revistas científicas.

Capítulo 1

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Taxonomy and abundance of epibenthic *Prorocentrum* (Dinophyceae) species from the tropical and subtropical Southwest Atlantic Ocean including a review of their global diversity and distribution

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Phylogeny

ABSTRACT

In the tropical and subtropical South Atlantic Ocean, studies on the taxonomy and abundance of benthic harmful algae are scarce and the region has been largely under investigated. In this study, morphological descriptions, molecular (LSU rDNA and ITS region) and abundance data of benthic *Prorocentrum* species from the tropical and subtropical Southwest Atlantic and three oceanic islands are presented. Moreover, a review of global benthic *Prorocentrum* species richness and distribution is presented. Eleven benthic *Prorocentrum* species were found in Brazil. Morphological and molecular data on *P. borbonicum, P. hoffmannianum, P. lima* species complex and *P. rhathymum* were provided. *Prorocentrum panamense, P.* cf. *caipirignum, P.* cf. *concavum, P.* cf. *norrisianum, P. emarginatum/fukuyoi/sculptile* complex and two not identified species were observed using scanning electron and/or light microscopy, and morphological descriptions are presented. *Prorocentrum lima* species complex was found at all investigated sites, in abundances up to 2×10^4 cells g^{-1} FW at the Northeast Brazil, while maximum abundance of all the remaining species did not exceed 1×10^3 cells g^{-1} FW. The Fernando de Noronha archipelago can be considered a hotspot of benthic *Prorocentrum* species diversity, with ten species registered. Data compiled in the literature review shows a clear latitudinal gradient with higher species richness in tropical and subtropical regions relative to temperate areas. It is also evident that there is a bias caused by taxonomic impediment and an uneven sampling effort, with many regions still to be investigated using a combined morphological and molecular effort. Therefore, the current knowledge on the global distribution of benthic *Prorocentrum* species is likely underestimated.

1. Introduction

The genus *Prorocentrum* Ehrenberg (1834) encompasses 84 valid species (Guiry and Guiry, 2022) and half of these are benthic/epibenthic and can be found associated with macroalgae, coral reefs, debris, and among sand grains in the marine environment (Fukuyo, 1981; Faust 1990; Tindall and Morton, 1998; Ten-Hage et al., 2000; Richlen and Lobel, 2011; Yong et al., 2018). Some benthic *Prorocentrum* species have been reported to produce toxins such as okadaic acid (OA) and its analogues, dinophysistoxins (DTXs) (Nakajima et al., 1981; Murakami et al., 1982; Holmes et al., 2001; Caillaud et al., 2010; Nascimento et al., 2017; Nishimura et al., 2020), responsible for diarrhetic shellfish poisoning (DSP) (Murakami et al., 1982).

Prorocentrum morphology is characterized by two lateral plates joined by a sagittal suture, with small platelets in the periflagellar area at the anterior end of the cell (Hoppenrath et al., 2013). The taxonomy of this genus is based on morphological criteria such as cell shape and size, cell surface ornamentation and pore pattern, intercalary band morphology, and number, shape and organization of platelets and structures (spines, collars and protrusions) in the periflagellar area (Hoppenrath et al., 2013). The periflagellar area is considered a valuable and promising taxonomic feature in the genus, while other

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morphological characters, such as cell shape and pore pattern may be variable in some species or present subtle differences among species (Hoppenrath et al., 2013). The analysis of molecular data is therefore necessary, in combination with morphological studies, to unambiguously identify the species of *Prorocentrum* and other dinoflagellates (Nagahama et al., 2011; Nascimento et al., 2017, 2019; Jang et al., 2018; Lim et al., 2019; Chomérat et al., 2020).

Prorocentrum species generally constitute a significant part of benthic dinoflagellate assemblages in tropical and subtropical areas and occur with several species of the genera *Amphidinium* Claperède & Lachmann, *Coolia* A. Meunier, *Gambierdiscus* R. Adachi & Y. Fukuyo and *Ostreopsis* J. Schmidt (Tindall and Morton, 1998; Delgado et al., 2006; Richlen and Lobel, 2011; Boisnoir et al., 2019). Many studies have revealed high *Prorocentrum* richness in benthic reef ecosystems in the Pacific and Indian Oceans, and particularly in the Caribbean Sea, where numerous benthic *Prorocentrum* species have been originally described (Faust, 1990, 1993a, 1993b, 1994, 1997; Faust et al., 2008). The Pacific Ocean was the type locality of some benthic *Prorocentrum* species as well (Fukuyo, 1981; Mohammad-Noor et al., 2007; Hoppenrath and Leander, 2008; Lim et al., 2019), while a smaller number has been described from the Indian Ocean (Ten-Hage et al., 2000; Chomérat et al., 2012). Only two benthic *Prorocentrum* species have been described from the South Atlantic Ocean (Nascimento et al., 2017; Arteaga-Sogamoso et al., 2023).

In the Atlantic Ocean, many studies have focused on the occurrence and toxicity of *Prorocentrum lima* species complex in temperate areas, such as the United States (Morton et al., 1999; Maranda et al., 2007a, 2007b), Canada (Lawrence et al., 2000; Levasseur et al., 2003), United Kingdom (Foden et al., 2005; Nascimento et al., 2005), Ireland (Kilcoyne et al., 2020), Portugal (Vale et al., 2009), Spain (Bravo et al., 2001) and Argentina (Gayoso et al., 2002). Some studies in the temperate Atlantic have also evaluated the distribution and diversity of other benthic *Prorocentrum* species in France (e.g. Chomérat et al., 2010, 2011), the Bay of Biscay (Laza-Martinez et al., 2011; David et al., 2014) and Sweden (Álvarez et al., 2022). In the tropical and subtropical Atlantic, apart from the Caribbean Sea and Florida, studies on the diversity and abundance of benthic *Prorocentrum* species are scarce and the region has been investigated only recently (Nascimento et al., 2016, 2017; Gómez et al., 2017; Fernández-Zabala et al., 2019, 2022; Mendes et al., 2019; Moreira-González et al., 2019a, 2019b, 2020; Godinho et al., 2022; Arteaga-Sogamoso et al., 2023).

Climate change is altering species distribution, strongly linked to the recent increase in global temperature (Lenoir and Svenning, 2015). Besides that, other anthropogenic stressors, like eutrophication, are taking place in coastal areas worldwide and have a detrimental effect on species diversity. It is important to characterize current species distribution and abundance patterns in a world under increasing pressure on coastal systems and their biodiversity, particularly in the high-diversity and less-studied tropical areas.

The aim of this work was to study the patterns of benthic *Prorocentrum* species richness and distribution along the tropical and subtropical Southwest Atlantic, including coastal sites and oceanic islands. Species morphological descriptions and molecular data were provided, including the analysis of field and isolated cells kept in culture. *Prorocentrum* species abundance from 14 sampling sites distributed along nearly 2000 km of coastline was determined and a global review of benthic *Prorocentrum* species richness and distribution is presented.

2. Materials and methods

2.1. Sample collection and treatment

Macroalgal samples were collected by diving from 12 locations along the Northeast and Southeast Brazilian coast and from three oceanic islands, from latitude 00°55′10″ N to 23°00′03″ S (Supplementary Table S1, Fig. 1). In total, 633 macroalgae samples were collected, 487 from the Southeast coast, 89 from the Northeast coast and 57 from the oceanic islands. Macroalgae species varied between sampling sites (see Supplementary Table S2 for a full list of genera). During sampling, macroalgae were placed in sealable plastic bags and were vigorously shaken for two minutes to detach the associated epiphytic cells. The epiphytic suspensions were preserved with 1% neutral Lugol iodine solution for species identification and quantification in the laboratory. Date of sampling, depth and seawater temperature (measured in situ at the time of sampling or estimated from satellites) from each sampling site are presented in Supplementary Table S1. Scientific research and collecting permit authorizing field studies were obtained from "Instituto Chico Mendes de Conservação da Biodiversidade" (ICMBio), Brazilian Ministry of the Environment (permit numbers: 35,192–1, 35,192–2, 35,192–3).

2.2. Cultures establishment

At six of the 15 sites, in addition to the samples preserved with Lugol,

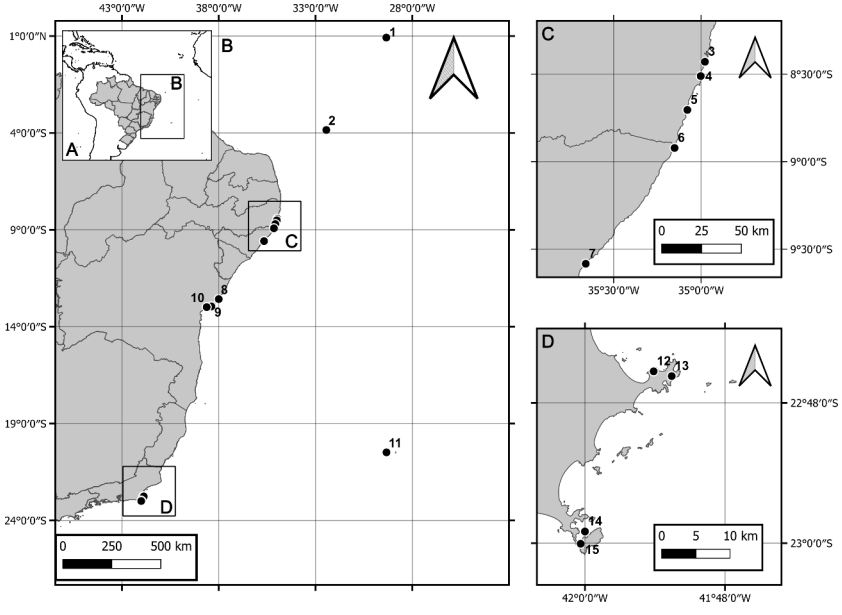


Fig. 1. Map showing sampling sites at the coast and oceanic islands of Brazil. (A). Brazil, South Atlantic Ocean, (B). Coastal and oceanic area showing the fifteen sampling sites, (C). Some sites at the Northeast coast, (D). Sites at the Southeast coast. 1. Saint Paul's Rocks Archipelago; 2. Fernando de Noronha Archipelago; 3. Muro Alto; 4. Porto de Galinhas; 5. Carneiros; 6. Maragogi; 7. Garça Torta; 8. Forte; 9. Placaford; 10. Penha; 11. Trindade Island; 12. Tartaruga; 13. Forno-AB; 14. Forno-AC; 15. Cabo Frio.

epiphyte suspensions were kept alive for the isolation of strains and the establishment of cultures in the laboratory, according to Nascimento et al. (2017). The place of origin of each strain is presented in Supplementary Table S1. Cultures were maintained in L1 medium (Guillard and Hargraves, 1993) that was modified by omitting silicate, nickel, vanadium and chromium. They were kept in a temperature-controlled cabinet at 24 ± 2 ºC with a light/dark cycle of 12 h/12 h and a photon flux density of 70 μmol m^{-2} s^{-1}, provided by cool-white fluorescent tubular lamps. Photosynthetically active radiation was measured with a QSL-100 quantum sensor (Biospherical Instruments, San Diego, California, USA).

2.3. Morphological characterization

Cultured cells and Lugol preserved field cells were observed by light microscopy (LM) and scanning electron microscopy (SEM). Cells were observed in a light microscope (ImagerA2, Zeiss, Germany) and images were captured with an AxioCam ICc1 digital camera (Zeiss, Germany). For observation of *Prorocentrum* cells kept in culture using SEM, cells were fixed with 2% glutaraldehyde SEM grade (Merck, Darmstadt, Germany) for 1 hour. Cells were then filtered through Durapore membrane filters (0.22 μm pore size, Millipore, USA), rinsed twice with distilled water for 10 min and subjected to dehydration through a series of ethanol (10, 30, 50, 70, 80, 95 and twice at 100%, 10 min each step), followed by three drops of hexamethildisilazane (HMDS) (Spectrum Chemical MFG. CORP. New Brunswick, NJ, USA).

Field cells preserved with Lugol were isolated under observation in LM and transferred to a 1.5 ml tube with filtered and autoclaved seawater. The isolated field cells were then harvested in Durapore membrane filters (0.22 μm pore size, Millipore, USA), rinsed once with distilled water and dehydrated in an ethanol series, followed by HMDS, as described above. After being air-dried overnight, cultured and field cells were coated with nickel or gold with a sputter coater (Leica EM ACE 600, Germany) and observed with a Micro Quanta FEG 250 scanning electron microscope (FEI Company, Hillsboro, Oregon, USA). Scanning electron microscopy images were presented on a black background using Adobe Photoshop CS6.

Exponentially growing cultured cells were preserved with Lugol for length (L) and width (W) measurement using Axiovision software (Zeiss, Germany). The L and W of Lugol preserved field cells were measured using the Axiovision software or with a microscope eyepiece ruler (Imager A2 or Primovert, Zeiss, Germany).

2.4. Molecular characterization

Cells of strains UNR-11, UNR-12, UNR-15, UNR-35, UNR-44, UNR-68, UNR-72 and UNR-86 were harvested in 2 ml tubes by centrifugation at 5000 × *g* for 15 min for DNA extraction. The supernatant was discarded and the cell pellet was stored at −80 °C for further analysis. Genomic DNA was extracted using the commercial kit NucleoSpin® Plant II (Macherey-Nagel, Germany) following the manufacturer's instructions, and then stored at −20 °C. DNA quantification was performed using Qubit® 3.0 Fluorometer (Life Technologies) and checked by electrophoresis on a 1% (w/v) agarose gel in 1XTAE buffer (Tris-acetate-EDTA) stained with GelRed (Biotium Inc., USA).

Two nuclear loci were analyzed: the ITS region (ITS1–5.8S-ITS2) and the D1-D2 domain of the Large Subunit (LSU) ribosomal DNA. To amplify the ITS and the LSU loci, first, several pairs of primers available from the literature were tested, such as: ITSAxITSB (Sato et al., 2011), ITS1xITS4 (White et al., 1990), ProITS-FxProITS-R (Nagahama et al., 2011), D1RxD2C (Scholin et al., 1994a), D1RxD3Ca (Scholin et al., 1994b), D1RxLSUB (Scholin et al., 1994a; Litaker et al., 2003) and D1RxD3B (Scholin et al., 1994a; Nunn et al., 1996). The ITS sequences of strains UNR-11 and UNR-12 were eventually obtained using the pair of primers ITS1xITS4 (White et al., 1990) and the LSU sequences were obtained using the pair of primers D1RxD2C (Scholin et al., 1994a). Regarding the *P. hoffmannianum* strain UNR-44, and the *P. lima* species complex strains UNR-15, UNR-35, UNR-68, UNR-72 and UNR-86 sequences were obtained using four new pair of primers (Table 1) designed based on ITS and LSU sequences of the *P. lima* – *P. caipirignum* – *P. hoffmannianum* clade, available from GenBank, using the standard parameters of the Geneious Prime v2020.2.4 software (www.geneious.com). Forward and reverse primers were designed within conserved regions of the ITS and LSU multiple sequence alignment.

The amplification reaction mixture of 25 μL contained 1 unit (U) Taq DNA polymerase (Thermo Scientific Inc, USA), 1x reaction buffer with NH_4SO_4, 2.5 mM $MgCl_2$, 0.16 mM dNTPs (Thermo Scientific Inc., USA), 8 pmol of each primer, 0.2 mg of Bovine Serum Albumin (BSA) and ~10 ng of genomic DNA. For the *P. borbonicum* and *P. rhathymum* strains the PCR cycling comprised an initial 5 min heating step at 95 °C, followed by 40 cycles of 95 °C for 1 min, 45 °C (for ITS) or 58 °C (for LSU) for 1 min, 72 °C for 1 min, and a final extension at 72 °C for 5 min. Regarding the *P. hoffmannianum* and *P. lima* species complex strains the PCR cycling comprised an initial 5 min heating step at 95 °C, followed by 10 cycles of 95 °C for 1 min, touchdown of 60 °C-55 °C (Δ = −0,5 ºC/cycle) for 1 min, 72 °C for 90 s, 35 cycles of 95 °C for 1 min, 55 °C for 1 min, 72 °C for 90 s and a final extension at 72 °C for 5 min. PCR products were checked by electrophoresis on 1% (w/v) agarose gel in 1X TAE buffer stained with GelRed. PCR products were purified and sequenced by Macrogen Inc. (Seoul, Korea) in both directions, using the same PCR primers, through the traditional capillary sequencing method.

Sequence reads were manually checked and edited using Chromas 2.6.6 (http://technelysium.com.au/wp/chromas) and MEGA 7.0 (Kumar et al., 2016) programs. The new sequences obtained in the present study were first BLAST searched against the GenBank database (www.ncbi.nlm.nih.gov/blast) to test for sequence homology with non-target taxa. All sequences obtained in this study were deposited in GenBank.

The sequences were then aligned with other *Prorocentrum* sequences retrieved from GenBank using MAFFT 7.0 (Katoh and Standley, 2013) with the iterative refinement method L-INS-i. Phylogenetic analyses were conducted separately for each molecular marker. Sequences of *Adenoides eludens* were used as outgroup. The MEGA software was used to select the best-fit model of nucleotide substitution (T92+G+I for both markers) and construct maximum likelihood (ML) phylogenetic trees with 1000 bootstrap (BS) replications. The phylogenetic relationships were also examined using Bayesian inference (BI) with MrBayes 3.2.7a (Ronquist et al., 2012). To sample across nucleotide substitution models, the command "lset nst=mixed" was used before running the analysis. Markov Chain Monte Carlo procedure consisted of two independent trials with four chains each. Each chain was run for 1.000.000 generations and sampled every 100th cycle. Posterior probability (PP) values

Table 1
PCR primers designed in the present study to amplify the ITS and D1-D3 LSU loci of *P. hoffmannianum* and *P. lima* complex strains.

Target locus	Primer name and primer sequence (5′−3′)	Expected size
ITS (ITS1–5.8S-ITS2)	PLSC_ITS_F1 GTTGATTACGTCCCTGCCCT	~1000bp
	PLSC_ITS_R1 ATGAAAGCCACCACCACCTT	
	PLSC_ITS_F2 TGCACATCAGGGCACATTAT	~550bp
	PLSC_ITS_R2 TTCACTGGCCTAACATCGTG	
LSU (D1-D3 domain)	PLSC_D1D3_F1 CAGGATTCCGTGAGCCAACA	~1250bp
	PLSC_D1D3_R1 AGGGAAACTTCGGAGGGAAC	
	PLSC_D1D3_F2 TCAGTAATGGCGAATGAACG	~1200bp
	PLSC_D1D3_R2 TCGGAGGGAACCAGCTACTA	

for the resulting 50% majority rule consensus tree were estimated after discarding the first 10% of trees as burn-in.

2.5. Abundance data

Total benthic dinoflagellates abundance was quantified in field samples preserved with neutral Lugol iodine solution using a Sedgewick Rafter or sedimentation chamber, and observation in a light inverted microscope (Primovert, Zeiss, Germany). Fresh weight of macroalgae was measured and the abundance of benthic dinoflagellates was determined as cells per gram of fresh macroalgae weight (cells g^{-1} FW). The relative abundance (%) of the genus and species of *Prorocentrum* were calculated in relation to the total benthic dinoflagellate abundance, to show the contribution of the genus and species of *Prorocentrum* to the total abundance. Abundance data is not available for the Carneiros site.

The morphological features on which *P. emarginatum, P. fukuyoi* and *P. sculptile* are reliably distinguished are not yet clear (Hoppenrath et al., 2013) and not positively recognized through observation using the light microscope, therefore, cell dimensions, morphological descriptions and abundance data for these species from field samples were presented combined.

2.6. Literature survey of benthic Prorocentrum species richness and distribution

A literature survey on the diversity of benthic *Prorocentrum* species was carried out using the "Web of Science" database choosing the option "topic". Keywords used for searching included "Benthic and *Prorocentrum*", as well as the names of each benthic *Prorocentrum* species (Supplementary Table S3). Species that had their names emended, were searched for both names (e.g. *Prorocentrum levis* and *Prorocentrum leve*), the same was applied to currently synonymized species.

In total, 1009 publications were retrieved from this search (Supplementary Table S3) and after reading the abstracts of all retrieved studies, 505 were excluded due to any of the following reasons: the content was not about any benthic *Prorocentrum* species, or the species used as the searching term was cited only marginally, or the papers did not present the geographic origin of the benthic *Prorocentrum* strains. After this first trial, from the 504 publications left, 231 were excluded as they were duplicated. The remaining 273 papers were read in full and 66 of them were excluded as they did not present the geographical coordinates of sites where benthic *Prorocentrum* species were found. Finally, 207 papers were considered eligible and were used to compile data on global benthic *Prorocentrum* species distribution (Supplementary Table S2). The following information was compiled for each Ocean basin, from each field study: geographic coordinates of the investigated sites, benthic *Prorocentrum* species found, and the substrate (macroalgae, sediment, sand, coral reef, invertebrates, water) sampled. Laboratory studies that investigated isolated strains were also included when the place of origin of the strain was mentioned. The geographic coordinates were retrieved from the articles when informed, or were estimated. When different papers cited the same strain, only one publication was considered. The search ended on 22th March 2023. Other eight publications that were not retrieved in the literature search were posteriorly included, and data from 215 publications were compiled in Supplementary Table S2.

3. Results

3.1. Morphology and distribution

Ten strains of benthic *Prorocentrum* species were established (Supplementary Table S1), and eight of them were identified through combined morphological (LM and SEM) and molecular (ITS region and LSU rDNA) analysis. These strains include the species *P. borbonicum* (strain UNR-12), *P. hoffmannianum* (UNR-44), *P. lima* species complex (UNR-15, UNR-35, UNR-68, UNR-72 and UNR-86) and *P. rhathymum* (UNR-11). The two remaining strains, *P. borbonicum* (UNR-13) and *P. hoffmannianum* (UNR-29), were identified based on morphology. Moreover, field cells of *P. emarginatum/fukuyoi/sculptile* species complex and *P. panamense* were tentatively identified through observation of cell morphology on LM and SEM and *P.* cf. *caipirignum, P.* cf. *concavum* and *P.* cf. *norrisianum* through LM. Other two not identified species (*Prorocentrum* sp. 1 and *Prorocentrum* sp. 2) were observed using SEM. Dimensions of strains and field cells of *Prorocentrum* species are presented in Table 2. Cells of *Prorocentrum* species are described below.

Species observed through LM and SEM:

Prorocentrum borbonicum Ten-Hage, Turquet, Quod, Puiseux-Dao & Couté (2000)

Prorocentrum borbonicum cells from strains UNR-12 (Fig. 2A) and UNR-13 (Fig. 2B-D) were oblong to ovoid and symmetric. Thecal surface foveate with scattered pores, without a marginal row of pores (Fig. 2B-C). Round pores of two size classes, both located inside depressions (Fig. 2B-C), that were deeper at the center of the right thecal plate (Fig. 2B). Periflagellar area wide and V-shaped excavating the right thecal plate and composed of eight platelets (platelet 7 was not observed) (Fig. 2D). Cells with many golden-brown chloroplasts and a centrally located pyrenoid (Fig. 2A).

Distribution: Maragogi (sequence obtained), Fernando de Noronha and Trindade (morphospecies).

Prorocentrum emarginatum Fukuyo (1981)/*Prorocentrum fukuyoi* Murray S., et Nagahama Y., 2007/*Prorocentrum sculptile* M.A. Faust (1994) complex

Prorocentrum emarginatum/fukuyoi/sculptile species complex field cells were round to oval and slightly asymmetric (Fig. 3A-I). Thecal surface ornamentation was variable, and cells were smooth (Fig. 3B-E) or strong (Fig. 3F-G), slight (Fig. 3H) or faint (Fig. 3I) foveate. In cells with a smooth surface (Fig. 3B-E) or a slight (Fig. 3H) and faint (Fig. 3I) foveate ornamentation, pores were round and of two size classes, arranged in radial rows in some specimens (Fig. 3E, H-I). Marginal row of pores visible in some specimens (Fig. 3B-E, H-I) and center of thecal plates devoid of pores (Fig. 3B-I). Periflagellar area deep, narrow and V-shaped excavating the right thecal plate, with a wing (Fig. 3B-C, F).

Distribution: St. Paul's Rocks, Fernando de Noronha, Porto de Galinhas, Maragogi, Penha, Trindade, Tartaruga, Forno-AC and Cabo Frio (morphospecies).

Prorocentrum hoffmannianum M.A. Faust (1990) emend. S. Fraga (2018)

Prorocentrum hoffmannianum cells of strains UNR-29 (Fig. 4A-E) and UNR-44 and field cells from St. Paul's Rocks and Fernando de Noronha (Fig. 4F-I) were symmetric, ovoid to broadly oval, narrow at the anterior end and wider in the middle region of the cell, with a rounded posterior margin. Most field cells from Trindade showed a different cell shape, and were wider below the middle of the cell (Fig. 4J-L). Thecal surface reticulate-foveate with scattered pores, except in the central area, and a marginal row of pores (Fig. 4B-D, G-H, J-K). Some depressions with one or two round pores, or two pores merged and a larger elongated pore (oblong or kidney-shaped) (Fig. 4E, I). Periflagellar area V-shaped excavating the right thecal plate (Fig. 4A-C, E-F, G, J, L). Cells with many golden-brown chloroplasts and a centrally located pyrenoid (Fig. 4A, F).

Distribution: St. Paul's Rocks and Trindade (morphospecies), Fernando de Noronha (sequence obtained).

Prorocentrum lima species complex (Ehrenberg) F. Stein (1878) emend. Nagahama et al. (2011)

Prorocentrum lima cells of strains UNR-15 (Fig. 5A-D), UNR-35, UNR-68 and UNR-72 were symmetric, ovate, narrow at the anterior end and wider in the middle region (Fig. 5A-C). Thecal surface smooth with scattered pores, except in the central area, and a marginal row of pores (Fig. 5B-C). Round to oblong pores (Fig. 5D). Periflagellar area V-shaped excavating the right thecal plate (Fig. 5B). Cells with many golden-brown chloroplasts and a centrally located pyrenoid (Fig. 5A). *Prorocentrum lima* cells of strain UNR-86 (Fig. 5E) presented similar

Table 2
Dimensions of cultured and field cells of *Prorocentrum* species, indicating site of origin and size range, mean value ± standard deviation and number of cells measured (n).

Species	Sampling sites	Length (L)	Width (W)	L/W	Origin
Prorocentrum borbonicum	Maragogi	23.4 - 26.8 (25.0 ± 0.8, *n* = 69)	19.6 - 22.8 (21.2 ± 0.8, *n* = 69)	1.12 - 1.24 (1.18, *n* = 69)	Strains UNR-12 and UNR-13
Prorocentrum cf. *concavum*	Fernando de Noronha	40.0 - 57.5 (45.8 ± 4.9, *n* = 24)	32.5 - 50.0 (40.3 ± 4.6, *n* = 24)	1.1 - 1.4 (1.1 ± 0.1, *n* = 24)	Field
Prorocentrum emarginatum/fukuyoi/sculptile species complex	Fernando de Noronha	27.5 - 42.5 (33.8 ± 3.0, *n* = 120)	25.0 - 37.5 (29.8 ± 2.6, *n* = 120)	1.0 - 1.3 (1.1 ± 0.1, *n* = 120)	Field
	Trindade	28.0 - 37.0 (33.0 ± 4.0, *n* = 50)	23.0 - 31.0 (27.0 ± 3.0, *n* = 50)	1.0 - 1.3 (1.2 ± 0.1, *n* = 50)	Field
Prorocentrum hoffmannianum	Fernando de Noronha	45.0 - 50.0 (47.9 ± 1.7, *n* = 50)	37.5 - 42.5 (39.4 ± 1.5, *n* = 50)	1.1 - 1.3 (1.2 ± 0, *n* = 50)	Strain UNR-44
	Fernando de Noronha	47.5 - 57.5 (53.2 ± 2.3, *n* = 102)	35.0 - 45.0 (42.0 ± 2.2, *n* = 102)	1.2 - 1.4 (1.3 ± 0.1, *n* = 102)	Field
	Trindade	41.3 - 47.0 (44.2 ± 1.5, *n* = 35)	37.3 - 45.0 (39.8 ± 1.6, *n* = 35)	1.06 - 1.15 (1.11, *n* = 35)	Strain UNR-29
	Trindade	41.0 - 48.0 (45.0 ± 5.0, *n* = 49)	35.0 - 40.0 (37.0 ± 3.5, *n* = 49)	1.1 - 1.3 (1.2 ± 0.2, *n* = 49)	Field
Prorocentrum lima species complex	Fernando de Noronha	35.0 - 37.5 (35.8 ± 1.2, *n* = 35)	27.5 - 32.5 (30.3 ± 1.5, *n* = 35)	1.1 - 1.3 (1.2 ± 0, *n* = 35)	Strain UNR-86
	Fernando de Noronha (morphotype 1)	32.5 - 47.5 (43.5 ± 3.1, *n* = 51)	22.5 - 25.0 (24.6 ± 1.0, *n* = 51)	1.3 - 2.0 (1.8 ± 0.1, *n* = 51)	Field
	Fernando de Noronha (morphotype 2)	32.5 - 47.5 (40.6 ± 5.1, *n* = 30)	27.5 (27.5 ± 0.0, *n* = 30)	1.2 - 1.7 (1.5 ± 0.2, *n* = 30)	Field
	Fernando de Noronha (morphotype 3)	32.5 - 47.5 (36.9 ± 2.4, *n* = 88)	30.0 - 37.5 (31.3 ± 1.9, *n* = 88)	0.9 - 1.6 (1.2 ± 0.1, *n* = 88)	Field
	Maragogi	36.4 - 41.1 (38.8 ± 1.1, *n* = 35)	27.6 - 31.9 (29.4 ± 1.1, *n* = 35)	1.25 - 1.39 (1.3, *n* = 35)	Strain UNR-15
	Trindade	30.0 - 42.0 (36.0 ± 3.8, *n* = 49)	20.0 - 29.0 (24.0 ± 6.5, *n* = 49)	1.3 - 1.8 (1.5 ± 0.5, *n* = 49)	Field
Prorocentrum cf. *norrisianum*	Fernando de Noronha	17.0 - 25.0 (23.0 ± 2.3, *n* = 23)	12.5 - 20.0 (16.5 ± 1.8, *n* = 23)	1.1 - 1.7 (1.4 ± 0.2, *n* = 23)	Field
Prorocentrum panamense	Fernando de Noronha	45.0 - 55.0 (47.3 ± 2.7, *n* = 15)	42.5 - 50.0 (44.0 ± 2.1, *n* = 15)	1.0 - 1.3 (1.1 ± 0.1, *n* = 15)	Field
Prorocentrum rhathymum	Fernando de Noronha	30.0 - 35.0 (33.5 ± 1.4, *n* = 30)	20.0 - 25.0 (22.9 ± 1.7, *n* = 30)	1.3 - 1.8 (1.5 ± 0.1, *n* = 30)	Field
	Cabo Frio	28.0 - 32.0 (29.9 ± 0.8, *n* = 35)	18.8 - 25.7 (23.0 ± 1.3, *n* = 35)	1.19 - 1.49 (1.31, *n* = 35)	Strain UNR-11
Prorocentrum sp. 1	Fernando de Noronha	45.0–60.0 (53.4 ± 3.4, *n* = 37)	42.5–57.5 (50.1 ± 3.6, *n* = 37)	1.0–1.1 (1.1 ± 0.0, *n* = 37)	Field
Prorocentrum sp. 2	Fernando de Noronha	42.5 - 47.5 (44.7 ± 1.8, *n* = 22)	32.5 - 40.0 (36.0 ± 2.0, *n* = 22)	1.1 - 1.3 (1.2 ± 0.0, *n* = 22)	Field

morphology of strains UNR-15, UNR-35, UNR-68 and UNR-72, except that they were wider (Table 2).

Prorocentrum lima field cells from Fernando de Noronha presented cell shapes that varied from narrow almost oblong (morphotype 1, Fig. 5F-G) to ovate (morphotype 2, Fig. 5H) and broadly ovate (morphotype 3, Fig. 5I). Morphotype 3 was morphologically similar to cultured cells of strain UNR-86. Cells from all morphotypes presented a smooth thecal surface with scattered pores (mostly round, but also oblong), except in the central area, and a marginal row of pores (Fig. 5F-I). Periflagellar area V-shaped excavating the right thecal plate (Fig. 5F, H-I). At all the remaining sampling sites, *P. lima* field cells were predominantly ovate, with cell shape similar to morphotype 2 cells from Fernando de Noronha.

Distribution: Present at all investigated sites. Fernando de Noronha, Carneiros, Maragogi and Forte (sequence obtained) and St. Paul's Rocks, Muro Alto, Porto de Galinhas, Garça Torta, Placaford, Penha, Trindade, Tartaruga, Forno-AB, Forno-AC and Cabo Frio (morphospecies).

Prorocentrum panamense Grzebyk et al. (1998)

Prorocentrum panamense field cells were heart-shaped and asymmetric. Thecal surface reticulate-foveate with scattered pores, except in

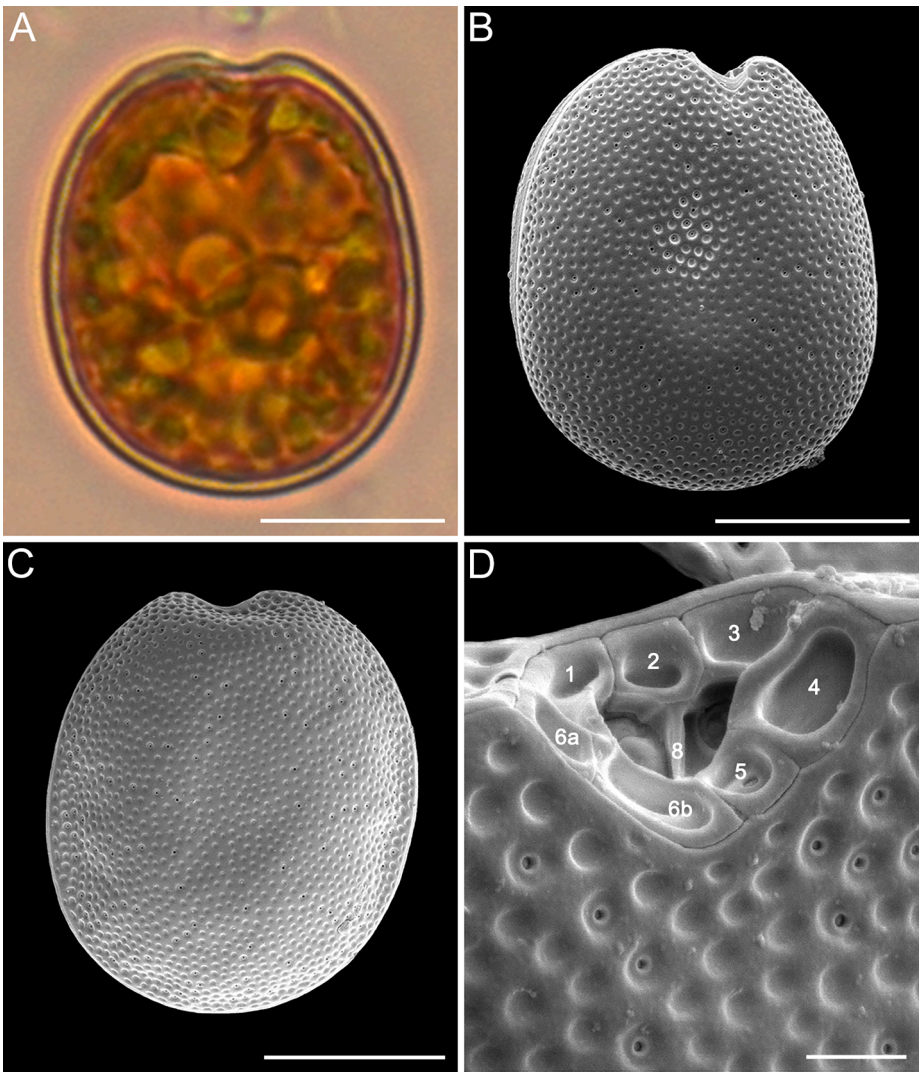


Fig. 2. (A) Light and (B-D) scanning electron micrographs of *Prorocentrum borbonicum*. (A) Strain UNR-12, (B-D) Strain UNR-13. (A-B) Right thecal plate view, (C) Left thecal plate view, (D) Detail of the periflagellar area. Scale bars: (A-C) 10 μm, (D) 1 μm.

the central area, and without a marginal row of pores. Round pores located inside depressions. Depressions shallower towards the center of the thecal plates, that was devoid of pores and depressions. Periflagellar area linear and not excavated (Fig. 6A).

Distribution: Fernando de Noronha and Trindade (morphospecies).

Prorocentrum rhathymum Loeblich et al. (1979)

Prorocentrum rhathymum cells of strain UNR-11 (Fig. 6B-C) and field cells (Fig. 6D-F) were oval to oblong and asymmetric. Thecal surface smooth with a characteristic pore pattern, showing one apical row and several posterior radial rows in shallow furrows, present in both thecal plates (large pores located inside depressions) (Fig. 6C-E). Small pores scattered on the surface of cells (Fig. 6C-E). Both pores round and the center of the thecal plates was devoid of pores (Fig. 6C-E). Periflagellar area wide V-shaped excavating the right thecal plate, with a wing on platelet 1 and a short wing at the most ventral platelet (Fig. 6F). Cells with many golden-brown chloroplasts (Fig. 6B).

Distribution: Fernando de Noronha, Tartaruga and Forno-AC (morphospecies) and Cabo Frio (sequence obtained).

Prorocentrum sp. 1

Prorocentrum sp. 1 field cells were broadly oval to almost round and symmetric (Fig. 7A-C). Thecal surface reticulate-foveate with scattered pores, with central area reticulate-foveate without pores and no marginal row of pores (Fig. 7A-C). Round pores located inside depressions (Fig. 7D), that were larger towards the periphery of the cell. Periflagellar area wide V-shaped, slightly excavating the right thecal plate (Fig. 7A).

Distribution: Fernando de Noronha and Trindade (morphospecies).

Prorocentrum sp. 2

Prorocentrum sp. 2 field cells were oblong and symmetric (Fig. 7E-F). Thecal surface smooth with scattered round to oblong pores, except in the central area, and a marginal row of pores (Fig. 7E-F). Periflagellar area V-shaped excavating the right thecal plate (Fig. 7E).

Distribution: Fernando de Noronha (morphospecies).

Species observed only through LM:

Prorocentrum cf. *caipirignum* S. Fraga, M. Menezes et S. Nascimento, 2017

Prorocentrum cf. *caipirignum* field cells were oblong and symmetric. Periflagellar area V-shaped excavating the right thecal plate.

Distribution: Cabo Frio (morphospecies).

Prorocentrum cf. *concavum* Fukuyo (1981)

Prorocentrum cf. *concavum* field cells were broadly oval and symmetric, with a centrally located pyrenoid. Periflagelar area V-shaped excavating the right thecal plate (Fig. 8A).

Distribution: Fernando de Noronha (morphospecies).

Prorocentrum cf. *norrisianum* Faust (1997)

Prorocentrum cf. *norrisianum* field cells were oval to oblong with straight sides, and the anterior end appears slightly oblique (Fig. 8B).

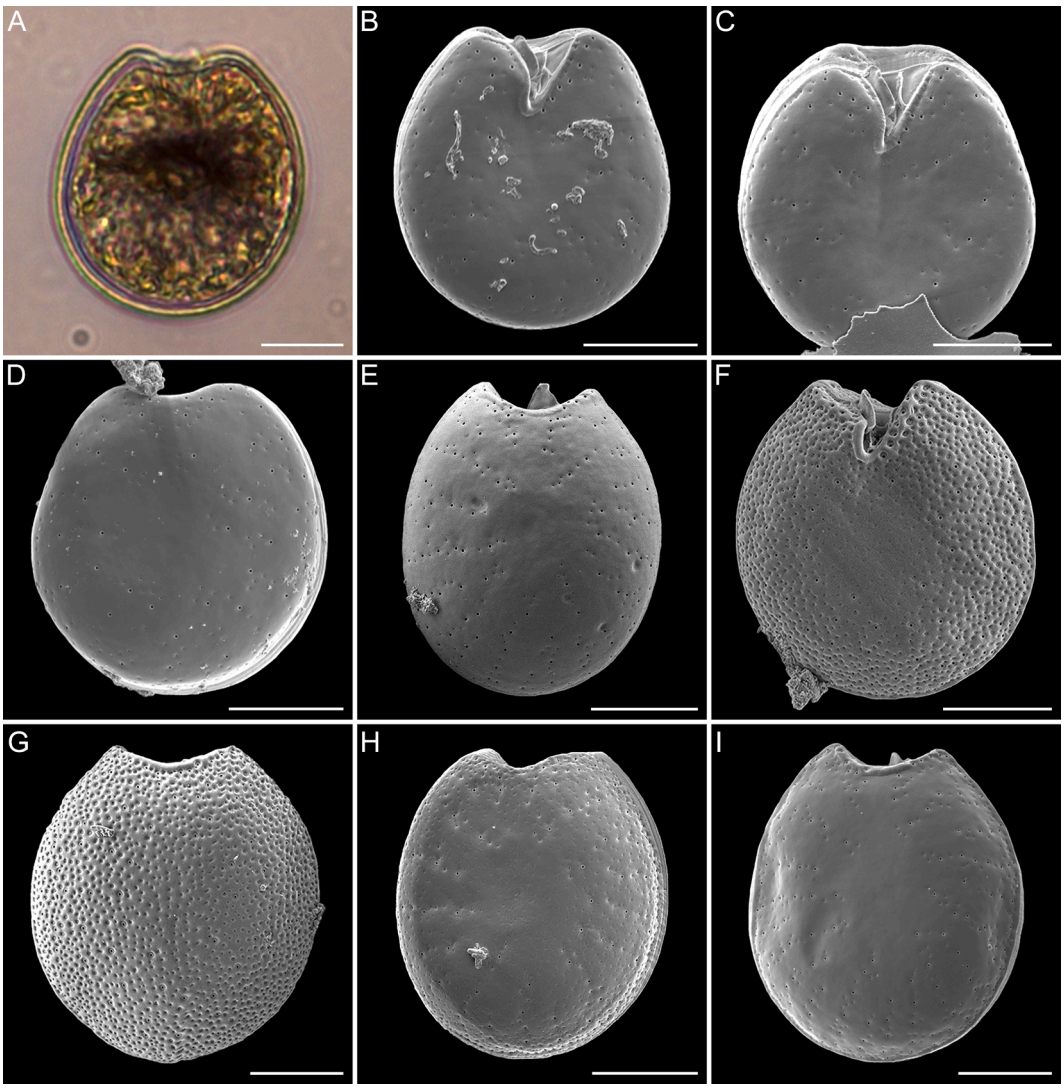


Fig. 3. (A) Light and (B-I) scanning electron micrographs of *Prorocentrum emarginatum/fukuyoi/sculptile* species complex (Fernando de Noronha field cells). (B-C, F) Right thecal plate view, (D-E, G-I) Left thecal plate view. Scale bars: 10 μm.

Distribution: Fernando de Noronha and Trindade (morphospecies).

3.2. Phylogenetic analysis

The ITS and LSU sequences were retrieved for seven strains of benthic *Prorocentrum* species: UNR-11, UNR-12, UNR-15, UNR-35, UNR-68, UNR-72 and UNR-86, and for the strain UNR-44 only the ITS sequence was obtained. The final alignment of the ITS sequences comparing 62 OTUs comprised 484 aligned nucleotides. The alignment of the LSU sequences comparing 80 OTUs included 478 aligned nucleotides. The general topology of the ML and BI trees agreed with previous studies (Luo et al., 2017; Moreira-González et al., 2019a; Chomérat et al., 2019; Lim et al., 2019; Nishimura et al., 2020) for ITS (Fig. 9) and LSU (Fig. 10). All species clades showed high support values (BS>95 and PP>0.95).

The phylogenetic analysis based on ITS and LSU loci grouped the sequences of five *Prorocentrum* strains from Brazil in the *P. lima* species complex. Considering the four clades of this complex (Nishimura et al., 2020), the strains UNR-15, UNR-35, UNR-68 and UNR-72 grouped in clade 1, while strain UNR-86 grouped in clade 3 (Fig. 9 and 10).

Two other *Prorocentrum* species were identified based on ITS and LSU sequences. Strain UNR-11 clustered within the clade of *P. rhathymum/P. mexicanum* and strain UNR-12 clustered within the clade of *P. borbonicum* (Fig. 9 and 10). Moreover, strain UNR-44 was identified as *P. hoffmannianum* based on the ITS sequences (Fig. 9).

3.3. Abundance

Prorocentrum was present at all investigated sites (Supplementary Table S4, Fig. 11) and high mean abundances of 1.4×10^3, 1.9×10^3 and 7.1×10^3 cells g^{-1} FW were observed at Fernando de Noronha, Porto de Galinhas and Forte, respectively (Supplementary Table S4, Fig. 11A). At Fernando de Noronha, this genus represented 58% of the mean total abundance of benthic dinoflagellates (Fig. 11B). *Prorocentrum* showed mean abundances between 1×10^2 and 5×10^2 cells g^{-1} FW at Maragogi, Tartaruga, Penha and Cabo Frio (Supplementary Table S4, Fig. 11A). At Cabo Frio, *Prorocentrum* represented 79% of the total mean dinoflagellate abundance (Fig. 11B). Saint Paul's Rocks, as well as the coastal sites of Muro Alto, Garça Torta, Placaford, Forno-AB and Forno-AC presented lower *Prorocentrum* mean abundances, below 1×10^2 cells g^{-1} FW (Supplementary Table S4, Fig. 11A).

Maximum *Prorocentrum* abundances higher than 1×10^3 cells g^{-1} FW were found at Cabo Frio, Trindade, Fernando de Noronha, Tartaruga, Porto de Galinhas and Forte (Supplementary Table S4, Fig. 11A). At Maragogi and Penha maximum abundances were 5×10^2 cells g^{-1} FW and 7×10^2 cells g^{-1} FW respectively, while at St. Paul's Rocks, Muro

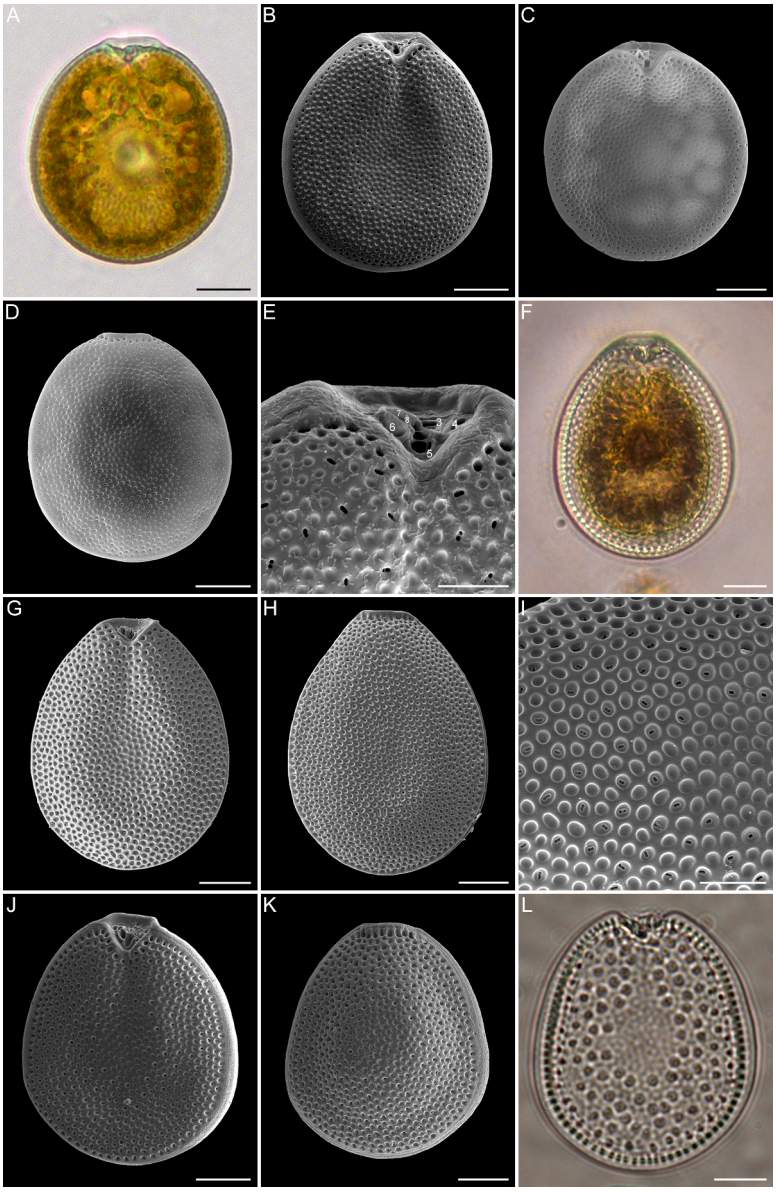


Fig. 4. (A, F, L) Light and (B-E, G-K) scanning electron micrographs of *Prorocentrum hoffmannianum*. (A-E) Strain UNR-29, (F-I) Fernando de Noronha field cells, (J-L) Trindade field cells. (A-C, F-G, J, L) Right thecal plate view, (D, H, K) Left thecal plate view, (E) Periflagellar area seen from the right lateral view, (I) Detail of the thecal surface. Scale bars: (A-D, F-H, J-L) 10 μm, (E) 4 μm, (I) 5 μm.

Alto, Garça Torta, Placaford, Forno-AB and Forno-AC maximum abundances were lower than 5×10^2 cells g^{-1} FW (Supplementary Table S4, Fig. 11A).

Prorocentrum lima species complex was the only species observed at all sites (Supplementary Table S4 and Figure S1A). Mean *P. lima* species complex abundance ranged between 1 at Forno-AB and 7×10^3 cells g^{-1} FW at Forte. Peak abundances of *P. lima* species complex were noteworthy at Forte (1.9×10^4 cells g^{-1} FW) and Porto de Galinhas (8.4×10^3 cells g^{-1} FW) (Supplementary Table S4, Fig. S1A). Other sites with high maximum abundances include Trindade (2×10^3 cells g^{-1} FW), Fernando de Noronha (2.1×10^3 cells g^{-1} FW), Cabo Frio (2.3×10^3 cells g^{-1} FW) and Tartaruga (6.7×10^3 cells g^{-1} FW) (Supplementary Table S4, Fig. S1A). *Prorocentrum lima* species complex represented, on average, more than 20% of the benthic dinoflagellate abundance in eight of the 14 sites (Fig. S1B). *Prorocentrum emarginatum/fukuyoi/sculptile* complex were found at nine of the 14 sites, in general at low abundances (Supplementary Table S4) and representing a minor component of total benthic dinoflagellates abundance (between 1 and 17%). Mean abundance of this complex ranged between not detected at Forno-AB and 2.4×10^2 cells g^{-1} FW at Trindade. Peak abundance was found at Tartaruga (9.8×10^2 cells g^{-1} FW) (Supplementary Table S4).

Prorocentrum hoffmannianum was registered only at the oceanic islands with mean abundances ranging between 2 at St. Paul's Rocks and 1.9×10^2 cells g^{-1} FW at Fernando de Noronha, where peak abundance of 7.4×10^2 cells g^{-1} FW was recorded (Supplementary Table S4). *Prorocentrum rhathymum* was found at Fernando de Noronha and at sampling sites on the Southeast coast of Brazil. Mean *P. rhathymum* abundance ranged between 0.2 at Forno-AC and 83 cells g^{-1} FW at Fernando de Noronha, where maximum abundance of 5.9×10^2 cells g^{-1} FW was registered (Supplementary Table S4). All other *Prorocentrum* species presented mean abundances lower than 70 cells g^{-1} FW (Supplementary Table S4).

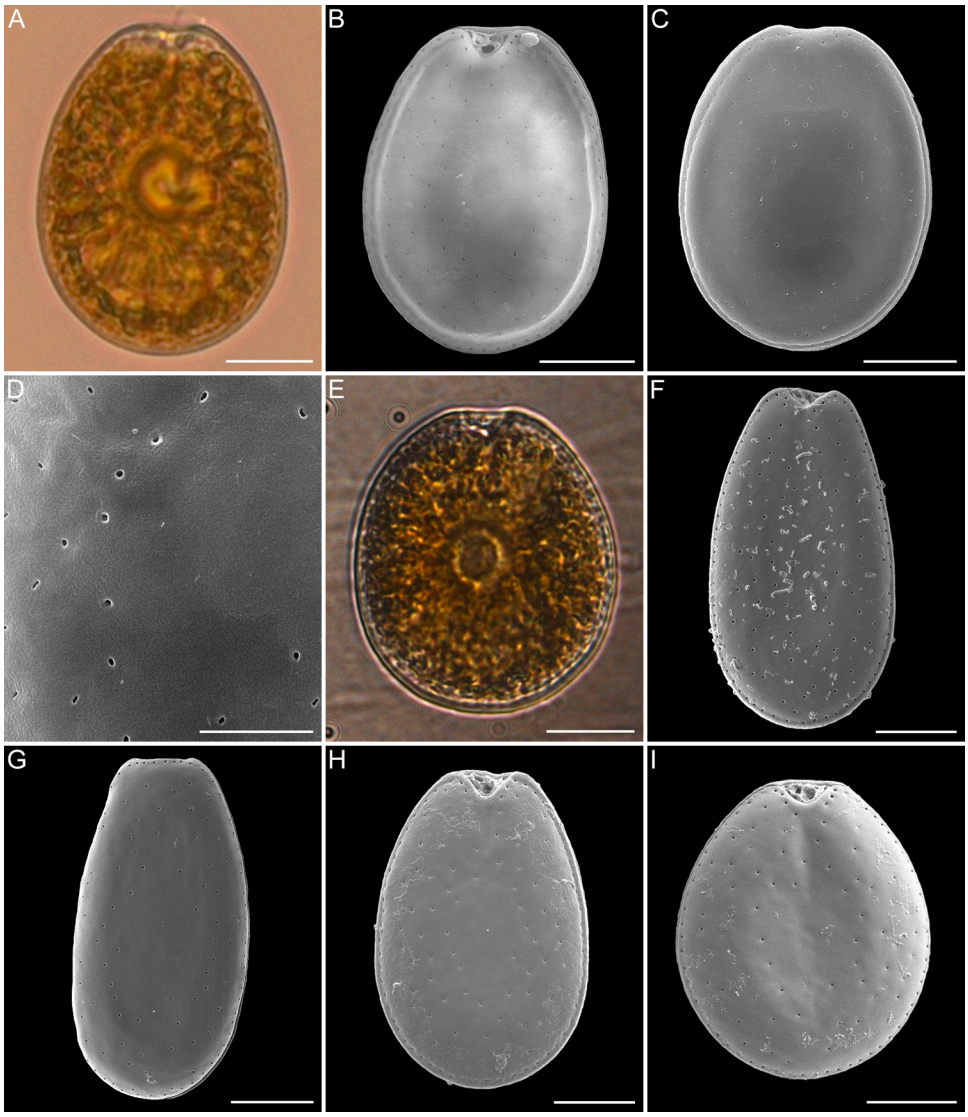


Fig. 5. (A, E) Light and (B-D, F-I) scanning electron micrographs of *Prorocentrum lima* species complex. (A-D) Strain UNR-15, (E) Strain UNR-86, (F-I) Fernando de Noronha field cells. (A-B) Right thecal plate view of strain UNR-15, (C) Left thecal plate view of strain UNR-15, (D) Detail of the thecal surface of strain UNR-15, (E) Right thecal plate view of strain UNR-86, (F) Right thecal plate view of morphotype 1, (G) Left thecal plate view of morphotype 1, (H) Right thecal plate view of morphotype 2, (I) Right thecal plate view of morphotype 3. Scale bars: (A-C, E-I) 10 μm, (D) 5 μm.

3.4. Literature survey of benthic Prorocentrum species richness and distribution

Information on benthic *Prorocentrum* species distribution was compiled from 215 publications and data on benthic *Prorocentrum* species and the substrate investigated is presented in Supplementary Table S2. Ninety-eight papers investigated the Atlantic Ocean, 15 studies at the South Atlantic, 45 at the North Atlantic and 38 in the Caribbean Sea. Seventy-eight studies were conducted in the Pacific Ocean, 19 in the South Pacific and 59 in the North Pacific. The Indian Ocean was less investigated, and 11 studies were conducted in the South Indian and 10 in the North Indian Ocean. The Mediterranean Sea, Black Sea, Baltic Sea, Suez Canal, and one inland water body were addressed by 37 studies.

Macroalgae was the substrata most investigated (Supplementary Table S2), and was collected in 57% of the locations, followed by sediment and sand, sampled in 41% of the sites, seagrass (19%), corals, coral rubbles, coral sand and dead corals (14%) and artificial substrate (5%). Seawater was sampled in 40% of the sites.

Prorocentrum lima species complex was registered in 80% of the locations in Supplementary Table S2, followed by *P. concavum* (40%), *P. rhathymum* and *P. emarginatum* (32%), *P. mexicanum* (27%), *P. hoffmannianum* (26%) and *P. fukuyoi* (18%), while the remaining benthic *Prorocentrum* species were present in less than 10% of the locations. *Prorocentrum bimaculatum, Prorocentrum pseudopanamense, Prorocentrum reticulatum* and *Prorocentrum sabulosum* were registered only at their type localities.

4. Discussion

4.1. Taxonomy and distribution

4.1.1. Prorocentrum borbonicum

Morphology of *P. borbonicum* cells was in agreement with the original description of the species (Ten-Hage et al., 2000), with cell dimensions slightly larger. *Prorocentrum borbonicum* was described from Réunion Island, Indian Ocean (Ten-Hage et al., 2000) and, so far, has been found in Tanzania (Hansen et al., 2001), Greece (Aligizaki et al., 2009), Saudi Arabia (Prabowo and Agusti, 2019), China (Zou et al., 2022) and Colombia (Arteaga-Sogamoso et al., 2022). In Brazil, the species occurrence was confirmed with molecular data at Maragogi in the Northeast coast and as a morphospecies at Fernando de Noronha and Trindade (Supplementary Table S2). The species was also reported at the Northeast coast of Brazil by Fernandes et al. (2021).

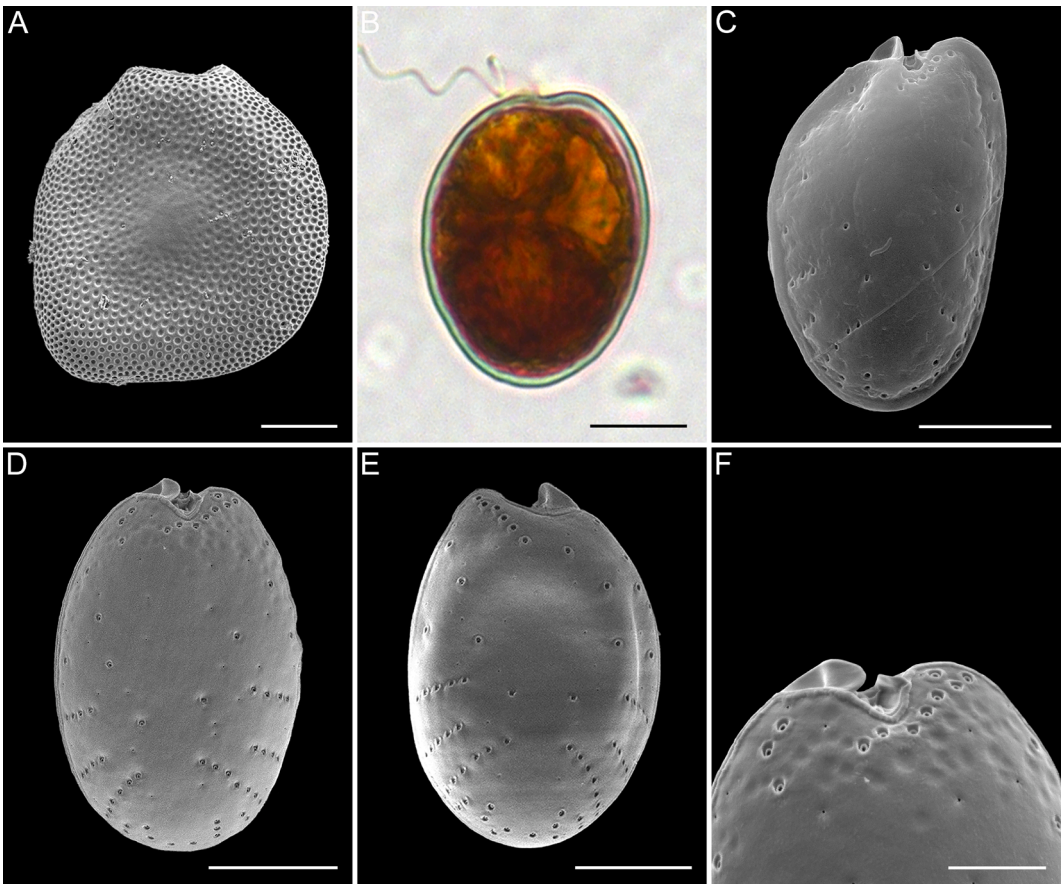


Fig. 6. (A, C-F) Scanning electron and (B) light micrographs of *Prorocentrum* species. (A) *Prorocentrum panamense* Fernando de Noronha field cell. (B-F) *Prorocentrum rhathymum*: (B-C) Strain UNR-11, (D-F) Fernando de Noronha field cells. (A-D) Right thecal plate view, (E) Left thecal plate view, (F) Periflagellar area seen from the right lateral view. Scale bars: (A-E) 10 μm, (F) 4 μm.

4.1.2. *Prorocentrum cf. caipirignum*

Prorocentrum caipirignum was reported from the Southeast and Northeast coasts of Brazil (Nascimento et al., 2017; Fernandes et al., 2021), and in the current study was found at Cabo Frio. The current distribution of the species includes Cuba (Herrera-Sepúlveda et al., 2015), China (Zhang et al., 2015; Luo et al., 2017; Zou et al., 2022), Malaysia (Lim et al., 2019) and Japan (Nishimura et al., 2020) (Supplementary Table S2).

4.1.3. *Prorocentrum cf. concavum*

Prorocentrum cf. *concavum* field cells found in Fernando de Noronha presented a similar shape to the original description of the species (Fukuyo, 1981) with a slightly wider range in length and width. However, a detailed study of the morphology and molecular analysis are necessary to confirm the identity of this morphospecies. *Prorocentrum concavum* was described from French Polynesia and New Caledonia, Overseas France and Ryukyu Islands, Japan (Fukuyo, 1981), and is currently found in several locations in the Atlantic, Indian and Pacific Oceans (Supplementary Table S2).

4.1.4. *Prorocentrum emarginatum/fukuyoi/sculptile species complex*

Prorocentrum emarginatum, P. fukuyoi and *P. sculptile* form a problematic group of species with similar morphology and the features that can reliably distinguish them are not yet clear (Hoppenrath et al., 2013). Specimens with radiating lines of pores and a completely smooth surface have been considered by many authors as *P. emarginatum*, however, this is in contradiction with Fukuyo's original description (Fukuyo, 1981) and these specimens likely correspond to a species in the *P. fukuyoi* complex (Chomérat et al., 2019). *Prorocentrum sculptile* was described with a rugose surface and shallow, round to oblong depressions evenly distributed (Faust, 1994). Later Chomérat et al. (2019) showed that in young specimens the center of the theca was smooth with pores arranged in radiating lines, and the foveate ornamentation was visible only on the margin. Moreover, the absence of molecular data associated with the original description of *P. emarginatum* (Fukuyo, 1981) and *P. sculptile* (Faust, 1994), and the considerable genetic variability observed in this species complex does not allow to conclude in the identity of the specimens (Laza-Martinez et al., 2011; Chomérat et al., 2019). In the current study, field cells of this species complex from two sites (Fernando de Noronha and Trindade) were observed using SEM and cells with a smooth and with a strong, or light or faint foveate ornamentation were observed. As molecular data from these specimens were not available, identification was not possible.

Prorocentrum emarginatum was described from the Ryukyu Islands, Japan (Fukuyo, 1981), while *P. fukuyoi* was described from Sydney, Australia (Murray et al., 2007) and *P. sculptile* from Carrie Bow Cay, Belize (Faust, 1994). Specimens from the *P. emarginatum/fukuyoi/sculptile* complex have been recorded in several locations in the world's oceans (Supplementary Table S2). In Brazil, *P. emarginatum* was found in the Northeast coast, with molecular data associated to the morphological description (Mendes et al., 2019), and *P.* cf. *fukuyoi* was reported from the South coast, although no details on cell morphology or molecular data were presented (Moreira-González et al., 2020). In this study, this species complex was found at other six sites from the Northeast and Southeast coasts, as well as three oceanic islands (Supplementary Table S2).

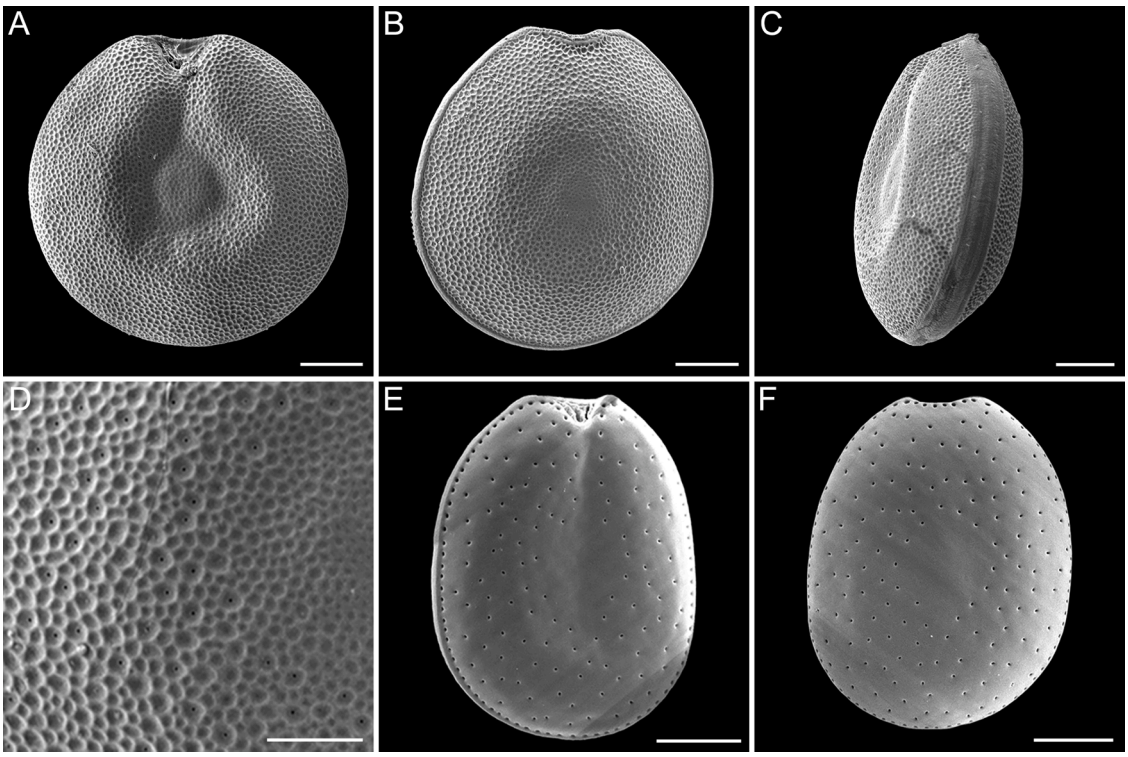


Fig. 7. (A-F) Scanning electron micrographs of *Prorocentrum* species. (A-D) *Prorocentrum* sp. 1., (E-F) *Prorocentrum* sp. 2. (A, E) Right thecal plate view, (B, F) Left thecal plate view, (C) Lateral view, (D) Detail of the thecal surface. Scale bars: (A-C, E-F) 10 μm, (D) 5 μm.

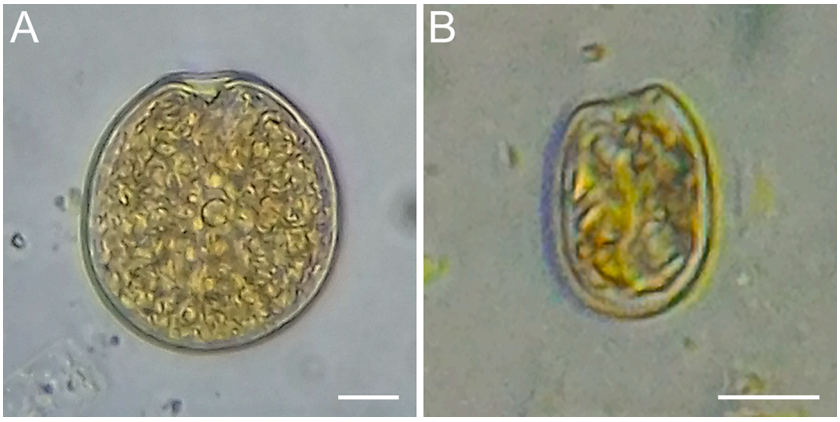


Fig. 8. Light micrographs of *Prorocentrum* species (Fernando de Noronha field cells). (A) *Prorocentrum* cf. *concavum*, (B) *Prorocentrum* cf. *norrisianum*. (A-B) Right thecal plate view. Scale bars: (A-B) 10 μm.

4.1.5. *Prorocentrum hoffmannianum*

Morphology of *P. hoffmannianum* cells kept in culture and from field samples was in agreement with the redescription of the species (Rodríguez et al., 2018). Cell shape was variable at different sampling sites, from ovoid to wider towards the posterior end of the cell, and all cells examined presented a foveate cell surface. Strain UNR-29, isolated from Trindade Island, corresponds to the Belize ribotype sensu Herrera-Sepúlveda et al. (2015). The species was described from Belize (Faust, 1990), that is also the type locality of *P. belizeanum* (Faust, 1993a) and *P. maculosum* (Faust, 1993b) that are now considered synonyms of *P. hoffmannianum* (Herrera-Sepúlveda et al., 2015; Rodríguez et al., 2018).

Prorocentrum hoffmannianum has a broad distribution and was reported from the Atlantic, Indian and Pacific Oceans (Supplementary Table S2). In Brazil, *P. hoffmannianum* was found at the Northeast and Southeast coasts (Fernandes et al., 2021), and this study expands its distribution to the oceanic islands of Trindade, Fernando de Noronha and St. Paul's Rocks (Supplementary Table S2).

4.1.6. *Prorocentrum lima species complex*

Prorocentrum lima species complex was ubiquitous in this study, found at all investigated sites. This species complex has a wide distribution in tropical, subtropical and temperate zones, along the Atlantic, Indian and Pacific Oceans (Supplementary Table S2). Four of the five Brazilian *P. lima* strains isolated in the current study grouped in clade 1 of the *P. lima* species complex sensu Nishimura et al. (2020), whereas one strain grouped in clade 3. Strains from clade 1 have been recorded from locations in the Atlantic (Table S4 by Nishimura et al., 2020), Indian (Oyeku and Mandal, 2021) and Pacific (Murray et al., 2009; Zhang et al., 2015; Luo et al., 2017; Nishimura et al., 2020) Oceans.

Strain UNR-86 grouped within clade 3 of the *P. lima* species complex and has a broad oval cell shape, wider than the *P. lima* strains from clade

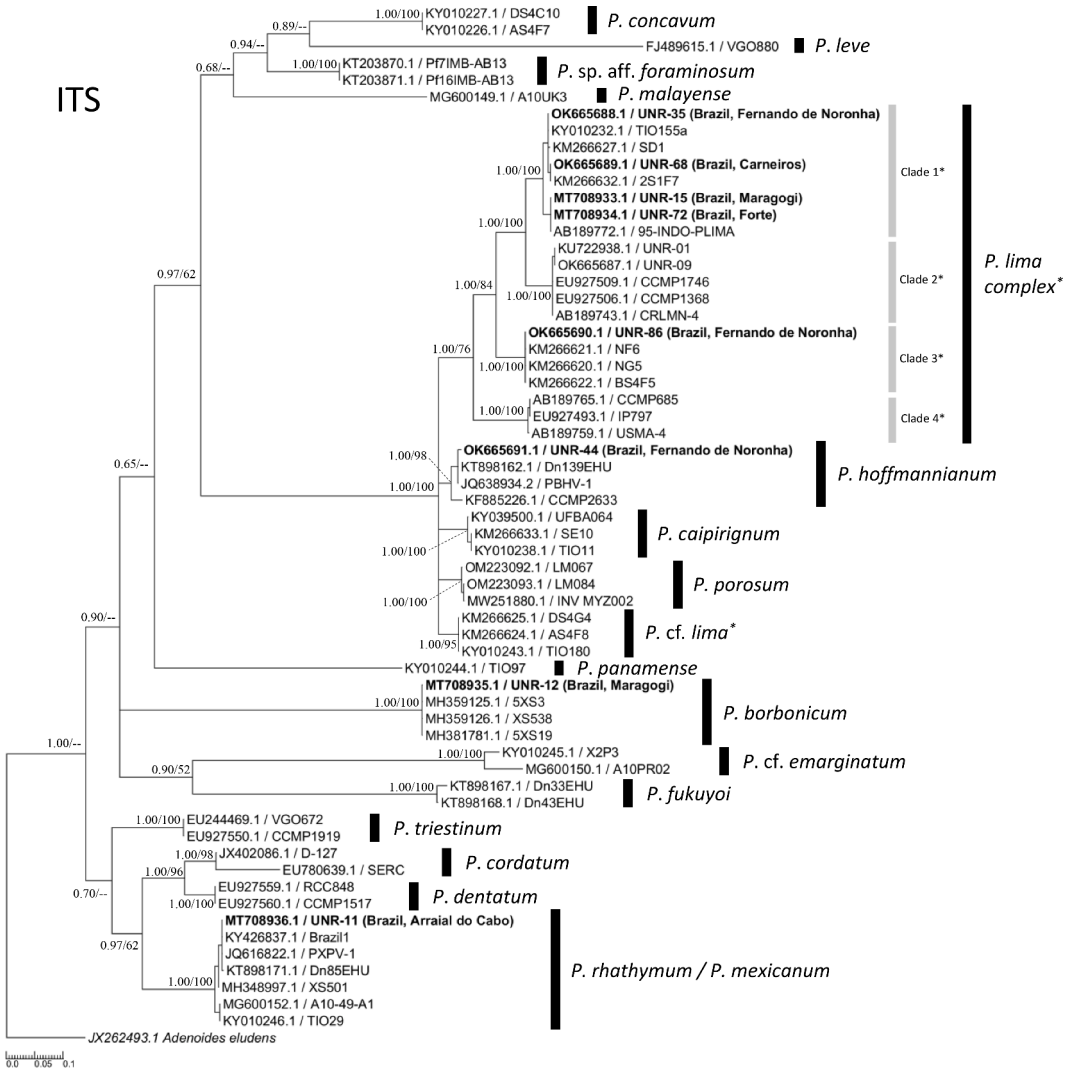


Fig. 9. Bayesian Inference phylogenetic tree based on ITS sequences of *Prorocentrum* species. Operational taxonomic units (OTUs) are identified by: GenBank accession number \ strain name (locality, for Brazilian strains). Numbers at nodes represents posterior probability from BI and bootstrap values from ML analyses, respectively (cut-off = 50% for both analyses). New sequences published in this study are displayed in bold (UNR-11, UNR-12, UNR-15, UNR-35, UNR-44, UNR-68, UNR-72 and UNR-86). *Clades and taxa names according to Nishimura et al. (2020).

1, in agreement with the morphology of the species *P. arenarium* M.A Faust (1994), that is currently considered a synonym of *P. lima* (Nagahama et al., 2011). In Brazil, sequences belonging to clade 3 were recorded only from Fernando de Noronha. At this oceanic island, the cell shape, particularly cell width, of *P. lima* species complex was variable, and three morphotypes (narrow, ovate and broadly ovate) were recognized. This island was the only site that presented narrow and broadly ovate cells, while at all the remaining sites *P. lima* species complex cells were ovate. Sequences of *P. lima* clade 3 were found at Australia (Murray et al., 2009), Hainan Island, China (Zhang et al., 2015), Canary Islands, Overseas Spain (Rodríguez et al., 2018), Martinique Island, Overseas France (Chomérat et al., 2019), Rawa Island, Malaysia (Lim et al., 2019) and Réunion Island (Nishimura et al., 2020).

4.1.7. *Prorocentrum cf. norrisianum*

Prorocentrum cf. *norrisianum* field cells from Fernando de Noronha and Trindade had similar shape and dimensions to the original description of the species (Faust, 1997) with a wider range in width, however, further morphological studies and molecular analyzes are necessary to confirm the identity of this morphospecies. *Prorocentrum norrisianum* was described from Belize (Faust, 1997) and, to date, has been found in Malaysia (Mohammad-Noor et al., 2007), Kuwait (Chomérat et al., 2012 and references therein) and Martinique Island (Chomérat et al., 2019).

4.1.8. *Prorocentrum panamense*

Morphology of *P. panamense* cells was in agreement with the original description of the species (Grzebyk et al., 1998), with slightly larger dimensions. *Prorocentrum panamense* was described from Panama (Grzebyk et al., 1998) and has been found in the Réunion Island (Hansen et al., 2001), Hainan Island (Luo et al., 2017), Martinique Island (Chomérat et al., 2019), Canary Islands (Fernández-Zabala et al., 2019; Gaiani et al., 2022), Selvagens Islands, Portugal (Godinho et al., 2022) and Brazil, where the species was found at the Northeast coast (Fernandes et al., 2021) and at the Fernando de Noronha and Trindade Islands (Supplementary Table S2).

4.1.9. *Prorocentrum rhathymum*

Morphology of *P. rhathymum* cells kept in culture and from field samples was in agreement with the species description (Loeblich et al., 1979). *Prorocentrum rhathymum* was originally found at the Virgin Islands, USA (Loeblich et al., 1979) and was later considered synonymous with *P. mexicanum* (Steidinger, 1983; Faust, 1990), however, Cortés-Altamirano and Sierra-Beltrán (2003) reestablished

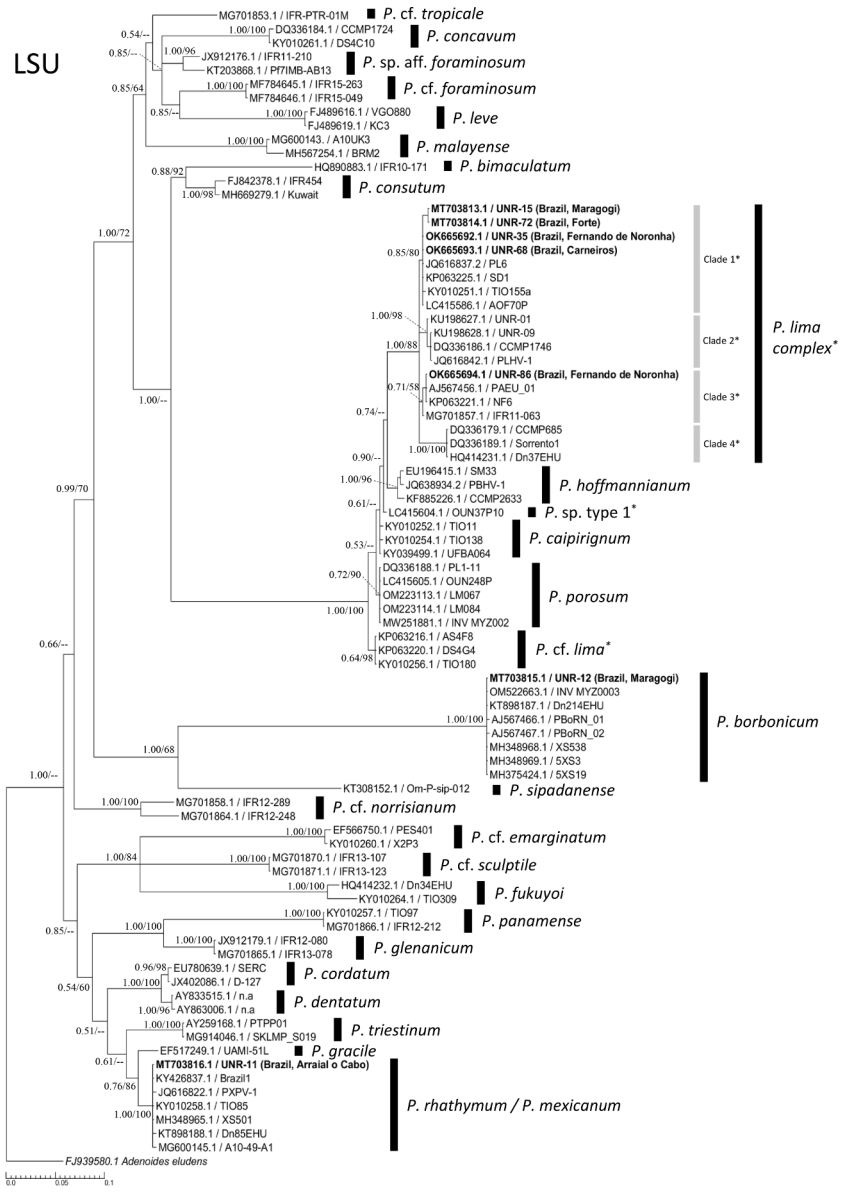


Fig. 10. Bayesian Inference phylogenetic tree based on LSU sequences of *Prorocentrum* species. Operational taxonomic units (OTUs) are identified by: GenBank accession number \ strain name (locality, for Brazilian strains). Numbers at nodes represents posterior probability from BI and bootstrap values from ML analyses, respectively (cut-off = 50% for both analyses). New sequences published in this study are displayed in bold (UNR-11, UNR-12, UNR-15, UNR-35, UNR-68, UNR-72 and UNR-86). *Clades and taxa names according to Nishimura et al. (2020).

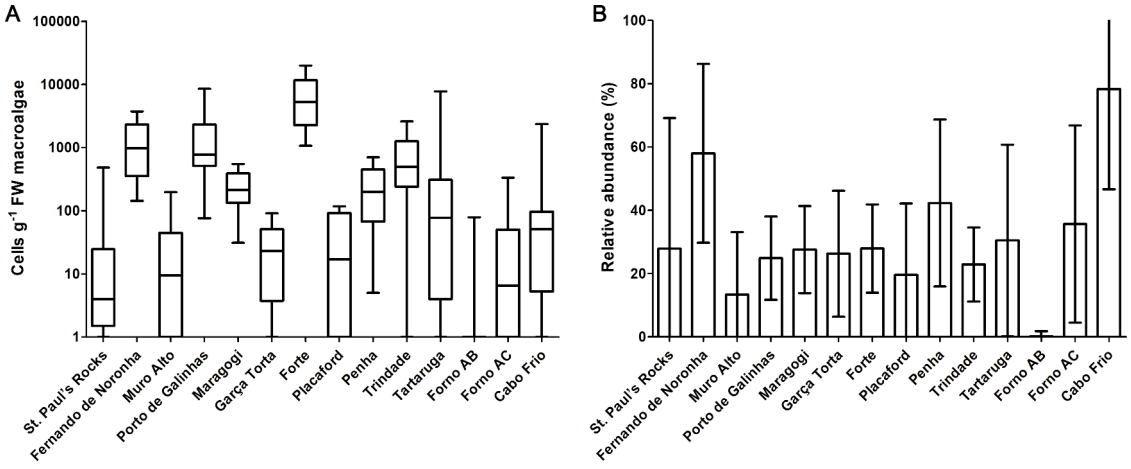


Fig. 11. *Prorocentrum* abundance values at 11 sites on the coast and three oceanic islands of Brazil. (A) *Prorocentrum* abundance showing median, 1st quartile, 3rd quartile, maximum and minimum values (cells g^{-1} FW macroalgae), (B) *Prorocentrum* relative abundance (%) with standard deviation.

P. rhathymum as an independent species. Gómez et al. (2017) presented morphological and molecular data seeking to reestablish synonymy. In this study, the nomenclature of the species followed Hoppenrath et al. (2013). However, there is confusion in the literature and apparently different authors use the names *P. rhathymum* and *P. mexicanum* to refer to the same species.

Prorocentrum rhathymum has a wide distribution and was found in the Atlantic, Indian and Pacific Oceans (Supplementary Table S2). In Brazil, *P. rhathymum* was found at the Northeast coast (Proença et al., 2009; Fernandes et al., 2021), and in the present study in the Southeast coast and Fernando de Noronha (Supplementary Table S2).

4.1.10. *Prorocentrum sp. 1*

Nearly round *Prorocentrum* specimens with a foveate cell surface and pores of one size class were observed at Fernando de Noronha and Trindade. Cells presented a thecal surface pattern similar to *P. concavum*, but were wider than this species. Further studies including molecular analysis will be necessary to complete the characterization of the species.

4.1.11. *Prorocentrum sp. 2*

Prorocentrum sp. 2 cells were similar to the recently described species *Prorocentrum porosum* (Arteaga-Sogamoso et al., 2023), presenting similar dimensions, smooth thecal surface with a large number of round to oblong pores (between 114 and 133 thecal pores and 72–79 marginal pores in *Prorocentrum* sp. 2), however, they differ in terms of cell shape. Therefore, further studies are important for the identification of this morphospecies.

4.2. *Global benthic Prorocentrum species richness and distribution*

Species of the genus *Prorocentrum* have a wide geographic distribution and can contribute a considerable part of benthic dinoflagellates assemblage. Altogether, 11 benthic *Prorocentrum* species were found in the present study, seven morphospecies and four species identified based on morphology and molecular sequences. A clear latitudinal gradient in species richness was observed. The largest number of species was found at the oceanic island of Fernando de Noronha (03°50′S, 10 species), followed by the Northeast coast (08º04'S - 18º02'S, 10 species in total), the Southeast coast (22°45′S - 23°04′S, 5 species in total) while at the South coast (25°30′S) fewer species were present (4 species in total, Supplementary Table S2). Species richness varied among the three oceanic islands studied, and while only three benthic *Prorocentrum* species were recorded at St. Paul's Rocks, seven were found at Trindade and 10 at Fernando de Noronha.

In the current study some sites were more intensively studied than others. While the Southeast coast has been more intensively sampled, with 487 samples analyzed, covering all seasons; fewer samples (89) have been investigated from the Northeast coast. Noteworthy is the fact that the oceanic islands were the sites with fewer (57) and less frequent sampling and, despite of that, Fernando de Noronha and Trindade showed high species richness.

In the global distribution data of benthic *Prorocentrum* species, an uneven sampling effort is also evident, and while many regions have been undersampled or sampled infrequently, only a few areas have been sampled intensively enough to give a reliable estimate of the real species richness, as noted by Hoppenrath et al. (2014). Another issue is that to discuss species distribution patterns requires a well-defined species concept (Lundholm and Moestrup, 2006). Molecular data greatly advanced the understanding of protist distribution and species number (Foissner, 2008), but genetic sequences are still not available from many sites that have been investigated worldwide. Therefore, the reliability of species identification may be problematic, particularly for closely related species that are difficult to distinguish. Moreover, there are uncertainties regarding species delimitations, and some species may present considerable intraspecific morphological variability, while in other cases morphologies of distinct species may largely overlap (Hoppenrath et al., 2014).

Despite of those drawbacks, there is sufficient evidence for the existence of several distribution patterns in marine phytoplankton (Lundholm and Moestrup, 2006) and the examination of the biogeography of marine benthic *Prorocentrum* species, compiled from the literature in Supplementary table S2 also revealed a few patterns. Higher species richness was found in the tropics and subtropics, with a decrease in the number of species reported towards the temperate latitudes (Supplementary Table S2). At latitudes higher than 40° North, *P. lima* species complex was frequently the only benthic *Prorocentrum* species reported. At higher latitudes in the South hemisphere, *P. lima* species complex was the only species found in Argentina and temperate New Zealand (Supplementary Table S2).

Places that have been more intensively studied clearly presented higher species richness. This is the case of Belize, in the Caribbean Sea, the location with the highest number of species (16, Supplementary Table S2). Morphospecies of benthic dinoflagellates have been investigated in Belize since the 1990s by Faust and this is the type locality of 15 benthic *Prorocentrum* species. Among them, *P. reticulatum* and *P. sabulosum* have been recorded only from their type locality and further investigation using molecular and morphological characterization is necessary. Other studies in Mexico and Colombia, in the Caribbean Sea, have also shown a high morphospecies richness, with 12 and nine species registered, respectively (Supplementary Table S2). Recently, Chomérat et al. (2019) provided molecular and morphological descriptions to specimens of *P.* cf. *tropicale, P.* cf. *foraminosum* and *P. norrisianum*, that have been described from Belize without an associated molecular sequence, and the morphospecies *P.* cf. *ruetzlerianum* from the Martinique Islands, East Caribbean. Twelve species were putatively identified from the same site at the Martinique Islands (Chomérat et al., 2019), confirming the Caribbean Sea is a hotspot of benthic *Prorocentrum* species diversity.

In the tropical Réunion Islands in the Indian Ocean, in Hainan and Xisha Islands in China, and in Hawaii in the USA, in latitudes 16 - 21°N, between seven and 10 species of benthic *Prorocentrum* were registered (Supplementary Table S2), reflecting their high species diversity; but also a high number of studies that included an integrated taxonomical approach combining molecular and morphological analysis to study benthic dinoflagellates. Kuwait and Thuwal, Saudi Arabia are also noteworthy for their high number of benthic *Prorocentrum* species (eight and 11, Supplementary Table S2), likely related to its subtropical location, shallow and protected coastline and by the high number of studies performed.

A comprehensive study of *Prorocentrum* species has been performed in Japan, along 27 sampling sites from subboreal, temperate and subtropical latitudes, comprising the molecular analysis of 244 isolated strains (Nishimura et al., 2020). Eight benthic *Prorocentrum* species have been reported from Japan, a number comparable to that found in tropical and subtropical latitudes elsewhere (Supplementary Table S2). This high species richness is likely related to the intensive sampling effort, and the use of molecular analysis, that largely improved the capability of species recognition, including one new phylotype, *Prorocentrum* sp. type 1 and the recently described *P. porosum* (Arteaga--Sogamoso et al., 2023), that were found in the subtropical zone of Japan (Nishimura et al., 2020).

Prorocentrum lima species complex presents a cosmopolitan distribution and was found in nearly all investigated sites, from tropical to temperate latitudes (Supplementary Table S2) and was frequently the only species reported in temperate latitudes. However, a high genetic variability is found in the *P. lima* species complex, that comprises four major clades (Nishimura et al., 2020). Clade 4 is restricted to temperate latitudes and presents high genetic divergence relative to clades 1, 2 and 3, compatible to that between different species (Nishimura et al., 2020). Clade 3 is consistently separated in *P. lima* phylogenies (Nascimento et al., 2016, 2017; Nishimura et al., 2020) and cells of this clade can be

morphologically distinguished by its broader cell width, corresponding to the morphospecies *P. arenarium*. Therefore, the *P. lima* species complex comprises different lineages that altogether present a cosmopolitan distribution.

The morphologically similar *P. emarginatum, P. fukuyoi* and *P. sculptile* have been frequently reported from many locations around the world, from the tropics to temperate latitudes, and until this species complex receives a detailed study, their identification and geographic distribution will be uncertain. The same holds for the widely distributed *P. rhathymum* and *P. mexicanum* species.

4.3. Abundance

Cell abundance data are crucial for establishing alarm concentration levels for harmful algal species and the associated risks. Moreover, the exposure of benthic fauna to low or intermediate abundances of toxic microalgae species for long periods can be detrimental (Neves et al., 2020). However, few data on benthic *Prorocentrum* abundance are available, particularly for the South Atlantic, where only the species *P. lima* complex/*P.* cf. *lima* (Gayoso et al., 2002; Brustolin et al., 2014; Moreira-González et al., 2020, 2022) and *P.* cf. *fukuyoi* (Moreira-González et al., 2020, 2022) have been quantified.

The *P. lima* species complex has been in a few occasions associated to the accumulation of okadaic acid (OA) in mollusks (mussels and oysters) in different regions of the world (e.g. Marr et al., 1992; Gayoso et al., 2002; Nascimento et al., 2005; Maranda et al., 2007b) and was considered a potential causative agent of DSP. Epiphytic *P. lima* cells may be ressuspended in the water from their substrate and become available for filter feeding mollusks. The macroalgae that serve as substrate to *P. lima* often grows on aquaculture ropes, close to the shellfish, and *P. lima* cells may become readily available. Gayoso et al. (2002) and Maranda et al. (2007b) found *P. lima* cells in the content and debris of stomach and digestive glands of mussels and oysters, respectively. Levasseur et al. (2003) found *P. lima* cells in the digestive glands of mussels at abundances of up to 1.7×10^2 cells g^{-1} wet digestive gland weight. In a shallow lagoon, the close proximity of oysters and cockles to macroalgae colonized by *P. lima* in abundances of up to 4×10^3 cells g^{-1} FW (Foden et al., 2005) indicated that *P. lima* was the most likely source of occasional DSP toxicity in the area, as no *Dinophysis* cells were detected in net samples (Nascimento et al., 2005).

Accumulation of DSP toxins in the mollusk *Mytilus* and *Aulacomya* was associated with *P. lima* abundances of 7.5×10^2 and 1.8×10^3 cells g^{-1} FW macroalgae, respectively in Argentina (Gayoso et al., 2002). In *Aulacomya*, OA concentrations were close to the regulatory guidance level by the U.S. Food and Drug Administration to prevent acute intoxication by OA in human consumers (FDA, 2020). Moreira-González et al. (2022) found low to moderate OA concentrations in marine benthic fauna (such as bivalves, gastropods, squid, crabs, echinoderms and fish) and indicated *P. lima* as the main vector. Highest OA concentrations were found in fish and in bivalves, when *P. lima* abundances were on average lower than 5×10^2 cells g^{-1} FW, and *Dinophysis* was not detected in the water column (Moreira-González et al., 2022).

In the current study, *P. lima* species complex abundances higher than 5×10^2 cells g^{-1} FW were found at eight of the 14 investigated sites, indicating the potential accumulation of DSP toxins in the benthic fauna, that needs to be verified. At sites where high ($>1 \times 10^3$ cells g^{-1} FW) *P. lima* abundances were found, the ecological and human health risks are higher. At some sites, *P. lima, P. caipirignum, P. hoffmannianum* and *P. borbonicum* were found together, representing a source of a suite of toxic compounds, including OA, DTXs, the fast acting toxin prorocentrolide (Nascimento et al., 2017), belizeanic acid (Cruz et al., 2008), corozalic acid (Napolitano et al., 2010) and borbotoxins (Ten-Hage et al., 2002). Therefore, there is a need to monitor species abundance in order to prevent the risks associated to the chronic and acute exposure to OA and other toxins, ensuring seafood safety.

5. Conclusion

This is the first study on the diversity of benthic *Prorocentrum* species along a wide latitudinal gradient of the tropical and subtropical Southwest Atlantic, reporting on species abundance, a scarce data globally and particularly at this region. A high species richness (10 species, and this values is likely underestimated) was revealed at the Fernando de Noronha oceanic island, that can be considered a hotspot of benthic *Prorocentrum* species diversity. *Prorocentrum borbonicum, P. hoffmannianum, P. lima* species complex and *P. rhathymum* were identified using molecular methods and morphological analysis. Field cells of *P. emarginatum/P. fukuyoi/P. sculptile* complex and *P. panamense* were observed using SEM and *P.* cf. *caipirignum, P.* cf. *concavum* and *P.* cf. *norrisianum* through light microscopy, and further studies combining molecular data with morphological descriptions are needed to confirm their identities. Two other species still need to be identified.

Different morphotypes of the *P. lima* species complex were observed at Fernando de Noronha and rDNA sequences from clades 1 and 3 were found at this island, but molecular diversity at this site is probably underestimated and deserves further studies. *Prorocentrum lima* complex was the only species recorded at all investigated sites and at certain places the abundance of this species may pose a risk to the marine ecosystem and human health. Further studies that expand the spatial and temporal scales investigated in Brazil are highly desirable.

The data compiled in the literature review shows a clear latitudinal gradient with higher species richness in tropical and subtropical regions. It is also evident that there is a bias caused by taxonomic impediment and an uneven sampling effort, with many regions still to be investigated. Therefore, the current knowledge on the global distribution of benthic *Prorocentrum* species is likely underestimated. The variable morphology of some benthic *Prorocentrum* species, such as in cell shape and surface ornamentation, as well as the similarities between closely related species, makes identification based solely on morphology inconclusive for a few species. This is particularly challenging in species for which the morphological conservative features with taxonomic value, that distinguishes them from their close relatives are still to be determined (such as in *P. emarginatum/P. fukuyoi/P. sculptile* complex). Therefore, the uncertainties in species distribution patterns will need a taxonomic approach that combines morphological and molecular data and that explores different regions of the world, particularly those poorly studied.

Author contributions

Conceptualization, S.M.N., F.S.; Formal analysis, G.T.B., S.M.N., F.S.; Investigation, G.T.B., S.M.N., F.S.; Resources, S.M.N., F.S., J.C.P; Data Curation, S.M.N., G.T.B., G.A.L.C., A.M.M., A.S.G.; Writing – Original Draft Preparation, G.T.B., S.M.N. and F.S.; Writing – Review & Editing, G.T.B., S.M.N., F.S.; Supervision, S.M.N. and F.S.; Funding Acquisition, S.M.N, F.S., J.C.P.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The authors do not have permission to share data.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.hal.2023.102470.

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Capítulo 2

Temporal dynamics of benthic dinoflagellates at the oceanic Fernando de Noronha Archipelago (Tropical South Atlantic) in a warming ocean

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Harmful algae, Time series, Sea surface temperature, *Prorocentrum*, *Ostreopsis*, *Gambierdiscus*

Abstract

Benthic dinoflagellates produce toxins with significant socioeconomic and health impacts, and their distribution is expected to shift due to global warming. Understanding their current diversity and abundance is, therefore, essential to assess the effects of anthropogenic stressors. This study presents a six-year monitoring of benthic dinoflagellate composition and abundance at the Fernando de Noronha Archipelago (tropical South Atlantic). We characterized the assemblage structure and investigated temporal trends and fluctuations in abundance across three sites within the Marine National Park, evaluating the influence of sea surface temperature (SST) and depth. The assemblage was primarily composed of *Prorocentrum*, *Ostreopsis*, *Amphidinium*, *Coolia*, and *Gambierdiscus*, with significant

increases in abundance over time, particularly in the post-COVID-19 pandemic period (2021–2023). These trends are likely driven by a historical warming of SST (past 40 years) combined with increased nutrient inputs from tourism expansion and inefficient wastewater treatment in the archipelago. These findings highlight the urgent need for improvements in the archipelago's sanitation infrastructure and underscore the importance of long-term monitoring as an early warning system for ecological and public health risks.

1. Introduction

Benthic dinoflagellates live associated to macroalgae, seagrasses, coral reefs, sand, sediments, and detritus (Tindall and Morton, 1998; Yong et al., 2018) and are found in tropical, subtropical, and temperate regions. The abundance and species composition of benthic dinoflagellate assemblages vary widely according to environmental factors (e.g., water temperature, salinity, light intensity, nutrient availability, hydrodynamics, and substrate availability and type) (Parsons and Preskitt, 2007; Richlen and Lobel, 2011; Cohu et al., 2013). Expanding knowledge of benthic dinoflagellates' geographic distribution, species composition, and abundance has become increasingly relevant, as different species can synthesize a variety of toxins that may cause harm to human health, and social and economic impacts (Friedman et al., 2017; Pavaux et al., 2020). Moreover, with rising sea temperatures resulting from global climate change, species distribution is expected to change, along with shifts in cell abundance (Tester et al., 2020). Therefore, to understand how climate change affects benthic dinoflagellates, prior knowledge of their diversity and distribution across the globe will be extremely important.

The benthic dinoflagellate genus *Gambierdiscus* has been extensively studied due to its direct association with Ciguatera Poisoning (CP) (Friedman et al., 2017; Chinain et al., 2021). CP is characterized by numerous gastrointestinal, neurological, and cardiovascular symptoms caused by the consumption of marine organisms, mainly fish, contaminated with ciguatoxins (CTXs) (Friedman et al., 2017; Chinain et al., 2021). CTXs are produced by species of *Gambierdiscus* and *Fukuyoa* and accumulate in food webs through the grazing of herbivorous fish; as these fish are preyed upon, the toxins are transferred to higher trophic levels. The highest CP incidence rates are reported in two historically CP-endemic regions: the Pacific Ocean and the Caribbean Sea (Chinain et al., 2021). In affected areas, CP poses a major threat to human health and causes significant economic impacts, including severe

financial losses to both local and international fish trade and the tourism industry (Chinain et al., 2021).

Gambierdiscus is commonly found co-occurring with *Ostreopsis*, *Prorocentrum*, *Coolia*, and *Amphidinium* in tropical and warm temperate areas. Considerable efforts have been directed towards studying *Ostreopsis* species, particularly *O*. cf. *ovata*, due to the production of palytoxin (PLTX) analogues, the most potent non-bacterial biotoxin (Pavaux et al., 2020). Human health impacts associated with *Ostreopsis* may occur through the consumption of seafood contaminated with PLTX analogues (Alcala et al., 1988; Randall, 2005) or through direct exposure to seawater and marine aerosols during bloom events, leading to general malaise and respiratory and dermatological symptoms in bathers, workers, and coastline residents (Vila et al., 2016; Pavaux et al., 2020). In addition, *Ostreopsis* blooms have been linked to negative effects and mass mortalities of marine organisms in the Atlantic (Ferreira, 2006) and Pacific (Shears and Ross, 2009) Oceans, as well as in the Mediterranean Sea (Blanfuné et al., 2012). Moreover, the presence of PLTX-like compounds, such as isobaric PLTX, ovatoxin-a (OVTX-a), OVTX-b, and OVTX-d has been detected in fish meal remains that caused Haff disease in Brazil (Cardoso et al., 2022).

Some benthic species of *Prorocentrum* produce toxic compounds, including okadaic acid (OA), dinophysistoxins (DTXs), borbotoxins, and prorocentrolides (Nakajima et al., 1981; Ten-Hage et al., 2002; Nascimento et al., 2016, 2017). OA and DTXs can accumulate in shellfish and subsequently cause Diarrhetic Shellfish Poisoning (DSP) in humans, with gastrointestinal symptoms (Lee et al., 2016). The genera *Coolia* and *Amphidinium* also produce various bioactive compounds (Holmes et al., 1995; Kobayashi and Kubota, 2007; Tibiriçá et al., 2020); however, to date, no ecological or human health impacts have been linked to these compounds.

Research on benthic dinoflagellates in the tropical South Atlantic has largely focused on the taxonomy, phylogeny, and/or toxicity of the main genera: *Ostreopsis* (Nascimento et al., 2012a, 2020; Gómez et al., 2017a; Mendes et al., 2017; Tibiriçá et al., 2019; Borsato et al., 2020), *Gambierdiscus* (Nascimento et al., 2015), *Prorocentrum* (Nascimento et al., 2016, 2017; Gómez et al., 2017b; Mendes et al., 2019; Moreira-González et al., 2019a, 2019b, 2022; Borsato et al., 2023), and *Coolia* (Gómez et al., 2016; Nascimento et al., 2019; Mendes et al., 2019; Moreira-González et al., 2019a; Tibiriçá et al., 2020). In contrast, ecological studies on geographic distribution and abundance remain scarce, and no long-term

monitoring of benthic dinoflagellate assemblages has been conducted in the region. Long-term ecological studies of benthic dinoflagellates are globally rare; however, they are crucial for understanding temporal dynamics, distinguishing natural variability from long-term trends, and assessing ecosystem responses to environmental changes, which is especially relevant under current and projected climate change scenarios (Birchenough et al., 2026). In addition, most studies have been conducted along the coast of Brazil, whereas oceanic islands, which are less directly affected by local anthropogenic activities, remain largely unexplored.

Therefore, the present study fills a gap regarding long-term monitoring data on the species composition and abundance of benthic dinoflagellates at an oceanic island in the tropical South Atlantic (Fernando de Noronha Archipelago) and aims to: (I) identify species/genus composition of benthic dinoflagellate assemblages; (II) investigate temporal trends in benthic dinoflagellates abundance over six years, and relate it to potential factors driving this dynamic; (III) analyze temporal trends in sea surface temperature (SST) and relate them to the temporal variation of benthic dinoflagellates; (IV) evaluate how benthic dinoflagellates abundance varies according to depth.

2. Materials and methods

2.1 Study area

Fernando de Noronha (FN) is a volcanic archipelago located approximately 545 km off the Northeast Brazilian coast, in the tropical South Atlantic. The archipelago consists of a large main island and 20 other small islands surrounding it, with a total area of 26 km² (Ibama and Funatura, 1990). The climate is tropical, with a rainy season from February to July and a dry season between August and January (Ibama and Funatura, 1990). Southeast trade winds predominate, with greater intensity from July to September (Calliari et al., 2016). The South Equatorial Current is the main surface current around the archipelago, flowing from East to West and characterized by warm (26-27°C) and oligotrophic waters, with salinity 36 (Matheus et al., 2019).

Benthic habitats of FN are primarily rocky reefs dominated by turf algae, macroalgae, and a diverse assemblage of calcifying organisms, including corals, crustose and articulated coralline algae, and rhodolith beds. Other components, such as cyanobacteria, sponges,

ascidians, sea stars, and polychaetes, occur at relatively lower abundances (Zamoner et al., 2021).

The archipelago, declared as a Natural World Heritage Site due to its biological significance (UNESCO, 2001) includes two Marine Protected Areas (MPAs): the Marine National Park (Brazil, 1988) and the Environmental Protection Area (Brazil, 1986), corresponding to International Union for Conservation of Nature (IUCN) categories II and VI, respectively (Dudley, 2008). The Marine National Park, where the current study was conducted, covers 70% of the archipelago and is a no-take zone, with only regulated ecotourism and scientific research being permitted.

2.2 Sea surface temperature

Daily Sea Surface Temperature (SST) data from January 1985 to March 2025 were obtained from the FN virtual station on NOAA Coral Reef Watch (https://coralreefwatch.noaa.gov/product/vs/gauges/fernando_de_noronha.php). Daily median SST values and the daily temperature range (i.e., the difference between the maximum and minimum values) were calculated and, subsequently, monthly averages were computed for each year.

2.3 Macroalgae collection and sample treatment

Macroalgae samples were collected by scuba diving for benthic dinoflagellates evaluation at three sampling sites within the FN Marine National Park: Cagarras (CGR), Laje Dois Irmãos (LDI), and Ponta da Sapata (PDS) (Fig. 1). Sampling was performed once a year, in October, during the austral spring season, from 2017 to 2023, except in 2020, due to COVID-19 restrictions to access the area (Table 1). Sampling occurred within the Long-Term Ecological Research Program of the Brazilian Oceanic Islands (PELD-ILOC) Project. A total of 84 macroalgae samples were collected: 34 from CGR, 32 from PDS, and 18 from LDI (Table 1). When possible, considering sea conditions for scuba diving, samples were collected at two depths at CGR and PDS (Table 1). Scientific research and collection permits authorizing fieldwork were obtained from the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio), Brazilian Ministry of the Environment (permit numbers: 74213-1, 74213-2, 74213-3, 74213-4).

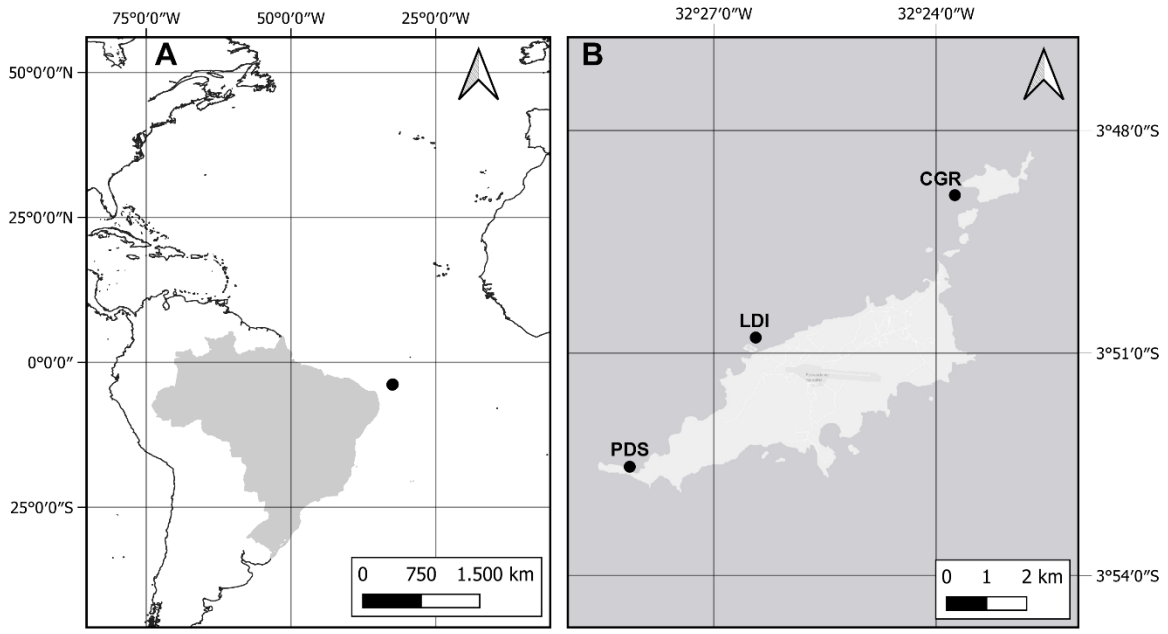


Figure 1. Study area. (A) Location of the Fernando de Noronha Archipelago in the tropical South Atlantic (Brazil in gray). (B) Sampling sites at the Fernando de Noronha Archipelago: Cagarras (CGR), Laje Dois Irmãos (LDI), and Ponta da Sapata (PDS).

Macroalgae were collected using sealable plastic bags filled the surrounding seawater, and the samples were then vigorously shaken for two minutes to detach associated epiphytic cells. The resulting suspension was separated from the macroalgae and preserved with neutral Lugol's iodine solution for identification and quantification of benthic dinoflagellates in the laboratory. Macroalgae were kept frozen for subsequent determination of fresh weight and species-level identification.

Table 1. Summary of sampling site information, including geographic coordinates, sampling years and depths, macroalgae species, and the number of specimens collected from each site at the Fernando de Noronha Archipelago.

Sampling sites	Latitude, Longitude	Sampling year and depth	Macroalgae sampled (number of individuals sampled)
Cagarras (CGR)	3°48'52.31"S, 32°23'44.80"W	2017: 6 and 15 m; 2018: 4 m; 2019: 5 m; 2021: 10 and 18 m; 2022: 5 and 17 m; 2023: 2, 4, and 10 m	*Canistrocarpus cervicornis* (23), *Canistrocarpus crispatus* (4), *Dictyota ciliolata* (1), *Dictyota pinnatifida* (1), *Galaxaura rugosa* (1), *Jania adhaerens* (1), *Jania capillacea* (1), *Tricleocarpa fragilis* (1), Set of red algae (*Jania adhaerens*, *Amphiroa fragilissima*, *Anotrichium tenue*, *Gayliela* sp. = 1)
Laje Dois Irmãos (LDI)	3°50'47.5"S, 32°26'26.1"W	2018-2023: 17-18 m	*Canistrocarpus cervicornis* (2), *Canistrocarpus crispatus* (11), *Dictyota* cf. *pinnatifida* (4), *Jania adhaerens* (1)
Ponta da Sapata (PDS)	3°52'32.0"S, 32°28'08.2"W	2017: 12 m; 2018: 8 m; 2019: 5 m; 2021: 8 and 14 m; 2022: 8 and 14 m; 2023: 4 and 10 m	*Canistrocarpus cervicornis* (5), *Canistrocarpus crispatus* (4), *Dictyopteris delicatula* (4), *Dictyota ciliolata* (2), *Dictyota menstrualis* (3), *Dictyota pinnatifida* (12), *Anotrichium tenue* and *Gayliela* sp. (1), *Jania adhaerens* and *Jania rubens* (1)

2.4 Benthic dinoflagellates abundance

Benthic dinoflagellates abundance was determined using a Sedgewick Rafter chamber or sedimentation chambers (2.5, 5, and 10 mL) and observed in a light inverted microscope (Primovert, Zeiss, Germany). Macroalgae's fresh weight was determined, and the volume of epiphyte samples was measured. Benthic dinoflagellates abundance was determined as cells per gram of macroalgae fresh weight (cells g^{-1} FW). Relative abundance (%) of each dinoflagellate genus was calculated in relation to the total benthic dinoflagellates abundance to assess the contribution of each genus to total abundance.

Ostreopsis, *Prorocentrum*, and *Sinophysis* were quantified at the species level. Among *Prorocentrum* species, the morphological characteristics that allow reliable discrimination among *P. emarginatum*, *P. fukuyoi*, and *P. sculptile* have not yet been established (Hoppenrath et al., 2013); therefore, abundance data for these species were presented together. The remaining benthic dinoflagellate genera were quantified at the genus level.

2.5 Species identification

Benthic dinoflagellates were examined using light microscopy (LM) (Zeiss Imager A2, Germany), and images were captured with a Zeiss AxioCam ICc1 digital camera. Scanning electron microscopy (SEM) was also performed. Sample preparation for SEM followed the protocol described by Borsato et al. (2023). Cells were then observed with a Quanta FEG 250 scanning electron microscope (FEI Company, Hillsboro, Oregon, USA).

2.6 Statistical analyses

Time series trend was tested using the non-parametric Mann-Kendall and Sen's methods to statistically assess whether there was a monotonic upward or downward trend, based on Kendall's Tau statistic, and applying the correction for data continuity. Analyses were performed independently for *Amphidinium*, *Coolia*, *Gambierdiscus*, *Ostreopsis*, and *Prorocentrum* to detect temporal trends in absolute (cells g^{-1} FW macroalgae) and relative (%) abundance at CGR, LDI, and PDS, from 2017 to 2023 (except 2020). Time series trend analysis was also applied to SST monthly averages (daily median and daily range), comprising 483 data points (January 1985 to March 2025). Time series analyses were performed at the significance level of 0.05 using the software Past 4.03.

The non-parametric Mann–Whitney U test was used to compare the total benthic dinoflagellates abundance and the abundance of each genus (*Amphidinium*, *Coolia*, *Gambierdiscus*, *Ostreopsis*, and *Prorocentrum*) between the periods 2017–2019 (before the COVID-19 pandemic) and 2021–2023 (after the COVID-19 pandemic), regardless of sampling depth, in order to increase the robustness of the statistical analysis. The test was performed using the software Statistica 10.0.

The influence of sampling depth on benthic dinoflagellates abundance was tested for the sampling sites CGR and PDS using data from 2017 to 2023, except for 2020. A Friedman ANOVA (ANOVA Chi Square) test was applied to the abundance data for each genus, testing by depth category: first depth and second depth. The number of replicates by depth category varied according to data availability for each site CGR (n=15) and PDS (n=11). Sampling depth varied between sites and within sites according to the study year. At CGR, the first sampling depth ranged between 4–10 m, while the second depth varied between 10–18 m. At PDS, the first depth was 4–8 m, and the second 10–14 m. Therefore, a depth range (and not absolute values) was used to evaluate differences in benthic dinoflagellates abundance.

A multivariate Principal Component Analysis (PCA) was applied to integrate the abundance data of benthic dinoflagellates genera (i.e., response variables) and the supplementary variables: SST, sampling year, and depth. Abundance data were transformed using Hellinger standardization. Before analysis, response data were log-transformed and standardized (centered), and the ordination was performed using a linear method based on unconstrained supplementary variable data. Multivariate analysis was performed using the software Canoco 5.04.

3. Results

3.1 Total benthic dinoflagellates abundance

Mean total benthic dinoflagellates abundance was $7.4x10^3$ cells g^{-1} FW at CGR (range: $9.5x10^2$ in 2019 and $1.5x10^4$ cells g^{-1} FW in 2021), $5.3x10^3$ cells g^{-1} FW at LDI ($2.1x10^2$ in 2019 and $1.1x10^4$ cells g^{-1} FW in 2022), and $4.5x10^3$ cells g^{-1} FW at PDS ($9.8x10^2$ in 2017 and $5.9x10^3$ cells g^{-1} FW in 2022) at PDS (Fig. 2). Lowest benthic dinoflagellates abundance was recorded in 2019, when filamentous cyanobacteria dominated the epiphytic environment, with mean abundances of $8.8x10^4$ at PDS and $2.1x10^5$ cells g^{-1} FW at CGR. Cyanobacteria was not recorded at LDI.

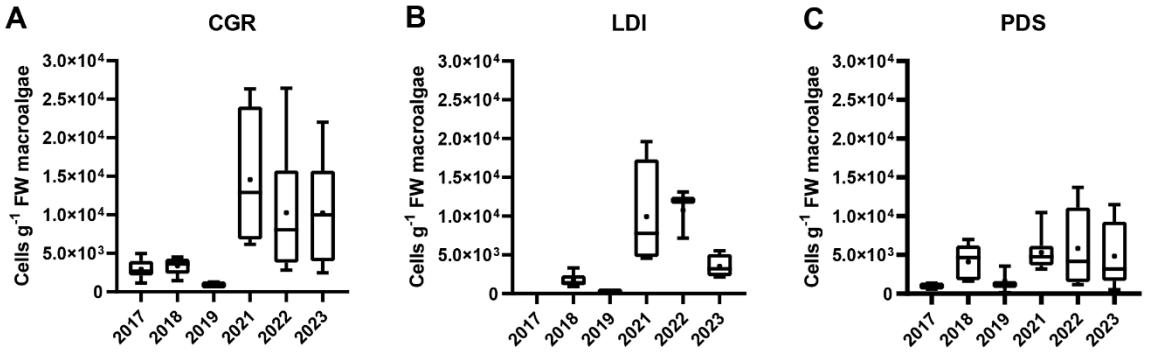


Figure 2. Total benthic dinoflagellates abundance (cells g^{-1} FW macroalgae) at each sampling site between 2017 and 2023, except 2020. Boxplots show 25th and 75th percentiles, median (-), mean (+), minimum, and maximum values.

3.2 Time series trend analysis

3.2.1 SST time series trend analysis

A significant increasing trend in SST median values was observed over the last 40 years (1985-2025; Mann-Kendall, $p < 0.0001$) at the FN Archipelago (Fig. 3A). Concurrently, a significant decreasing trend in daily temperature range was also verified (Mann-Kendall, $p < 0.0001$), indicating a tendency of narrower variability of increased SST values throughout the last four decades (Fig. 3B). During the study period, SST varied from 26.5 to 29.3 °C.

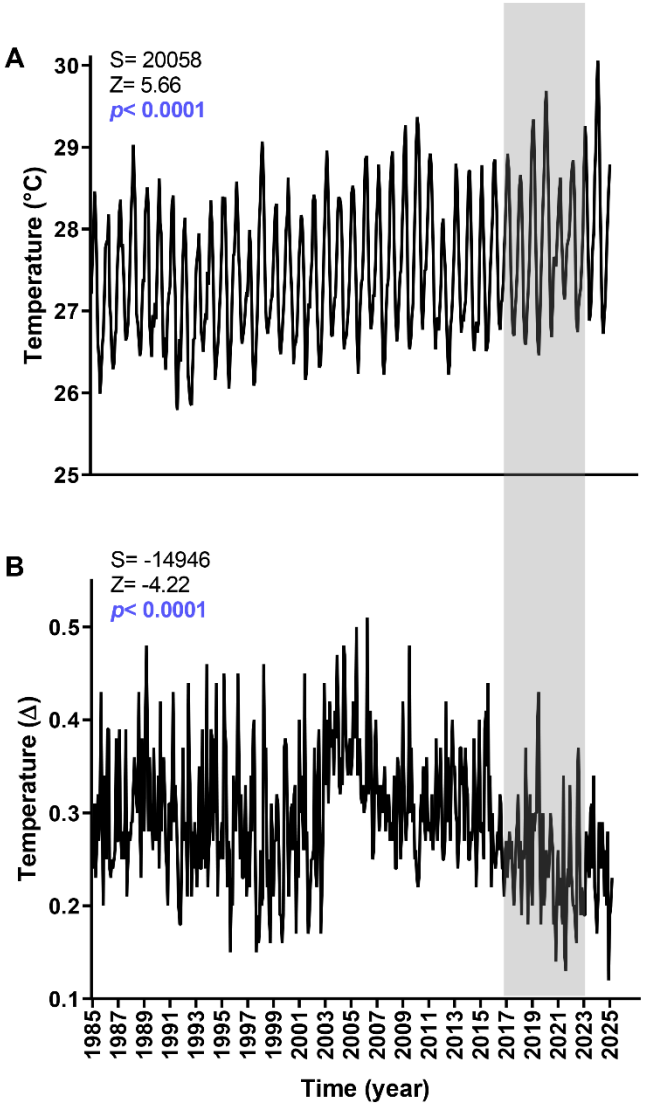


Figure 3. Results of the Mann-Kendall trend test in sea surface temperature (SST) at Fernando de Noronha Archipelago over 40 years (1985-2025). (A) Daily temperature median values (ºC); (B) Daily temperature range (maximum-minimum). Data are plotted as mean values by month. SST during this study is marked in gray.

3.2.2 Time series trend analysis of benthic dinoflagellates abundance and relative abundance

From 2017 to 2023, there was a significant increasing trend in *Amphidinium* abundance at the three sites (Mann-Kendall, $p < 0.0001$ at CGR, $p = 0.0029$ at LDI, and $p = 0.050$ at PDS, Fig. 4A, F, K). A significant increasing trend in *Coolia* abundance was observed at CGR (Mann-Kendall, $p = 0.0293$, Fig. 4B), while at LDI, although abundance values were higher lately, the increase was not significant (Mann-Kendall, $p = 0.5185$, Fig. 4G). At PDS, *Coolia* showed a non-significant decreasing trend (Mann-Kendall, $p = 0.330$, Fig. 4L).

A decreasing trend in *Gambierdiscus* abundance was found at PDS (Mann-Kendall, $p < 0.0001$, Fig. 4M) and CGR (Mann-Kendall, $p = 0.099$, Fig. 4C); however, this trend was significant only at PDS. At LDI, *Gambierdiscus* showed a significant increasing trend (Mann-Kendall, $p = 0.020$, Fig. 4H).

Significantly increasing trends in *Ostreopsis* abundance were observed at CGR (Mann-Kendall, $p = 0.0004$, Fig. 4D) and LDI (Mann-Kendall, $p = 0.0049$, Fig. 4I), while at PDS there was a non-significant decreasing trend (Mann-Kendall, $p = 0.8584$, Fig. 4N). *Prorocentrum* abundances showed non-significant increasing trends at the three sites (Mann-Kendall, $p = 0.1267$ at CGR, $p = 0.1297$ at LDI, and $p = 0.2365$ at PDS, Fig. 4E, J, O).

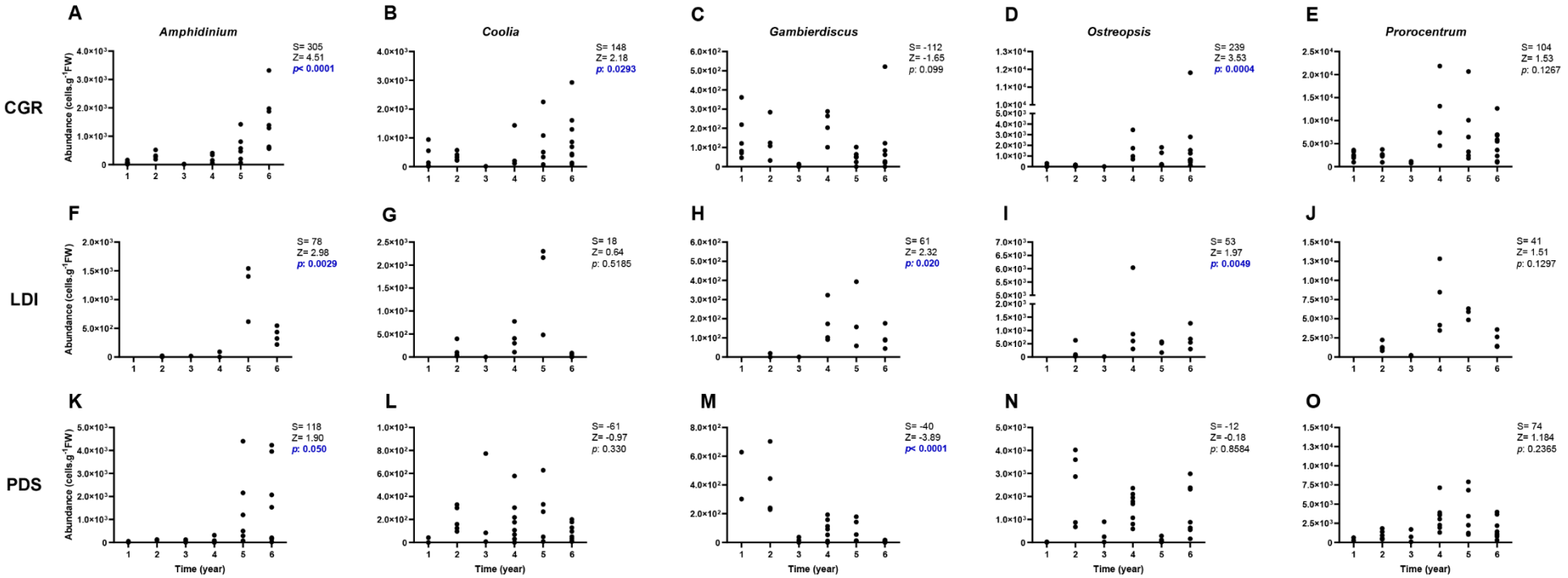


Figure 4. Results of the Mann-Kendall trend test applied to abundance data (cells g^{-1} FW macroalgae) of the genera *Amphidinium*, *Coolia*, *Gambierdiscus*, *Ostreopsis*, and *Prorocentrum* from the sampling sites CGR (A–E), LDI (F–J), and PDS (K–O) over six years. The x-axis shows the years, 1 = 2017, 2 = 2018, 3 = 2019, 4 = 2021, 5 = 2022, 6 = 2023. Statistically significant trends ($p \leq 0.05$) are highlighted in blue. Note the scale variation on the y-axis.

Amphidinium relative abundance showed an increasing trend at the three sites, and was significant at CGR (Mann-Kendall, $p = 0.0006$, Fig. 5A) and LDI (Mann-Kendall, $p = 0.0046$, Fig. 5F), and not significant at PDS (Mann-Kendall, $p = 0.5285$, Fig. 5K). A decreasing trend in *Coolia* relative abundance was recorded at LDI (Mann-Kendall, $p = 0.8184$, Fig. 5G) and PDS (Mann-Kendall, $p = 0.0183$, Fig. 5L) and was significant only at PDS. A non-significant increasing trend was observed for this genus at CGR (Mann-Kendall, $p = 0.4545$, Fig. 5B).

Gambierdiscus relative abundance showed a significant decreasing trend at CGR (Mann-Kendall, $p = 0.0001$, Fig. 5C) and PDS (Mann-Kendall, $p < 0.0001$, Fig. 5M), and a significant increasing trend at LDI (Mann-Kendall, $p = 0.0026$, Fig. 5H).

An increasing trend in *Ostreopsis* relative abundance was observed at the three sites (Fig. 5D, I, N) but was significant only at CGR (Mann-Kendall, $p = 0.0004$, Fig. 5D). There was a significant decreasing trend in *Prorocentrum* relative abundance at CGR (Mann-Kendall, $p = 0.0002$, Fig. 5E) and LDI (Mann-Kendall, $p = 0.0030$, Fig. 5J), while at PDS there was a non-significant increasing trend in *Prorocentrum* relative abundance (Mann-Kendall, $p = 0.2358$, Fig. 5O).

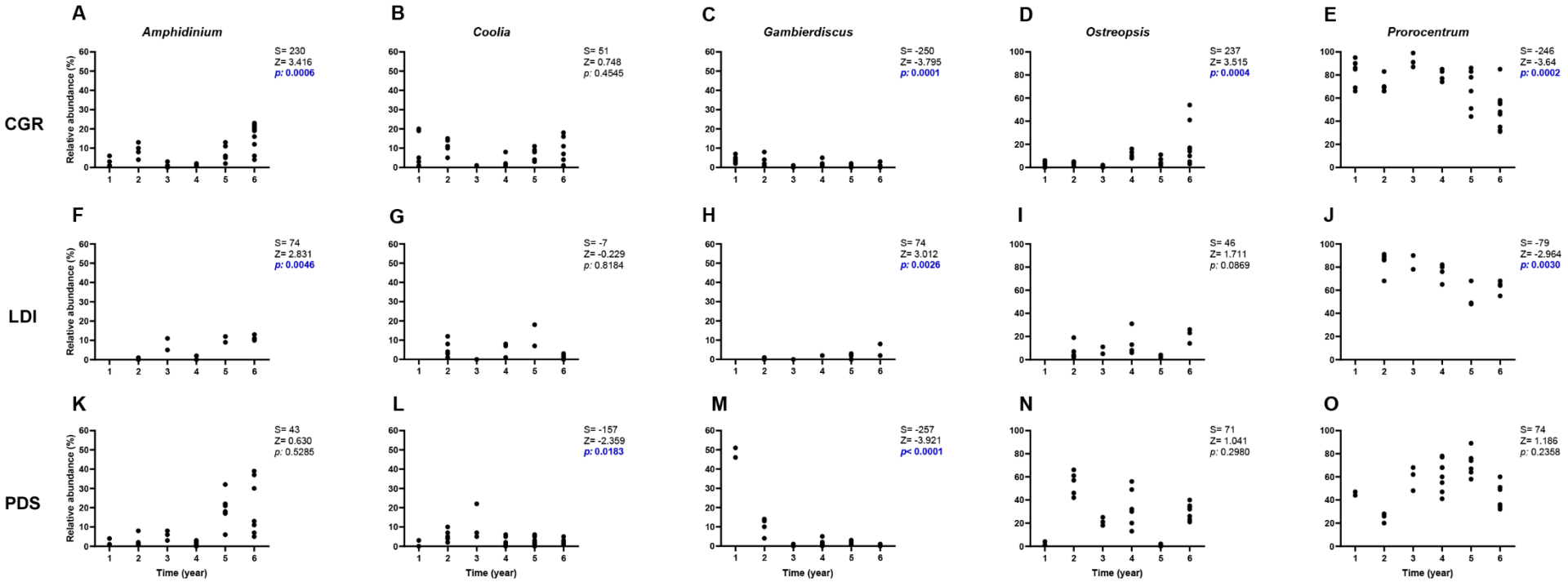


Figure 5. Results of the Mann-Kendall time series trend of the relative abundance of each genus (%) in relation to total benthic dinoflagellates abundance at the sampling sites CGR (A–E), LDI (F–J), and PDS (K–O) over six years. The x-axis shows the years, 1= 2017, 2= 2018, 3= 2019, 4= 2021, 5= 2022, 6= 2023. Statistically significant trends ($p \leq 0.05$) were highlighted in blue. Note the scale variation on the y-axis.

Mean abundance (cells g^{-1} FW macroalgae) and mean relative abundance (%) of each benthic dinoflagellate genus at the three sampling sites over the six-year study period is presented in Table S1. *Prorocentrum* was the most abundant genus in all years and sites, except at PDS in 2017 and 2018, where *Gambierdiscus* showed the highest abundance in 2017 and *Ostreopsis* in 2018. *Sinophysis*, *Cabra*, and *Bysmatrum* were minor components of the benthic dinoflagellates assemblage.

3.3 Comparison of abundance data in 2017-2019 and 2021-2023

In the first three years (2017–2019), mean total benthic dinoflagellates abundance considering the three sites, varied between $1.3x10^2$ and $7.0x10^3$ cells g^{-1} FW (mean = $2.4x10^3$), while in the last three years of the study (2021–2023), abundances were significantly higher (Mann-Whitney U, $p < 0.0001$) and ranged between $5.0x10^2$ and $2.6x10^4$ cells g^{-1} FW (mean = $8.0x10^3$).

Significantly higher abundances of *Prorocentrum* (Mann-Whitney U, $p < 0.0001$), *Ostreopsis* (Mann-Whitney U, $p < 0.0001$), *Coolia* (Mann-Whitney U, $p = 0.0168$), and *Amphidinium* (Mann-Whitney U, $p < 0.0001$) were found in 2021-2023 relative to 2017-2019. In contrast, *Gambierdiscus* showed higher abundances in 2017- 2019. In the first three years, mean abundance of *Amphidinium*, *Coolia*, *Gambierdiscus*, *Ostreopsis*, and *Prorocentrum* was 91, $1.9x10^2$, $1.4x10^2$, $4.8x10^2$, and $1.5x10^3$ cells g^{-1} FW at FN, respectively, while in 2021-2023 mean abundance of these genera was $8.4x10^2$, $4.9x10^2$, 93, $1.3x10^3$, and $4.9x10^3$ cells g^{-1} FW, respectively.

3.4 Benthic dinoflagellates abundance according to depth

Amphidinium, *Coolia*, and *Prorocentrum* abundances were significantly higher at the first sampling depth (4 to 8 m) relative to the second depth (10 to 14 m) at PDS (ANOVA Chi Square, $p = 0.00091$ for *Amphidinium* and *Coolia*, $p = 0.03481$ for *Prorocentrum*). *Gambierdiscus* and *Ostreopsis* abundance was not different between sampling depths at PDS. There was no significant difference in benthic dinoflagellates genera abundance between sampling depths (4-10 and 10-18 m) at CGR.

3.5 Integrated Principal Component Analysis (PCA)

The first and second PCA axes explained 52.04% and 17.07% of the variance, respectively, and supplementary variables (SST, sampling year, and depth) accounted for 29.10% (Fig. 6). Principal Component 1 (PCA 1) was negatively correlated with depth

(cc= -0.252) and positively correlated with sampling year (cc= 0.283), and SST (cc= 0.256) (Fig. 6). PCA1 mostly distinguished samples associated with high *Ostreopsis* abundances (negatively correlated to axis 1) in more recent years, higher SST, and lower depth (Fig. 6). *Prorocentrum*, *Coolia*, and *Amphidinium* were negatively correlated with PCA 1 and very closely related suggesting co-occurrence (Fig. 6). Samples did not show a clear group formation by sampling site.

Principal Component 2 (PCA 2) was negatively correlated with sampling year (cc= -0.173) and positively correlated with sampling depth (cc= 0.249) and SST (cc= 0.201) (Fig. 6). Sample ordination on PCA 2 mostly separated *Gambierdiscus*, that was positioned on the negative side of the axis (Fig. 6).

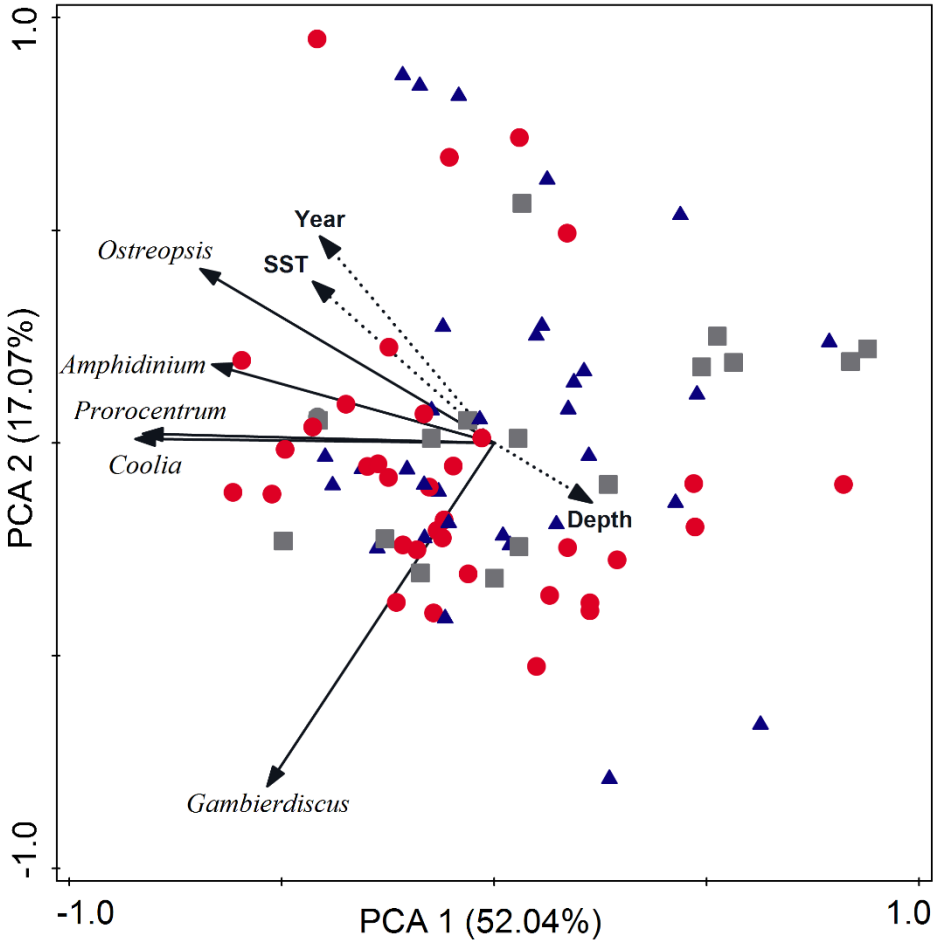


Figure 6. Biplot of the main genera of benthic dinoflagellate (full line vectors) from three sites at the Fernando de Noronha Archipelago. Dashed line vectors indicate supplementary variables: sea surface temperature (SST), sampling year, and depth. Different symbols indicate distinct sampling sites: Cagarras (•), Laje Dois Irmãos (■), and Ponta da Sapata (▲).

3.6 Benthic dinoflagellates species composition

Specimens of the genera *Amphidinium* (Fig. 7A), *Cabra* (Fig. 7B), *Ostreopsis* (Fig. 7C-D), *Bysmatrum* (Fig. 8A-B), *Coolia* (Fig. 8C-E), *Prorocentrum* (Fig. 8F-K), *Sinophysis* (Fig. 8L), and *Gambierdiscus* (Fig. 9) were found at all sampling sites.

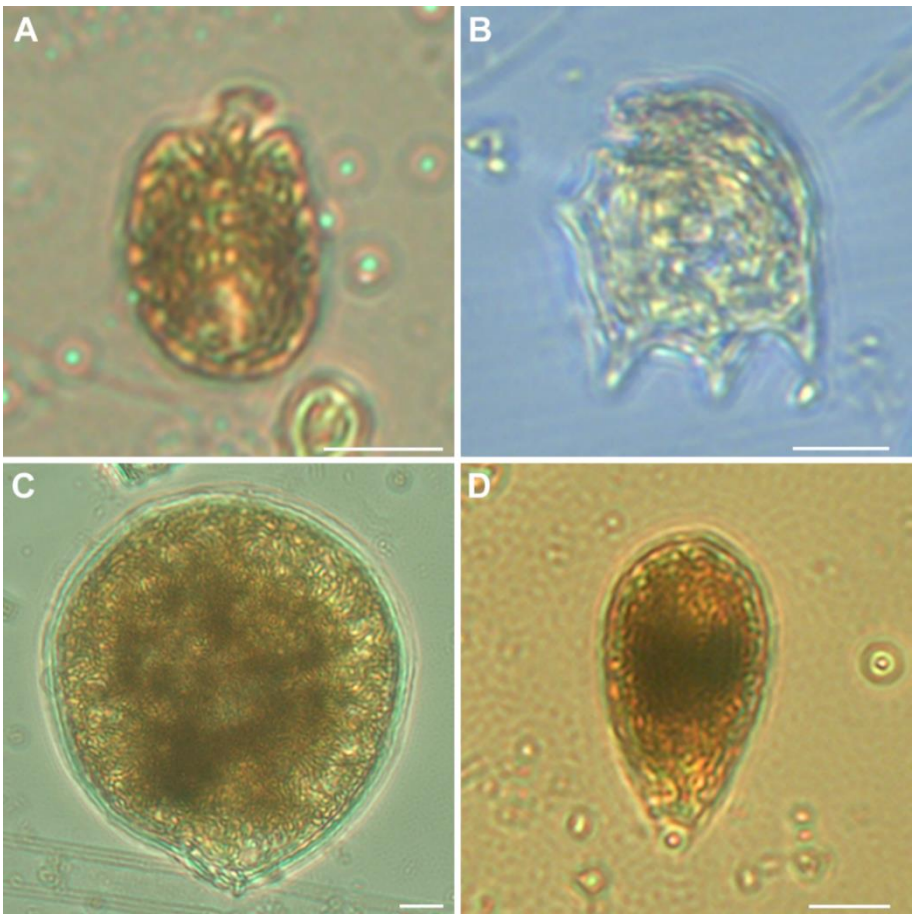


Figure 7. Light micrographs of specimens of (A) *Amphidinium* sp., (B) *Cabra* sp., (C) *Ostreopsis lenticularis*, and (D) *Ostreopsis* cf. *ovata* from the Fernando de Noronha Archipelago. Scale bar: 10 μm.

Species of *Cabra* (*C*. cf. *aremorica* and *C*. cf. *reticulata*), *Ostreopsis* (*O*. *lenticularis* Fig. 7C, and *O*. cf. *ovata* Fig. 7D), *Bysmatrum* (*B*. cf. *gregarium*, Fig. 8A-B), and *Coolia* (*Coolia* sp. Fig. 8C, *C*. cf. *canariensis* Fig. 8D, and *C*. cf. *malayensis* Fig. 8E) were observed. High *Prorocentrum* species richness was found, including *P*. *arenarium* (Fig. 8F-G), *P*. cf. *borbonicum*, *P*. cf. *concavum*, *P*. *emarginatum*/*fukuyoi*/*sculptile* complex (Fig. 8H), *P*. *hoffmannianum* (Fig. 8I), *P*. *lima* (Fig. 8J), *P*. cf. *norrisianum*, *P*. *panamense*, *P*. *rhathymum* (Fig. 8K), and two species not identified. *Sinophysis* cf. *canaliculata*, *Sinophysis* cf. *microcephala* (Fig. 8L), and *Sinophysis* cf. *stenosoma* were

observed at FN. *Gambierdiscus* cf. *belizeanus* (Fig. 9A-B) and *Gambierdiscus* cf. *silvae* (Fig. 9C-E) were also found.

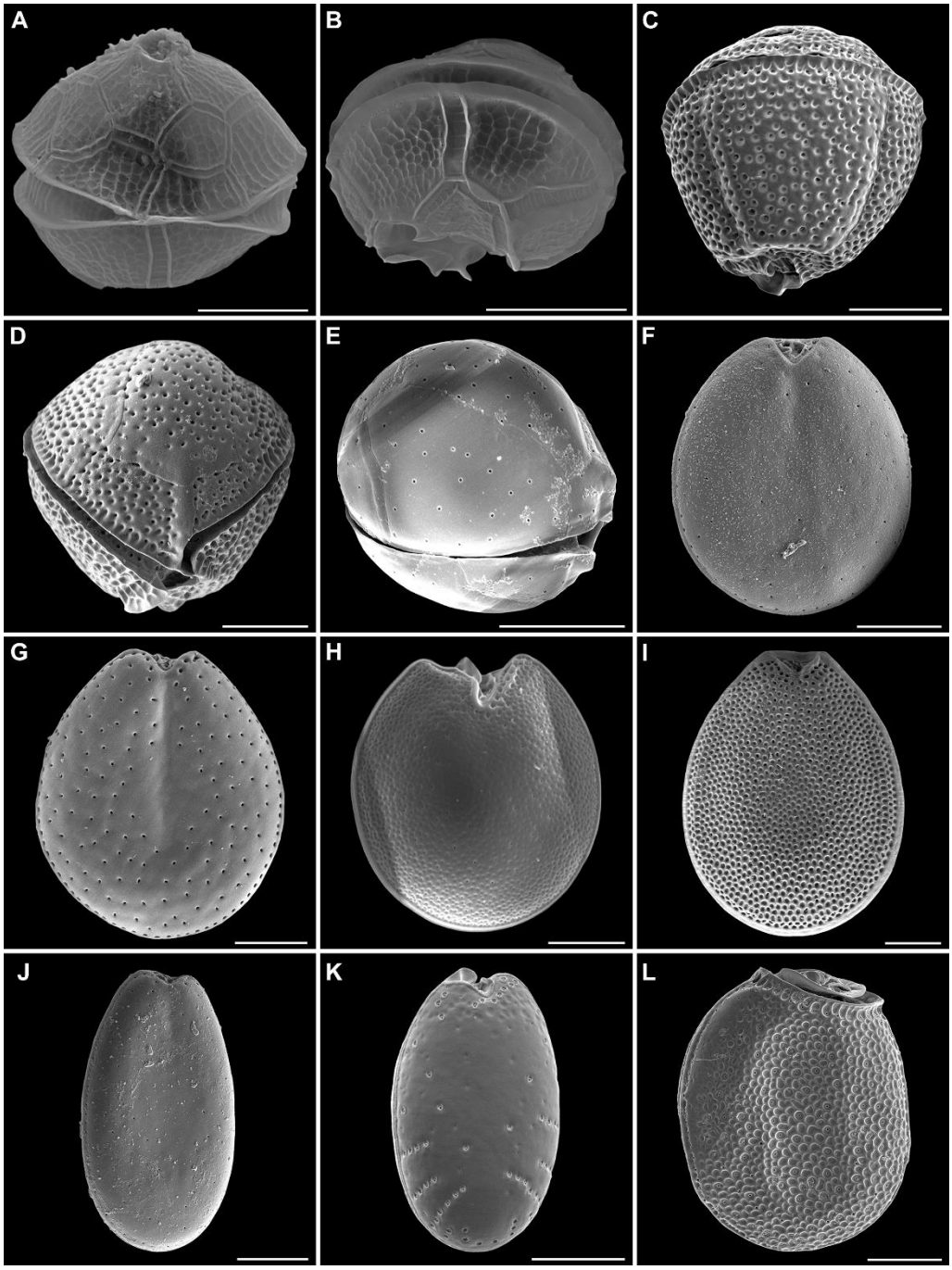


Figure 8. Scanning electron micrographs of specimens of (A-B) *Bysmatrum* cf. *gregarium*, (C) *Coolia* sp., (D) *Coolia* cf. *canariensis*, (E) *Coolia* cf. *malayensis*, (F-G) *Prorocentrum* cf. *arenarium*, (H) *Prorocentrum emarginatum*/*fukuyoi*/*sculptile* complex, (I) *Prorocentrum hoffmannianum*, (J) *Prorocentrum lima*, (K) *Prorocentrum rhathymum*, and (L) *Sinophysis* cf. *microcephala* from the Fernando de Noronha Archipelago. Scale bar: 10 μm.

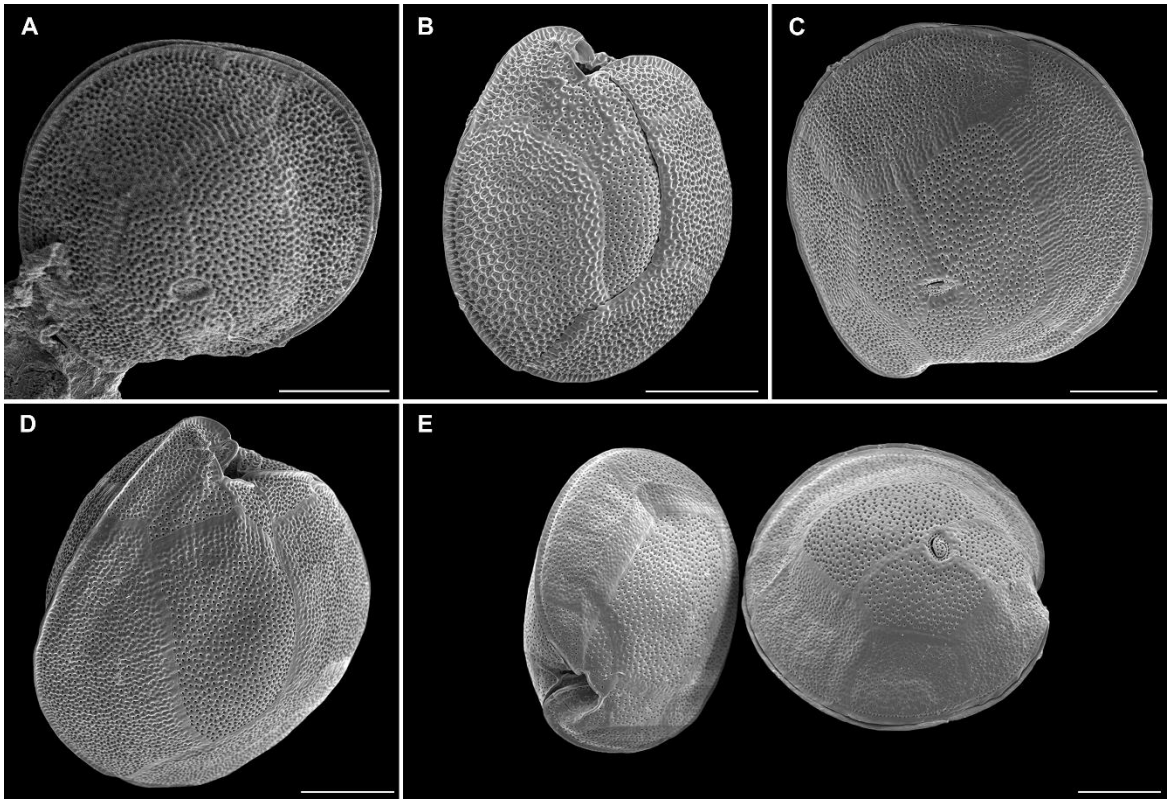


Figure 9. Scanning electron micrographs of *Gambierdiscus* species from the Fernando de Noronha Archipelago. (A-B) *Gambierdiscus* cf. *belizeanus*, (C-E) *Gambierdiscus* cf. *silvae*. (A, C) Apical view, (B, D) Antapical view, (E) Ventral to antapical and lateral-apical views. Scale bar: A-D: 20 μm, E: 40 μm.

3.7 Benthic dinoflagellates species abundances

At CGR, *Prorocentrum lima* (mean abundance between $1.5x10^2$ and $9.2x10^3$ cells g^{-1} FW) and *P. arenarium* ($1.5x10^2$ – $1.0x10^3$ cells g^{-1} FW) were the most abundant species of the genus *Prorocentrum*, and contributed up to 61% and 46%, respectively, to total benthic dinoflagellates abundance at this site. Mean *O.* cf. *ovata* abundance ranged between 7 and $2.1x10^3$ cells g^{-1} FW, and was higher than that of *O. lenticularis* (0 and $4.7x10^2$ cells g^{-1} FW). Mean relative abundance of *O.* cf. *ovata* and *O. lenticularis* did not exceed 17% and 4% at CGR, respectively. Regarding *Sinophysis*, *S.* cf. *microcephala* showed mean abundance of 62 cells g^{-1} FW, while *S.* cf. *canaliculata* 14 cells g^{-1} FW, and *S.* cf. *stenosoma* only 1 cell g^{-1} FW.

At LDI, *P. emarginatum*/*fukuyoi*/*sculptile* complex was the most abundant *Prorocentrum* in three of the five sampling years, with mean abundance up to $1.4x10^3$ cells g^{-1} FW, contributing 45% to total dinoflagellates abundance at this site.

Prorocentrum lima was also abundant at LDI (mean up to $3.7x10^3$ cells g^{-1} FW and 39%). *Ostreopsis lenticularis* mean abundance ranged from 15 to $1.0x10^3$ cells g^{-1} FW, and *O.* cf. *ovata* from 0 to $9.3x10^2$ cells g^{-1} FW. Mean relative abundance of *O. lenticularis* and *O.* cf. *ovata* did not exceed 8% and 17%, respectively. *Sinophysis* cf. *microcephala* mean abundance was 34 cells g^{-1} FW, and that of *S.* cf. *canaliculata* was 4 cells g^{-1} FW.

At PDS, *Prorocentrum emarginatum*/*fukuyoi/sculptile* complex (57 – $6.3x10^2$ cells g^{-1} FW) and *P. lima* ($1.1x10^2$ – $2.7x10^3$ cells g^{-1} FW) were the more abundant *Prorocentrum* species, with mean relative abundance up to 11% and 51% at this site, respectively. *Ostreopsis* cf. *ovata* was the most abundant *Ostreopsis* species at PDS, with mean abundance ranging from 16 to $1.7x10^3$ cells g^{-1} FW, and *O. lenticularis* between 0 and $6.8x10^2$ cells g^{-1} FW. *Ostreopsis* cf. *ovata* and *O. lenticularis* mean relative abundance did not exceed 38% and 17%, respectively. At PDS, *S.* cf. *microcephala* mean abundance was 11 cells g^{-1} FW, and that of *S.* cf. *canaliculata* was 23 cells g^{-1} FW.

4. Discussion

This was the first spatial and temporal investigation of benthic dinoflagellates at the Fernando de Noronha (FN) Archipelago, one of the most diverse marine areas in the tropical South Atlantic. The assemblage was mainly represented by the genera *Prorocentrum*, *Ostreopsis*, *Amphidinium*, *Coolia*, and *Gambierdiscus*, as has been observed in other tropical areas. *Bysmatrum*, *Sinophysis*, and *Cabra* were present in lower abundances.

Benthic dinoflagellates abundance at the sites CGR and LDI showed an increase trend from 2017 to 2023, except *Gambierdiscus* at CGR. At the site PDS, only *Amphidinium* and *Prorocentrum* abundances showed an increasing trend, while *Coolia*, *Gambierdiscus*, and *Ostreopsis* showed a decreasing trend. When comparing the period before (first three) and after (last three years of the study) the COVID-19 pandemic, both total and *Prorocentrum*, *Ostreopsis*, *Coolia*, and *Amphidinium* abundances were significantly higher in 2021-2023 relative to 2017-2019. Concomitantly, the annual tourist influx to the archipelago increased from 303,829 tourists in 2017-2019 (101,276 visitors per year, Marinho, 2018, 2019, 2020) to 387,384 in 2021-2023 (129,128 visitors per year, Marinho, 2022, 2023, 2024), a 27.5% rise. In 2020, due to the COVID-19 pandemic, access to the archipelago was restricted for five months, from March to August 2020, and the island was fully reopened in December 2020.

The increased number of visitors has raised serious concerns related to basic sanitation efficiency, as the island's wastewater treatment infrastructure has not kept pace with the population increase (Cristiano et al., 2020; Araújo et al., 2023; Mello et al., 2025; Adam et al., 2025). Moreover, failure in both the operation and infrastructure of wastewater treatment plants have been reported, including incomplete or inadequate treatment according to regulatory guidelines, as well as reliance on outdated pipeline systems prone to cracks and blockages, which further limit treatment effectiveness (Cristiano et al., 2020; Silva, 2023). In parallel, the resident population at FN increased from 2,630 inhabitants in 2010 to 3,167 in 2022 (IBGE, 2010, 2022).

This scenario has likely contributed to the deterioration of seawater quality, as inefficient wastewater treatment and the discharge of untreated effluents into the sea have resulted in significant nutrient enrichment at FN Environmental Protection Area (EPA) (Mello et al., 2025). To a lesser extent, nutrient enrichment, along with contamination by metals, microplastics, and polycyclic aromatic hydrocarbons (PAHs), has also been recorded within the FN Marine National Park (MNP) (Mello et al., 2025), where the present study was conducted. Studies from 2013–2014 at various sites in FN reported lower nutrient concentrations than those observed in 2022 by Mello et al. (2025), indicating a rise over the past decade (Assunção et al., 2016; Bertini and Braga et al., 2022). This condition is worsened by the discharge of effluents from a desalination plant used to produce potable water (Cristiano et al., 2020). The increased input of nutrients and pollutants, due to growing human pressure, is likely an important driver of the increase in benthic dinoflagellates abundance observed at FN.

In addition to nutrient enrichment, SST in the archipelago has increased significantly over the past 40 years, accompanied by a narrowing in daily SST amplitude. This pattern is consistent with an increase in global SST of ~0.18 °C per decade since 1981 (~0.7 °C until 2022) (Martinez-Lopez et al., 2024), as well as a decreasing trend in daily SST amplitude in the tropics (Chan et al., 2025). Temperature was shown to be the most important factor affecting the growth of three benthic dinoflagellate species from different genera (*O.* cf. *ovata*, *P. lima*, *C.* cf. *malayensis*) under controlled laboratory conditions, having a direct positive effect on growth rate (Grigoriyan et al., 2024).

Moreover, the intensity, duration, and frequency of thermal stress episodes have increased in the South Atlantic since 1985 (Destri et al., 2025). In 2019, during an intense marine heatwave, biofilms with high benthic filamentous cyanobacteria abundances

covered the epilithic algal matrix (turf algae) and macroalgae at the sites studied in the current study (Zamoner et al., 2021). Benthic cyanobacteria growth and dominance in 2019 resulted in the lowest benthic dinoflagellates abundance recorded in the present study. In 2024, thermal stress anomalies persisted for five months along the entire Brazilian coast, and FN experienced 40 days of moderate thermal stress and 46 days of severe stress (Mies et al., 2025). Preliminary analyses of samples from 2024 also showed high filamentous cyanobacteria abundances (data not shown).

In two Caribbean reefs, a shift from calcifying organisms (corals and crustose coralline algae) to a community dominated by algae and, subsequently, by benthic cyanobacterial mats was observed over a 40-year period (Bakker et al., 2017). The deterioration of seawater quality due to nutrient enrichment and increasing seawater temperatures were suggested as the main drivers of changes in reef benthic communities (Bakker et al., 2017).

Several studies have shown that different types of disturbances affecting coral reefs, both natural and anthropogenic, such as storms, hurricanes, and bleaching events, can result in a reduction in coral cover, thereby freeing space that may be colonized by macroalgae and turf algae (Hughes et al., 2010; Elma et al., 2023; Hernández-Delgado et al., 2024). As a consequence, more substrate becomes available for epiphytic microalgae colonization, a process that has been recognized as a factor promoting the growth of benthic dinoflagellates, particularly *Gambierdiscus* (Randall, 1958; Yasumoto et al., 1980; Chinain et al., 1999; Lehane and Lewis, 2000; Holmes and Lewis, 2025). Southwestern Atlantic reefs, including those of FN, are naturally algae-dominated, with the turf algae and macroalgae comprising the main components of reef benthic communities, while corals represent less than 5% of benthic cover (Aued et al., 2018; Zamoner et al., 2021). Therefore, this high algae coverage represents a favorable environment for epiphytic microalgae colonization, including benthic dinoflagellates.

Besides high substrate (macroalgae and turf algae) availability, seawater temperature and irradiance are within the optimal range for the growth of many benthic dinoflagellate species at FN (SST ranged from 26.5 to 29.3 °C during the current study). However, conditions of thermal stress caused by marine heatwaves may displace seawater temperature to values that exceed benthic dinoflagellate species upper thermal tolerance, beyond which growth slows significantly (Tester et al., 2020). At FN, the thermal stress appears to benefit benthic cyanobacteria over dinoflagellates.

Most studies assessing the distribution and abundance of benthic dinoflagellates in tropical regions have been conducted in shallow waters, generally down to 5 m depth (e.g., Martínez-Cruz et al., 2015; Aguilar-Trujillo et al., 2017; Irola-Sansores et al., 2018; Boisnoir et al., 2019a, 2019b) and less is known about their distribution at deeper depths (e.g., Richlen and Lobel, 2011; Boisnoir et al., 2018). In the current study, depth range was considered in the statistical analysis because sampling depths varied between years, compromising a more precise comparison of benthic dinoflagellates abundance across depths. The analysis indicated that *Gambierdiscus* and *Ostreopsis* abundances did not vary significantly with depth at PDS and CGR, while *Amphidinium*, *Coolia*, and *Prorocentrum* showed significantly higher abundances at 4-8 m relative to 10-14 m at PDS. No significant difference in benthic dinoflagellates abundance at 4-10 m and 10-18 m was observed at CGR. Higher light incidence in shallow coastal environments likely favors the growth of these species, and therefore, higher abundances would be expected. However, at FN, the water is clear, and light may reach a depth of 50 m (Matheus et al., 2019). Among benthic dinoflagellates, *Ostreopsis* is generally more abundant at shallow waters, down to 4 m depth (Totti et al., 2010; Cohu and Lemée, 2012; Richlen and Lobel, 2011; Boisnoir et al., 2018), while in the present study, samples were collected at depths $\geq$ 4 m.

Boisnoir et al. (2018) evaluated benthic dinoflagellates abundance in relation to depth at Gosier and Rivière Sens, in the Guadeloupe Archipelago (Caribbean Sea). *Ostreopsis* was negatively correlated with depth, showing higher abundances at depths $\leq$ 4 m at both sites, as was *Gambierdiscus* abundances, which was higher at $\leq$ 2 m in Gosier. A positive correlation was observed between *Amphidinium* and depth, with higher abundance at 15 m in Rivière Sens (Boisnoir et al., 2018). *Prorocentrum* and *Coolia* peak abundances were observed at different depths at the two sites studied by Boisnoir et al. (2018). At the Johnston Atoll in the Pacific Ocean, *Gambierdiscus* (highest at 13 m) and *Prorocentrum* (higher between 11–13 m) abundances showed a significant positive correlation with depth, whereas *Ostreopsis* showed a significant negative correlation (higher at 3 m) (Richlen and Lobel, 2011).

At the Guadeloupe Archipelago, depth was not an ecological factor influencing the total benthic dinoflagellates abundance. However, it partially structured the distribution of several dinoflagellate genera, suggesting responses other ecological parameters, such as temperature and salinity (Boisnoir et al., 2018). At Johnston Atoll,

besides depth, habitat type and water motion significantly affected both dinoflagellate abundance and community composition among sampling stations (Richlen and Lobel, 2011). Therefore, the relation between benthic dinoflagellates abundance and depth is variable according to environmental features of different sites. Benthic dinoflagellate assemblages are structured according to their responses to a combination of factors, such as temperature, light, nutrient concentrations, salinity, substrate availability, hydrodynamics, as well as biotic interactions, and organism's ability to persist after disturbances, resulting in fluctuations in abundance and species composition.

Prorocentrum, *Ostreopsis*, *Coolia*, and *Amphidinium* abundance values observed at FN were similar to those reported at other locations in the tropical Atlantic Ocean, such as the Caribbean Sea (Delgado et al., 2006; Tester et al., 2014; Boisnoir et al., 2018, 2019a, 2019b), the Yucatan Peninsula (Martínez-Cruz et al., 2015; Aguilar-Trujillo et al., 2017; Irola-Sansores et al., 2018), and the Gulf of Mexico (Okolodkov et al., 2007, 2014). *Sinophysis*, *Bysmatrum*, and *Cabra* abundances are rarely reported in the literature, and are low in the tropical Atlantic (Okolodkov et al., 2014; Martínez-Cruz et al., 2015; Aguilar-Trujillo et al., 2017; Boisnoir et al., 2019b). *Cabra* species are rarely observed, and the few studies that have identified this genus in the Caribbean Sea and the Gulf of Mexico did not determine its abundance.

To date, few studies have assessed the abundance of benthic dinoflagellates associated with macroalgae on tropical oceanic islands. In the Cape Verde Islands (tropical Atlantic), *Prorocentrum* (up to $8.9x10^2$ cells g^{-1} FW) and *Coolia* (up to $3.6x10^2$ cells g^{-1} FW) mean abundances were within the range reported for FN, while *Ostreopsis* abundances were higher (from $4.8x10^3$ to $1.5x10^5$ cells g^{-1} FW, Fernández-Zabala et al., 2019). At Guadeloupe and Martinique Islands (Lesser Antilles, Caribbean Sea) a similar pattern was observed, while most genera displayed mean abundances within the range found at FN, *Ostreopsis* reached higher values in Guadeloupe ($2.5x10^4$ cells g^{-1} FW, Boisnoir et al., 2019b) compared to our results. In the tropical Pacific, at Hawaii (Parsons and Preskitt, 2007) and Johnston Atoll (Richlen and Lobel, 2011), *Ostreopsis*, *Prorocentrum*, *Coolia*, and *Amphidinium* mean abundances were consistently below $6.0x10^2$ cells g^{-1} FW. In Bali (tropical Indian Ocean), *Gambierdiscus*, *Ostreopsis*, and *Prorocentrum* abundances were low, and up to $1.0x10^2$ cells g^{-1} FW, although higher *Ostreopsis* abundances (up to $3.0x10^3$ cells g^{-1} FW) were observed (Skinner et al., 2011). Overall, these abundance values are lower than those found at FN.

Ostreopsis cf. *ovata* (up to $2.1x10^3$ cells g^{-1} FW) and *O. lenticularis* (up to $1.0x10^3$ cells g^{-1} FW) abundances found in the current study, at sites within the FN Marine National Park can be considered moderate to low. In contrast, in a previous study that included sites within the Environmental Protection Area, high *O. lenticularis* ($7.6x10^4$ cells g^{-1} FW) abundances were found at a site close to the discharge of sewage and desalination plant effluents in 2018 (Borsato et al., 2020) and then again in 2022, when a biofilm of *O. lenticularis* was seen covering macroalgae, with a mean abundance of $1.5x10^4$ cells g^{-1} FW (data not published). In the tropical South Atlantic, *O.* cf. *ovata* blooms (up to 10^5 cells g^{-1} FW) have been reported at the Saint Paul Rocks oceanic archipelago, that is 630 km away from FN (Nascimento et al., 2012b); and along the Brazilian coast, at Rio de Janeiro in the Southeast Brazil (Nascimento et al., 2008, 2010), where sea urchin (*Echinometra lucunter*) mortality were recorded (Ferreira, 2006), and at the Currais coastal archipelago, Southern Brazil (Tibiriçá et al., 2019).

Gambierdiscus maximum abundance observed during the current study was $7.0x10^2$ cells g^{-1} FW at FN Marine National Park. Cases of ciguatera poisoning have been reported yearly at FN since 2022 (Nascimento et al., 2025), and recently the presence of Caribbean ciguatoxins (C-CTXs) was confirmed in fish samples involved in ciguatera cases at FN (Hoff et al., 2026). This was the first finding of these toxins in fish from the South Atlantic Ocean.

Many harmful species listed in the IOC-UNESCO Taxonomic Reference List of Harmful Microalgae (Lundholm et al., 2026) were recorded at FN, including *O.* cf. *ovata*, *G.* cf. *belizeanus*, *G.* cf. *silvae*, *P. lima*, *P. hoffmannianum*, *P. rhathymum*, *P.* cf. *borbonicum*, *P.* cf. *concavum*, *C.* cf. *canariensis*, and *C.* cf. *malayensis*. The presence of these species at FN raises concerns regarding the impacts of biotoxins, including CTXs, PLTX analogs, OA, and their derivatives to the marine biota in this archipelago of high marine biodiversity.

Overall, benthic dinoflagellates abundance increased between 2017 and 2023, with distinct patterns among sites and genera, and was significantly higher during 2021-2023 compared to 2017-2019 for most taxa. Thus, the present study provides baseline data on harmful benthic dinoflagellates at FN, which is essential for assessing potential future impacts of anthropogenic activities. Over the past 40 years, an increase in SST and a narrowing of the thermal amplitude have been observed at FN. Warming seas, combined with increased nutrient inputs from inefficient wastewater treatment, associated with

population growth and tourism expansion are likely drivers of the increasing trend in benthic dinoflagellates abundance. In this context, improving sewage infrastructure and ensuring effective wastewater treatment are crucial measures to mitigate eutrophication in the archipelago. Furthermore, these findings highlight the importance of long-term monitoring of marine systems to understand benthic dinoflagellates dynamics under climate change and local anthropogenic stressors; as well as their use as an early warning system for threats to public health and marine ecosystems.

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Capítulo 3

Influence of marine pollution on benthic dinoflagellates assemblage of a Marine Protected Area in the Tropical South Atlantic Ocean

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1. Introduction

The ocean is fundamental to the maintenance of life on the planet and provides a wide range of ecosystem services, including the provision of food resources, climate regulation, habitat provision, cultural services, and the biogeochemical cycling of nutrients (Hattam et al., 2015). However, the integrity and resilience of marine ecosystems are under increasing pressure due to climate change and the intensification of human activities. Eutrophication is one of the major threats to the health of marine ecosystems and is considered a global problem, with coastal regions worldwide being affected by elevated nutrient inputs (Devlin and Brodie, 2023).

Nutrient fluxes, mainly nitrogen (N) and phosphorus (P), to the marine ecosystem may originate from point sources, such as sewage effluents (treated or untreated) and discharges from industrial facilities, as well as from diffuse sources, primarily surface runoff from agricultural watersheds (Devlin and Brodie, 2023). Nutrient loads cause a variety of impacts, including high chlorophyll-a concentrations, excessive growth of marine macroalgae, harmful algal blooms, reductions in biodiversity, changes in species composition, and decreased water transparency. At more advanced stages, high bacterial levels, foam formation, fungal proliferation, hypoxia, and ultimately anoxia are observed (Devlin and Brodie, 2023).

While high-income countries treat approximately 70% of municipal and industrial effluents, in low-income countries only about 8% of effluents undergo some form of treatment, and it is estimated that more than 80% of global effluents are discharged without any treatment (WWAP, 2017), and may ultimately reach the ocean. In the North Atlantic, pollutants are derived mainly from industrial activities and fossil fuel combustion, whereas in South America the primary source of pollution has been identified as the lack of adequate sewage systems and wastewater treatment plants (WWAP, 2017).

Harmful algal blooms (HABs) are increasing in coastal waters worldwide (Anderson et al., 2002; Glibert and Burkholder, 2018). These blooms, especially when formed by toxic species, are detrimental to marine ecosystems and can negatively affect fauna (Berdalet et al., 2017; Pavaux et al., 2020), as well as impact human health (Vila et al., 2016) and the economy, with significant losses to fisheries resources and tourism (Berdalet et al., 2017).

HABs may be associated with anthropogenic nutrient enrichment through elevated concentrations of inorganic and/or organic nutrients and changes in their relative proportions (Glibert and Burford, 2017). Resource ratio theory (Tilman, 1977, 1982, 1985; Smayda, 1997) predicts that, as the ratios of different essential elements change, community structure also shifts as a result of competition among algae with different optimal nutrient ratios. With changes in nutrient availability, species with different requirements may experience physiological stress or be favored.

Pollution, habitat modification, resource exploitation, invasive species, and climate change have been identified as the main drivers of biodiversity loss (Young et al., 2016). One of the principal strategies adopted globally for marine conservation is the establishment

of marine protected areas (MPAs) (Roberts and Hawkins, 2000; Dalongeville et al., 2022); however, these areas are currently exposed to threats that may compromise their ability to deliver conservation outcomes (Abessa et al., 2018).

The reasons for establishing MPAs often include the need to protect critical habitats of commercially or recreationally important species, or areas that serve as particularly good examples of a given habitat type (Kelleher, 1999). Thus, in many cases, sites selected to become MPAs are assumed to exhibit pristine conditions, in which the respective environments show little or no degradation. However, sporadic cases may include degraded marine areas that are intended to be restored through the control of pollution sources. Accordingly, the establishment of a given MPA is expected to ensure that local species and ecosystems are effectively protected from anthropogenic stressors, among which marine pollution is recognized as one of the major threats to MPAs (IUCN, 1994; Chatwin, 2007; Selig et al., 2014).

Oceanic islands are remote areas often regarded as near-pristine environments (Quimbayo et al., 2019). Due to their evolutionary history marked by isolation, these islands may support unique marine biota, constituting areas of high conservation value. The Fernando de Noronha (FN) Archipelago is widely recognized for its ecological importance. It and was designated a UNESCO World Natural Heritage site (UNESCO, 2021) and identified as a priority Marine Protected Area for the conservation of endemic species and marine communities in the South Atlantic. The archipelago is divided into a Marine National Park (MNP) and an Environmental Protection Area (EPA).

Recent studies have reported a significant increase in pollution at FN, associated with a higher number of inhabitants and intensified tourism, which leads to increased discharge of pollutants from various sources (Cristiano et al., 2020; Araújo et al., 2023; Mello et al., 2005). To date, changes in macroalgal community composition, reduced fish abundance (Mello et al., 2025), and genomic damage in shark (Araújo et al., 2023) and crab (Adam et al., 2025) species have been linked to pollution at FN. In the present study, the effects of nutrient (N and P) concentrations on abundance, species composition, and richness of harmful benthic dinoflagellates were assessed at sites within the MNP and the EPA.

2. Materials and methods

2.1 Study area

FN is a volcanic archipelago with an approximate area of 26 km², located about 545 km off the Northeast Brazilian coast, in the tropical South Atlantic (Ibama and Funatura, 1990). The climate is tropical, and the region is under the influence of the westward-flowing South Equatorial Current, which is characterized by warm (26–27 °C), saline (36), and oligotrophic waters (Matheus et al., 2019). The combined action of winds and ocean currents leads to the formation of two distinct regions in FN: the leeward coast, oriented towards the Northwest and sheltered from the direct influence of winds and currents, where 11 of the 12 sampling sites in this study are located; and the windward coast, oriented toward the Southeast and characterized by high hydrodynamic (Matheus et al., 2019).

The archipelago comprises two Marine Protected Areas: a Marine National Park (MNP) (Brazil, 1988) and an Environmental Protection Area (EPA) (Brazil, 1986). The MNP comprises 70% of the main island's land area, the secondary islands, and the insular shelf, including the entire windward coast and part of the leeward coast. Within the MNP, human activities are largely restricted; only regulated ecotourism and scientific research are permitted, and it is a no-take area. The remaining 30% corresponds to the EPA, a partially protected area designated for sustainable use, where various human activities are allowed, such as fishing, diving, boating, and urban development, although subject to established guidelines (ICMBio, 2017).

The main island is the only one inhabited and supports a population of approximately 3,341 people (IBGE, 2025). Tourism is the archipelago's main economic activity and has been growing exponentially, with 387,384 visitors recorded between 2021 and 2023 (129,128 visitors per year; Marinho, 2022, 2023, 2024). There are two wastewater treatment plants (WWTPs) in the archipelago, both located within the EPA. The WWTPs carry out preliminary treatment (screening and grit chamber), secondary treatment (upflow anaerobic reactors, anaerobic filters, stabilization ponds), and tertiary treatment (effluent disinfection system), followed by sludge treatment. One of the WWTPs is located at Boldró and discharges its effluents at the same site, while the other is situated at Cachorro, with its effluents released at Biboca. The archipelago does not support significant agricultural activities, and the use of fertilizers is prohibited. Livestock farming is restricted and involves a small number of animals, estimated at fewer than 400 individuals (Mello et al., 2025).

Given the scarcity of natural freshwater sources in the island, the desalination system is a central component of the potable water supply for residents and visitors of FN. The

archipelago has no natural springs and relies on harvested and stored rainfall, together with desalination, to supplement its water supply. Untreated hypersaline water from the desalination plant is discharged at Boldró (Cristiano et al., 2020).

Most of the municipal solid waste generated in FN is transported by ship to the mainland, where it undergoes further sorting and final disposal, as a result of space constraints and the lack of capacity for a sanitary landfill on the island.

2.2 Macroalgae collection for benthic dinoflagellates analyses and sample treatment

Macroalgae were collected by scuba or free diving at 12 sampling sites at FN Archipelago: six within the Marine National Park (MNP) (Cagarras, Laje Dois Irmãos, Sancho, Baía dos Golfinhos, Ponta da Sapata, and Atalaia) and six within the Environmental Protection Area (EPA) (Porto, Biboca 1, Biboca 2, Meio Beach, Conceição, and Boldró), for benthic dinoflagellates analyses (Fig. 1, Table 1). In Biboca, sampling was conducted at two sites: one closer to Porto (Biboca 1) and another one near the effluent discharge area (Biboca 2). Sampling was performed from 23rd to 30th October 2023, except at Boldró, where sampling took place on 13th October 2022. In total, 73 macroalgal samples were collected: 46 from the MNP and 27 from the EPA (Table 1).

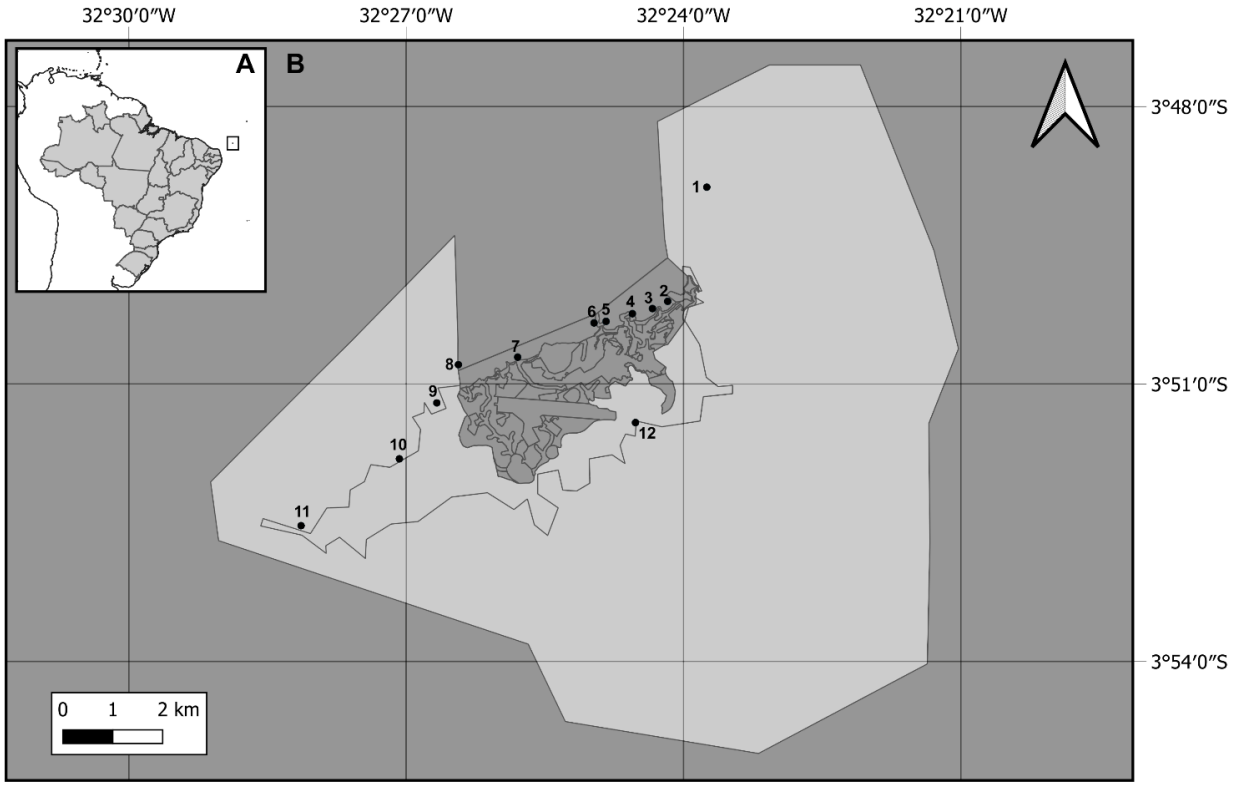


Figure 1. Study area. (A) South America showing Brazil in gray; the rectangle shows the location of the Fernando de Noronha Archipelago; (B) Sampling sites at Fernando de Noronha: 1. Cagarras, 2. Porto, 3. Biboca 1, 4. Biboca 2, 5. Meio, 6. Conceição, 7. Boldró, 8. Laje Dois Irmãos, 9. Sancho, 10. Baía dos Golfinhos, 11. Ponta da Sapata, and 12. Atalaia. Dark gray indicates the Environmental Protection Area (EPA), while light gray indicates the Marine National Park (MNP).

Macroalgae were collected using sealable plastic bags with the surrounding seawater. Samples were transferred to the laboratory in cool boxes and were posteriorly shaken for two minutes to detach associated epiphytic microalgae cells. The resulting suspensions were separated from the macroalgae and preserved with neutral Lugol's iodine solution for later identification and quantification of benthic dinoflagellates. Macroalgae were kept frozen for subsequent determination of fresh weight and identification to species level. Scientific research and collection permit authorizing fieldwork were obtained from the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio), Brazilian Ministry of the Environment (permit number: 74213-4).

Table 1. Summary of sampling site information, including the protected marine area in which they are located (Marine National Park - MNP or Environmental Protection Area - EPA), geographic coordinates, sampling depths, macroalgae species, and the number of specimens collected at each site at the Fernando de Noronha Archipelago.

Marine Protected Area	Sampling sites	Latitude/ Longitude	Depth (m)	Macroalgae sampled (number of individuals sampled)
MNP	Cagarras	3°48'52.31"S, 32°23'44.80"W	2, 4 and 10	*Canistrocarpus cervicornis* (6), *Canistrocarpus crispatus* (2), *Dictyota ciliolata* (1)
EPA	Porto	3°50'06.4"S, 32°24'10.2"W	2	*Canistrocarpus crispatus* (3), *Dictyopteris delicatula* (1)
EPA	Biboca 1	3°50'11.1"S, 32°24'20.1"W	2	*Dictyota jamaicensis* (4), *Canistrocarpus crispatus* (3)
EPA	Biboca 2	3°50'14.4"S, 32°24'33.1"W	2	*Canistrocarpus crispatus* (4)
EPA	Meio	3°50'19.4"S, 32°24'50.2"W	2	*Canistrocarpus crispatus* (3)
EPA	Conceição	3°50'20.4"S, 32°24'58.0"W	2	*Canistrocarpus crispatus* (4)
EPA	Boldró	3°50'42.6"S, 32°25'47.6"W	3	*Canistrocarpus crispatus* (3), *Galaxaura rugosa* (2)
MNP	Laje Dois Irmãos	3°50'47.5"S, 32°26'26.1"W	17	*Dictyota* cf. *pinnatifida* (4)
MNP	Sancho	3°51'12.3"S, 32°26'40.1"W	2	*Canistrocarpus crispatus* (5), *Padina gymnospora* (3)
MNP	Baía dos Golfinhos	3°51'48.6"S, 32°27'04.4"W	2 and 9	*Canistrocarpus crispatus* (4), *Dictyota jamaicensis* (2)
MNP	Ponta da Sapata	3°52'32.0"S, 32°28'08.2"W	4 and 10	*Dictyopteris delicatula* (4), *Dictyota ciliolata* (2), *Dictyota* cf. *pinnatifida* (2)
MNP	Atalaia	3°51'25.1"S, 32°24'31.1"W	1	*Sargassum cymosum* (4), *Galaxaura rugosa* (3), *Canistrocarpus crispatus* (3), *Canistrocarpus cervicornis* (1)

2.3 Nutrient analysis

Seawater samples were collected from each sampling site, except for Laje Dois Irmãos. Samples were syringe filtered through Whatman GF/F filters (0.7 µm porosity) and kept frozen at -20 °C until further analysis. Dissolved inorganic nutrients including orthophosphate (PO_4^{3-}), nitrate (NO_3^-), and ammonium (NH_4^+) were analyzed following the methods described in Grasshoff et al. (1983) and Strickland and Parsons (1972). For the determination of total dissolved nitrogen and total dissolved phosphorus (TDN and TDP), a

simultaneous oxidation of organic nitrogen and phosphorus compounds was performed using an alkaline persulfate solution. This procedure allows the analysis of their oxidized forms (NO_3^-–N and PO_4^{3-}–P) and enables the calculation of the dissolved organic N (DON) and P fractions (DOP). Absorbances were measured with a UV–visible spectrophotometer (Shimadzu UV-1800) using quartz cuvettes, following Grasshoff et al. (1999).

2.4 Benthic dinoflagellates abundance

Benthic dinoflagellates abundance was determined using a Sedgewick Rafter chamber or sedimentation chambers (2.5, 5, and 10 mL) and observed in a light inverted microscope (Primovert, Zeiss, Germany). Macroalgae's fresh weight was determined, and the volume of epiphyte samples was measured. Benthic dinoflagellates abundance was determined as cells per gram of macroalgae fresh weight (cells g^{-1} FW). Relative abundance (%) of each dinoflagellate genus was calculated in relation to the total benthic dinoflagellates abundance to assess the contribution of each genus to total abundance.

2.5 Statistical analyses

Nutrient (PO_4^{3-}, DOP, DIN, DON, NH_4^+, NO_3^-) concentrations were tested between four sites at the MNP and six sites at the EPA to determine if there were significant differences between the two areas. First, the normality of nutrient data (PO_4^{3-}, DOP, DIN, DON, NH_4^+, NO_3^-), expressed as µM, and the N:P ratio were tested using the Shapiro-Wilk test. For variables with a normal distribution (DON and DOP), the Levene's test was applied to assess the homogeneity of variances, followed by a t-test. For the remaining nutrients that did not follow a normal distribution, the Mann-Whitney test was used.

Nutrient data from the Atalaia site, located within the MNP, were not included in the analysis because it is a shallow (maximum depth 0.9 m) tidal pool that differs from the other sites. It also receives discharge from a small creek originating in one of the most populated areas of the island, where cattle are frequently present (Mello et al., 2023).

Additionally, a Mann–Whitney test was performed to evaluate whether total benthic dinoflagellates abundance and *Ostreopsis* abundance differed significantly between the EPA area (6 sites) and the MNP area (6 sites). Statistical analyses were conducted using R (version 4.5.1) and RStudio (version 2025.09.1).

Spearman's rank correlation coefficients were used to examine potential relationships between *Ostreopsis* abundance (cells g^{-1} FW) and ecological variables. Correlations were performed between *Ostreopsis* abundance at each site and the distance (km) of each site to the place of effluent discharge (Biboca 2 and Boldró). Correlations were also performed between *Ostreopsis* abundance and benthic dinoflagellates richness at each site. Spearman's correlation was chosen due to its suitability for non-normally distributed data and its ability to detect monotonic relationships. Statistical significance was set at $\alpha = 0.05$, and all analyses were conducted using GraphPad Prism v.8.

3. Results

3.1 Nutrients

Nutrient concentrations were not significantly different at the EPA and the MNP areas (Mann-Whitney, $p > 0.05$). At the EPA, highest PO_4^{3-}, NH_4^+, NO_3^-, DIN, and DON concentrations were recorded at Boldró, along with the highest N:P ratio (Table 2). Among the other sites at the EPA, Porto followed regarding NH_4^+, NO_3^-, DIN, and DON concentrations, while Biboca 2 presented high PO_4^{3-} and DOP values (Table 2). At the MNP, Atalaia presented highest NH_4^+, NO_3^-, and DIN concentrations, while the highest PO_4^{3-} and DON values were recorded at Cagarras (Table 2). N:P ratios between 4 and 7 were found at the EPA sites, except at Boldró (16.5), while at the MNP, values ranged between 5 and 11, and was highest at Atalaia (11.2) (Table 2).

Table 2. Orthophosphate (PO_4^{3-}), dissolved organic phosphorus (DOP), ammonium (NH_4^+), nitrate (NO_3^-), dissolved inorganic nitrogen (DIN), dissolved organic nitrogen (DON) concentrations (μM), and the N:P ratio at 11 sampling sites at the Fernando de Noronha Archipelago.

Marine Protected Area	Sampling sites	PO_4^{3-}	DOP	NH_4^+	NO_3^-	DIN	DON	N:P ratio
EPA	Porto	0.25	0.26	0.73	0.68	1.41	10.02	5.65
EPA	Biboca 1	0.18	0.27	0.55	0.65	1.20	6.89	6.52
EPA	Biboca 2	0.27	0.32	0.56	0.58	1.14	7.74	4.27
EPA	Meio	0.21	0.37	0.41	0.57	0.98	7.38	4.62
EPA	Conceição	0.16	0.24	0.48	0.64	1.12	7.83	7.18
EPA	Boldró	0.29	0.30	3.54	1.24	4.78	10.95	16.53
MNP	Cagarras	0.24	0.25	0.63	0.59	1.23	9.98	5.12
MNP	Sancho	0.15	0.17	0.52	0.69	1.20	5.55	8.17
MNP	Baía dos Golfinhos	0.16	0.30	0.46	0.63	1.09	1.98	6.97
MNP	Ponta da Sapata	0.15	0.29	0.65	0.60	1.26	7.83	8.65
MNP	Atalaia	0.17	0.21	0.74	1.22	1.96	6.89	11.23

3.2 Benthic dinoflagellates abundance

Porto, Boldró and Biboca 1, located at the EPA, showed highest mean benthic dinoflagellates abundances of $2.6x10^5$, $1.6x10^5$, and $7.8x10^4$ cells g^{-1} FW, respectively (Fig. 2A). Conceição presented the lowest mean abundance ($5.3x10^3$ cells g^{-1} FW) among sites at the EPA (Fig. 2A). At the MNP, mean abundances ranged from $3.5x10^3$ at Laje Dois Irmãos to $2.2x10^4$ cells g^{-1} FW at Baía dos Golfinhos (Fig. 2A). Benthic dinoflagellates abundance was significantly higher at the EPA than at the MNP (Mann-Whitney, $p < 0.001$, Fig. 2B).

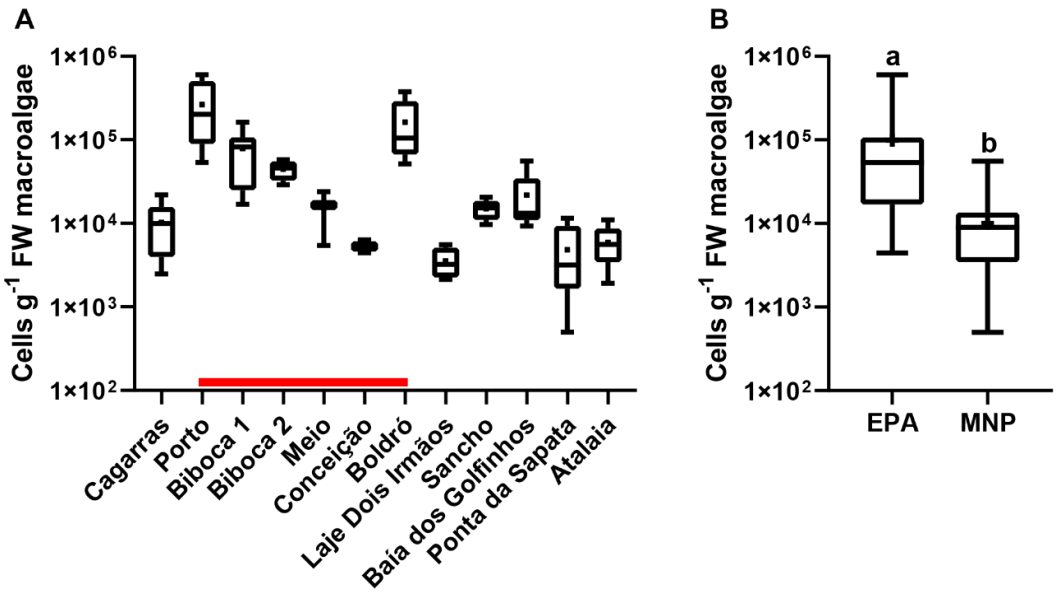


Figure 2. Benthic dinoflagellates total abundance (cells g^{-1} FW macroalgae) of each sampling site (A) and values at the EPA and MNP areas (B) of the Fernando de Noronha Archipelago. In A, the red line indicates the EPA sites. In B, different letters indicate a significant difference between the two protected areas. Boxplots show 25^{th} and 75^{th} percentiles, median (-), mean (+), minimum, and maximum values.

3.3 Benthic dinoflagellates assemblage structure at the EPA and at the MNP

Environmental Protection Area (EPA)

Ostreopsis abundance was significantly higher at the EPA than at the MNP (Mann-Whitney, $p < 0.001$). Two species of *Ostreopsis* were found at FN, *O.* cf. *ovata* and *O. lenticularis*, and the former was more abundant at most sites (Table 3). *Ostreopsis* cf. *ovata* mean abundance ranged from $1.4x10^2$ cells g^{-1} FW at Boldró to $2.2x10^5$ cells g^{-1} FW at Porto, and was higher than 10^4 cells g^{-1} FW at Biboca 1, Biboca 2, and Meio, while *O. lenticularis* mean abundance ranged from $3.1x10^2$ cells g^{-1} FW at Meio to $1.6x10^5$ cells g^{-1} FW at Boldró (Table 3). *Ostreopsis* was dominant at the EPA area, with relative abundance ranging from 84% at Meio to 97% at Boldró, and exceeding 90% at Porto and Biboca 1. A different pattern was observed only at Conceição (Fig. 3, Table 3).

Ostreopsis abundance was significantly higher near Biboca 2 (Spearman $r = -0.536$, $p < 0.0001$) (Fig. 4A) and Boldró (Spearman $r = -0.264$, $p = 0.024$) (Fig. 4B), the two sites that receive effluents from the two wastewater treatment plants and the desalination system at Boldró.

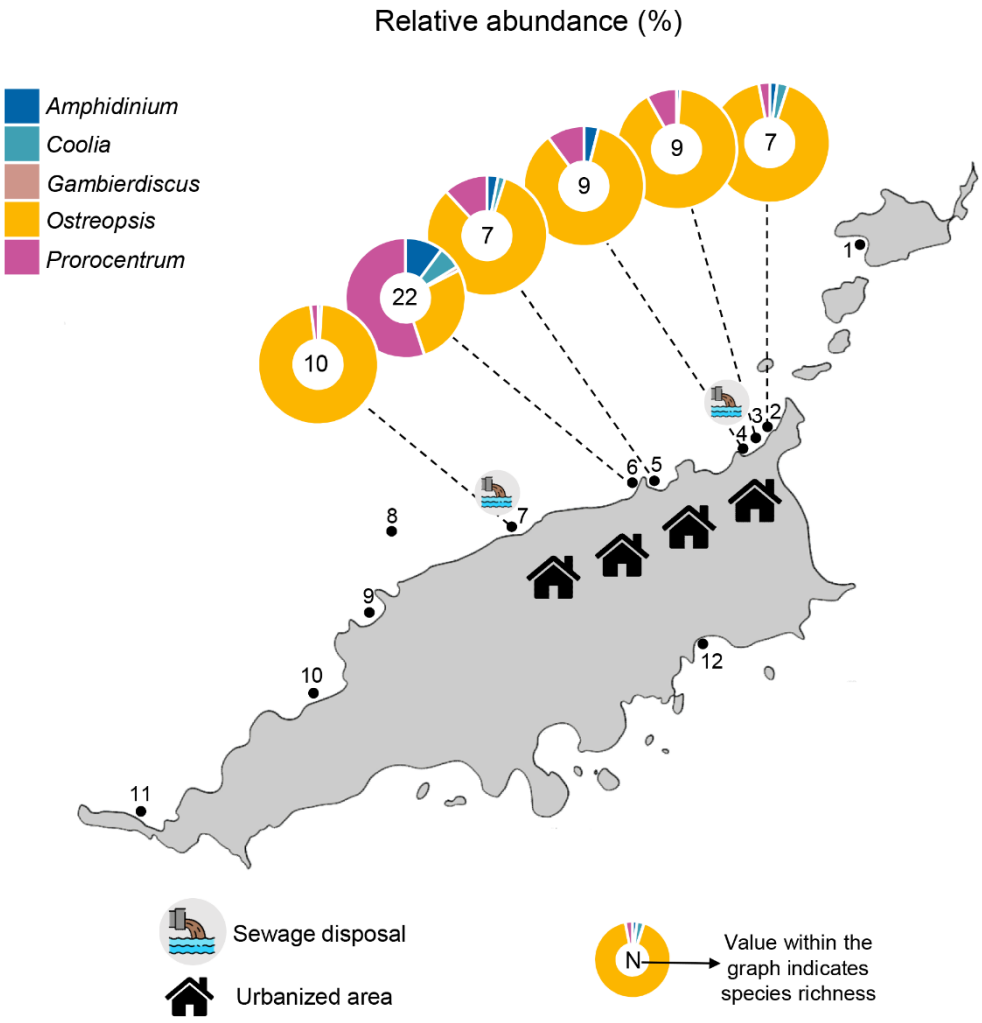


Figure 3. Benthic dinoflagellates genera relative abundance (%) and species richness at the EPA sites: (2) Porto, (3) Biboca 1, (4) Biboca 2, (5) Meio, (6) Conceição, and (7) Boldró.

Conceição presented a different community structure, more similar to that observed at the MNP, with *Ostreopsis* representing only 27% and *Prorocentrum* 54% of the total dinoflagellate abundance (Table 3). Total abundance was lower ($5.3x10^3$ cells g^{-1} FW) and mean *Prorocentrum* and *Ostreopsis* abundances were $2.9x10^3$ and $1.4x10^3$ cells g^{-1} FW, respectively (Table 3).

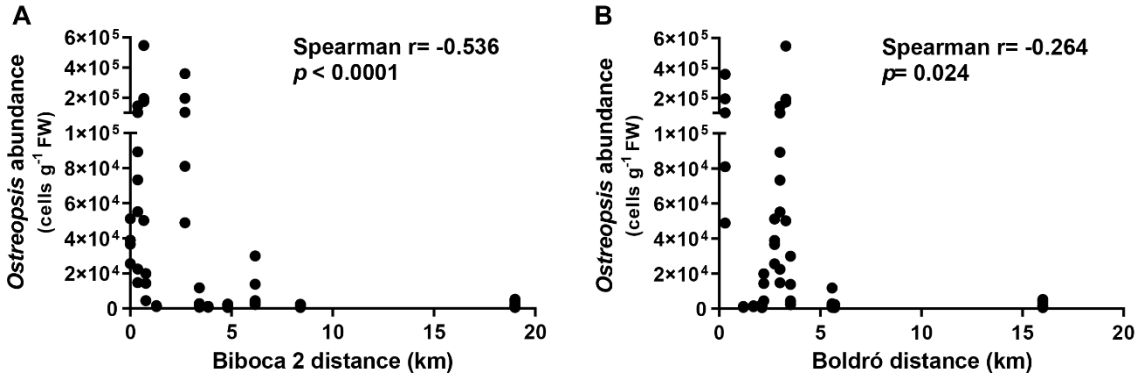


Figure 4. Spearman's rank correlations between *Ostreopsis* abundance (cells g^{-1} FW macroalgae) and distance (km) from Biboca 2 (A) and Boldró (B) sites, showing significant negative monotonic relationships, with a moderate correlation at Biboca 2 and a weaker correlation at Boldró.

Marine National Park (MNP)

In contrast to the results of the EPA sites, lower *Ostreopsis* mean abundances were found at the MNP, ranging from $7.0x10^2$ at Laje Dois Irmãos to $9.5x10^3$ cells g^{-1} FW at Baía dos Golfinhos (Table 3). *Ostreopsis* relative abundance varied between 10 and 37% at sites within the MNP (Fig. 5, Table 3). *Prorocentrum* was the genus with higher abundances, that ranged from $1.8x10^3$ at Ponta da Sapata to $8.9x10^3$ cells g^{-1} FW at Sancho (Table 3), representing 41-63% of the total abundance (Fig. 5, Table 3). Only at Baía dos Golfinhos *Ostreopsis* was more abundant than *Prorocentrum* (Table 3). Among *Ostreopsis* species, *O.* cf. *ovata* was more abundant ($5.9x10^2$ - $9.3x10^3$ cells) than *O. lenticularis* ($1.1x10^2$ – $6.5x10^2$ cells), except at Atalaia ($1.8x10^3$ cells g^{-1} FW) (Table 3).

At the MNP, the genera *Amphidinium*, *Coolia*, and *Gambierdiscus* contributed on average 8-22%, 1-18%, and 0-3%, respectively (Table 3). The mean abundances of these genera ranged from $3.8x10^2$ to $2.0x10^3$ cells g^{-1} FW, 41 to $2.8x10^3$ cells g^{-1} FW, and 0 to $2.2x10^2$ cells g^{-1} FW for *Amphidinium*, *Coolia*, and *Gambierdiscus*, respectively (Table 3). The maximum abundance of *Gambierdiscus* was recorded at Cagarras ($5.2x10^2$ cells g^{-1} FW).

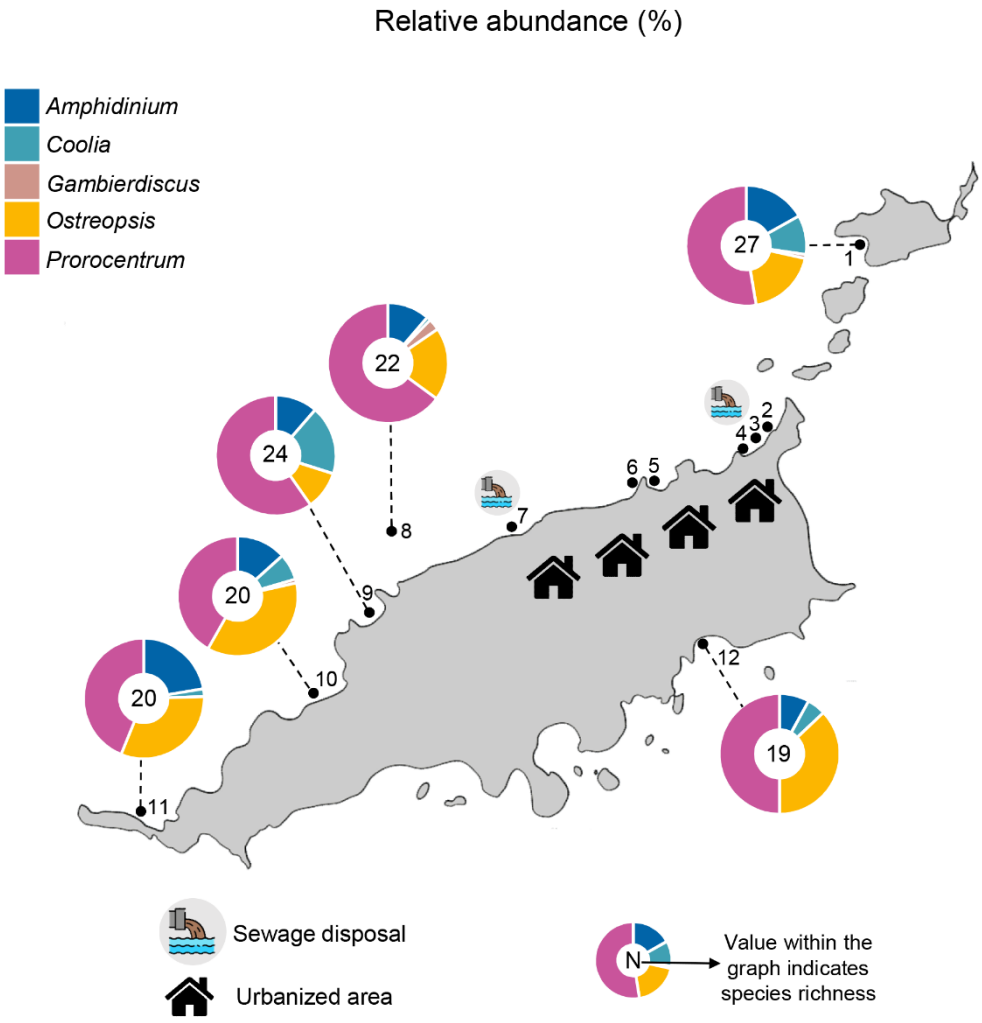


Figure 5. Benthic dinoflagellates genera relative abundance (%) and species richness at the MNP sites: (1) Cagarras, (8) Laje Dois Irmãos, (9) Sancho, (10) Baía dos Golfinhos, (11) Ponta da Sapata, and (12) Atalaia.

Table 3. Benthic dinoflagellates genera and *Ostreopsis* species mean abundance (cells g^{-1} FW macroalgae) and relative abundance (%) at 12 sampling sites at the Fernando de Noronha Archipelago.

Sampling sites	*Amphidinium*	*Coolia*	*Gambierdiscus*	*Ostreopsis*	*O.* cf. *ovata*	*O. lenticularis*	*Prorocentrum*
Cagarras	$1.4x10^3$ 16%	$9.4x10^2$ 10%	93 1%	$2.2x10^3$ 18%	$2.1x10^3$ 17%	$1.1x10^2$ 1%	$5.1x10^3$ 50%
Porto	$3.7x10^3$ 2%	$1.0x10^4$ 3%	0 0%	$2.4x10^5$ 92%	$2.2x10^5$ 83%	$2.5x10^4$ 8%	$9.6x10^3$ 3%
Biboca 1	$8.2x10^2$ 1%	$1.5x10^2$ 0%	0 0%	$7.1x10^4$ 90%	$6.1x10^4$ 75%	$1.0x10^4$ 15%	$6.1x10^3$ 8%
Biboca 2	$1.9x10^3$ 4%	$1.7x10^2$ 0%	0 0%	$3.8x10^4$ 86%	$3.7x10^4$ 83%	$1.1x10^3$ 3%	$4.2x10^3$ 10%
Meio	$2.9x10^2$ 3%	$2.3x10^2$ 2%	0 0%	$1.3x10^4$ 84%	$1.3x10^4$ 82%	$3.1x10^2$ 2%	$1.8x10^3$ 12%
Conceição	$5.0x10^2$ 10%	$3.2x10^2$ 6%	37 1%	$1.4x10^3$ 27%	$1.0x10^3$ 21%	$3.3x10^2$ 6%	$2.9x10^3$ 54%
Boldró	$1.6x10^3$ 1%	$1.1x10^2$ 0%	0 0%	$1.6x10^5$ 97%	$1.4x10^2$ 0%	$1.6x10^5$ 97%	$4.2x10^3$ 2%
Laje Dois Irmãos	$3.8x10^2$ 11%	41 1%	99 3%	$7.0x10^2$ 19%	$5.9x10^2$ 17%	$1.1x10^2$ 3%	$2.3x10^3$ 63%
Sancho	$1.5x10^3$ 11%	$2.8x10^3$ 18%	54 0%	$1.5x10^3$ 10%	$9.0x10^2$ 6%	$6.5x10^2$ 4%	$8.9x10^3$ 58%
Baía dos Golfinhos	$2.0x10^3$ 13%	$1.0x10^3$ 7%	$2.2x10^2$ 1%	$9.5x10^3$ 36%	$9.3x10^3$ 35%	$2.1x10^2$ 1%	$8.7x10^3$ 41%
Ponta da Sapata	$1.5x10^3$ 22%	88 2%	8 0%	$1.4x10^3$ 31%	$1.1x10^3$ 27%	$2.6x10^2$ 4%	$1.8x10^3$ 43%
Atalaia	$4.3x10^2$ 8%	$2.7x10^2$ 5%	0 0%	$2.2x10^3$ 37%	$4.6x10^2$ 7%	$1.8x10^3$ 29%	$2.9x10^3$ 50%

3.4 Benthic dinoflagellates species richness

At five of the six EPA sites, benthic dinoflagellates richness was up to 10 species, with 7 species recorded at Porto and Meio, 9 at Biboca 1 and Biboca 2, and 10 at Boldró (Fig. 3). At Conceição, 22 species were observed (Fig. 3). Species richness was higher at the MNP sites, with 27 species recorded at Cagarras, 24 at Sancho, 22 at Laje Dois Irmãos, 20 at Baía dos Golfinhos and Ponta da Sapata, and 19 at Atalaia (Fig. 5). *Ostreopsis* abundance was negatively correlated to species richness (Spearman r= -0.714, $p < 0.0001$), indicating lower richness at sites with high *Ostreopsis* abundance and dominance (Fig. 6).

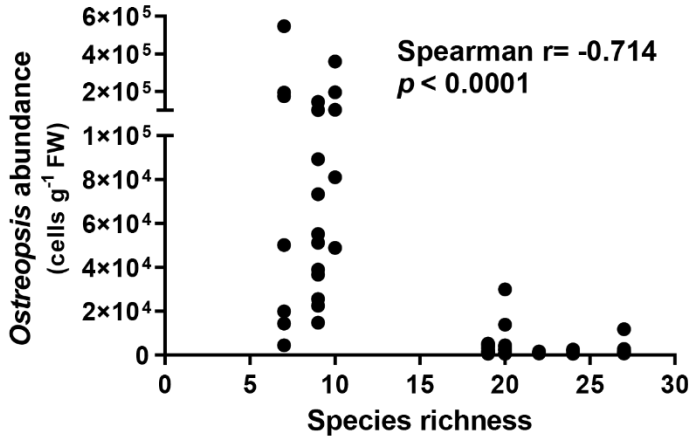


Figure 6. Spearman's rank correlation between *Ostreopsis* abundance (cells g^{-1} FW macroalgae) and species richness, showing a strong and significant negative monotonic relationship.

The species *O*. cf. *ovata* and *O. lenticularis,* as well as *Amphidinium* spp. and *Coolia* spp. were recorded at all MNP and EPA sites. *Prorocentrum lima* was the only species of the genus *Prorocentrum* found at all sites. Higher *Prorocentrum* species richness was found at sites within the MNP, with 11 species recorded (*P*. *arenarium*, *P*. cf. *borbonicum*, *P*. cf. *concavum*, *P*. *emarginatum*/*fukuyoi*/*sculptile* complex, *P*. *hoffmannianum*, *P*. *lima*, *P*. cf. *norrisianum*, *P*. *panamense*, *P*. *rhathymum*, and two not identified *Prorocentrum* species), whereas at five of the six EPA sites, only six *Prorocentrum* species were recorded (*P*. *arenarium*, *P*. *emarginatum*/*fukuyoi*/*sculptile* complex, *P*. *lima*, *P*. *rhathymum*, and two not identified *Prorocentrum* species), and at Conceição, there were 9 species of *Prorocentrum*. At the EPA, *Gambierdiscus* was found only at Conceição, while the genus was observed at all sites at the MNP, except at Atalaia.

4. Discussion

Benthic dinoflagellates community structure, including abundance, species composition and richness, was significantly different between sites among the EPA and the MNP. Higher total benthic dinoflagellate and *Ostreopsis* abundances, and lower species richness, characterized the EPA sites relative to the MNP. Nutrient concentrations did not differ significantly but tended to be higher at the EPA than at the MNP, particularly at Boldró, Porto, and Biboca 1 and 2 sites.

There are two wastewater treatment plants (WWTPs) at FN, both located within the EPA. The WWTPs discharges their effluents at Boldró and Biboca, and therefore these two sites are constantly affected by pollution due to the continuous input of wastewater and inadequately treated effluents (Mello et al., 2025). The effluents discharged by the WWTPs at Biboca and Boldró did not meet the standards established by Brazilian legislation, in a study performed in April 2022 by Mello et al. (2025), confirming the inefficiency of the archipelago's sewage treatment processes. The Porto site, located close to Biboca, receives diffuse sewage discharge from local restaurants and constitutes the main hub of nautical activities in the archipelago. It is also impacted by effluent leaks from the vessel responsible for transporting solid waste generated from the island to the mainland.

Biological assimilation of anthropogenic nitrogen by macroalgae was found throughout the EPA, based on isotopic signatures, and at Biboca, Boldró and Porto, macroalgae presented $\delta^{15}N$ enrichment, indicating chronic exposure to sewage, in addition to elevated levels of orthophosphate and coprostanol (Mello et al., 2025). The differences in benthic dinoflagellates abundance, species composition, and richness found in the current study between the EPA and MNP areas are therefore likely related to pollution and intensified urbanization in the EPA, where substantial inputs of nutrients and pollutants occur. Such conditions favor the growth of certain species over others, leading to dominance of one or a few species, as observed in the present study, as *O.* cf. *ovata* dominated the benthic dinoflagellates assemblage at most EPA sites. Another consequence of eutrophication is the reduction in local diversity, and at FN, species richness ranged from 7 to 10 at the EPA sites and from 19 to 27 at the MNP sites, that does not directly receive effluents and is therefore less polluted.

Fernando de Noronha has experienced significant population and tourism growth over the past decade. Currently, it is estimated that approximately 3,341 people live on the archipelago (IBGE, 2025). In 2024, FN received 131,503 tourists (Marinho, 2025). The high number of people on the archipelago has raised concerns, as inefficiencies in the island's sewage treatment process have been documented (Cristiano et al., 2020; Araújo et al., 2023; Silva, 2023; Mello et al., 2025). Operational and infrastructural problems have been reported at the WWTPs, including treatment steps that were not properly carried out in accordance with established guidelines, thereby hindering the treatment process (Silva, 2023), as well as the use of old pipelines with cracks and blockages (Cristiano et al., 2020). Approximately 66% of the residences in FN are connected to the sewage system, which conveys effluents to the two WWTPs (Boldró and Cachorro). About 31% of the buildings rely on septic tanks, whereas the remaining 3% discharge effluents directly into the environment (Cristiano et al., 2020). Fernando de Noronha generates approximately $7x10^5$ m^3 of sewage per year. In 2022, $2.5x10^5$ m^3 were discharged into the environment without treatment (SINISA, 2023).

The urbanization process, combined with higher population density, increases water pollution and alters coastal habitats, including macroalgal communities (Mangialajo et al., 2008), which can affect the distribution and abundance of *Ostreopsis*, as evidenced in previous studies (Briggs and Leff, 2007; Ungano et al., 2010; Cohu et al., 2013; Meroni et al., 2018). Higher *Ostreopsis* abundances have been associated with areas of higher anthropogenic impact, due to increased urbanization and nutrient inputs (Briggs and Leff, 2007; Ungano et al., 2010; Cohu et al., 2013; Meroni et al., 2018). For example, in the coastal areas of Apulia on the Adriatic Sea, analyses conducted by Ungano et al. (2010) showed that *O*. cf. *ovata* abundance increased in locations with higher levels of microbiological contamination of anthropogenic origin, associated with the region's high population density. Similar results were found by Meroni et al. (2018) in the Ligurian Sea, with significantly higher values of *O*. cf. *ovata* recorded at the most urbanized site, highlighting that coastal areas subjected to more intense anthropogenic exploitation are generally more prone to the proliferation of *O*. cf. *ovata*, both in the benthic stock and in the planktonic pool.

Baía dos Golfinhos, although located within the MNP, exhibited a distinct structure from other sites in the same area, with higher *Ostreopsis* abundance (mostly *O*. cf. *ovata*). Baía dos Golfinhos is under the influence of nutrients and pollutants discharged at the EPA,

which are transported by currents toward this site (Mello et al., 2025), and may cause the observed changes, favoring the proliferation of *Ostreopsis*.

Benthic dinoflagellate assemblage structure and abundance at Conceição were similar to those observed at MNP sites. This is likely due to the location of Conceição, that is relatively distant from both Biboca and Boldró, where effluents are discharged. Moreover, predominant marine currents will transport the effluents discharged at Boldró in the opposite direction, towards Baía dos Golfinhos.

Ostreopsis cf. *ovata* blooms recorded at EPA in the present study are of concern, as this species produces palytoxin analogues (the most potent non-bacterial toxin of biological origin), namely ovatoxins (Pavaux et al., 2020). *O*. cf. *ovata* has been extensively studied because it is associated with frequent massive blooms in the Mediterranean Sea (Table 1 from Gladan et al., 2019), which have caused impacts on human health, affecting bathers, workers, and coastal residents (e.g., Sansoni et al., 2003; Durando et al., 2007), as well as the death of marine organisms (e.g., Ciminiello et al., 2006; Totti et al., 2010; Blanfuné et al., 2012). In Brazil, sea urchins mass mortality has been linked to *O*. cf. *ovata* blooms along the coast of Rio de Janeiro (Ferreira, 2006).

In an *O*. cf. *ovata* bloom ($4.6x10^4$ cells g^{-1} FW) at the Saint Paul's Rocks Archipelago, in the Southwestern Atlantic Ocean, Nascimento et al. (2012) suggested that industrial fishing activities and upwelling events may have contributed to the bloom. Additionally, the Saint Paul's Rocks is rich in seabird guano, which fertilizes the upper ocean layer in this region and plays an important role in enriching food webs (Andrades et al., 2024). Nutrient inputs derived from seabird guano likely favored the bloom of *O*. cf. *ovata* at Saint Paul's Rocks.

Results from field studies indicate divergent findings regarding the relationship between nutrients and *Ostreopsis* dynamics. In Hawaii, *O*. cf. *ovata* abundance showed no correlation with nutrients, while *Ostreopsis* sp. 1 abundance was positively correlated with nitrate, nitrite, phosphate, and silicate concentrations (Parsons and Preskitt, 2007). In the Strait of Gibraltar and in Catalonia, Spain, in the Mediterranean Sea, significant negative correlations were observed between *O*. cf. *ovata* abundance and nitrate, nitrite, and ammonium concentrations (Ibghi et al., 2022; Carnicer et al., 2015), while a significant positive correlation between phosphate and *O*. cf. *ovata* abundance was found only in the

Strait of Gibraltar (Ibghi et al., 2022). Furthermore, using principal component analysis, the authors confirmed that silicate, dissolved inorganic nitrogen, ammonium, nitrate, and nitrite were inversely associated with the abundance of harmful algal blooms in this region (Ibghi et al., 2022). In a study along the Gulf of Lion and the Ligurian coast in the Mediterranean Sea, Cohu et al. (2013) highlighted significant negative correlations between nitrite and both epiphytic and planktonic *O*. cf. *ovata* abundances, while nitrate and silicate concentrations were weakly and negatively correlated with *O*. cf. *ovata* abundances, only one macroalgae and in the water column. In contrast, phosphate concentrations were positively correlated with *O*. cf. *ovata* epiphytic cells on all substrates and with planktonic cells. The mechanism for bloom development of this dinoflagellate is complex and far from fully understood, and its relationship with nutrients requires further investigation.

For *O. lenticularis*, there are still no studies demonstrating the influence of nutrient availability on its growth. Considering the higher abundance of this species (10^4-10^5 cells g^{-1} FW) at locations with higher nutrient concentrations at FN (Boldró, Porto, and Biboca 1), it seems that increased nutrient inputs may favor its growth. Another bloom of this species was recorded at Boldró in October 2018, when it reached $7.6x10^4$ cells g^{-1} FW macroalgae (Borsato et al., 2020). The pattern of high *O. lenticularis* abundances at Boldró suggests the presence of a set of abiotic and biotic factors that are particularly favorable for the growth of this species at this site. In contrast, at Porto and Biboca 1 and 2, *O*. cf. *ovata* was more abundant than *O. lenticularis* reaching up to 10^5 cells g^{-1} FW. However, *O. lenticularis* still presented between 10^3-10^4 cells g^{-1} FW in these sites.

The sites within the EPA with the lowest N:P ratios (Biboca 2 = 4.3, Meio = 4.6, Porto = 5.7, and Biboca 1 = 6.5) exhibited the highest *O*. cf. *ovata* abundances, whereas at sites with the highest N:P ratios (Boldró = 16.5 and Atalaia = 11.2), *O. lenticularis* was the most abundant species of the genus. Evidence that microalgal biodiversity changes under modified stoichiometric conditions is substantial, both in freshwater and marine systems (Glibert, 2017). However, the relationship between the N:P ratio and benthic dinoflagellates in field studies remains poorly investigated (Cohu et al., 2013; Ibghi et al., 2022), and although these studies reported a significant negative correlation between the N:P ratio and *Ostreopsis* abundance in the Mediterranean Sea, N:P values were not presented, hindering comparison.

Higher nutrient input, resulting from an increased population (residents and tourists), as well as from inefficient wastewater treatment at FN, likely played an important role in benthic dinoflagellate species richness loss and the development of higher *Ostreopsis* abundances at the EPA. In addition, sea surface temperature (26.9–29.3 °C) is within the optimal range for many benthic dinoflagellate species (Tester et al., 2020) in FN and has increased significantly over the past 40 years (Borsato et al., in prep.). Growing evidence indicates that human-driven factors, particularly climate change such as rising sea surface temperatures and nutrient pollution, are key contributors to the global increase in harmful algal bloom occurrences (Glibert, 2020).

5. Conclusions

Marked differences in benthic dinoflagellates abundance, species composition, and richness were found between the two marine protected areas of Fernando de Noronha, likely as a result of local anthropogenic impacts. Overall, in the area directly affected by pollution, *Ostreopsis* blooms and dominance were observed, concurrently with a reduction in dinoflagellates richness. Higher *Ostreopsis* abundance was recorded near effluent discharges from wastewater treatment plants. In contrast, sites within the less impacted area exhibited more diverse benthic dinoflagellate communities, with a greater contribution of other genera. Benthic dinoflagellates assemblage proved to be a good bioindicator of changes caused by eutrophication.

Taken together, these findings indicate that anthropogenic stressors acting at different scales, including local pollution combined with global warming of surface seawater, may be driving the occurrence of *Ostreopsis* blooms at Fernando de Noronha. These findings raise important concerns regarding ecological impacts, human health, and the effectiveness of current environmental management strategies for the conservation of marine biodiversity at the archipelago. Therefore, this study highlights the need for actions to reduce pollution in this high biodiverse area of the Atlantic Ocean in order to preserve biodiversity and maintain ecosystems services, as well as to avoid food contamination with biotoxins from toxic microalgae at FN. Moreover, the need to monitor water quality and marine communities in the long term is essential.

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Conclusões gerais

Esta tese integrou abordagens taxonômicas e ecológicas, em escalas espacial e temporal, para investigar a diversidade, a distribuição e a dinâmica dos dinoflagelados bentônicos no Arquipélago de Fernando de Noronha, no Oceano Atlântico Sul, contribuindo de forma inédita para o conhecimento desses organismos em uma região ainda pouco estudada. Em conjunto, os resultados demonstram que Fernando de Noronha abriga elevada riqueza de dinoflagelados bentônicos, confirmando o arquipélago como um importante *hotspot* de diversidade do gênero *Prorocentrum*. Os dados compilados na revisão da literatura sobre esse gênero, que compõem o capítulo 1 desta tese, mostraram um claro gradiente latitudinal, com maior riqueza de espécies bentônicas de *Prorocentrum* em regiões tropicais e subtropicais. Observa-se, ainda, a existência de um viés espacial associado a impedimentos taxonômicos em algumas áreas e a um esforço de amostragem desigual, com muitas regiões ainda a serem investigadas. Dessa forma, o conhecimento atual sobre a distribuição global das espécies bentônicas de *Prorocentrum* é provavelmente subestimado.

A análise temporal da abundância de dinoflagelados bentônicos em Fernando de Noronha (Capítulo 2) revelou um aumento significativo na abundância entre 2021 e 2023, em comparação ao período de 2017 a 2019, bem como um aumento significativo da temperatura da superfície do mar e a redução da amplitude térmica ao longo dos últimos 40 anos no arquipélago. O aumento da temperatura da superfície do mar, associado ao incremento no despejo de nutrientes, decorrente do crescimento populacional, da expansão do turismo e da limitada eficiência do tratamento de efluentes, está provavelmente relacionado ao aumento da abundância de dinoflagelados no arquipélago. A ocorrência de espécies tóxicas, como *Gambierdiscus excentricus*, *G. silvae*, *G. belizeanus*, *G. carpenteri*, *Ostreopsis* cf. *ovata* e *Prorocentrum lima*, levanta preocupações relevantes quanto aos riscos à saúde humana e aos impactos ecológicos nesse *hotspot* de biodiversidade marinha.

Os resultados sobre a elevada abundância de *Gambierdiscus* em 2017 e 2018 em Fernando de Noronha (Capítulo 2), bem como os sintomas da ciguatera, foram apresentados no auditório do ICMBio em Fernando de Noronha, em outubro de 2021, durante uma palestra que contou com a presença da população, além de agentes do ICMBio e da Vigilância em Saúde local. O objetivo foi alertar sobre as abundâncias de *Gambierdiscus* no arquipélago, que eram superiores às encontradas na costa brasileira, e chamar a atenção para a doença, aumentando a percepção dos agentes de saúde sobre a ciguatera. Os primeiros

casos da doença foram registrados em Fernando de Noronha cinco meses após a apresentação, em março de 2022. Há relatos de que casos esporádicos de ciguatera podem ter ocorrido antes de março de 2022, mas não foram notificados devido ao desconhecimento sobre a doença. Assim, os dados de abundância gerados nesta tese foram de extrema importância para alertá-los sobre a possível ocorrência da doença no arquipélago.

As análises espaciais de dinoflagelados bentônicos em sítios da APA e do PARNAMAR de Fernando de Noronha (Capítulo 3) evidenciaram variações marcantes na composição, abundância e riqueza da assembleia de dinoflagelados bentônicos, com diferenças claras entre sítios e entre a APA e o PARNAMAR, submetidos a distintos níveis de pressão antrópica. Sítios na APA, áreas mais impactadas pelo enriquecimento de nutrientes e descargas de efluentes, apresentaram dominância e florações do gênero *Ostreopsis*, especialmente da espécie tóxica *O.* cf. *ovata*, além de diminuição da riqueza de espécies. Em contraste, sítios no PARNAMAR apresentaram assembleias com maior riqueza de espécies e menor abundância, evidenciando a sensibilidade desses organismos à eutrofização e seu elevado potencial como bioindicadores de alterações ambientais.

De forma integrada, esta tese estabelece um conhecimento de base sobre a assembleia de dinoflagelados bentônicos no Arquipélago de Fernando de Noronha e demonstra que a interação entre estressores antrópicos locais e processos associados às mudanças climáticas globais exerce papel central na estruturação da assembleia de dinoflagelados bentônicos e na ocorrência de florações nocivas no arquipélago. Os resultados reforçam a urgência de ações voltadas à melhoria da gestão de efluentes, ao controle da poluição e à implementação de programas de monitoramento ambiental de longo prazo. Tais medidas são fundamentais para a conservação da biodiversidade, para a manutenção dos serviços ecossistêmicos e para o embasamento de estratégias eficazes de gestão e conservação em um dos arquipélagos mais biodiversos do Oceano Atlântico. Além disso, contribuem para garantir a saúde humana, a segurança alimentar, proteger atividades econômicas extremamente importantes, como a pesca e o turismo, e evitar impactos sociais à população local.

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Apêndice 1

Atividades de divulgação científica e popularização da ciência

Em 2023 e 2025, a discente participou de atividades de divulgação científica e popularização da ciência junto à equipe do Laboratório de Microalgas Marinhas da UNIRIO no Arquipélago de Fernando de Noronha. Essas ações tiveram como objetivo informar a comunidade da ilha sobre a doença Ciguatera, incluindo sua causa, organismos vetores, sintomas e consequências para a saúde pública, promovendo a conscientização e a adoção de medidas preventivas para reduzir o número de casos de intoxicação por pescado. Em 2023, as atividades foram realizadas com o apoio da Agência Pernambucana de Vigilância Sanitária (APEVISA), a Unidade de Vigilância em Saúde de Fernando de Noronha e do ICMBio. Já em 2025, as atividades foram realizadas no âmbito do projeto "Ciência oceânica na formação de cidadãos engajados na conservação das ilhas oceânicas brasileiras" (ONDA ILOC), apoiado pelo CNPq. Essas atividades integraram estratégias de ensino e extensão, aproximando estudantes e a comunidade das pesquisas em microalgas, promovendo a participação cidadã e fortalecendo a comunicação entre cientistas e a sociedade.

As atividades desenvolvidas foram:

- Realização de uma palestra e de uma roda de conversa com pescadores e moradores da ilha (outubro de 2023);
- Realização de palestras para estudantes do ensino médio da Escola Arquipélago, envolvendo ao todo 48 alunos, abordando os temas "microalgas nocivas" e "Ciguatera", seguidas de experiências práticas, incluindo a visualização de células vivas de dinoflagelados bentônicos tóxicos por meio de microscópio digital, a exploração de modelos tridimensionais de microalgas e a observação de exsicatas de macroalgas coletadas anteriormente em Fernando de Noronha. Ao final, os alunos foram convidados a atuar como cientistas cidadãos, contribuindo para a comunicação de casos de Ciguatera na ilha por meio de um formulário disponibilizado pela Secretaria de Saúde do Estado de Pernambuco (fevereiro de 2025);
- Realização de um bate-papo com 53 participantes da comunidade local, com o objetivo de informar sobre a ciguatera, aumentar a conscientização da população e estimular o engajamento da comunidade na prevenção e no monitoramento de casos, além de apresentar dados preliminares do capítulo 3 desta tese, que aborda a

influência das atividades antrópicas, especialmente a poluição, sobre o ecossistema marinho da ilha (fevereiro de 2025).

A discente também participou da criação do capítulo “Microalgas Nocivas e Ciguatera” do Manual do Cientista Cidadão de Noronha produzido pelo projeto ONDA ILOC (**Anexo**).

Além disso, foram realizadas atividades de divulgação científica sobre o tema “algas nocivas”, no âmbito do projeto de extensão “Conhecendo as HABs – Harmful Algal Blooms” da UNIRIO, em diferentes eventos, tais como: na oficina Sentinelas do Mar, oferecida durante a 2ª edição do evento Guardiões das Águas, organizado pelo Núcleo Maré e por professores da UFRJ, UERJ e UNIRIO; na IV Mostra do CCBS da UNIRIO, com apresentação interna e externa (Museu da República); na II Mostra do IBIO da UNIRIO; e no V Simpósio do PPGBIO. Por fim, foram produzidos conteúdos de divulgação para o Instagram do Laboratório de Microalgas Marinhas (@microalgas.unirio).






Manual do Cientista Cidadão em Noronha







ONDA ILOC



Microalgas Nocivas e Ciguatera

Autores: Silvia M. Nascimento, Geovanna T. Borsato

O que são microalgas?

Já imaginou ter uma célula só? As microalgas são assim, organismos formados por uma única célula e que, muitas vezes, medem muito menos que um milímetro! Por isso, só podem ser observadas com um microscópio.

Onde estão?

Vivem em rios, lagos e oceanos do mundo inteiro. Podem ser encontradas livres na coluna d'água ou associadas a macroalgas, corais, grãos de areia e sedimentos do fundo.

E o que fazem?

As microalgas possuem papel essencial nos ambientes aquáticos por realizarem a **fotossíntese**, e servirem de alimento para os animais, sendo a "base" das cadeias alimentares aquáticas.

Além disso, pela fotossíntese as microalgas retiram CO_2 da atmosfera, auxiliando na **redução dos gases do efeito estufa**, e **produzem o oxigênio**.

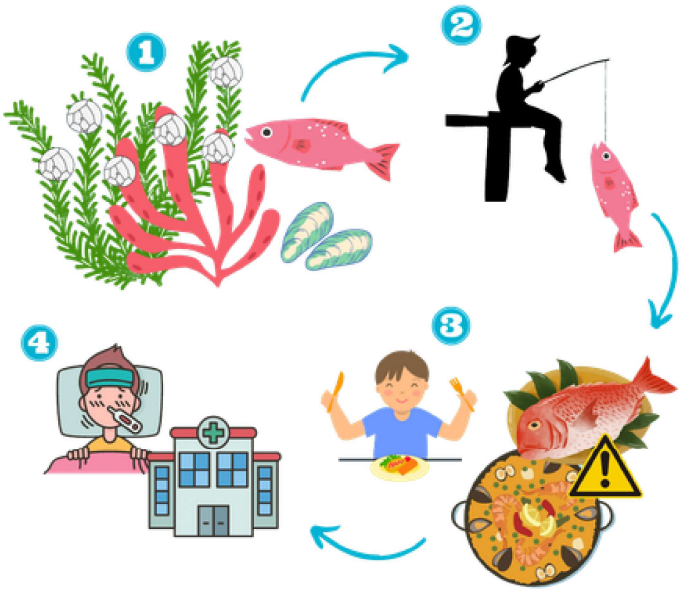
Mas atenção pro excesso!

Em determinadas condições, as microalgas podem se reproduzir muito e mudar a cor da água para verde, marrom ou avermelhada e formar espumas. Algumas espécies de microalgas produzem **toxinas potentes**, que podem ser acumuladas em moluscos (como mexilhões e ostras) e em peixes. **Essas toxinas podem afetar a saúde humana quando os frutos do mar contaminados são consumidos**.

Ciguatera, o que é?

A **Ciguatera** é uma doença que afeta os seres humanos através do consumo de peixes que se alimentaram da microalga nociva chamada *Gambierdiscus*, e acumularam em seu corpo as toxinas produzidas por ela. Os peixes contaminados não possuem cor, cheiro, gosto ou textura diferente dos demais, portanto, **não é possível detectar a contaminação ao olhar ou comer o peixe**. Essas toxinas, conhecidas como ciguatoxinas, não são degradadas pelo cozimento ou fritura do peixe.

O ciclo é o seguinte:



Um caso de ciguatera é definido pelo **consumo de peixe marinho** horas antes do início dos sintomas típicos da doença. Não há tratamento específico para a ciguatera, portanto, a medicação é usada para tratar os sintomas. Em caso de suspeita de ciguatera, busque atendimento médico o quanto antes, e relate o consumo recente de peixe.

Caso o peixe não tenha sido inteiramente consumido, não jogue o restante fora, entre em contato com a vigilância sanitária da ilha, para que o peixe possa ser enviado para análise. As análises serão realizadas pelo MAPA - Ministério da Agricultura e Pecuária.

Sintomas de Ciguatera



Já foram registrados 175 sintomas diferentes dessa intoxicação, entre eles:

Vômito;
Diarréia;
Dor abdominal;
Náusea;
Alodínia ao frio;
Formigamento/dormência nas extremidades;
Gosto metálico;
Sensação de dentes soltos;
Coceira;
Dor muscular;
Dor nas articulações;
Dor de cabeça;
Tontura;
Batimento cardíaco acelerado.



E em Noronha?

A ciguatera tem sido registrada em Fernando de Noronha desde 2022 e pesquisas estão em andamento para:

1) identificar as espécies da microalga *Gambierdiscus* que ocorrem na ilha;
2) determinar os locais onde elas ocorrem em maior quantidade;
3) compreender os fatores que levaram à ocorrência de ciguatera na ilha.

Quais peixes estão associados a ciguatera?

Os principais peixes vetores das ciguatoxinas, ou seja, que causam a ciguatera em Fernando de Noronha, são a **barracuda**, a **guarajuba**, o **chicharro** e o **dentão**.

Como lidar com a ciguatera na ilha?

Para se prevenir da ciguatera, o ideal é evitar comer os peixes vetores, principalmente a barracuda e a guarajuba. Em caso de intoxicação, procure atendimento médico. Isso será importante para amenizar os sintomas e para registrar a ocorrência da doença. Se tiver sobrado parte do peixe consumido, guarde-o no congelador e entre em contato com a vigilância sanitária da ilha. Caso conheça alguém que teve ciguatera e que não foi ao médico, oriente a preencher o formulário online para registrar o caso.

Quer registrar um caso?

Basta escanear o QR code com a câmera de seu celular!

Apêndice 2

Materiais Suplementares

Capítulo 1

Table S1. Summary of samples analyzed in this study, indicating the sampling sites, date of collection, number of macroalgae collected, sample origin (strain or field), depth of collection, water temperature range and mean value. ND: Not determined. The asterisk indicates temperature values obtained from satellite.

Sampling sites	Date	Number of macroalgae collected	Origin	Depth	Seawater Temperature (°C) Minimum - Maximum (Mean)
1 - Saint Paul's Rocks Archipelago (00°55'10"N, 29°20'33"W)	November 2017, September 2018	9	Field	3 - 18 m	26.1 - 27. 9 (27.0)*
2 - Fernando de Noronha Archipelago (03°50'52.3"S, 32°26'31.8"W)	October 2017, March and October 2018	32	Strains UNR-35, UNR-44, UNR-86 and Field	4 - 15 m	19.4 - 31.8 (27.6)
3 - Muro Alto, Pernambuco (08°25'45"S, 34°58'40"W)	July 2012	16	Field	1 - 2 m	26.0 - 28.8 (27.4)*
4 - Porto de Galinhas, Pernambuco (08°30'40"S, 35°00'07"W)	January 2013	8	Field	1 - 2 m	25.9 - 28.7 (27.3)*

5 - Carneiros, Pernambuco (08°42'16"S, 35°04'43"W)	November 2016	1	Strain UNR-68	1 - 2 m	ND
6 - Maragogi, Alagoas (08°55'18"S, 35°09'05.8"W)	January 2015	7	Strains UNR-12, UNR-13, UNR-15 and Field	1 - 2 m	25.9 - 28.5 (27.2)*
7 - Garça Torta, Alagoas (09°35'00"S, 35°39'35"W)	July 2012	12	Field	1 - 2 m	25.9 - 28.2 (27.0)*
8 - Forte, Bahia (12°34'41.0"S, 38°00'04.7"W)	January 2013	12	Strain UNR-72 and Field	1 - 2 m	25.3 - 28.2 (26.5)*
9 - Placaford, Bahia (12°57'20"S, 38°22'45"W)	July 2012	15	Field	1 - 2 m	25.3 - 28.1 (26.4)*
10 - Penha, Bahia (12°59'27"S, 38°37'29"W)	July 2012	18	Field	1 - 2 m	25.3 - 28.4 (26.8)*
11 - Trindade Island (20°29'22.2"S, 29°20'04.2"W)	October 2015, September 2014 and 2017	16	Strain UNR-29 and Field	7 - 14 m	23.4 - 27.7 (25.5)
		248	Field	1 - 2 m	21.2 - 25.2 (23.0)*

12 - Tartaruga, Armação dos Búzios, Rio de Janeiro (22°45'18"S, 41°54'07"W)	June and September 2006; January, March-November 2007; February, April, May, September, October and December 2012; January-May 2013; February 2014				
13 - Forno, Armação dos Búzios - AB, Rio de Janeiro (22°45'42.5"S, 41°52'34.28"W)	May, September, October and December 2012; January-May 2013; February and December 2014	149	Field	1 - 2 m	21.2 - 25.2 (23.0)*
14 - Forno, Arraial do Cabo - AC, Rio de Janeiro (22°59'S, 42°00'W)	July, September, November and December 2006; January-October 2007	78	Field	1 - 2 m	17.5 - 26.8 (23.2)
15 - Cabo Frio Island, Arraial do Cabo, Rio de Janeiro (23°00'03"S, 42°00'22"W)	March 2007, October 2015	12	Strain UNR-11 and Field	1 - 2 m	ND

Table S2. Benthic *Prorocentrum* species found at the Northeast, Southeast and oceanic islands of Brazil and in various places of the world, including species richness at each place and the substrate that has been investigated in each study. Species names in bold denote its type locality. The asterisk denotes that the species are synonyms and therefore only one of them was counted in the species richness. *Prorocentrum rhathymum* and *P. mexicanum* were used as synonyms for the purpose of quantifying the number of species in each location, as different authors used the names *P. rhathymum* and *P. mexicanum* to refer to the same species. *Prorocentrum emarginatum*/*fukuyoi*/*sculptile* species complex was counted as only one species, however, it may contain up to three species. NI: Not informed.

Place	Latitude	Number of species	Benthic species	Substrata	References
South Atlantic Ocean					
Fernando de Noronha, Brazil	03°50'S	10	*P*. cf. *borbonicum*, *P*. cf. *concavum*, P. *emarginatum*/*fukuyoi*/*sculptile* complex, *P*. *hoffmannianum*, *P*. *lima*, *P*. cf. *norrisianum*, *P*. *panamense*, *P*. *rhathymum*, *Prorocentrum* sp. 1, *Prorocentrum* sp. 2	Macroalgae (*Bryothamnion*, *Canistrocarpus*, *Dictyopteris*, *Dictyota*, *Jania*, *Stypopodium*, *Tricleocarpa*)	Current study
Northeast Brazil	08°04'S - 18°02'S	10	*P*. *borbonicum*, *P*. *caipirignum*, *P*. *emarginatum*, *P*. *emarginatum*/*fukuyoi*/*sculptile* complex, *P*. *hoffmannianum*, *P*. *leve*, *P*. *lima*, *P*. *panamense*, *P*. *porosum*, *P*. *rhathymum*	Macroalgae (*Agardhiella*, *Amansia*, *Amphiroa*, *Bryopsis*, *Canistrocarpus*, *Dictyopteris*, *Dictyota*, *Dictyotales*, *Gelidiella*, *Gelidium*, *Gracilaria*, *Halimeda*, *Hypnea*, *Lobophora*, *Ochtodes*, *Padina*, *Plocamium*, *Sargassum*) and artificial substrate	Current study, Proença et al. (2009), Nascimento et al. (2017), Mendes et al. (2019), Moreira-González et al. (2019a), Fernandes et al. (2021), Leite et al. (2021), Arteaga-Sogamoso et al. (2023)
Trindade, Brazil	20°29'S	7	*P*. cf. *borbonicum*, *P*. *emarginatum*/*fukuyoi*/*sculptile* complex, *P*. *hoffmannianum*, *P*. *lima*, *P*. cf. *norrisianum*, *P*. *panamense*, *Prorocentrum* sp. 1	Macroalgae (*Canistrocarpus*, *Dictyopteris*, *Dictyota*)	Current study
Southeast Brazil	22°45'S - 23°04'S	5	***P. caipirignum***, *P*. *emarginatum*/*fukuyoi*/*sculptile* complex, *P*. *hoffmannianum*, *P*. *lima*, *P*. *mexicanum*, *P*. *rhathymum*	Macroalgae (*Amphiroa*, *Arthrocardia*, *Canistrocarpus*, *Caulerpa*, *Cladophora*, *Cladophoropsis*, *Codium*, *Dictyopteris*, *Dictyota*, *Hincksia*, *Hypnea*, *Jania*, *Laurencia*, *Padina*,	Current study, Naves et al. (2006), Nascimento et al. (2016, 2017), Gomez et al. (2017), Fernandes et al. (2021)

				Plocamium, *Sargassum*, *Spyridia*, *Ulva*, *Zonaria*)	
South Brazil	25°30'S	4	*P*. cf. *fukuyoi*, *P*. cf. *lima*, *P*. cf. *lima* morphotype 5, *Prorocentrum* sp.	Macroalgae (*Acanthophora*, *Chaetomorpha*, *Hypnea*, *Ulva*), seagrass (*Halodule*), sediment and bare sand	Moreira-González et al. (2019a,b, 2020)
San Matías Gulf, San José Gulf, Nuevo Gulf and Beagle Channel, Argentina	~ 42°S - 55°S	1	*P. lima*	Macroalgae (*Anotrichium*, *Ceramium*, *Dictyota*, *Ulva*) and seawater	Gayoso et al. (2002), Krock et al. (2018 and references therein), D'Agostino et al. (2019)
Caribbean Sea					
Venezuela	~ 8°N - 11°N	4	*P. concavum*, *P. emarginatum*, *P. lima*, *P. mexicanum*, *P. rhathymum*	NI	Durán-Riveroll et al. (2019 and references therein), Sunesen et al. (2021 and references therein)
Barú Island, Concha Bay and Chengue Bay, Colombia	10°8'N - 11°20'N	9	*P. borbonicum*, *P*. cf. *concavum*, *P. emarginatum*, *P. hoffmannianum*, *P. lima*, *P. mexicanum*, ***P. porosum***, *P. rhathymum*, *Prorocentrum* sp. 1, *Prorocentrum* sp. 2	Seagrass (*Syringodium*, *Thalassia*)	Gomez and Pineda et al. (2019), Durán-Riveroll et al. (2019 and references therein), Arbelaez et al. (2020), Arteaga-Sogamoso et al. (2022, 2023)
San Andrés Island, Colombia	12°28'N - 12°36'N	5	*P. belizeanum**, *P. concavum*, *P. emarginatum*, *P. hoffmannianum*, *P. lima*, *P. maculosum**, *P. rhathymum*	Macroalgae (*Canistrocarpus*, *Sargassum*, *Turbinaria*) and seagrass (*Syringodium*, *Thalassia*)	Mancera-Pineda et al. (2014)
Martinique Island, Overseas France	14°31.538'N	12	*P. concavum*, *P*. cf. *foraminosum*, *P*. cf. *fukuyoi*, *P. glenanicum*, *P. hoffmannianum*, *P. lima*, *P*. cf. *maculosum**, *P*. cf. *norrisianum*, *P. panamense*, *P. rhathymum*, *P*. cf.	Surface sediment	Chomérat et al. (2019)

			ruetzlerianum, *P*. cf. *sculptile*, *P*. cf. *tropicale*		
Carrie Bow Cay, Twin Cays and South Water Cay, Belize	16°48'N - 18°48'N	16	***P. arenarium****, **P. belizeanum****, **P. caribbaeum***, *P. concavum*, ***P. elegans***, *P. emarginatum*, ***P. foraminosum***, ***P. formosum***, ***P. hoffmannianum***, ***P. leve***, *P. lima*, ***P. maculosum****, *P. mexicanum*, ***P. norrisianum***, ***P. reticulatum***, ***P. ruetzlerianum***, ***P. sabulosum***, ***P. sculptile***, ***P. tropicale***	Floating detritus, surface sediment, colored sand, coral rubble and macroalgae (*Dictyota*)	Faust (1990, 1993a, 1993b, 1994, 1995, 1997), Morton and Faust (1997), Morton et al. (1998), Faust et al. (2008)
Saint Barthélemy, Overseas France	~ 17°N	1	*P. lima*	NI	Diogéne et al. (1995)
British and United States Virgin Islands	~ 18°N	4	*P. concavum*, *P. hoffmannianum*, *P. lima*, *P. maculosum**, *P. mexicanum*, ***P. rhathymum***	Macroalgae (*Dictyota*)	Loeblich et al. (1979), Tindall and Miller (1987), Kelly et al. (1992), Kohler and Kohler (1992), Morton and Bomber (1994), Zhou and Fritz (1994), Morton and Tindall (1996), Durán-Riveroll et al. (2019 and references therein)
Quintana Roo, Campeche, Veracruz and Yucatan, Mexico	~ 18°N - 22°N	12	*P. arenarium**, *P. belizeanum**, *P. caribbaeum*, *P. concavum*, *P. emarginatum*, *P. foraminosum*, *P. fukuyoi*, *P. hoffmannianum*, *P.* cf. *leve*, *P. lima*, *P. maculosum**, *P. mexicanum*, *P. rhathymum*, *P. sculptile*, *P.* cf. *sipadanense*, *Prorocentrum* sp.	Macroalgae (*Acanthophora*, *Acetabularia*, *Acicularia*, *Amphiroa*, *Avrainvillea*, *Batophora*, *Bryothamnion*, *Caulerpa*, *Ceramium*, *Chaetomorpha*, *Chondria*, *Codium*, *Dictyota*, *Digenia*, *Enteromorpha*,	Okolodkov et al. (2007, 2014), Almazan-Becerril et al. (2015), Poot-Delgado et al. (2015), Aguilar-Trujillo et al. (2017), Irola-Sansores et al. (2018), Nunez-Vazquez et al. (2018 and references therein), Durán-Riveroll et al. (2019 and references therein), Tarazona-Janampa et al. (2020), Cembella et al. (2021)

				Eucheuma, *Gracilaria*, *Halimeda*, *Halymenia*, *Heterosiphonia*, *Jania*, *Laurencia*, *Padina*, *Penicillus*, *Sargassum*, *Stypopodium*, *Udotea*, *Ulva*), seagrass (*Halodule*, *Ruppia*, *Syringodium*, *Thalassia*), sediment, sponge, dead coral (*Millepora*, *Acropora*), attached buoy rope and seawater	
Cienfuegos and Havana, Cuba	21°55'N - 23°N	5	*P. belizeanum**, *P. caipirignum* (as *P. maculosum**), *P. concavum*, *P. hoffmannianum*, *P. lima*, *P. mexicanum*	Macroalgae (*Chaetomorpha*, *Dictyota*, *Dictyotales*, *Padina*, *Ulva*) and sediment	Delgado et al. (2006), Herrera-Sepulveda et al. (2015), Moreira-González et al. (2019a,b), Durán-Riveroll et al. (2019 and references therein)
North Atlantic Ocean					
Saint Paul's Rocks, Brazil	00°55'N	3	*P. emarginatum*/*fukuyoi*/*sculptile* complex, *P. hoffmannianum*, *P. lima*	Macroalgae (*Dictyota*)	Current study
Lagos, Nigeria	6°N	1	*P. lima*	Seawater	Ajuzie and Houvenaghel (2009)
Florida, United States	~ 24°42'N - 25°15'N	5	*P. concavum*, *P. emarginatum*, *P. hoffmannianum*, *P. lima*, *P. mexicanum*, *P. rhathymum*	Macroalgae (*Acanthophora*, *Ceramium*, *Halimeda*, *Hypnea*, *Palisada*, *Polysiphonia*) and seagrass (*Ruppia*, *Syringodium*, *Thalassia*)	Morton et al. (1992), Morton and Tindall (1996), Murray et al. (2009), An et al. (2010), Sugahara et al. (2011), Herrera-Sepulveda et al. (2015), Accoroni et al. (2018, 2020), Durán-Riveroll et al. (2019 and references therein)

Canary Islands, Overseas Spain	27°38.3'N - 29°13.1'N	4	*P. hoffmannianum*, *P. lima*, *P. maculosum**, *P. panamense*, *P. rhathymum*	Macroalgae (*Asparagopsis*, *Caulerpa*, *Colpomenia*, *Cystoseira*, *Dictyota*, *Galaxaura*, *Halimeda*, *Halopteris*, *Jania*, *Lobophora*, *Padina*, *Sargassum*, *Zonaria*) and artificial substrate	Rodriguez et al. (2018), Fernandez-Zabala et al. (2019, 2022), Gaiani et al. (2022)
Selvagens Islands, Portugal	30°01'N - 30°08'N	6	*P. concavum*, *P. emarginatum*, *P. hoffmannianum*, *P. lima*, *P. panamense*, *P. rhathymum*	Artificial substrate	Godinho et al. (2022)
Galé and Lisbon, Portugal	37°N - 38°41'N	1	*P. lima*	Macroalgae and seawater	Vale et al. (2009), David et al. (2018)
Great South Channel, Rhode Island and Maine, United States	40°55'N - 44°27'N	1	*P. lima*	Oyster cages, lines, buoys, rafts, macroalgae (*Ascophyllum*, *Ectocarpus*, *Fucus*), seagrass (*Zostera*) and seawater	Morton et al. (1999), Maranda et al. (1999, 2007)
Vigo, Ria de Vigo, Ria de Pontevedra, Zierbena, Arrigorri, San Sebastian and beaches of the south-eastern Bay of Biscay, Spain	~ 42°N - 43°N	5	*P. elegans*, *P. emarginatum/fukuyoi* group, *P. leve*, *P. lima*, *P. rhathymum*	Macroalgae (*Cladostephus*, *Corallina*, *Cystoseira*, *Dictyota*, *Gelidium*, *Plocamium*, *Stypocaulon*) and seawater	Lee et al. (1989), Bravo et al. (2001), Varkitzi et al. (2010), Laza-Martinez et al. (2011), David et al. (2014, 2018)
Nova Scotia, New Brunswick and Gulf of St. Lawrence, Canada	~ 44°N - 47°N	2	*P. lima*, *P. mexicanum*	Epibionts (composed of hydrozoans and macroalgae intertwined around a mussel sock) and seawater	Marr et al. (1992), Hu et al. (1995, 2017), Lawrence and Cembella (1999), Lawrence et al. (2000), Bauder et al. (2001), Levasseur et al. (2003)

Gironde, Brittany and Wimereux, France	44°38'N - 50°46'N	6	***P. consutum*****,** *P*. cf. *fukuyoi*, ***P. glenanicum***, *P. leve*, *P. lima*, ***P. pseudopanamense***	Sandy sediment, sediments and seawater	Chomérat et al. (2010, 2011), Gomez and Artigas (2014), Mertens et al. (2017)
Groix Island and Moutons Island, France	~ 47°N	4	*P. clipeus*, *P. foraminosum*, *P.* cf. *fukuyoi*, *P. tsawwassenense*	NI	Hoppenrath et al. (2013)
Dorset, United Kingdom	50°37'N	1	*P. lima*	Macroalgae (*Ascophyllum*, *Calliblepharis*, *Ceramium*, *Chaetomorpha*, *Ectocarpaceae* spp., *Enteromorpha*, *Fucus*, *Gracilaria*, *Sargassum*, *Ulva*) and seagrass (*Ruppia*, *Zostera*) and seawater	Nascimento et al. (2005), Foden et al. (2005), Aquino-Cruz et al. (2018)
Ireland	~ 51°N - 52°N	1	*P. lima*	NI	Kilcoyne et al. (2020)
Netherlands	~ 51°N - 53°N	1	*P. lima*	Seawater	van der Fels-Klerx et al. (2012)
Helgoland and Sylt, Germany	~ 54°N	3	***P. clipeus***, *P. foraminosum*, *P.* cf. *fukuyoi*	Sand	Hoppenrath (2000), Hoppenrath et al. (2013)
Gothenburg, Tjärnö, Kristineberg and Hovåsbadet, Sweden	57°33'N - 58°52'N	4	*P.* cf. *foraminosum*, *P. fukuyoi* complex, *P.* cf. *hoffmannianum*, *P. lima*	Macroalgae (*Ceramium*, *Polysiphonia*) and artificial substrate	Álvarez et al. (2022)
Kandalaksha Gulf, Russia	66°33'N	1	*P. lima*		Vershinin et al. (2006)

				Macroalgae (*Ascophyllum*, *Cladophora*, *Fucus*)	
Mediterranean Sea					
Alexandria, Egypt	~ 31°N	1	*P. lima*	Macroalgae (*Corallina*, *Hypnea*, *Jania*, *Laurencia*, *Sargassum*, *Ulva*)	Ismael and Halim (2012)
Gulf of Gabes, Gulf of Tunis, Ghar El Melh lagoon, Mahdia, Bizerte Lagoon and Bizerte Bay, Tunisia	34°0'N - 37°16'N	4	*P. concavum*, *P. emarginatum*, *P. lima*, *P. rhathymum*	Macroalgae (*Asparagopsis*, *Codium*, *Corallina*, *Cystoseria*, *Dictyopteris*, *Dictyota*, *Enteromorpha*, *Gracilaria*, *Jania*, *Laurencia*, *Mesophyllum*, *Padina*, *Penicillus*, *Sargassum*, *Ulva*), seagrass (*Cymodocea*, *Halophila*, *Posidonia*, *Ruppia*, *Zostera*), surface sediment and seawater	Turki (2005), Mabrouk et al. (2011), Zina et al. (2012), Dhib et al. (2013), Sahraoui et al. (2013), Aissaoui et al. (2014), Ben Gharbia et al. (2016, 2017), Moncer et al. (2017), Loukil-Baklouti et al. (2018), Hachani et al. (2018), Feki-Sahnoun et al. (2019), Ben Gharbia et al. (2019), Malika et al. (2021), Feki et al. (2022)
Tétouan-Chefchaouen coast and Gibraltar Strait, Morocco	35°20'N - 35°54'N	1	*P. lima*	Macroalgae (*Asparagopsis*, *Cladostephus*, *Dictyota*, *Halopteris*, *Plocamium*) and seawater	Leblad et al. (2020), Aboualaalaa et al. (2022), Ibghi et al. (2022)
Mellah lagoon, Algeria	36.54°N	1	*P. lima*	Seawater	Draredja et al. (2019)
Ibiza and Catalonia, Spain	38°N - 42°N	1	*P. lima*	Macroalgae (*Corallina*, *Dictyota*, *Dilophus*, *Halopteris*, *Jania*), sediment and seawater	Vila et al. (2001), David et al. (2018)
Greece	40°N - 41°N	5			Aligizaki et al. (2009)

			P. borbonicum, *P. emarginatum*, *P. leve*, *P. lima* species complex, *P. rhathymum*	Macroalgae (*Codium*, *Corallina*, *Cystoseira*, *Padina*, *Ulva*), sediment and seawater	
Sorrento, Genoa, Ortona, Francavilla, Pescara, Emilia-Romagna and Sacca di Goro, Italy	~ 40°N - 44°50'N	2	*P.* cf. *leve*, ***P. lima***	Macroalgae (*Halopteris*), seagrass and seawater	Nagahama and Fukuyo (2005), Ingarao et al. (2009), Vanucci et al. (2010), Nagahama et al. (2011), Pistocchi et al. (2012), Giussani et al. (2017)
French Catalonia, Languedoc, Provence, French Riviera, Villefranche-sur-Mer and Corsica, France	41°24'N - 43°46'N	1	*P. lima*	Macroalgae (*Asparagopsis*, *Caulerpa*, *Ceramium*, *Cladophora*, *Cladostephus*, *Corallina*, *Cystoseira*, *Dictyopteris*, *Dictyota*, *Flabellia*, *Gelidiella*, *Gelidium*, *Haliptylon*, *Halopitys*, *Halopteris*, *Jania*, *Laurencia*, *Liagora*, *Padina*, *Parviphycus*, *Plocamium*, *Polysiphonia*, *Taonia*, *Ulva*, *Womersleyella*)	Cohu and Lemée (2012), Blanfuné et al. (2015), David et al. (2018)
Kaštela Bay, Šibenik Bay and Istria Peninsula, Croatia	~ 43°N - 45°N	1	*P. lima*	NI	Arapov (2013 and references therein)
Suez Canal					
Temsah Lake, Egypt	30°33'N - 30°35'N	1	*P. lima*	Seawater	Mona et al. (2022)
Black Sea					

Sevastopol, Crimea	44°36'N	1	*P. lima*	Macroalgae (*Cystoseira*)	Ryabushko (2020)
Bolshoy Utrish, Russia	44°44'N	1	*P. lima*	Seawater	Morton et al. (2009)
Baltic Sea					
Neva Estuary, Russia	60°N	1	*P. lima*	Seawater	Golubkov et al. (2019)
South Indian Ocean					
Zanzibar, Tanzania	~ 6°S	7	*P. borbonicum*, *P. concavum*, *P. elegans*, *P. emarginatum*, *P. hoffmannianum* (as *P. belizeanum** and *P. maculosum**), *P. lima*, *P. mexicanum*	Dead coral with algal turf and seawater	Hansen et al. (2001)
Mayotte Island, Overseas France	12°41'S	1	*P. arenarium**, *P. lima*	Algal turf	Grzebyk et al. (1998), Bouaicha et al. (2001)
Ste. Marie, Madagascar	~ 16°S - 17°S	2	*P. arenarium**, *P. concavum*, *P. lima*	Benthic samples and seawater	Hansen et al. (2001)
Broome, Australia	17°97'S	2	*P. concavum*, *P. malayense*	Sandy intertidal sediments	Verma et al. (2019)
Mauritius Island, Overseas France	~ 20°S	6	*P. belizeanum**, *P. concavum*, *P. elegans*, *P. emarginatum*, *P. hoffmannianum*, *P. lima*, *P. mexicanum*	Macroalgae (*Gracilaria*, *Hypnea*, *Jania*) and seawater	Hansen et al. (2001), Bouaicha et al. (2001)
Réunion Island, Overseas France	~ 20°S - 21°S	9	*P. arenarium**, *P. belizeanum**, ***P. borbonicum***, *P. concavum*, *P.*		Diogéne et al. (1995), Grzebyk et al. (1998),

			elegans, *P. emarginatum*, *P. hoffmannianum*, *P. lima*, *P. mexicanum*, *P. panamense*, *P. sculptile*	Algal turf (Cerarniales, Gelidiales), coral, sand and seawater	Ten-Hage et al. (2000a), Hansen et al. (2001), Bouaicha et al. (2001), Escoffier et al. (2007), Hoppenrath et al. (2013), Dominguez et al. (2021)
Europa Island, Overseas France	22°20'S	1	*P. arenarium**, *P. lima*	Surface sand and coral rubbles	Ten-Hage et al. (2000b), Bouaicha et al. (2001)
KwaZulu-Natal, South Africa	30°S	2	*P. emarginatum*, *P. rhathymum*	NI	Hoppenrath et al. (2013)
Wilson Inlet, Australia	~ 34°S	1	*P. mexicanum*	Seawater	Mansour et al. (1999)
North Indian Ocean					
Tamil Nadu, Malabar coast and Dona Paula Bay, India	9.281933°N - 15°30'N	2	*P. lima*, *P. rhathymum*	Seawater	Naik et al. (2018), Oyeku and Mandal (2021), Sankaranarayanan et al. (2021)
Lakshadweep Archipelago, India	10°56'N	1	*P. rhathymum*	Macroalgae (*Gracilaria*) and seawater	Thomas et al. (2021)
Kadan Island, Myanmar	~ 12°N	1	*P. rhathymum*	Seawater	Su-Myat and Koike (2013)
Dhofar, Oman	16°49'N - 16°58'N	1	*P. sipadanense*	Macroalgae (*Padina*) and sediment	Saburova and Chomérat (2016)
Thuwal, Saudi Arabia	22.25°N - 22.39°N	11	*P. borbonicum*, *P. clipeus*, *P. concavum*, *P. consutum*, *P.*	Seagrass, surface sediment and seawater	Prabowo and Agusti (2019)

			elegans, *P. emarginatum*, *P. hoffmannianum*, *P. leve*, *P. lima*, *P. rhathymum*, *P. tropicale*		
Karachi, Pakistan	24°47'N - 24°49'N	3	*P. concavum* (as *P. faustiae**), *P. emarginatum*, *P. lima*	Seawater	Munir et al. (2013)
Hormozgan, Iran	26°50'N - 27°10'N	1	*P. lima*	Seawater	Mohebbi-Nozar et al. (2022)
Kuwait	28°46'N - 29°20'N	8	*P. arenarium**, ***P. bimaculatum***, *P. concavum*, *P. consutum*, *P. emarginatum*, *P. fukuyoi*, *P. lima*, *P. norrisianum*, *P. rhathymum*	Intertidal sediments	Chomérat et al. (2012 and references therein)
South Pacific Ocean					
Tropical Australia		3	*P. hoffmannianum*, *P. lima*, *P. rhathymum*	NI	Murray et al. (2009)
Queensland, Australia	~ 23°S - 27°28'S	3	*P. concavum* (as ***P. faustiae****), *P. lima*, *P. mexicanum*	Macroalgae, seagrass (*Cymodocea*, *Halodule*, *Halophila*, *Zostera*) and intertidal coral sand	Morton and Tindall (1995, 1996), Morton (1998), Takahashi et al. (2008)
French Polynesia, Overseas France	17°30'S	3	*P. arenarium**, ***P. concavum,*** *P. lima*, *P. mexicanum*	Macroalgae (*Amphiroa*, *Jania*, *Turbinaria*) and algal turf	Fukuyo (1981), Murakami et al. (1982), Grzebyk et al. (1998), Murray et al. (2009)
New Caledonia, Overseas France	~ 20°S	2	***P. concavum,*** *P. lima*	Macroalgae (*Amphiroa*, *Jania*, *Turbinaria*)	Fukuyo (1981), Holmes et al. (2001)
New Zealand subtropical zone	~ 29°S	5	*P.* cf. *emarginatum*, *P. fukuyoi*, *P. hoffmannianum*, *P. lima*, *P. maculosum**, *P. rhathymum*	Macroalgae (*Asparagopsis*, *Caulerpa*, *Dasya*, *Microdictyon*, *Spyridia*), corals and sediment	Rhodes et al. (2014, 2017), Rhodes and Smith (2019 and references therein)

New Zealand temperate zone	~ 34°S - 46°S	1	*P. lima*	Macroalgae on mussel growing lines, seagrass (*Zostera*), sediments and seawater	Rhodes et al. (1995), Chang et al. (2000), MacKenzie et al. (2011), Rhodes and Smith (2019 and references therein)
New South Wales, Australia	34°S	2	***P. fukuyoi***, *P. mexicanum*	Sediment	Lovejoy et al. (1998), Murray et al. (2007)
Cook Islands	35°S	2	*P.* cf. *hoffmannianum* (as *P.* cf. *maculosum**), *P. lima*	Macroalgae (*Halimeda*)	Rhodes et al. (2010)
Little Swanport, Tasmania	~ 42°S	1	*P. rhathymum*	Seawater	Pearce et al. (2005)
North Pacific Ocean					
Singapore Strait	1°N	3	*P. concavum*, *P. emarginatum*, *P. lima*	Sediments and seawater	Tan et al. (2016)
Sarawak and Sabah, East Malaysia	01°36'N - 07°38.65"N	9	*P. arenarium**, *P. concavum*, *P. emarginatum*, *P.* cf. *faustiae**, *P. foraminosum*, *P. formosum*, *P. lima*, *P. mexicanum*, *P. norrisianum*, *P. rhathymum*, *P. sculptile*, ***P. sipadanense***	Macroalgae (*Padina*, *Sargassum*), seagrasses, dead corals and sand	Mohammad-Noor et al. (2007a,b), Wu et al. (2022)
Manado, Indonesia	1°46'N	2	*P. concavum*, *P.* cf. *sculptile*	Sand	Wu et al. (2022)
Parque Nacional Isla del Coco, Costa Rica	~ 5°N	1	*P. concavum*	Macroalgae and seawater	Vargas-Montero et al. (2012)

Perhentian Islands, Peninsular Malaysia	05°57'N	6	*P. caipirignum*, *P. concavum*, *P.* cf. *emarginatum*, *P. lima*, ***P. malayense***, *P. mexicanum*	Seaweeds, coral rubble and sediment	Usup et al. (2008), Lim et al. (2019)
Kelantan, Malaysia	06°1'N	1	*P. mexicanum*	Sand and seawater	Wu et al. (2022)
Contadora Island, Panama	08°38'N	3	*P. concavum*, *P. hoffmannianum* (as *P. maculosum**), ***P. panamense***	Algal turf	Grzebyk et al. (1998)
Chumphon, Trat and Sichang, Thailand	10°33'N - 13°7'N	3	*P. concavum*, *P. fukuyoi*, *P. mexicanum*	Sand	Wu et al. (2022)
Nha Trang Bay, Vietnam	~ 12°N	5	*P. concavum*, *P. emarginatum*, *P. lima*, *P. rathymum*, *Prorocentrum* sp.	Artificial substrate	Nguyen-Ngoc et al. (2022)
El Salvador	~ 13°N	1	*P. lima*	NI	Durán-Riveroll et al. (2019 and references therein)
Zhongsha Islands, South China Sea	15°50.347'N - 16°13.191'N	6	*P. concavum*, *P. emarginatum*, *P. hoffmannianum*, *P. lima*, *P. rhathymum*, *P.* cf. *sculptile*	Macroalgae (*Amphiroa*, *Halimeda*, *Padina*) and coral sand	Xie et al. (2022)
Salina Cruz, Oaxaca, Mexico	16°9'N	1	***P. mexicanum***		Osorio-Tafall (1942)
Xisha Islands, South China Sea	16°34'N - 16°57'N	7	*P. borbonicum*, *P. caipirignum*, *P. concavum*, *P. elegans*, *P.* cf. *emarginatum*, *P. lima* complex, *P. rhathymum*	Macroalgae, seagrasses, dead coral reefs, and sediments	Zou et al. (2022)
Johnston Atoll, United States	16°44'N	4	*P. concavum*, *P. emarginatum*, *P. lima*, *P.* cf. *rhathymum*	Macroalgae (*Caulerpa*)	Richlen and Lobel (2011)

Hainan Island, South China Sea	18°09.61"N - 19.63°N	10	*P. caipirignum* (as *P. lima* morphotype 4 and *P.* cf. *maculosum**), *P. concavum*, *P.* cf. *emarginatum*, *P. fukuyoi*, *P. hoffmannianum*, *P. lima*, *P. malayense*, *P. panamense*, *P. rhathymum*, *Prorocentrum* morphotype 5	Macroalgae (*Caulerpa*, *Colpomenia*, *Dictyota*, *Padina*, *Sargassum*, *Spatoglossum*, *Ulva*), seagrass (*Enhalus*, *Halophila*, *Thalassia*), dead coral reef, sediments, sand and seawater	Li et al. (2012), Zhang et al. (2015), Luo et al. (2017), Yin et al. (2018), Lim et al. (2019), Zou et al. (2020), Wu et al. (2020), Liu et al. (2022), Wu et al. (2022)
Yitong Shoal and Shenhu Shoal, South China Sea	19°10.560'N - 19°31.924'N	3	*P. lima*, *P. rhathymum*, *P.* cf. *sculptile*	Macroalgae (*Halimeda*) and coral sand	Xie et al. (2022)
Hawaii, United States	19°30'N	7	*P. belizeanum**, *P. concavum*, *P. emarginatum*, *P. hoffmannianum*, *P. lima*, *P. mexicanum*, *P. ruetzlerianum*, *Prorocentrum* sp.	Macroalgae (*Acanthophora*, *Ahnfeltiopsis*, *Alsidium*, *Amansia*, *Amphiroa*, *Anotrichium*, *Caulerpa*, *Centroceras*, *Ceramium*, *Chondria*, *Cladophoropsis*, *Coelothrix*, *Dictyopteris*, *Dictyosphaeria*, *Enteromorpha*, *Eucheuma*, *Galaxaura*, *Gelidiella*, *Gelidiopsis*, *Gelidium*, *Gracilaria*, *Grateloupia*, *Halimeda*, *Haloplegma*, *Halymenia*, *Hypnea*, *Martensia*, *Microdictyon*, *Padina*, *Portieria*, *Pterocladia*, *Pterocladiella*, *Sargassum*, *Spyridia*, *Tolypiocladia*,	Landsberg et al. (1999), Parsons and Preskitt (2007)

				Trichogloea, *Tricleocarpa*, *Turbinaria*, *Ulva*), seagrass (*Halophila*), cyanobacteria, rock and sand	
Daya Bay, Guangxi and Fujian, China	~ 20°N - 26°N	4	*P. caipirignum* (as *P.* cf. *maculosum**), *P. fukuyoi*, *P. lima*, *P. mexicanum*	Macroalgae, seagrass, dead coral reef, sediments and sand	Luo et al. (2017), Wu et al. (2020), Gong et al. (2021), Wu et al. (2022)
Taiwan Island, China	~ 22°N	2	*P. lima*, *P. mexicanum*	NI	Lu et al. (2001, 2005), Yang et al. (2018)
Bahía de Mazatlán and Baja California Sur, Mexico	23°10'N - 24°35'N	5	*P. concavum*, *P. emarginatum*, *P. hoffmannianum* (as *P. belizeanum**), *P. lima*, *P. mexicanum*, *P. rhathymum*	Macroalgae (*Sargassum*, *Ulva*), rocky substrate, sediment with detritus and seawater	Hernandez-Becerril et al. (2000), Heredia-Tapia et al. (2002), Cortes-Altamirano and Sierra-Beltran (2003), Alonso-Rodriguez and Ochoa (2004), Band-Schmidt et al. (2008), Mucino-Marquez et al. (2015), Nunez-Vazquez et al. (2018 and references therein), Cembella et al. (2021)
Ryukyu Islands, Japan	~ 25°N	2	***P. concavum*, *P. emarginatum***	Macroalgae (*Amphiroa*, *Jania*, *Turbinaria*)	Fukuyo (1981)
Japan (subtropical and temperate zones)	26°14'N - 43°12'N	8	*P. caipirignum*, *P.* cf. *concavum*, *P.* cf. *emarginatum*, *P. fukuyoi*, *P. lima* complex, *P. mexicanum*, *P. porosum*, *P.* cf. *rhathymum*, *Prorocentrum* sp. type 1	Macroalgae (*Callophyllis*, *Carpopeltis*, *Codium*, *Coccophora*, *Dichotomaria*, *Distromium*, *Gelidium*,	Torigoe et al. (1988), Koike et al. (1991, 1998), Murata et al. (1998), Grzebyk et al. (1998), Izumikawa et al. (2000), Murray et al. (2007, 2009),

				Gracilaria, *Grateloupia*, *Heterochordaria*, *Laurencia*, *Lobophora*, *Padina*, *Palisada*, *Ptilonia*, *Sargassum*, *Turbinaria*, *Ulva*) and sediment	Amar et al. (2018), Nishimura et al. (2020a,b), Arteaga-Sogamoso et al. (2023)
West coast of the United States	~ 32°N - 48°N	1	*P. lima*	NI	Anderson et al. (2021)
Yeosu and Geomundo Island, Korea	~ 34°N	1	*P. lima*	Macroalgae (*Sargassum*)	Yang et al. (2017), You et al. (2020)
Jeju Island, Korea	33°12'N - 33°32'N	5	*P. concavum*, *P. emarginatum*, *P. fukuyoi*, *P. lima*, *P. rhathymum*	Macroalgae (*Champia*, *Chondrus*, *Cladophora*, *Codium*, *Colpomenia*, *Corallina*, *Dictyopteris*, *Ecklonia*, *Enteromorpha*, *Galaxaura*, *Gelidium*, *Gracilaria*, *Grateloupia*, *Hizikia*, *Hypnea*, *Jania*, *Martensia*, *Plocamium*, *Pterocladiella*, *Sargassum*, *Ulva*, *Wrangelia*) and sandy sediment	Shah et al. (2013), Lee et al. (2015), Yoo et al. (2018), You et al. (2020)
Qingdao and Qinhuangdao, China	36.08°N - 40.01°N	3	*P. fukuyoi*, *P. lima*, *P. tsawwassenense*	Sand and seawater	Liu et al. (2019), Wu et al. (2020), Wu et al. (2022)
Peter the Great Bay and Zhitkova Bay, Sea of Japan	42°30'N - 43°50'N	3	*P. foraminosum*, *P. fukuyoi*, *P. lima*	Macroalgae (*Ahnfeltiopsis*, *Bryopsis*, *Campylaephora*, *Ceramium*, *Champia*, *Chondria*, *Chondrus*,	Selina and Levchenko (2011), Selina et al. (2014), Kameneva et al. (2015), Selina (2017)

				Chorda, *Chordaria*, *Chrysymenia*, *Codium*, *Coccophora*, *Costaria*, *Cystoseira*, *Dasya*, *Delesseria*, *Desmarestia*, *Dictyota*, *Gracilaria*, *Grateloupia*, *Laurencia*, *Neorhodomela*, *Neosiphonia*, *Palmaria*, *Polysiphonia*, *Prionitis*, *Ptilota*, *Punctaria*, *Sargassum*, *Symphyocladia*, *Tichocarpus*, *Ulva*), seagrass (*Phyllospadix*) and sediment	
British Columbia, Canada	49°0.0'N	1	***P. tsawwassenense***	Sand	Hoppenrath and Leander (2008)
Inland Waterbody					
Lake Manych-Gudilo, Russia	46°20'N	1	*P. leve*	Seawater and aquatic vegetation	Glushchenko et al. (2019)

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Table S3. Keywords used in the literature survey on the diversity of benthic *Prorocentrum* species, number of publications retrieved for each entry and the number of selected papers for further reading for each keyword. The total number of publications considering all keywords searched and the total number of publications selected for full reading as well as the number of publications used to compile the data are presented at the bottom of the table.

Keyword	Total number of publications	Publications selected for full reading
Benthic and *Prorocentrum*	232	119
Prorocentrum arenarium	9	7
Prorocentrum belizeanum	25	12
Prorocentrum bimaculatum	1	1
Prorocentrum borbonicum	5	4
Prorocentrum caipirignum	7	4
Prorocentrum caribbaeum	2	1
Prorocentrum clipeus	1	1
Prorocentrum concavum	39	29
Prorocentrum consutum	2	1
Prorocentrum elegans	9	4
Prorocentrum emarginatum	22	22
Prorocentrum faustiae	5	3
Prorocentrum foraminosum	9	5
Prorocentrum formosum	1	1
Prorocentrum fukuyoi	10	9
Prorocentrum glenanicum	2	2
Prorocentrum hoffmannianum	39	20
Prorocentrum leve	4	2
Prorocentrum levis	5	4
Prorocentrum lima	432	173
Prorocentrum maculosum	22	10
Prorocentrum malayense	2	2

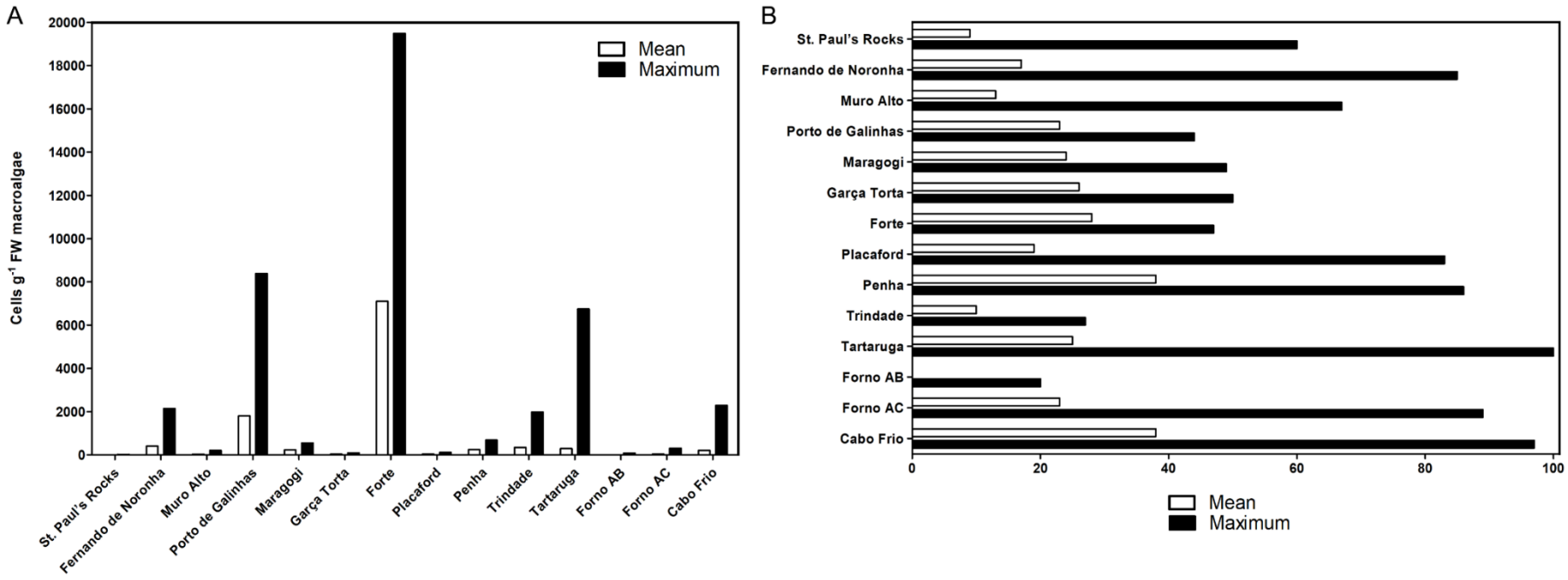
Prorocentrum mexicanum	39	25
Prorocentrum norrisianum	2	2
Prorocentrum panamense	3	3
Prorocentrum porosum	1	1
Prorocentrum pseudopanamense	1	1
Prorocentrum reticulatum	24	2
Prorocentrum rhathymum	30	20
Prorocentrum ruetzlerianum	2	2
Prorocentrum sabulosum	1	1
Prorocentrum sculptile	5	4
Prorocentrum sipadanense	1	1
Prorocentrum sipadanensis	2	2
Prorocentrum tropicale	1	1
Prorocentrum tropicalis	10	1
Prorocentrum tsawwassenense	2	2
Total	1009	504
After removing repeated selected publications		273
Publications used to compile the data presented in this study		215

Table S4. Minimum, maximum and mean abundances (in parentheses) of each *Prorocentrum* species, as well as total abundance of the genus *Prorocentrum* (cells g^{-1} FW macroalgae) at 11 sites at the coast and three oceanic islands of Brazil. NI*: Not identified.

Sampling sites	*P.* cf. *borbonicum*	*P.* cf. *caipirignum*	*P.* cf. *concavum*	*P. emarginatum/fukuyoi/ sculptile* complex	*P. hoffmannianum*	*P. lima* complex	*P.* cf. *norrisianum*	*P. panamense*	*P. rhathymum*	*Prorocentrum* sp. 1	*Prorocentrum* sp. 2	*Prorocentrum* NI*	*Prorocentrum* abundance
Saint Paul's Rocks				0 - 471 (54)	0 - 15 (2)	0 - 19 (5)						0 - 1 (0)	0 - 482 (62)
Fernando de Noronha	0 - 142 (25)		0 - 188 (16)	0 - 621 (158)	0 - 740 (191)	0 - 2141 (404)	0 - 221 (31)	0 - 86 (5)	0 - 586 (83)	0-117 (17)	0 - 164 (15)	0 - 242 (25)	143 - 3738 (1374)
Muro Alto						0 - 197 (31)							0 - 197 (31)
Porto de Galinhas				0 - 139 (48)		76 - 8389 (1804)						0 - 444 (64)	76 - 8527 (1916)
Maragogi				0 - 188 (36)		0 - 550 (227)							31 - 550 (263)
Garça Torta						0 - 91 (33)							0 - 91 (33)
Forte						1026 - 19487 (7099)						0 - 342 (38)	1067 - 19829 (7137)

Placaford					0 - 113 (35)					0 - 17 (1)	0 - 117 (37)
Penha			0 - 20 (4)		3 - 684 (236)					0 - 68 (14)	5 - 703 (254)
Trindade	0 - 37 (5)		0 - 826 (243)	0 - 714 (163)	0 - 1984 (347)	0 - 13 (1)				0 - 19 (1)	0 - 2590 (760)
Tartaruga			0 - 977 (45)		0 - 6746 (286)		0 - 41 (1)			0 - 81 (3)	0 - 7722 (334)
Forno, AB					0 - 79 (1)						0 - 79 (1)
Forno, AC			0 - 140 (4)		0 - 305 (36)		0 - 7 (0)			0 - 77 (3)	0 - 333 (43)
Cabo Frio		0 - 16 (4)	0 - 15 (3)		1 - 2288 (204)		0 - 58 (8)			0 - 55 (20)	1 - 2353 (238)

Figure S1. *Prorocentrum lima* abundance values at 11 sites on the coast and three oceanic islands of Brazil. (A) *Prorocentrum* abundance showing median, 1st quartile, 3rd quartile, maximum and minimum values (cells g^{-1} FW macroalgae), (B) *Prorocentrum* relative abundance (%) with standard deviation.



Capítulo 2

Table S1. Mean abundance (cells g^{-1} FW macroalgae) and mean relative abundance (%) of benthic dinoflagellate genera at each sampling site (Cagarras - CGR, Laje Dois Irmãos - LDI, and Ponta da Sapata - PDS) and year at Fernando de Noronha Archipelago.

Amphidinium abundance						
Sampling site	Years					
	2017	2018	2019	2021	2022	2023
CGR	70 3%	$3.0x10^2$ 9%	12 1%	$2.4x10^2$ 2%	$5.9x10^2$ 7%	$1.4x10^3$ 16%
LDI		7 0%	15 8%	23 0%	$1.2x10^3$ 11%	$3.8x10^2$ 11%
PDS	29 2%	$1.2x10^2$ 4%	68 6%	77 1%	$1.4x10^3$ 19%	$1.5x10^3$ 22%
Bysmatrum abundance						
Sampling site	Years					
	2017	2018	2019	2021	2022	2023
CGR				13 0%	$4.5x10^2$ 7%	$3.1x10^2$ 3%
LDI				$1.2x10^2$ 1%	$8.9x10^2$ 8%	15 1%
PDS				9 0%	$1.7x10^2$ 3%	22 0%
Cabra abundance						
Sampling site	Years					
	2017	2018	2019	2021	2022	2023
CGR		32 1%	10 1%	54 0%	25 0%	46 0%
LDI						

		2 0%	0 0%	0 0%	$1.0x10^2$ 1%	0 0%
PDS		0 0%	0 0%	7 0%	25 0%	6 0%
Coolia abundance						
Sampling site	Years					
	2017	2018	2019	2021	2022	2023
CGR	$2.5x10^2$ 7%	$3.6x10^2$ 11%	9 1%	$4.9x10^2$ 3%	$7.9x10^2$ 7%	$9.4x10^2$ 10%
LDI		$1.2x10^2$ 6%	0 0%	$4.0x10^2$ 6%	$1.6x10^3$ 14%	41 1%
PDS	21 2%	$2.0x10^2$ 6%	$2.9x10^2$ 11%	$1.9x10^2$ 3%	$2.2x10^2$ 3%	88 2%
Gambierdiscus abundance						
Sampling site	Years					
	2017	2018	2019	2021	2022	2023
CGR	$1.4x10^2$ 4%	$1.2x10^2$ 3%	7 1%	$2.1x10^2$ 2%	48 1%	93 1%
LDI		4 0%	0 0%	$1.7x10^2$ 2%	$2.0x10^2$ 2%	99 3%
PDS	$4.7x10^2$ 49%	$3.7x10^2$ 10%	17 1%	78 2%	75 1%	8 0%
Ostreopsis abundance						
Sampling site	Years					
	2017	2018	2019	2021	2022	2023
CGR	75 2%	$1.2x10^2$ 3%	9 1%	$1.7x10^3$ 12%	$6.4x10^2$ 5%	$2.2x10^3$ 18%
LDI		$1.7x10^2$ 7%	15 8%	$2.0x10^3$ 15%	$4.2x10^2$ 4%	$7.0x10^2$ 19%

PDS	16 2%	$2.4x10^3$ 55%	$3.9x10^2$ 22%	$1.5x10^3$ 31%	82 1%	$1.4x10^3$ 31%

Prorocentrum abundance

Sampling site	Years					
	2017	2018	2019	2021	2022	2023
CGR	$2.4x10^3$ 83%	$2.4x10^3$ 71%	$8.7x10^2$ 92%	$1.2x10^4$ 80%	$7.5x10^3$ 68%	$5.1x10^3$ 50%
LDI		$1.3x10^3$ 84%	$1.8x10^2$ 84%	$7.2x10^3$ 76%	$5.7x10^3$ 55%	$2.3x10^3$ 63%
PDS	$4.5x10^2$ 45%	$1.0x10^3$ 25%	$8.4x10^2$ 59%	$3.4x10^3$ 62%	$3.8x10^3$ 71%	$1.8x10^3$ 43%

Sinophysis abundance

Sampling site	Years					
	2017	2018	2019	2021	2022	2023
CGR	17 1%	22 1%	32 3%	91 1%	39 0%	59 1%
LDI		18 1%	0 0%	34 0%	24 0%	31 1%
PDS	0 0%	1 0%	19 1%	35 0%	13 0%	7 0%