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Baleias e golfinhos em águas costeiras e oceânicas: uma abordagem integrada para distribuição, exposição a atividades humanas e conservação das espécies no Brasil e no mundo.

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Tese apresentada, como requisito parcial para obtenção do título de Doutor, ao Programa de Pós-Graduação em Ecologia e Evolução, da Universidade do Estado do Rio de Janeiro.

Orientadores: Prof.ª Dra. Maria Alice dos Santos Alves
Prof. Dr. Clinton Neil Jenkins
Coorientador: Prof. Dr. Rodrigo Hipolito Tardin Oliveira

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RESUMO

MARICATO, Guilherme Azevedo Barreiros. *Baleias e golfinhos em águas costeiras e oceânicas:* uma abordagem integrada para distribuição, exposição a atividades humanas e conservação das espécies no Brasil e no mundo. 120 f. Tese (Doutorado em Ecologia e Evolução) – Instituto de Biologia Roberto Alcantara Gomes, Universidade do Estado do Rio de Janeiro, Rio de Janeiro, 2023.

A distribuição das espécies é de extrema importância para garantir a proteção adequada das espécies e dos ecossistemas. Cetáceos (baleias e golfinhos) desempenham papéis cruciais na regulação de ecossistemas marinhos, mas a compreensão da distribuição de organismos marinhos, especialmente cetáceos, ainda é limitada. O presente estudo visou preencher esta lacuna por meio de uso de modelagem de adequabilidade para avaliar a distribuição dessas espécies e sua relação com o ambiente. A presente tese foi constituída por três capítulos. No primeiro capítulo, por meio de revisão sistemática, evidenciou a necessidade de um protocolo analítico bem estabelecido para a replicabilidade das análises de baleias. Fatores como concentração de clorofila, profundidade e distância da costa foram essenciais para explicar sua distribuição, variando de acordo com o tipo de habitat e zona marítima. O segundo capítulo abordou a exposição de cetáceos a atividades humanas cumulativas e a sobreposição das áreas mais adequadas com Áreas Marinhas Protegidas (AMPs). Os resultados mostraram que muitas AMPs não abrangem áreas oceânicas com alta exposição às atividades humanas cumulativas. Águas sobre a plataforma continental foram identificadas como mais adequadas para baleias-de-bryde (*Balaenoptera brydei*) e golfinhos-nariz-de-garrafa (*Tursiops truncatus*), principalmente na região Sudeste do Brasil, onde as atividades humanas cumulativas são maiores. No terceiro capítulo, foi investigado o comportamento alimentar dos botos-cinza (*Sotalia guianensis*), que foi influenciado pela concentração de clorofila, profundidade e tráfego de embarcações. Redes de pesca representaram riscos, exigindo medidas eficazes para reduzir conflitos e melhorar a eficácia das AMPs locais. O foco na conservação de espécies guarda-chuva, como baleias e golfinhos, pode beneficiar outras espécies compartilhando os mesmos habitats. Entretanto, considerar diferentes escalas espaciais e as particularidades de cada espécie é essencial para estratégias de conservação eficazes. A criação e aprimoramento de AMPs são importantes para conservar essas espécies e a biodiversidade marinha, reduzindo impactos humanos. Os resultados podem embasar tomadas de decisões pelas partes cabíveis, de forma que o esforço coletivo possa garantir a conservação da biodiversidade e dos ecossistemas.

Palavras-chave: Conservação marinha. Impactos ambientais. Mamíferos marinhos. Modelagem espacial. Oceano Atlântico Sul Ocidental.

ABSTRACT

MARICATO, Guilherme Azevedo Barreiros. *Whales and dolphins in coastal and oceanic waters:* an integrated approach to species distribution, exposure to human activities, and conservation in Brazil and worldwide. 120 f. Tese (Doutorado em Ecologia e Evolução) – Instituto de Biologia Roberto Alcantara Gomes, Universidade do Estado do Rio de Janeiro, Rio de Janeiro, 2023.

The distribution of species is of utmost importance to ensure proper protection of both species and ecosystems. Cetaceans (whales and dolphins) play crucial roles in regulating marine ecosystems, yet our understanding of the distribution of marine organisms, especially cetaceans, remains limited. This study aimed to fill this gap by using suitability modeling to assess the distribution of these species and their relationship with the environment. The present dissertation consisted of three chapters. In the first chapter, through a systematic review, the need for a well-established analytical protocol to ensure the replicability of whale analyses was highlighted. Factors such as chlorophyll concentration, depth, and distance from the coast were essential in explaining cetacean distributions, varying according to habitat type and marine zone. The second chapter addressed the exposure of cetaceans to cumulative human activities and the overlap of the most suitable areas with Marine Protected Areas (MPAs). The results showed that many MPAs do not cover oceanic areas with high exposure to cumulative human activities. Waters over the continental shelf were identified as more suitable for Bryde's whales (*Balaenoptera brydei*) and bottlenose dolphins (*Tursiops truncatus*), especially in Southeastern Brazil, where cumulative human activities are more significant. In the third chapter, the feeding behavior of Guiana dolphins (*Sotalia guianensis*) was investigated, influenced by chlorophyll concentration, depth, and vessel traffic. Fishing gear represented risks, necessitating effective measures to reduce conflicts and improve the effectiveness of local MPAs. Focusing on the conservation of umbrella species like whales and dolphins can benefit other species sharing the same habitats. However, considering different spatial scales and specificities of each species is essential for effective conservation strategies. The establishment and improvement of MPAs is crucial in conserving cetacean species and reducing human impacts in general on marine biodiversity. The findings may inform decision-making by relevant parties, ensuring that collective efforts can lead to the conservation of biodiversity and ecosystem.

Keywords: Marine conservation. Environmental impacts. Marine mammals. Spatial modeling. Southwestern Atlantic Ocean.

SUMÁRIO

INTRODUÇÃO

Compreender os processos que influenciam a distribuição das espécies é importante no campo da ecologia, com implicações significativas para a conservação de espécies e ecossistemas. Diversas espécies possuem amplas áreas de vida, o que as torna suscetíveis a diversos impactos ambientais. Uma estimativa imprecisa da distribuição desses organismos pode ter um impacto direto na eficácia das medidas de conservação adotadas. Por essa razão, a investigação cuidadosa dos padrões de distribuição é essencial para garantir a proteção adequada das espécies e dos ecossistemas em que habitam (REDFERN et al., 2006).

Estudos de distribuição de organismos terrestres têm ganhado destaque, mas a compreensão da distribuição de organismos marinhos ainda é incipiente (REDFERN et al., 2006; ROBINSON et al., 2011). Mamíferos marinhos, como os cetáceos (baleias e golfinhos), enfrentam desafios únicos devido à sua alta mobilidade e por viverem em ambientes com nenhuma ou poucas barreiras físicas que limitem esses movimentos (SIMS et al., 2008; MELO-MERINO; REYES-BONILLA; LIRA-NORIEGA, 2020). Sua distribuição varia ao longo do tempo, de acordo com as exigências biológicas e ecológicas da espécie (COSTA; MARESH, 2018). Essa alta mobilidade resulta em uma área de vida significativamente maior em comparação com mamíferos terrestres de tamanho similar (TUCKER; ORD; ROGERS, 2014).

Uma das técnicas para determinar a amplitude da distribuição geográfica das espécies é a Modelagem de Distribuição de Espécies (*Species Distribution Modeling*). Esse tipo de modelagem permite gerar mapas preditivos de padrões de distribuição das espécies, por meio da utilização de registros de presença/ausência e de variáveis explanatórias (DE MARCO-JÚNIOR; SIQUEIRA, 2009). No presente estudo, utilizamos o termo Modelagem de Adequabilidade (*Suitability Modeling*), que avalia a adequabilidade de um determinado ambiente ou área para uma ou mais espécies (GUISAN; THUILLER; ZIMMERMANN, 2017). Esses mapas são valiosos para a identificação de áreas prioritárias para conservação e a compreensão da relação das espécies com o ambiente, auxiliando no planejamento e nas tomadas de decisão (DE MARCO-JÚNIOR; SIQUEIRA, 2009; GUISAN; THUILLER; ZIMMERMANN, 2017).

Embora estudos recentes tenham mostrado diferentes respostas às variáveis que explicam a distribuição das espécies de acordo com a escala, poucos consideram diferentes escalas nas análises. Essa variação na escala espacial pode fazer com que variáveis explanatórias respondam de forma diferente ao mesmo conjunto de variáveis dependentes

(WITMAN; ETTER; SMITH, 2004; FERNANDEZ et al., 2018). Dessa forma, é necessário entender como o efeito da escolha da escala e das variáveis explanatórias influenciam na adequabilidade das espécies para uma conservação mais efetiva da biodiversidade.

Na presente tese, as espécies-modelo selecionadas para abordar a modelagem de distribuição de espécies foram os cetáceos. As baleias e os golfinhos são considerados predadores de topo, ocupando posições cruciais nas cadeias alimentares marinhas. Desempenham um papel fundamental na regulação das populações de presas e no equilíbrio dos ecossistemas. Sua presença pode ter efeitos em cascata por todo o ambiente marinho, influenciando a estrutura da comunidade e a biodiversidade (ROMAN et al., 2014; KISZKA; WOODSTOCK; HEITHAUS, 2022). Além disso, como sentinelas de ecossistemas, esses cetáceos oferecem informações sobre as condições ambientais e suas alterações, tornando-os bons indicadores para compreender e gerenciar ecossistemas marinhos (BOSSART, 2011; HAZEN et al., 2019).

Os cetáceos também são considerados espécies guarda-chuva, pois representam um grupo mais amplo de espécies com requisitos de habitat semelhantes, e ao proteger essas, espera-se preservar o habitat como um todo, assim como a comunidade de espécies associadas a elas (SERGIO et al., 2006). Por essas características, os cetáceos podem ser definidos como espécies-chave na conservação da biodiversidade e dos ecossistemas (LIBRALATO; CHRISTENSEN; PAULY, 2006; VALLS; COLL; CHRISTENSEN, 2015). Além disso, a popularidade e o carisma dessas espécies os tornam espécies-bandeira, capazes de angariar apoio financeiro e conscientização pública para a conservação marinha como um todo (SERGIO et al., 2006, 2008).

Para proteger os cetáceos, e consequentemente a biodiversidade marinha, além da redução da sobrepesca e destruição do habitat, uma das ferramentas mais importantes é a criação de Áreas Marinhas Protegidas (AMPs), uma vez que já foi reportado que estas levam ao aumento da biomassa e da biodiversidade conjuntamente (BOONZAIER; PAULY, 2016; GRORUD-COLVERT et al., 2021). Recentemente, o Brasil atingiu a marca de 25% de proteção do ecossistema marinho por meio de AMPs, porém a eficácia destas é contestada, uma vez que os diferentes usos por parte dos seres humanos continuam a acontecer dentro de grande parte dessas AMPs de forma descontrolada (MAGRIS; PRESSEY, 2018).

O objetivo geral da presente tese foi utilizar modelos de distribuição como uma ferramenta para subsidiar ações para a conservação de baleias e golfinhos no Brasil. A tese está constituída de três capítulos. O primeiro abordou uma revisão sistemática com o objetivo de avaliar os fatores ambientais que influenciam na distribuição das baleias, o segundo teve como objetivo avaliar as áreas de maior exposição de cetáceos considerando AMPs e atividades humanas cumulativas, e o terceiro consistiu em avaliar as características ambientais que influenciam o comportamento de alimentação do boto-cinza e suas táticas coordenadas de pesca.

1 WHAT INFLUENCES THE DISTRIBUTION OF WHALES WORLDWIDE? A SYSTEMATIC REVIEW

Abstract: Comprehending the factors that affect the distribution of a particular species is important to support more assertive decision-making for its conservation. Although modeling techniques are among the most used tools to predict species distributions, studies on whales (Mysticeti) in general do not follow a well-established analytical protocol that allows for replicability. Our systematic review investigated the biotic and abiotic factors that influence whale distributions worldwide. The systematic literature survey was carried out using the PRISMA protocol at the Scopus® database. Papers from 2001 to 2020 were evaluated. The initial search found 1,090 studies and, after sorting, 64 papers were considered. In general, the most important characteristics to explain a mysticete distribution were chlorophyll concentration, depth, distance from the coastline, sea surface temperature, and seabed slope. The results showed that the response of the species occurrence to the characteristics depends on the habitat area (breeding, feeding, and permanent) and maritime zone (coastal and ocean) of the explanatory variables. Mysticetes tended to occur in warmer waters and steeper slopes. Chlorophyll concentration, depth and sea surface temperature had different relationships, depending on the habitat area. In feeding grounds and permanent habitat areas, mysticetes tended to occur in areas of greater chlorophyll concentration, depths, and distance from the coastline, while the opposite occurred in breeding grounds. Looking at the results without comprehending the parameters used to generate them can lead to various types of errors, including making decisions that are not suitable for protecting the species. We recommend considering the parameters used to reduce bias and avoid misinterpretation, bringing the results closer to reality and making them more assertive and replicable.
Keywords: Mysticeti. Baleen whales. Suitability. Habitat. Biogeography.

Resumo: Entender os fatores que afetam a distribuição de uma determinada espécie é importante para embasar tomadas de decisão mais assertivas para sua conservação. Embora técnicas de modelagem estejam entre as ferramentas mais utilizadas para prever a distribuição de espécies, estudos com espécies de baleias (subordem Mysticeti), em geral, não seguem um protocolo analítico bem estabelecido que permita a replicabilidade. A presente revisão sistemática investigou os fatores bióticos e abióticos que influenciam a distribuição de baleias ao redor do mundo. O levantamento da literatura foi conduzido seguindo o protocolo PRISMA por meio do banco de dados Scopus®. Foram pesquisados artigos de 2001 a 2020.

A busca inicial resultou em 1.090 estudos e, após a triagem, foram considerados 64 artigos. De forma geral, as variáveis que mostraram mais importância para explicar a distribuição de misticetos foram concentração de clorofila, profundidade, distância da linha de costa, temperatura superficial do mar e declive do relevo submarino. Os resultados apontaram que a resposta da ocorrência das espécies às características vai depender da área de habitat (reprodução, alimentação e permanente), zona marítima (costeira e oceânica) e resolução espacial das variáveis explanatórias. Os misticetos tenderam a ocorrer em águas mais quentes e íngremes. A concentração de clorofila, a profundidade e a temperatura superficial do mar tiveram relações diferentes conforme a área de residência. Em áreas de alimentação e permanentes, os misticetos tenderam a ocorrer mais em maiores concentrações de clorofila, profundidades e distâncias da linha de costa, enquanto o oposto ocorreu em áreas de reprodução. Olhar para os resultados sem compreender os parâmetros utilizados para chegar até eles pode levar a vários tipos de erros, incluindo tomadas de decisões inadequadas para a conservação das espécies. Recomendamos considerar os parâmetros utilizados para reduzir viés e evitar interpretação errônea, aproximando os resultados da realidade e tornando-os mais assertivos e replicáveis.

Palavras-chave: Mysticeti. Baleias verdadeiras. Adequabilidade. Habitat. Biogeografia.

Introduction

Understanding a species' distribution is crucial for various biological and ecological applications. It can help researchers better understand the species' habitat requirements, determine their role in ecosystem functioning and assess population viability (e.g., Morris and Doak, 2002; Meynecke et al., 2021). Furthermore, species distribution information can be used to predict the potential impacts of environmental change on the species, aiding conservation efforts and the development of management plans for their conservation (e.g., Ehrlén and Morris, 2015; Ye et al., 2021).

A species' distribution is influenced by life history and ecological factors. Unraveling this is important and determined by many biotic and abiotic conditions, dispersal ability, and adaptive capacity. Biotic conditions are intra or interspecific interactions, which can be positive (e.g., mutualism and pollination) or negative (e.g., parasitism and predation) in terms of population increase. Abiotic conditions include environmental aspects, such as depth, slope, and precipitation. The dispersal ability represents the movement of individuals to accessible regions, and the adaptive capacity is linked to evolutionary characteristics of adjusting or responding to environmental changes (Soberón and Peterson, 2005).

Species distribution is constantly changing because of global environmental changes, and may increase, decrease, or be fragmented (Chen et al., 2011). Human activities have altered species distributions, especially after the industrial revolution. Activities such as predatory fishing, hunting, urban sprawl, and unbridled land use change are some of those that have had a negative impact on biodiversity (Hunter, 2007). These activities can cause many species to have their range reduced, and even eliminated (e.g., Cruz et al., 2018; Main et al., 2020; O'Donnell and DelBarco-Trillo, 2020). However, some species may benefit from human activities by adapting quickly to new stressors and having fewer local competitors and predators, resulting in increased ranges (e.g., Firn et al., 2011; Parker et al., 2013).

Modeling has become an increasingly common approach for determining the range of species distributions, both in current and future scenarios (Guisan et al., 2017). For prediction and projection models, the Species Distribution Modeling (SDM) technique allows species distribution maps to be generated by using occurrence records (presence and absence) and explanatory environmental, biological, and anthropic variables (Guisan et al., 2017).

Distribution studies of terrestrial organisms have been growing rapidly over the years (Redfern et al., 2006). In parallel, the understanding of the distribution of marine organisms is also increasing, although the number of publications is lower than terrestrial studies (Robinson et al., 2011). Studying marine species with high mobility has been a great challenge for researchers over time due to the physical and biological characteristics of the habitats and species (Redfern et al., 2006; Robinson et al., 2011). The logistics for data sampling in marine environments is often complicated, depending on boat rentals and favorable meteo-oceanographic conditions for navigation. Marine mammals, such as whales, live in open and fluid environments with few physical barriers to limit their movements and those of their prey (Sims et al., 2008; Melo-Merino et al., 2020). As a result, these animals are highly mobile and tend to have a much larger ranges than similarly sized terrestrial mammals (Tucker et al., 2014).

Whales, categorized within the Mysticeti group (mysticetes), generally move looking for food resources, sexual partners, and suitable areas to live. These movements have spatiotemporal characteristics and may consist of large-scale migrations between polar regions (feeding grounds) and tropical/temperate regions (breeding areas). The migration route may vary according to the life history and individual experience of the animals, being commonly associated with productive, stable feeding grounds, and safe habitats for both adults and offspring, as well as a trade-off between the cost to move and the daily energetic requirements (Abrahms et al., 2019; Riekkola et al., 2020). The migration can vary according to multiple factors, such as biological characteristics and extreme weather events, influencing the timing of the beginning and end of migration, as well as the route taken. Biological characteristics, such as age and sex, may be related to hormonal differences and energy requirements that influence reproductive success, while extreme weather events (e.g., El Niño/La Niña and marine heatwaves) may influence environmental characteristics, such as sea temperature and primary productivity (Craig et al., 2003; Rasmussen et al., 2007). Some populations perform longitudinal movements, such as Bryde's whales in the Western South Atlantic, while others do not perform these movements and remain in the same habitat, such as a population of fin whales in the Mediterranean Sea (Lodi and Borobia, 2013; Geijer et al., 2016; Stern and Friedlaender, 2018).

Whales' distributions depend on biotic and abiotic factors that may be associated with physical and chemical characteristics of water masses, as well as organisms living in them, and may be present in coastal (estuarine or near-shore), neritic (on the continental shelf) and/or oceanic (after the shelf break) regions (Forcada, 2018). Biotic factors include the distribution and abundance of their prey, predation pressure, competitors, and availability of sexual partners, for example. Abiotic factors include, for example, water temperature, salinity, chlorophyll concentration, depth, submarine relief gradient, substrate type, and distance from land, among others. In addition to these two components, anthropic factors can influence the distribution of whales and include characteristics that can alter the species habitat, such as organic, chemical and noise pollution, ship strikes, and fishing activity (Santora et al., 2014; Tardin et al., 2019; Lodi et al., 2020; Stephenson et al., 2020).

Whales play a fundamental role in ecosystems. Because they have high metabolic demand, they feed upon tons of prey per day and their iron and nitrogen-rich feces fertilizes the ocean, increasing primary productivity in oligotrophic environments (Freitas et al., 2023). Some of their species are top predators, having the potential to regulate the food web from a top-down control, but also being at risk of biomagnification, accumulating several contaminants in high concentration, and can be used as indicators of environmental quality (Smith and Gangolli, 2002; Roman et al., 2014). As well, because they reach dozens of meters in length and can weigh tons, whales have a great potential to store and sequester carbon, helping to fight climate change. Finally, when they die, whale carcasses serve as a food source (Lavery et al., 2010; Pershing et al., 2010; Roman et al., 2014; Smith et al., 2019).

Due to their charismatic nature, whales may serve as flagship species with great potential to raise public awareness and funding for environmental actions (Sergio et al., 2006; Verissimo et al., 2011). They also have large ranges, with some species being cosmopolitan; that is, their conservation can make it possible to conserve several co-occurring species (Sergio et al., 2008). Given whales' role in structuring their food webs, they can also be recognized as keystone species (Libralato et al., 2006).

Despite their fundamental role in conservation, studies aimed at understanding the relationship of whale species with the environment have been limited to relatively small study areas compared to the species' home ranges. Therefore, the present study aimed to analyze which environmental factors influence whale distributions worldwide, and how they do so, to clarify general trends and facilitate decision-making.

1.1 Methods

1.1.1 Literature survey

The literature search was conducted following the Preferred Reporting Items for Systematic reviews and Meta-Analyses (PRISMA) statement (Page et al., 2021) through Scopus® (https://www.scopus.com), a peer-reviewed literature database. The survey was conducted using "*Article title*, *Abstract*, *Keywords*" and the search terms used were: BALAEN*; DISTRIBUTION; ESCHRICH*; "HABITAT USE"; MODEL*; NEOBALAEN*; NICHE, OCCURRENCE; WHALE*. For this purpose, the concepts of ecological niche, distribution, and habitat use were considered as equivalent. In total, four combinations were used (Table 1).

Table 1 – Keyword queries used to find scientific papers in the present study.

Search	**Query**
1	MODEL* AND DISTRIBUTION AND (BALAEN* OR ESCHRICH* OR NEOBALAEN* OR WHALE*)
2	MODEL* AND "HABITAT USE" AND (BALAEN* OR ESCHRICH* OR NEOBALAEN* OR WHALE*)
3	MODEL* AND OCCURRENCE AND (BALAEN* OR ESCHRICH* OR NEOBALAEN* OR WHALE*)
4	MODEL* AND NICHE AND (BALAEN* OR ESCHRICH* OR NEOBALAEN* OR WHALE*)

Papers were searched from 1960 to 2020 and went through the following screening process: i) it was identified whether the theme appeared in the title or abstract; ii) it was evaluated if the theme in question was an objective of the paper or just mentioned, without having been explicitly tested. If the theme was addressed as an objective, it was included in the set of papers selected for analysis.

The following information was obtained from the selected papers, considering the appropriate protocols for SDM studies (Zurell et al., 2020): year of publication, target species, study area, habitat area, maritime zone, model type, algorithms used, nature of occurrence data, explanatory variables, significant explanatory variables, model selection criterion, metric for model performance evaluation, and uncertainty assessment.

1.1.2 Definition of terms and data collecting

The study area was classified according to ecoregion, following the definitions proposed by Spalding et al. (2007). Habitat areas were divided into breeding, feeding, and migratory route (when there were migratory movements), and permanent (when there were no migratory movements). Areas up to 12 nautical miles from the coastline were defined as coastal, while areas more distant than 12 nautical miles were defined as oceanic (UNCLOS, 1982).

Absence data were grouped as being i) true absence, where systematic monitoring occurred to assess whether the species occurred in the area, ii) artificial (pseudo-absence and background), or iii) presence-only (no absence data). The explanatory variables were separated into three categories: (i) physiographic, which depend on the geological characteristics of the oceans and do not change in the short to medium term (e.g., depth and distance to coast), (ii) oceanographic, which are dynamic and depend on meteo-oceanographic conditions (e.g., sea surface temperature and turbidity), and (iii) anthropic, which depend on any action performed by humans (e.g., distances to fishing grounds and boat routes).

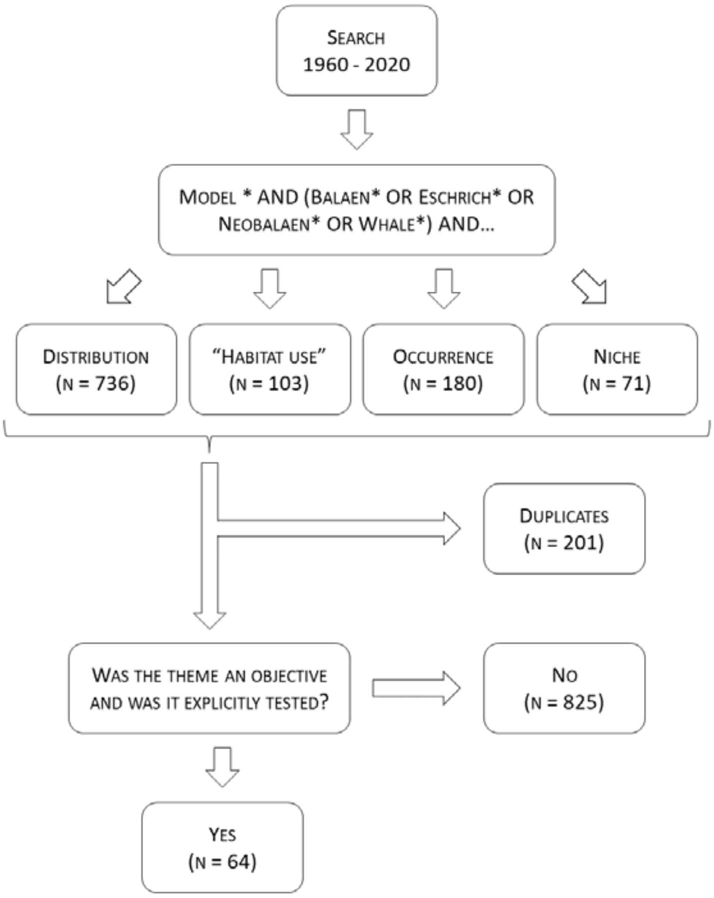
The criteria used for selecting explanatory variables of the models in each paper were also extracted. Variable selection is performed to choose a model with a good fit to the data and with the minimum number of variables possible to simplify the results and facilitate interpretation (Heinze et al., 2018). Model evaluation metrics were also compiled for each study. This step is crucial, as it determines how well the models represent reality through the data provided. There are several metrics, and the most common ones use residuals (Guisan et al., 2017).

Finally, the variable importance was obtained from each study analyzing how each variable influenced species distribution (e.g., positive, negative or no trend) by model coefficients and/or inference from prediction graphs that depicted the relationship between the response and explanatory variable. The relationship of the importance of each variable for the mysticete occurrence was evaluated according to habitat area (seasonal and permanent) and the maritime zone (coastal or oceanic).

1.2 Results

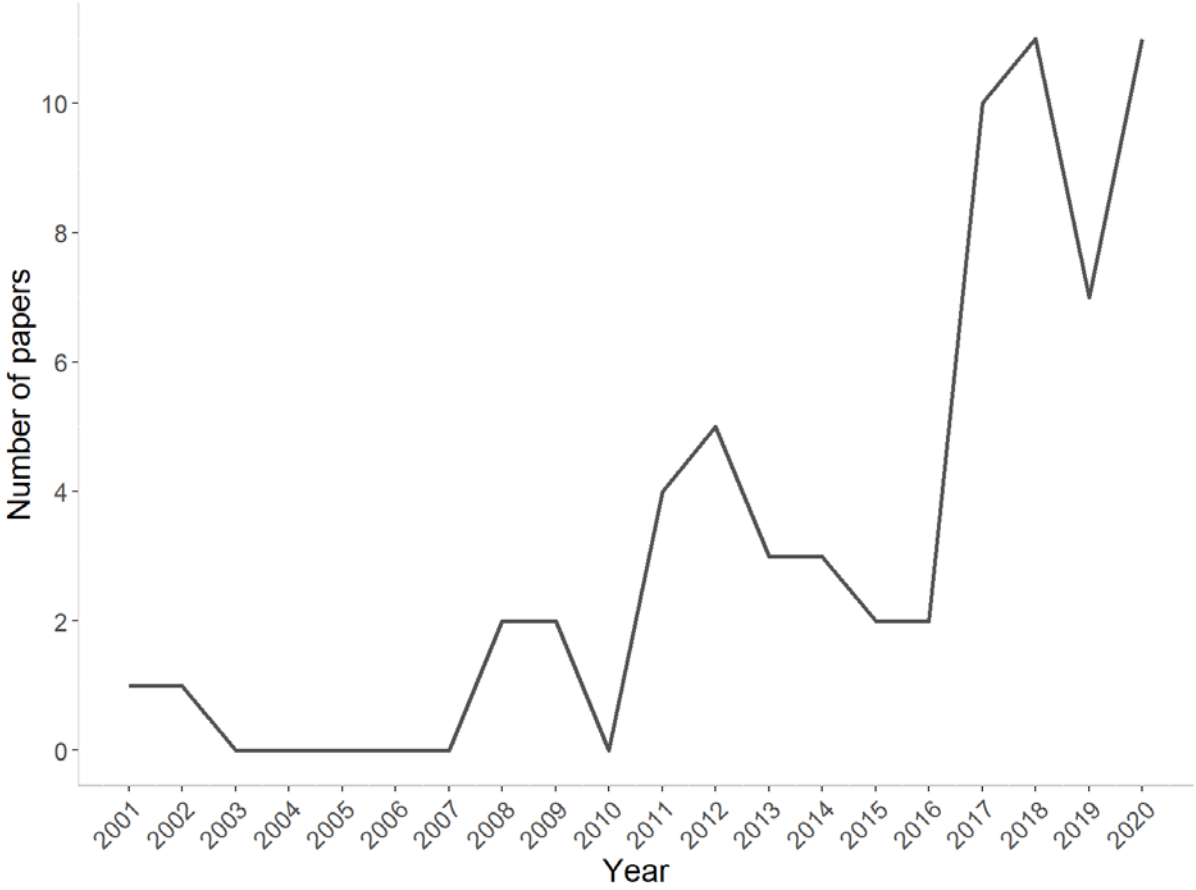
The survey resulted in 1,090 papers that appeared in more than one combination. After the screening process, 64 papers that modelled the factors that influence the distribution of whale species were selected for analysis (Figure 1). Some papers addressed more than one species independently and were therefore counted more than once.

Figure 1 – Flowchart showing the screening process of modeling papers published from 1960 to 2020.



The papers analyzed were published between 2001 and 2020 (Figure 2). In general, it was possible to observe an increase in the number of papers published over the years.

Figure 2 – Number of whale distribution modeling papers published between 2001 and 2020.



A total of 11 mysticete species were contemplated in the studies. Fin whale, *Balaenoptera physalus* (18.9%), humpback whale, *Megaptera novaeangliae* (18,1%), and blue whale, *Balaenoptera musculus* (15,0%) represented more than half of the records (Figure 3).

The studies covered 158 of the 232 existing ecoregions (68.1%). The northeast and northwest Atlantic Ocean and the northeast Pacific Ocean were the most represented regions (Figure 4).

Figure 3 – Number of mysticete species in modeling papers. *B.* = *Balaenoptera**, *E.* = *Eubalaena*, *M.* = *Megaptera*. *Except in *B. mysticetus* = *Balaena mysticetus*.

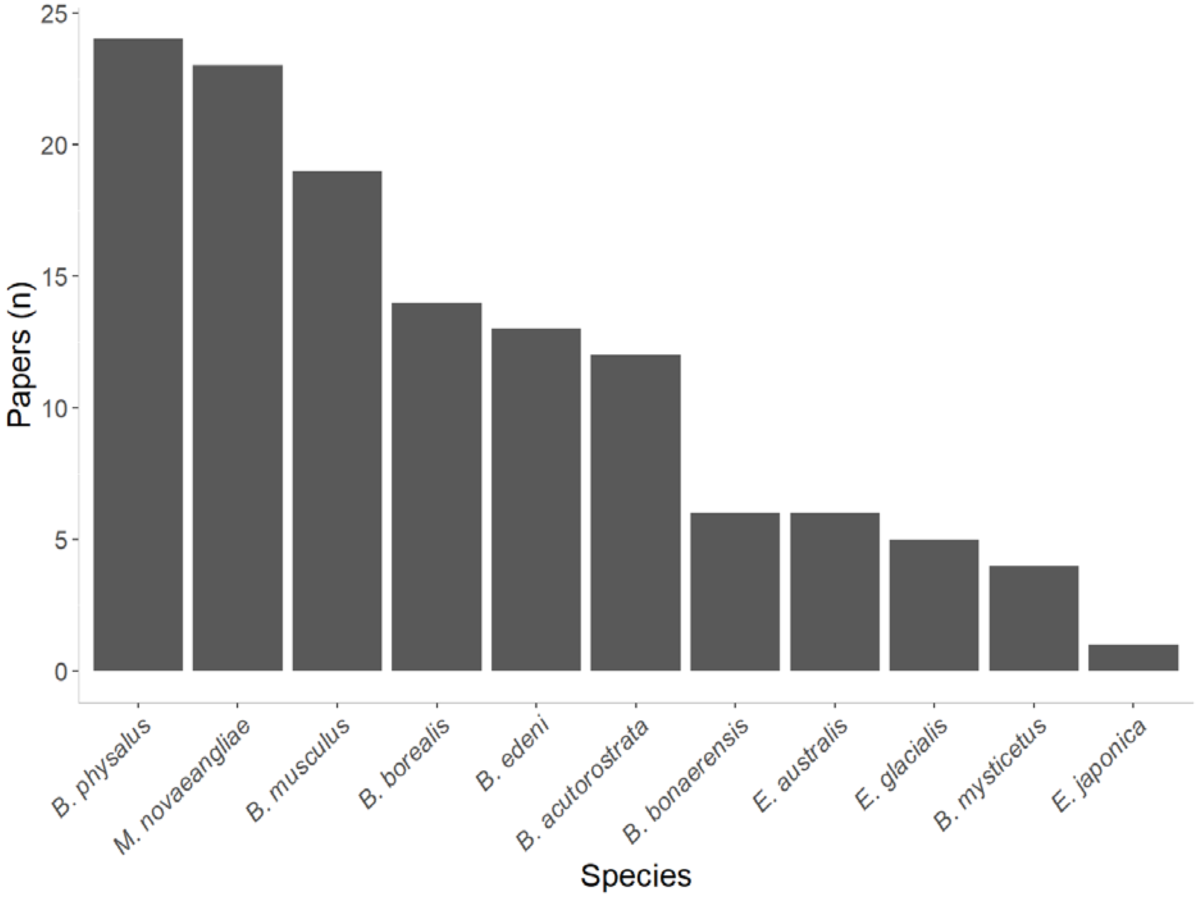
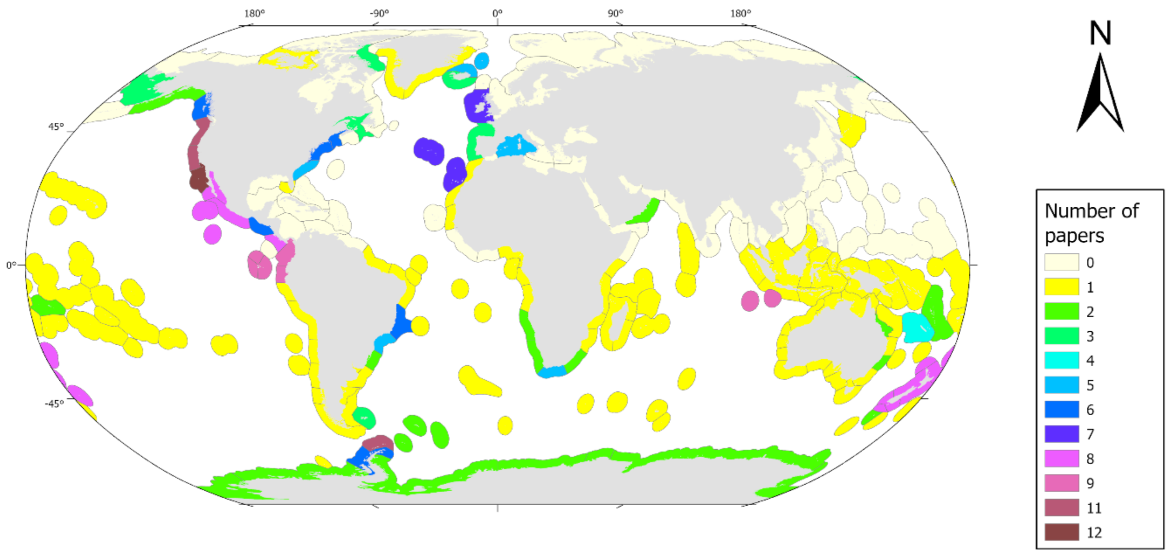


Figure 4 – Ecoregions studied in whale species modeling papers. Robinson projection, WGS 1984 datum.



Most of the papers analyzed populations in feeding grounds (50.9%), while only 18.1% analyzed populations in breeding grounds. Some studies analyzed regions that spanned feeding and breeding grounds (8.6%), while others analyzed populations on migratory routes (8.6%). Some populations of *B. edeni* and *B. physalus* were considered permanent residents in 13.8% of the studies. Most studies occurred in the oceanic zone (59.6%), while 40.4% occurred in the coastal zone.

The most used algorithms were the regression models - generalized additive (GAM) and linear (GLM) - and Maximum Entropy (MaxEnt), with GAM used in more than half of the studies. Another 13 algorithms were also used (Table 2). Many studies did not present a metric to select the models subsequently used (46.3%); that is, only a single model was used. Among the papers that used multi-model inference, Akaike Information Criterion (AIC) was the most used. Five other tests were also used (Table 3).

To evaluate the performance of SDMs, ten different tests were used. In 38.2% of the models no evaluation tests were used. Considering the studies that used at least one of the tests, the Area Under the Curve (AUC) of the Receiver Operating Characteristic (ROC) was the most popular (Table 4). The evaluation of model uncertainty was measured in 69.2% of the papers. In another 30.8% this information was not available. Information on the nature of absence data was unavailable in 30.9% of the papers. When available, most of the papers used true absence data in the analyses (Table 5). A total of 35 different explanatory variables were used, 13 physiographic, 15 oceanographic, and seven anthropic. A description of each can be found in Supplementary Table 2. Supplementary Table 2 lists the frequencies in which each variable was used, the significance level, and the relationship (positive, negative, or unidentified) to the mysticete occurrence. Not all papers showed a clear tendency if the variables were positive, negative, or had no correlation with mysticete distribution.

Table 2 – Algorithms used, their corresponding acronyms, and the frequency in which each algorithm was used by the total number of whale distribution modeling papers (n = 64).

Algorithm	**Acronym**	**%**
Generalized Additive Model	GAM	59.6
Maximum Entropy	MaxEnt	23.1
Generalized Linear Model	GLM	20.2
Boosted Regression Tree	BRT	12.5
Random Forest	RF	5.8
Conditional Auto-Regressive	CAR	2.9
Classification And Regression Tree	CART	2.9
Machine Learning Regression Algorithms	MLRA	2.9
Environmental Niche Factor Analysis	ENFA	1.9
Support Vector Machine	SVM	1.9
Artificial Neural Network	ANN	1.0
Classification Tree Analysis	CTA	1.0
Multiple Adaptive Regression Splines	MARS	1.0
Minimum Cross-Entropy	MinxEnt	1.0
Partial Least Squares	PLS	1.0
Principal Component Analysis	PCA	1.0

Table 3 – Criteria used to select the best models, their corresponding acronyms, and the frequency in which each test was used by the total number of whale distribution modeling papers (n = 64).

Criterion	**Acronym**	**%**
Akaike Information Criterion	AIC	68.2
Generalized Cross-Validation	GCV	15.2
Restricted Maximum Likelihood	REML	9.1
Deviance Information Criterion	DIC	3.0
Unbiased Risk Estimator	UBRE	3.0
Quasi Information Criterion	QIC	1.5

Table 4 – Metrics used to evaluate models' performance, their corresponding acronyms, and the frequency in which each test was used by the total number of whales distribution modeling papers (n = 64).

Metric	**Acronym**	**%**
Receiver Operating Characteristic	ROC	60.5
True Skill Statistic	TSS	13.2
Adjusted R-squared	Adjusted R^2	11.8
Pseudo-R-squared	Pseudo-R^2	5.3
Root Mean Square Error	RMSE	2.6
Boyce Index	Boyce	1.3
Conditional Predictive Ordinate	CPO	1.3

Table 5 – Absence type and the frequency in which each type was used by the total number of whales distribution modeling papers (n = 64).

Absence	**%**
True	36.1
Pseudoabsence	24.7
Background	23.7
Presence-only	15.5

Only the five most frequent variables combining all studies (chlorophyll, depth, distance to coast, sea surface temperature and slope) were used to investigate how the variables influenced mysticete occurrence. In general, regardless of habitat area, mysticetes tended to occur in regions with local lower sea surface temperature and steeper slopes (Table 6). The other selected variables had different relationships according to habitat area. Model prediction indicated that the mysticete occurrence, in breeding grounds, was higher in shallower waters and near-shore, and lower chlorophyll concentration, while in feeding grounds they were found in deeper waters, farther from the coastline and with higher chlorophyll concentration (Table 6, details in Supplementary Table 3). In permanent grounds, more mysticetes were observed in deeper waters, near the coastline and with higher chlorophyll concentration. It was not possible to assess the importance of the variables in migratory routes due to a low number of papers.

Analyzing the significant explanatory variables by species, sea surface temperature and/or depth were the most often found significant for all species. The relationship of the explanatory variables to mysticete occurrence varied by species (Table 7, see Supplementary Tables 4 to 14 for details).

Table 6 – Direction of the importance of the main explanatory variables in relation to habitat area (breeding, feeding, or permanent) and maritime zone (coastal or oceanic) to explain mysticete occurrence. Positive (↗), neutral (→) and negative (↘) relations. C = Coastal, O = Oceanic.

Habitat area	**Breeding**		**Feeding**		**Permanent**	
Maritime zone	**C**	**O**	**C**	**O**	**C**	**O**
Chlorophyll	↘	-	→	↗	↗	↗
Depth	↘	↘	↗	↗	↗	↗
Distance to coast	↘	↘	↗	↗	↗	-
Sea surface temperature	↗	-	↗	↗	↗	↘
Slope	-	↗	↗	↗	↗	-

Table 7 – Direction of the importance of the main explanatory variables in relation to the most frequent explanatory variables to explain mysticete occurrence. Positive (↗), neutral (→), and negative (↘) relations. Chl. = Chlorophyll; D. C. = Distance to coast; SST = Sea Surface Temperature.

Species	**Chl.**	**Depth**	**D. C.**	**SST**	**Slope**
Balaena mysticetus	↗	↘	↘	↗	↗
Balaenoptera acutorostrata	↘	↗	→	↘	→
Balaenoptera bonaerensis	-	↘	↘	↗	-
Balaenoptera borealis	↗	↗	↗	→	↗
Balaenoptera edeni	↗	↗	↘	↘	→
Balaenoptera musculus	↘	↘	↘	↘	↗
Balaenoptera physalus	↘	↗	↗	→	↗
Eubalaena australis	→	↘	↘	→	→
Eubalaena glacialis	↘	↘	↘	→	-
Eubalaena japonica	-	↗	-	↘	-
Megaptera novaeangliae	→	↘	↘	↘	↗

1.3 Discussion

The results of the present study revealed some trends in studies addressing distribution models of whales worldwide. In general, whales in breeding grounds tend to be found in shallower waters, close to the coast and with low concentrations of chlorophyll. On the feeding grounds and permanent habitat areas, whales are more likely to be found in deeper areas, far from the coast and with more productive waters. This indicated that animals tend to respond to environmental variables differently depending on the habitat area and maritime zone of the explanatory variables, which can make it difficult to compare and interpret the results.

Although 35 different explanatory variables were recorded, only five of these were used in more than half of the papers analyzed (chlorophyll concentration, depth, distance to the coastline, sea surface temperature and slope). These five variables also appeared the most often with a significant response to the mysticete occurrence.

Sea surface temperature showed a positive relationship with the mysticete occurrence in all habitat areas and maritime zones, except in areas of permanent residence in oceanic zones. The species occurrence in warmer waters may be related to the optimization of energetic costs over the lifetime, as well as increasing growth, reproductive success, and survival rates of offspring, and even decreasing the risk of predation mainly in breeding grounds (Brodie, 1975; Corkeron and Connor, 1999; Rasmussen et al., 2007). In coastal zones of permanent residence, the occurrence of species at lower temperatures may be related to more nutrient-rich waters, reflecting the upwelling, as reported for Bryde's whales in Brazil (Tardin et al., 2017).

Depth showed different responses according to habitat areas. Mysticete occurrence was higher in deeper water in feeding grounds and permanent habitat areas, while the opposite occurred in breeding grounds. Shallow waters are generally associated with more sheltered and safer regions since there may be fewer predators or make it difficult for them to detect calves (e.g., Zeh et al., 2022). The same result was found for distance from the coastline, which is usually correlated with depth due to regional characteristics, with the further from the coastline, the deeper it is (Kowsmann, 2015). Both variables can have a direct relationship with the occurrence of whales and the availability of their prey (Forcada, 2018; Ramírez-León et al., 2021). Studies conducted in the Gulf of Mexico and the Mediterranean Sea, for example, indicate that species with larger body sizes tend to occupy deeper waters (Davis et al., 1998, 2002; Cañadas et al., 2002). Larger areas may promote a greater carrying capacity for predators, as they sustain a larger number of prey (McIntosh et al., 2018). The presence of whales in deeper waters may also be related to the need for space in the water column for the movement of these animals.

Mysticete occurrence was higher in steeper areas. The underwater bottom slope may be associated with greater heterogeneity of habitats, which can lead to greater availability of microhabitats and prey diversity, both in coastal waters, such as near islands, and in oceanic waters, such as the continental shelf break. These animals also have some mechanisms to avoid predators (Nielsen et al., 2019). Steeper regions may cause the sound to disperse less than in flatter regions. Slope can influence other factors, such as current dynamics, primary productivity, and vessel traffic (e.g., Kowsmann, 2015; Thompson et al., 2018).

Chlorophyll concentration positively influenced the mysticete occurrence in feeding grounds and permanent habitat areas. The greater chlorophyll concentration may reflect the primary productivity of the habitat, which may favor the prey occurrence. In breeding grounds, mysticetes occurrence was higher in low chlorophyll sites and may be related to individuals not being focused on feeding at these sites. It may also be related to excessive chlorophyll concentration, as known in eutrophication, which is common where bays and estuaries are present and nearby due to the influence of rivers, and human activities such as sewage outfalls and proximity to urban centers (Malone and Newton, 2020; Castelo et al., 2021).

Publication of papers addressing mysticete distribution models has occurred since 2001, but there has only been a substantial increase in such publications since 2017. Although studies modeling the distribution of terrestrial organisms have been occurring for longer, the use of the tool with marine species has been growing since 2005 (Robinson et al., 2011, 2017; Melo-Merino et al., 2020). Late growth in studies modeling mysticete distribution may be because of the difficulty of studying marine environments due to their three-dimensionality and the lack of data layers in the intermediate depths of the water column (Bentlage et al., 2013). There is also a bias in obtaining presence points, as most of the efforts is focused on coastal regions (Robinson et al., 2011), and true absence points, as mysticetes have a high dispersal capacity and are not always visible on the sea surface.

In addition, most studies comprise ecoregions on the northeast coast of the Pacific and Atlantic Ocean and around New Zealand. As countries located in these regions tend to invest more resources in research and development (Unesco, 2021), the greater number of studies in these ecoregions may reflect a greater research effort. Increased efforts result in initiatives for long-term monitoring, which is crucial in successful actions for biodiversity conservation (Sukhotin and Berger, 2013; Miranda et al., 2020).

Variations in the spatial scale, such as habitat area and maritime zone, may cause the independent explanatory variables to respond differently to the same set of dependent variables (e.g., Witman et al., 2004; Fernandez et al., 2018). Differences in resolution can result in the modifiable areal unit problem, which is characterized as the influence of different sized analysis units on the results of some analyses (Dungan et al., 2002). Considering the spatial scale when interpreting results is crucial to properly represent the dynamic nature of marine ecosystems, especially in the case of highly mobile species (Melo-Merino et al., 2020).

Regression models (GAM and GLM) and machine learning (MaxEnt) were the most common algorithms used by the authors. Regression analyses are among the oldest and most established in ecological studies, and to this day are well accepted in this type of study, mainly because these algorithms are appropriate when the studies require presence and absence data of species, reflecting the large occurrence of studies containing systematized scientific expeditions (Guisan et al., 2002; Austin, 2007). MaxEnt is a relatively new algorithm that has been in use since 2006 and has become very popular because it is robust even with small sample sizes and without the need for absence data (Elith et al., 2006; Phillips et al., 2006; Proosdij et al., 2016). For marine organisms in general, MaxEnt is the most widely used algorithm (Melo-Merino et al., 2020), but it is still not as popular as regression models in studies of mysticetes species.

To select the best model, most studies used the Akaike Information Criterion (AIC), one of the oldest and most popular methods for model selection (Guisan et al., 2017). This selection method allows the scientists to model whales' occurrence as a function of different combinations of oceanographic and explanatory variables. The Area Under the Curve (AUC) of the Receiver Operating Characteristic was the most widely used to evaluate the models, included in more than half of the papers. Problems are reported when using AUC to evaluate the accuracy of SDMs, mainly because the total extent to which the models are run influences the rate of predicted absences (Lobo et al., 2008). Therefore, even if poorly fitted (underestimated or overestimated), a model can still score well (Hosmer et al., 2013). The good score of a model gives a false sense of reliability even if it does not represent reality well, which can cause misinterpretation of the results. A good alternative to evaluate the accuracy of SDMs would be through the TSS (Shabani et al., 2016, 2018), which was only used in 13.2% of the papers analyzed in this study.

Most of the studies used true absence data. In general, most records of mysticetes come from systematic monitoring, which allows the collection of absence and presence data. This systematic monitoring strengthens the ability to model where the species is present or absent, but at the same time makes large-scale distribution studies very difficult. Currently, several modeling techniques do not require true absence data, generating and using pseudo-absences (Barbet-Massin et al., 2012; Guisan et al., 2017). This allows data collected in a non-systematic way, such as whale watching and citizen science, to be used in modeling studies. However, it is important to note that the use of unsystematically collected data needs pre-processing, since the data can be biased spatially and temporally.

In the present study, almost 70% of the reviewed papers presented some metric to assess uncertainty. In a study on best practices in SDMs of marine species, Robinson et al. (2017) reported that 94% of studies did not assess uncertainty. Melo-Merino et al. (2020) also exposed the need to reduce and report errors and uncertainties associated with models. The results obtained in the present study show that there has been a breakthrough regarding the transparency of SDMs with mysticetes through uncertainty assessment and the reporting of associated errors. Uncertainty detection is important for SDMs, particularly for studies that target threatened species and predict changes in their distributions (Robinson et al., 2017). Understanding the relationship between species and the environment allows for identifying and prioritizing biologically important areas, as well as assisting in impact assessment and decision-making (Guisan and Thuiller, 2005; Elith and Leathwick, 2009). Therefore, an incorrect estimate of the organism distribution can directly implicate their conservation (Redfern et al., 2006).

Our study found that the response of whale occurrence to environmental variables varies depending on the spatial characteristics, such as habitat area and maritime zone. It is crucial to consider these factors when interpreting the results, as ignoring them may lead to inaccurate conclusions and inappropriate conservation actions. Therefore, we recommend that future studies on whale ecology and conservation should account for the spatial characteristics of their habitats to ensure that the results are reliable and relevant for management and conservation efforts.

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Supplementary material

Supplementary Table 1 – Description of the explanatory variables used in whale distribution modeling papers subdivided by their corresponding groups.

Group	Variable	Description
Physiographic	Aspect	Direction of the angle in degrees relative to North
	Benthic sediment disturbance	Benthic sediment disturbance from wave action
	Depth	Sea surface height relative to the Earth's geoid in meters
	Distance to coast	Shortest distance to the coastline in meters
	Distance to currents	Shortest distance to the nearest ocean current in meters
	Distance to ice	Shortest distance to the nearest ice layer in meters
	Distance to islands	Shortest distance to the nearest island in meters
	Distance to isobaths	Shortest distance to 200, 1000, and 2000 meters isobaths
	Distance to reefs	Shortest distance to the nearest coral reef in meters
	Distance to shelf break	Shortest distance to the nearest shelf break in meters
	Habitat complexity	Rate of change of slope in a given habitat
	Slope	Underwater bottom slope in degrees
	Stratification	Density difference between the surface and a depth
Oceanographic	Chlorophyll	Chlorophyll concentration in mg/m3 (minimum, mean, maximum and range)
	Current	Current speed in m/s
	Dissolved organic matter	Dissolved organic matter concentration in g.m-3
	Euphotic zone	Euphotic zone depth in meters
	Ice	Ice concentration in %
	Photosynthetically active radiation	Photosynthetically active radiation in Einstein/m²/day

	Prey biomass	Prey biomass in g/m3
	Primary productivity	Dissolved organic matter concentration in mgC.m.2/day
	Sea surface height	Sea surface height in meters
	Sea surface salinity	Sea surface salinity in ppt (mean and range)
	Sea surface temperature	Sea surface temperature in °C (minimum, mean, maximum and range)
	Thermocline depth	Lower thermocline depth in meters
	Turbidity	Suspended organic matter in g.m-3
	Upwelling	Upwelling index m.s-1
	Wind speed	Wind speed in m/s
Anthropic	Distance to anchoring areas	Distance to anchoring areas in meters
	Distance to dive boat routes	Distance to dive boat routes in meters
	Distance to fishing boat routes	Distance to fishing boat routes in meters
	Distance to fishing grounds	Distance to fishing areas in meters
	Distance to port complexes	Distance to port complexes in meters
	Distance to marine outfall	Distance to marine outfalls in meters
	Distance to tourist boat routes	Distance to tourist boat routes in meters

Supplementary Table 2 – Explanatory variables subdivided by their respective groups, the frequency that each was used (Total) and significant (Sig.) relative to the total number of papers analyzed, and the frequency and direction of significance relative to the number of models in which the respective variable was significant in explaining the occurrence of whales. Positive (Pos.), negative (Neg.), and unidentified (U/I) relations.

Group	Variable	Total	Sig.	Pos.	Neg.	U/I
Physiographic	Depth	85.3	62.6	45.2	38.7	16.1
	Distance to coast	57.8	46.3	22.6	48.4	29.0
	Slope	53.4	41.9	57.7	15.4	26.9
	Stratification	15.5	50.0	66.7	11.1	22.2
	Distance to shelf break	13.8	25.0	0.0	75.0	25.0
	Aspect	8.6	0.0	0.0	0.0	0.0
	Distance to currents	8.6	80.0	12.5	75.0	12.5
	Benthic sediment disturbance	7.8	0.0	0.0	0.0	0.0
	Distance to ice	6.0	57.1	25.0	75.0	0.0
	Distance to isobaths	6.0	28.6	0.0	50.0	50.0
	Habitat complexity	1.7	50.0	0.0	0.0	100.0
	Distance to islands	0.9	100.0	100.0	0.0	0.0
	Distance to reefs	0.9	100.0	0.0	0.0	100.0
Oceanographic	Sea surface temperature	92.2	62.6	35.8	46.3	17.9
	Chlorophyll	49.1	43.9	40.0	44.0	16.0
	Sea surface salinity	19.0	45.5	60.0	10.0	30.0
	Primary productivity	15.5	61.1	63.6	36.4	0.0
	Sea surface height	14.7	70.6	8.3	66.7	25.0
	Current	12.9	73.3	27.3	63.6	9.1
	Wind speed	10.3	75.0	11.1	77.8	11.1
	Prey biomass	9.5	72.7	75.0	25.0	0.0
	Photosynthetically active radiation	7.8	0.0	0.0	0.0	0.0
	Dissolved organic matter	6.0	28.6	0.0	0.0	100.0
	Turbidity	6.0	14.3	0.0	0.0	100.0
	Ice	5.2	66.7	75.0	25.0	0.0
	Upwelling	2.6	66.7	100.0	0.0	0.0
	Thermocline depth	1.7	100.0	0.0	100.0	0.0
	Euphotic zone	1.7	0.0	0.0	0.0	0.0
Anthropic	Distance to fishing grounds	2.6	33.3	0.0	100.0	0.0
	Distance to anchoring areas	0.9	100.0	0.0	100.0	0.0
	Distance to port complexes	0.9	100.0	0.0	100.0	0.0
	Distance to marine outfall	0.9	0.0	0.0	0.0	0.0

Distance to dive boat routes	0.9	0.0	0.0	0.0	0.0
Distance to tourist boat routes	0.9	0.0	0.0	0.0	0.0

Supplementary Table 3 – Frequency and direction of the importance of the main explanatory variables in relation to habitat area (breeding, feeding, or permanent) and maritime zone (coastal or oceanic) to explain mysticete occurrence. Positive (+) and negative (-) relations.

Habitat area	**Breeding**				**Feeding**				**Permanent**			
Maritime zone	**Coastal**		**Oceanic**		**Coastal**		**Oceanic**		**Coastal**		**Oceanic**	
Variable relation	**(+)**	**(-)**	**(+)**	**(-)**	**(+)**	**(-)**	**(+)**	**(-)**	**(+)**	**(-)**	**(+)**	**(-)**
Chlorophyll	0.0	100.0	NA	NA	50.0	50.0	100.0	0.0	100.0	0.0	100.0	0.0
Depth	25.0	75.0	0.0	100.0	100.0	0.0	52.9	47.1	52.9	47.1	100.0	0.0
Distance to coast	33.3	66.7	0.0	100.0	75.0	25.0	80.0	20.0	80.0	20.0	NA	NA
Sea surface temperature	100.0	0.0	NA	NA	66.7	33.3	56.3	43.8	56.3	43.8	33.3	66.7
Slope	NA	NA	100.0	0.0	80.0	20.0	87.5	12.5	87.5	12.5	NA	NA

Supplementary Table 4 – Significant explanatory variables to explain the occurrence of the common minke whale, *Balaenoptera acutorostrata*. Positive (Pos.), negative (Neg.), and unidentified (U/I) relations.

Variable	**Total (%)**	**Pos. (%)**	**Neg. (%)**	**U/I (%)**
Depth	66.7	33.3	16.7	16.7
Sea surface temperature	58.3	25.0	33.3	0.0
Slope	33.3	16.7	16.7	0.0
Distance to the coast	25.0	8.3	8.3	8.3
Primary productivity	16.7	0.0	16.7	0.0
Chlorophyll	16.7	0.0	8.3	8.3
Distance to currents	8.3	0.0	8.3	0.0
Prey biomass	8.3	8.3	0.0	0.0
Ice	8.3	8.3	0.0	0.0
Habitat complexity	8.3	0.0	0.0	8.3
Dissolved organic matter	8.3	0.0	0.0	8.3
Turbidity	8.3	0.0	0.0	8.3

Supplementary Table 5 – Significant explanatory variables to explain the occurrence of the Antarctic minke whale, *Balaenoptera bonaerensis*. Positive (Pos.), negative (Neg.), and unidentified (U/I) relations.

Variable	**Total (%)**	**Pos. (%)**	**Neg. (%)**	**U/I (%)**
Depth	50.0	16.7	33.3	0.0
Sea surface temperature	50.0	33.3	16.7	0.0
Primary productivity	33.3	0.0	33.3	0.0
Distance to coast	16.7	0.0	16.7	0.0
Habitat complexity	16.7	0.0	0.0	16.7

Supplementary Table 6 – Significant explanatory variables to explain the occurrence of the sei whale, *Balaenoptera borealis*. Positive (Pos.), negative (Neg.), and unidentified (U/I) relations.

Variable	**Total (%)**	**Pos. (%)**	**Neg. (%)**	**U/I (%)**
Sea surface temperature	57.1	21.4	21.4	14.3
Depth	42.9	21.4	7.1	14.3
Primary productivity	21.4	14.3	7.1	0.0
Slope	21.4	7.1	0.0	14.3
Distance to coast	14.3	7.1	0.0	7.1
Sea surface height	7.1	0.0	7.1	0.0
Chlorophyll	7.1	7.1	0.0	0.0
Distance to currents	7.1	0.0	7.1	0.0
Ice	7.1	7.1	0.0	0.0
Habitat complexity	7.1	0.0	0.0	7.1
Turbidity	7.1	0.0	0.0	7.1

Supplementary Table 7 – Significant explanatory variables to explain the occurrence of the Bryde's whale, *Balaenoptera edeni*. Positive (Pos.), negative (Neg.), and unidentified (U/I) relations.

Variable	**Total (%)**	**Pos. (%)**	**Neg. (%)**	**U/I (%)**
Sea surface temperature	53.8	15.4	23.1	15.4
Depth	38.5	23.1	0.0	15.4
Chlorophyll	30.8	30.8	0.0	0.0
Distance to coast	23.1	0.0	7.7	15.4
Sea surface salinity	23.1	0.0	0.0	23.1
Stratification	15.4	15.4	0.0	0.0
Slope	15.4	0.0	0.0	15.4
Sea surface height	7.7	0.0	7.7	0.0
Distance to anchoring areas	7.7	0.0	7.7	0.0
Distance to fishing grounds	7.7	0.0	7.7	0.0
Distance to islands	7.7	7.7	0.0	0.0
Wind speed	7.7	0.0	7.7	0.0
Habitat complexity	7.7	0.0	0.0	7.7
Turbidity	7.7	0.0	0.0	7.7

Supplementary Table 8 – Significant explanatory variables to explain the occurrence of the blue whale, *Balaenoptera musculus*. Positive (Pos.), negative (Neg.), and unidentified (U/I) relations.

Variable	**Total (%)**	**Pos. (%)**	**Neg. (%)**	**U/I (%)**
Sea surface temperature	57.9	10.5	36.8	10.5
Sea surface height	36.8	5.3	26.3	5.3
Depth	36.8	10.5	15.8	10.5
Chlorophyll	31.6	10.5	15.8	5.3
Wind speed	26.3	5.3	21.1	0.0
Distance to coast	26.3	5.3	10.5	10.5
Distance to shelf break	21.1	0.0	15.8	5.3
Sea surface salinity	15.8	15.8	0.0	0.0
Slope	15.8	10.5	0.0	5.3
Stratification	10.5	10.5	0.0	0.0
Distance to currents	5.3	0.0	5.3	0.0
Primary productivity	5.3	5.3	0.0	0.0
Upwelling	5.3	5.3	0.0	0.0
Distance to isobaths	5.3	0.0	0.0	5.3

Supplementary Table 9 – Significant explanatory variables to explain the occurrence of the bowhead whale, *Balaena mysticetus*. Positive (Pos.), negative (Neg.), and unidentified (U/I) relations.

Variable	**Total (%)**	**Pos. (%)**	**Neg. (%)**	**U/I (%)**
Sea surface temperature	100.0	75.0	25.0	0.0
Distance to ice	75.0	25.0	50.0	0.0
Distance to currents	50.0	25.0	25.0	0.0
Depth	50.0	0.0	50.0	0.0
Chlorophyll	25.0	25.0	0.0	0.0
Slope	25.0	25.0	0.0	0.0
Distance to coast	25.0	0.0	25.0	0.0
Ice	25.0	0.0	25.0	0.0
Prey biomass	25.0	0.0	25.0	0.0

Supplementary Table 10 – Significant explanatory variables to explain the occurrence of the fin whale, *Balaenoptera physalus*. Positive (Pos.), negative (Neg.), and unidentified (U/I) relations.

Variable	**Total (%)**	**Pos. (%)**	**Neg. (%)**	**U/I (%)**
Depth	62.5	41.7	8.3	12.5
Sea surface temperature	58.3	20.8	20.8	16.7
Chlorophyll	29.2	4.2	16.7	8.3
Slope	20.8	20.8	0.0	0.0
Primary productivity	20.8	16.7	4.2	0.0
Prey biomass	12.5	8.3	4.2	0.0
Current	12.5	8.3	4.2	0.0
Distance to coast	8.3	8.3	0.0	0.0
Sea surface height	8.3	0.0	4.2	4.2
Distance to isobaths	4.2	0.0	4.2	0.0
Stratification	4.2	4.2	0.0	0.0
Ice	4.2	4.2	0.0	0.0
Thermocline depth	4.2	0.0	4.2	0.0
Sea surface salinity	4.2	4.2	0.0	0.0
Wind speed	4.2	0.0	4.2	0.0
Habitat complexity	4.2	0.0	0.0	4.2
Distance to currents	4.2	0.0	0.0	4.2
Dissolved organic matter	4.2	0.0	0.0	4.2
Turbidity	4.2	0.0	0.0	4.2

Supplementary Table 11 – Significant explanatory variables to explain the occurrence of the Southern right whale, *Eubalaena australis*. Positive (Pos.), negative (Neg.), and unidentified (U/I) relations.

Variable	**Total (%)**	**Pos. (%)**	**Neg. (%)**	**U/I (%)**
Depth	50.0	16.7	33.3	0.0
Slope	50.0	16.7	16.7	16.7
Sea surface temperature	50.0	16.7	16.7	16.7
Chlorophyll	33.3	16.7	16.7	0.0
Distance to coast	33.3	0.0	33.3	0.0
Sea surface height	16.7	0.0	16.7	0.0
Distance to current	16.7	0.0	16.7	0.0
Stratification	16.7	0.0	16.7	0.0

Supplementary Table 12 – Significant explanatory variables to explain the occurrence of the North Atlantic right whale, *Eubalaena glacialis*. Positive (Pos.), negative (Neg.), and unidentified (U/I) relations.

Variable	**Total (%)**	**Pos. (%)**	**Neg. (%)**	**U/I (%)**
Sea surface temperature	80.0	40.0	40.0	0.0
Depth	60.0	0.0	60.0	0.0
Distance to coast	40.0	0.0	40.0	0.0
Chlorophyll	20.0	0.0	20.0	0.0
Wind speed	20.0	0.0	20.0	0.0

Supplementary Table 13 – Significant explanatory variables to explain the occurrence of the North Pacific right whale, *Eubalaena japonica*. Positive (Pos.), negative (Neg.), and unidentified (U/I) relations.

Variable	**Total (%)**	**Pos. (%)**	**Neg. (%)**	**U/I (%)**
Depth	100.0	100.0	0.0	0.0
Sea surface temperature	100.0	0.0	100.0	0.0

Supplementary Table 14 – Significant explanatory variables to explain the occurrence of the humpback whale, *Megaptera novaeangliae*. Positive (Pos.), negative (Neg.), and unidentified (U/I) relations.

Variable	**Total (%)**	**Pos. (%)**	**Neg. (%)**	**U/I (%)**
Depth	60.9	17.4	39.1	4.3
Distance to coast	43.5	13.0	26.1	4.3
Sea surface temperature	39.1	13.0	21.7	4.3
Slope	21.7	13.0	4.3	4.3
Prey biomass	13.0	13.0	0.0	0.0
Sea surface salinity	13.0	8.7	4.3	0.0
Stratification	13.0	4.3	0.0	8.7
Chlorophyll	8.7	4.3	4.3	0.0
Upwelling	4.3	4.3	0.0	0.0
Distance to port complexes	4.3	0.0	4.3	0.0
Thermocline depth	4.3	0.0	4.3	0.0
Sea surface height	4.3	0.0	4.3	0.0
Wind speed	4.3	0.0	0.0	4.3
Distance to ice	4.3	0.0	0.0	4.3
Distance to reefs	4.3	0.0	0.0	4.3

2 UNVEILING THE EXPOSURE OF BRYDE'S WHALES AND BOTTLENOSE DOLPHINS TO CUMULATIVE HUMAN ACTIVITIES IN COASTAL AND MARINE SEAS

Abstract: Human activities have led to the accumulation of environmental impacts, posing a significant threat to biodiversity in marine ecosystems. The establishment of marine protected areas (MPAs) has emerged as a crucial tool to address these challenges. This study aimed to identify priority areas for the conservation of Bryde's whales (*Balaenoptera brydei*) and bottlenose dolphins (*Tursiops truncatus*) along the Brazilian coast, considering their exposure to cumulative human activities and the overlap with existing MPAs. Using suitability modeling, we ran models for each species to identify suitable areas for them. As explanatory variables, we chose current velocity, depth, primary productivity, sea surface salinity, sea surface temperature, and seabed slope. The results showed that the most suitable areas for Bryde's whales and bottlenose dolphins are primarily located in Southeastern Brazil, which also exhibits a higher number of human activities. Shallower waters, characterized by higher primary productivity and nutrient richness, were found to be more suitable for both species. The Southeastern region also harbors the largest number of highly and fully protected MPAs, although many of them are in coastal regions and do not encompass oceanic areas with high exposure to cumulative human activities. Given the economic significance of the Southeastern region and the increasing human activities, it is crucial to prioritize conservation efforts and implement mitigation measures to reduce conflicts between biodiversity conservation and human activities. The findings of this study provide valuable insights into the management and conservation of Bryde's whales and bottlenose dolphins in Brazil's waters.
Keywords: Human activities. Environmental conflicts. Public policies. Atlantic Ocean. Species Distribution Modeling.

Resumo: As atividades humanas têm levado ao acúmulo de impactos ambientais, representando uma ameaça significativa à biodiversidade nos ecossistemas marinhos. O estabelecimento de Áreas Marinhas Protegidas (AMPs) tem se mostrado uma ferramenta crucial para enfrentar esses desafios. Este estudo teve como objetivo identificar áreas prioritárias para a conservação de baleias-de-bryde (*Balaenoptera brydei*) e golfinhos-nariz-de-garrafa (*Tursiops truncatus*) ao longo da costa brasileira, considerando sua exposição às atividades humanas cumulativas e a sobreposição com as AMPs existentes. Utilizando a modelagem de adequabilidade, executamos 180 modelos para cada espécie a fim de

identificar áreas adequadas para elas. Como variáveis explanatórias, escolhemos velocidade da corrente, profundidade, produtividade primária, salinidade superficial do mar, temperatura superficial do mar e declive do relevo submarino. Os resultados mostraram que as áreas mais adequadas para baleias-de-bryde e golfinhos-nariz-de-garrafa estão principalmente localizadas no Sudeste do Brasil, região que também apresenta um maior número de atividades humanas. Águas mais rasas, caracterizadas por maior produtividade primária e riqueza de nutrientes, foram consideradas mais adequadas para ambas as espécies. A região Sudeste abriga o maior número de AMPs altamente e totalmente protegidas, embora muitas delas estejam em regiões costeiras e não abranjam áreas oceânicas com alta exposição às atividades humanas cumulativas. Dada a importância econômica da região Sudeste e o aumento das atividades humanas, é crucial priorizar esforços de conservação e implementar medidas de mitigação para reduzir conflitos entre a conservação da biodiversidade e as atividades humanas. Os resultados deste estudo fornecem informações valiosas para o manejo e a conservação de baleias-de-bryde e golfinhos-nariz-de-garrafa no mar territorial do Brasil.
Palavras-chave: Atividades humanas. Conflitos ambientais. Políticas públicas. Oceano Atlântico. Modelagem de Distribuição de Espécies.

Introduction

Multiple institutions and researchers have been expressing their concern about the cumulative human activities (IPBES, 2019; IPCC, 2023). Human activities continue to increase at an alarming rate, resulting in the accumulation of environmental impacts (Halpern et al., 2015). These cumulative human activities pose a significant threat to biodiversity across various taxonomic groups, such as fragmentation, change and loss of habitat, and increase in contaminant levels, which can cause even loss of species (Buschke & Vanschoenwinkel, 2014; Halpern et al., 2019; Su et al., 2021). In marine ecosystems this is evident, where many activities, such as vessel traffic, oil and gas exploration, and overfishing, contribute to the degradation of habitats and ecosystems (Cordes et al., 2016). To address these challenges and mitigate conflicts, the establishment of protected areas has emerged as a crucial tool (Kriegl et al., 2021; Rechciński et al., 2019).

Marine protected areas (MPAs) encompass a range of conservation levels and strategies, ranging from sustainable use to complete preservation. Despite progress, it was recently shown that most countries only partially met the Aichi Biodiversity Target of safeguarding at least 10% of marine and coastal areas (CBD, 2020). At the same time, studies have been indicating that several MPAs are neither effective nor representative for protecting marine biodiversity (Rodríguez-Rodríguez & Martínez-Vega J., 2022). In 2018, Brazil made significant progress toward achieving this goal by announcing the creation of two large offshore MPAs, increasing from 1.5% to the proposed 25%, seemingly meeting the conservation target. However, the effectiveness of Brazilian MPAs in conserving biodiversity is a subject of ongoing debate (Magris & Pressey, 2018), as their location may not always align with the most critical areas for species conservation.

To gain insights into identifying suitable areas for conservation, Species Distribution Modeling (SDM) has become an increasingly utilized approach (Melo-Merino et al., 2020; L. M. Robinson et al., 2011). This tool uses occurrence data, including species presence, absence, and pseudo-absence, to predict the most suitable areas for species' occurrence (Guisan et al., 2017). However, applying SDM in marine environments presents unique challenges compared to terrestrial systems. In addition to the high mobility of marine species, marine environments have a complex and dynamic environment, with many factors that can influence the behavior and distribution of marine species, such as ocean currents, temperature, salinity, and the absence of physical barriers (Libralato et al., 2015; Seebens et al., 2016).

Bottlenose dolphin (*Tursiops truncatus*) is a widespread delphinid living in tropical and temperate waters and displaying plastic behavior throughout its distribution. Its cosmopolitan nature exposes it to human pressures from different sources, rendering it as a good candidate to evaluate the impacts of cumulative human activities on its distribution. In Brazil, the species is not usually resident and can travel long distances along coastal and oceanic waters looking for areas to feed and breed (Lodi et al., 2017). In Southeastern Brazil, this dolphin is found nearshore and at port regions, which renders it particularly susceptible to the impacts of diverse human activities (Maricato et al., 2022). The dolphins' preference for these coastal areas intensifies their exposure to anthropogenic stressors, underscoring the need for targeted conservation efforts in these vulnerable habitats.

Bryde's whale (*Balaenoptera edeni*) is a poorly known baleen whale and one that does not engage in long-distance latitudinal migration. For that reason, it is exposed year-round to both coastal and offshore cumulative human activities, unlike many migratory whales. Recent studies have shed light on the morphological and genetic distinctiveness of the population of this whale inhabiting the Brazilian coast (Pastene et al., 2015; Wada et al., 2003), giving rise to a scientific discussion on whether this population should be recognized as a different species, *Balaenoptera brydei* (Wada et al., 2003). For this reason, we have decided to refer to

B. brydei hereafter. Despite not engaging in migrations, Bryde’s whales exhibit latitudinal movements and habitat shifts during the warm and cold seasons (Dalpaz et al., 2023), exposing them to multiple anthropogenic activities across their range.

Whales and dolphins provide important ecosystem services, such as ocean fertilization, carbon sequestration, and recreational activities, and their conservation can benefit the conservation of many other species (Hazen et al., 2019; Kiszka et al., 2022). Because of the extensive home range of cetaceans, many MPAs may not be effective for their conservation (Hooker et al., 2011; Tardin et al., 2020). Since human activities and their impacts are increasing, the present study goal was to evaluate species’ exposure to cumulative human activities and the overlap of these areas with existing MPAs along the Brazilian coast. The presence of upwelling and the influence of the South Atlantic Central Waters make the Southeastern coast one of the most productive areas (Coelho-Souza et al., 2012; Palma & Matano, 2009). Simultaneously, the region hosts the largest and most urbanized cities in the country, where the oceanic basins around congregate multiple pressures, such as intense vessel traffic and oil and gas activities (ANP, 2023). Therefore, we hypothesize that both species’ degree of human activities exposure will be higher in Southeastern Brazil, both in coastal and marine waters, than in other regions.

2.1 Methods

2.1.1 Study area

The Brazilian coastline, located in the Southwestern Atlantic Ocean, is one of the largest in the world. The Brazilian Exclusive Economic Zone covers approximately 4.5 million km². Among these, 25% are protected areas through a total of 211 partially or exclusively marine protected areas (MPAs). The MPA protection level ranges from Ia to IV (according to IUCN categories), and they are managed at various administrative levels, from municipal to federal (MMA, 2023).

Brazil is a major player in the oil and gas industry, harboring two important sedimentary basins for exploration: Campos Basin and Santos Basin. In 2022, Brazil produced over 3 million oil and gas barrels per day (ANP, 2023). These activities are linked to vessel traffic, underwater noise, and the risk of spills (Cordes et al., 2016). Additionally, Brazil engages in multiple fishing activities, including artisanal and industrial fishing, which can result in overfishing and bycatch (Drakopulos et al., 2023; Hamilton & Baker, 2019). In Santos Basin, which is the only region with systematic fishing effort monitoring, over 110,000 tons of fish were extracted in the first half of 2022 (PMAP-BS, 2022).

2.1.2 Data collection

Occurrence data of the target species were obtained from multiple sources, including public databases, scientific papers, and collaborative projects (Supplementary Table 1). The explanatory variables used in the habitat suitability models were the average values of current velocity, depth, primary productivity, sea surface salinity, sea surface temperature, and seabed slope. All variables were obtained from Bio-ORACLE at a resolution of 5 arcminutes (Assis et al., 2017), except for slope, which was obtained from MARSPEC at a resolution of 30 arcseconds (Sbrocco & Barber, 2013).

2.1.3 Data analyzes

2.1.3.1 Habitat suitability modeling

We conducted the modeling analysis in the R environment (R Core Team, 2023) using the biomod2 package (Thuiller et al., 2023). To calibrate the models, we considered the entire IUCN range map and restricted it to the Atlantic Ocean, as there is evidence of significant genetic structure differences between Bryde’s whale populations in the Atlantic and Pacific oceans, suggesting limited movement between these two oceans (Pastene et al., 2015). The same is likely to be true for bottlenose dolphins. We also restricted the modeled area to Brazil’s boundaries.

We standardized the resolution of all explanatory variables to 5 arcminutes and checked for multicollinearity using the usdm package (Naimi et al., 2014). To avoid spatial autocorrelation, we randomly filtered occurrence data within a 100 km radius using the spThin package (Aiello-Lammens et al., 2015), ensuring that there was no more than one occurrence point within the same radius. The distance was defined based on the target species' mobility capacity to ensure record independence.

As true absence points could not be obtained, we generated three sets of pseudo-absences with three times the number of occurrences after the filtering process (Barbet-Massin et al. 2012). We used an environmental stratified strategy to generate pseudo-absences at a minimum distance of 100 km from each other or from an occurrence point.

We used modeling algorithms of two types: presence-absence using regression (Generalized Linear Model - GLM and Generalized Additive Model - GAM), boosting (Random Forest - RF and Generalized Boosting Model - GBM), and discriminant technique (Flexible Discriminant Analysis - FDA); and presence-background using Maximum Entropy - MaxEnt (see Guisan et al., 2017 for more details). To calibrate the models, each algorithm was run ten times using 80% of the records for training and 20% for testing (Guisan et al., 2017).

The performance of the models was evaluated using the True Skill Statistic (TSS). TSS is a simple and intuitive metric that evaluates the model performance based on the values of sensitivity (true presence rate), specificity (true absence rate), commission (presence where it should be absence), and omission (absence where it should be presence) (Allouche et al., 2006). After evaluating the model performance, an ensemble model was made calculating weighted mean values for all models with TSS > 0.7, as models with performance above this threshold are considered good (Araújo & New, 2007; Guisan et al., 2017). Finally, we calculated the importance of variables, which is estimated by randomly permuting one predictor variable at a time, and generated response curves (Guisan et al., 2017).

2.1.3.2 Marine Protected Areas

The listing of MPAs was obtained from The National Registry of Conservation Units (CNUC) of the Brazilian government (MMA, 2023). The categorization of the MPAs followed the MPA Guide, a science-driven framework that helps to clarify the definition of "protection" and likely MPA outcomes (Grorud-Colvert et al., 2021). It categorizes MPAs by stage of establishment and level of protection, specifies the resulting direct and indirect outcomes for biodiversity and human well-being, and describes the key conditions necessary for positive outcomes (Figure 1). The MPA Guide is intended to aid the design, evaluation, and tracking of MPAs to achieve conservation goals. It can be used by scientists, managers, policymakers, and communities to improve the effective design, implementation, assessment, and tracking of existing and future MPAs.

Therefore, we inserted all Brazilian MPAs into the MPA Guide. The data for each MPA required for inclusion in the MPA Guide were primarily obtained from official documents such as the creation decree and management plan, and secondarily from unofficial databases that were confirmed by experts through a screening and validation process. MPAs could be ranked on a scale from most to least protective: Fully Protected, Highly Protected, Lightly Protected, Minimally Protected, and Incompatible with the conservation of nature. More details about the categories are in Figure 1 and Grorud-Colvert et al. (2021).

Figure 1 – Marine Protected Areas (MPAs) level of protection system based on the maximum allowed impact of seven potential activities into each MPA. Source: Grorud-Colvert et al. (2021).

2.1.3.3 Cumulative human activities

In ArcGIS Pro v3.1.1, we created the cumulative human activities layer by overlaying seven variables: port complexes (2 km radius) (ANTAQ, 2023), exploration blocks and production fields from the oil and gas industry (ANP, 2023), and vessel traffic from fishing, commercial, leisure, and oil and gas activities (Cerdeiro et al., 2020). We used binary values, i.e., presence or absence of the activity. For the layers of port complexes, exploration blocks, and production fields, the absence of activity was represented as 0, while the presence was represented as 1. For the vessel traffic layers, which were not binary, the absence of traffic was considered 0, while any other value different from 0 was considered 1 (presence of traffic, regardless of density).

2.1.3.4 Exposure index

To overlay the layers and create the exposure index (EI), we utilized the Reclassify and Raster to Polygon ArcGIS Pro tools to convert raster layers into shapefiles. Subsequently, we employed the Union tool to merge all the layers. We calculated the exposure index using the formula:

$$EI = \text{habitat suitability} \times \text{cumulative human activities} \times \text{MPA category}$$

Habitat suitability was standardized from 0 to 1, where the lowest value (0) was represented by itself, and the highest value (1000) was 1. The same was used for cumulative human activities, where the overlapping human activities values from 0 to 7 were standardized between 0 and 1. Finally, the MPA category was also standardized, where the most restrictive category (Fully Protected) was the lowest exposure value (0), and the least restrictive one (Incompatible) as the highest value (1).

2.1.4 Caveats

We note two caveats about the present study. One was the limitation to quantify the intensity of some human activities layers, and a consequent use of binary values in order to standardize the values of all layers. Although binary values are commonly used, we lost the refinement of some layers when transforming them from continuous to binary. A second point was the unequal effort in the sampling of species occurrence data in Brazil. Although the method utilized in this study minimizes effort issues by spatial rarefaction and the results matched with what we expected, Northern and Northeastern Brazil have less effort in oceanic waters than Southern and Southeastern Brazil.

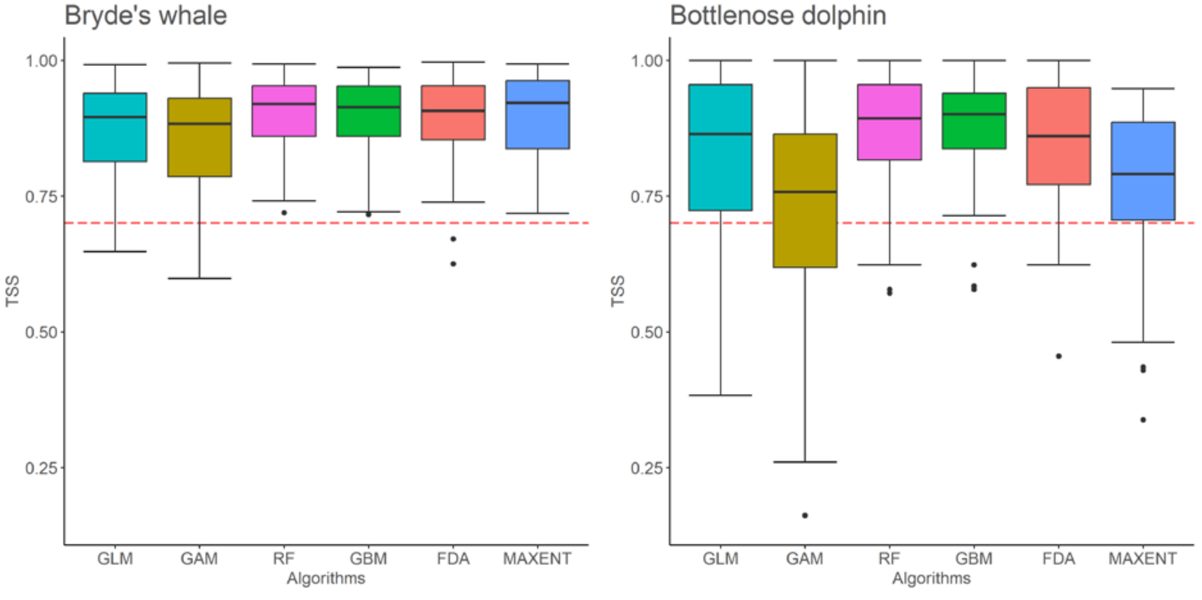
2.2 Results

2.2.1 Habitat suitability modeling

The filtering technique resulted in the retention of 485 occurrence records for bottlenose dolphins out of a total of 115,273, and 72 records for Bryde's whale out of 5,752. No issues were detected in the assessment for multicollinearity and all six explanatory variables were included.

In the ensemble models, we included only individual models with a TSS value > 0.7 out of a total 180 models (three sets of pseudo-absences * six algorithms * ten runs). For the bottlenose dolphin ensemble model, 122 models were selected, while 170 models were selected for the Bryde's whale one. In general, the boosting algorithms exhibited better performance, whereas the GAM showed the lowest average for both ensemble models (Figure 2).

Figure 2 – True Skill Statistic (TSS) validation values of each algorithm for the validation of Bryde's whale, *Balaenoptera brydei*, (left) and bottlenose dolphin, *Tursiops truncatus*, (right) habitat suitability models in the Atlantic Ocean. The red dashed line indicates the TSS threshold = 0.7. Dots are outliers.



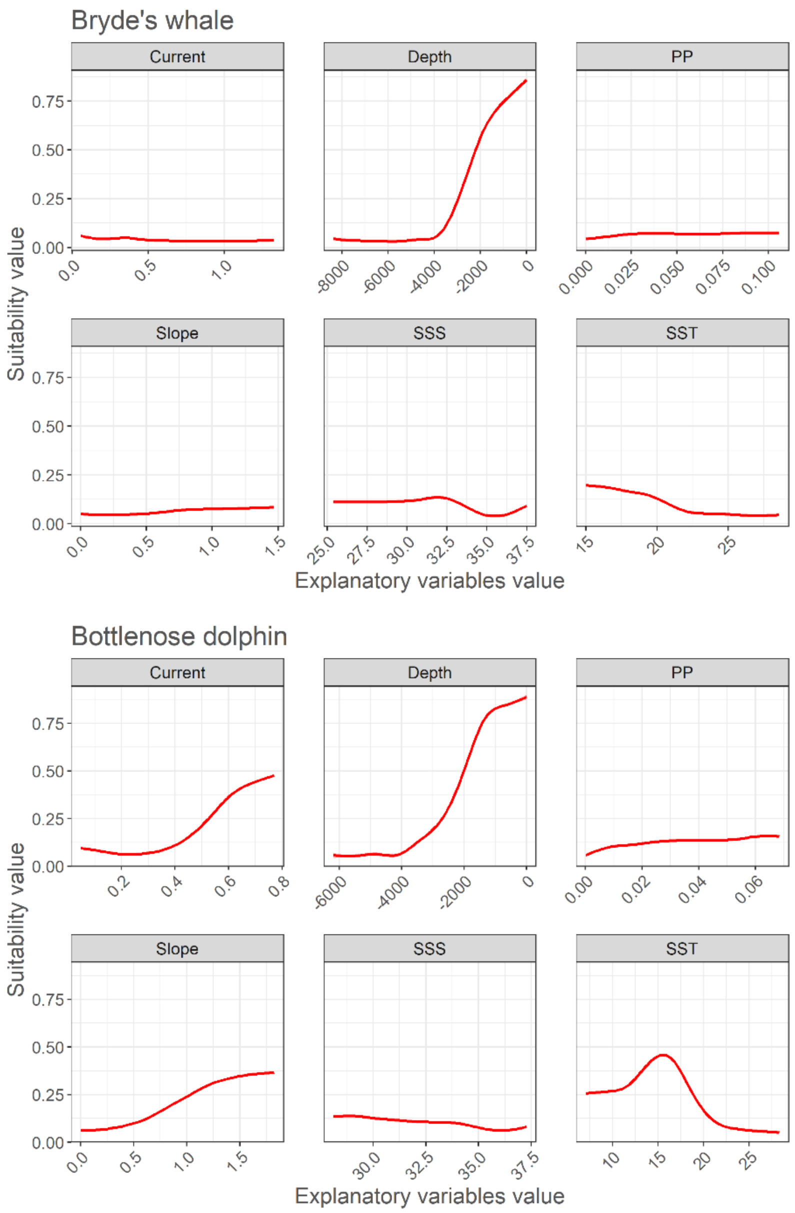
Depth was the most important variable in explaining the habitat suitability of both Bryde's whale and bottlenose dolphin. Temperature was also important in explaining the most suitable areas for bottlenose dolphins (Table 1). Overall, the most suitable areas for Bryde's whales and bottlenose dolphins were characterized by shallower depths (up to 1,000 meters).

Additionally, for bottlenose dolphins, higher suitability is observed in regions with greater current velocity, steeper slopes, and temperatures around 15ºC, while no clear trend was observed for Bryde's whale (Figure 3). Maps of the explanatory variables can be found in Supplementary Figures 1 and 2.

Table 1 – Importance of explanatory variables in explaining the habitat suitability of Bryde's whales, *Balaenoptera brydei*, and bottlenose dolphins, *Tursiops truncatus*, in the Atlantic Ocean. Values in bold represent the highest ones.

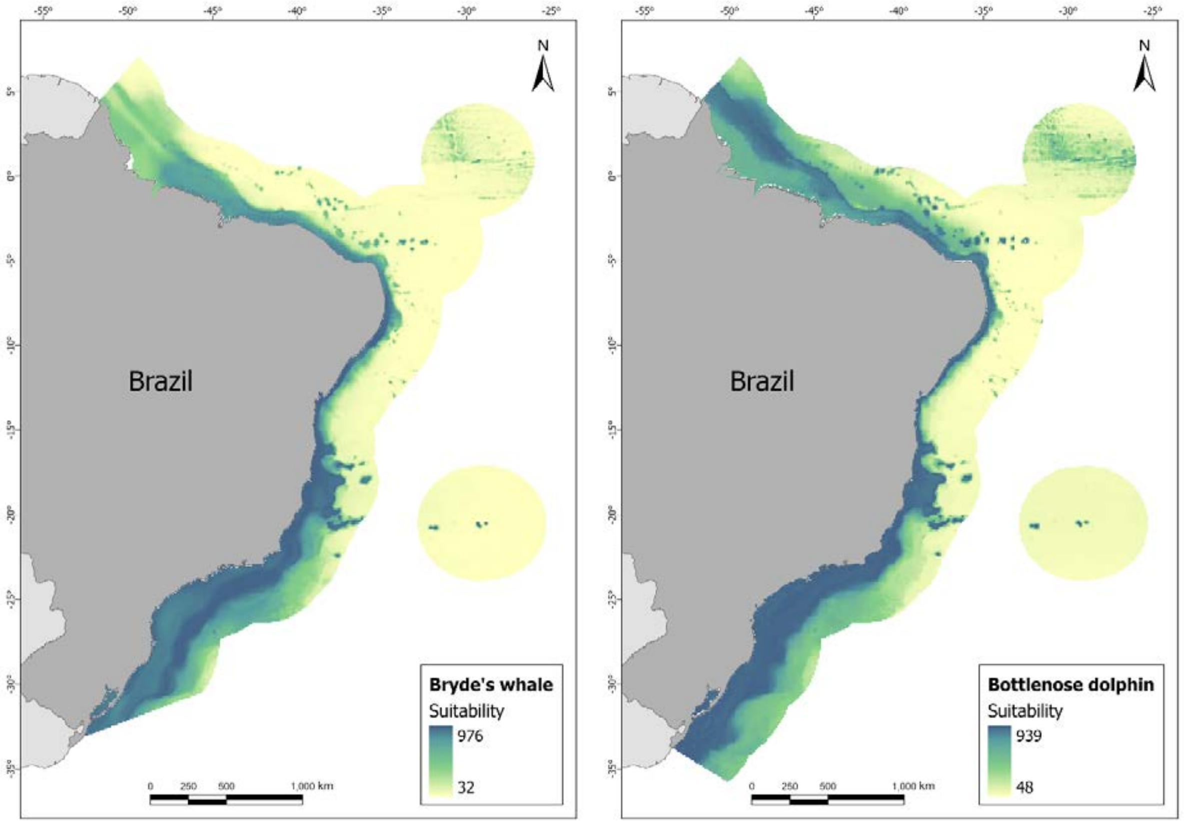
Explanatory variable	**Bryde's whale**	**Bottlenose dolphin**
Current velocity	0.01	0.04
Depth	**0.95**	**0.70**
Primary productivity	0.00	0.01
Sea surface salinity	0.02	0.00
Sea surface temperature	0.02	0.17
Seabed slope	0.00	0.03

Figure 3 – Response curves of the ensemble habitat suitability model for Bryde's whale, *Balaenoptera brydei*, (top) and bottlenose dolphin, *Tursiops truncatus*, (bottom), considering weighted mean, in the Atlantic Ocean.



The continental shelf break in Southern and Southeastern Brazil was suitable for both species, as well as coastal areas in the Northeast. Bottlenose dolphin habitat was also suitable in coastal waters in the South and Southeast. In the North, there was no suitability in coastal waters, but more offshore waters were suitable for bottlenose dolphins (Figure 4). Following the standard protocol for reporting SDM proposed by Zurell et al. (2020), we presented the habitat suitability models for the calibration area, the binary maps with occurrence data and the uncertainty maps in Supplementary Figures 3 to 8.

Figure 4 – Habitat suitability of Bryde’s whale, *Balaenoptera brydei*, (left) and bottlenose dolphin, *Tursiops truncatus*, (right) in Brazil.



2.2.2 Marine Protected Areas

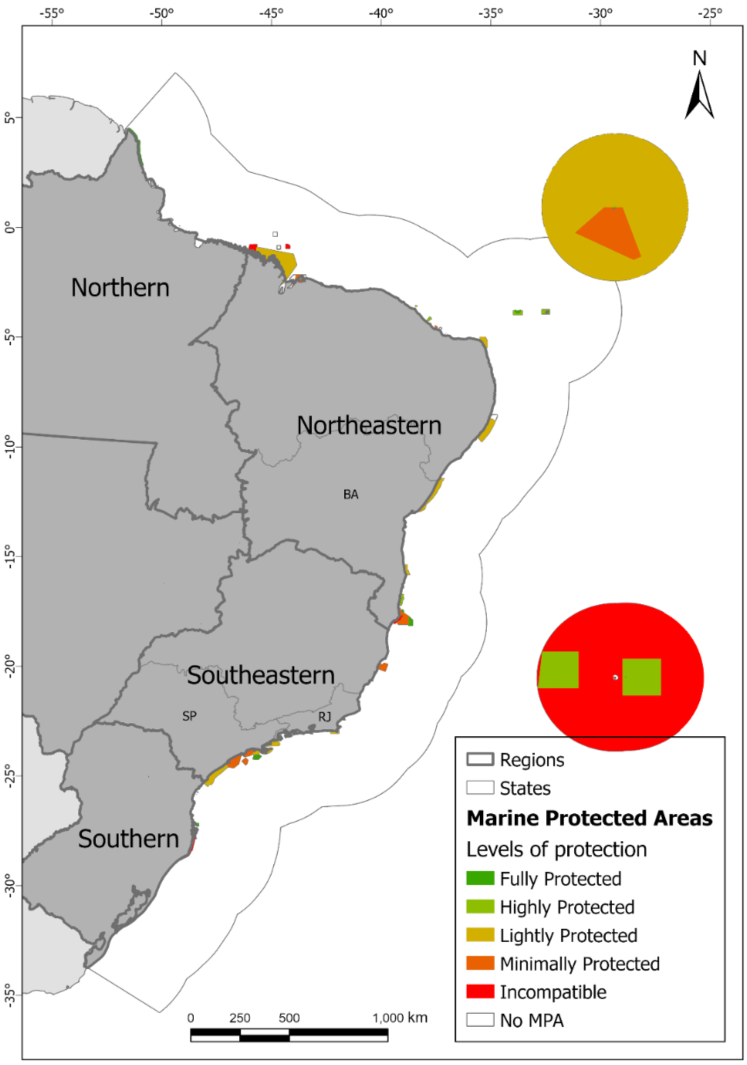
A total of 188 MPAs were inserted into the MPA Guide. Of these, it was not possible to obtain sufficient information for 33 MPAs (17.6%) to categorize them within the MPA Guide. Of those that were categorized, 24 (15.5%) were Incompatible, 21 (13.5%) Minimally Protected, 51 (32.9%) Lightly Protected, 33 (21.3%) Highly Protected, and 26 (16.8%) Fully Protected (Table 2).

Table 2 – Categories of Marine Protected Areas (MPAs) by region and state in Brazil. Some MPAs are in more than one state and duplicated. IN = Incompatible, MP = Minimally Protected, LP = Lightly Protected, HP = Highly Protected, FP = Fully Protected.

Region	**State**	**IN**	**MP**	**LP**	**HP**	**FP**	**Total**
Northern	Amapá	0	0	1	2	1	4
	Pará	3	4	5	1	0	13
	- *Subtotal*	*3*	*4*	*6*	*3*	*1*	*17*
Northeastern	Maranhão	5	1	1	0	0	7
	Piauí	1	0	0	0	0	1
	Ceará	1	5	2	5	0	13
	Rio Grande do Norte	3	0	1	1	1	6
	Paraíba	0	1	2	0	1	4
	Pernambuco	0	2	2	1	1	6
	Alagoas	0	0	3	0	0	3
	Sergipe	0	1	0	0	0	1
	Bahia	6	2	6	5	1	20
	- *Subtotal*	*16*	*12*	*17*	*12*	*4*	*61*
Southeastern	Espírito Santo	0	2	2	1	3	8
	Rio de Janeiro	3	0	12	6	9	30
	São Paulo	0	2	7	7	5	21
	- *Subtotal*	*3*	*4*	*21*	*14*	*17*	*59*
Southern	Paraná	1	0	4	1	0	6
	Santa Catarina	2	1	3	3	3	12
	Rio Grande do Sul	1	0	2	0	1	4
	- *Subtotal*	*4*	*1*	*9*	*4*	*4*	*22*

Most of the MPAs are located in coastal regions, but oceanic waters exhibit greater overlap with protected areas due to the presence of the four largest MPAs (Figure 5).

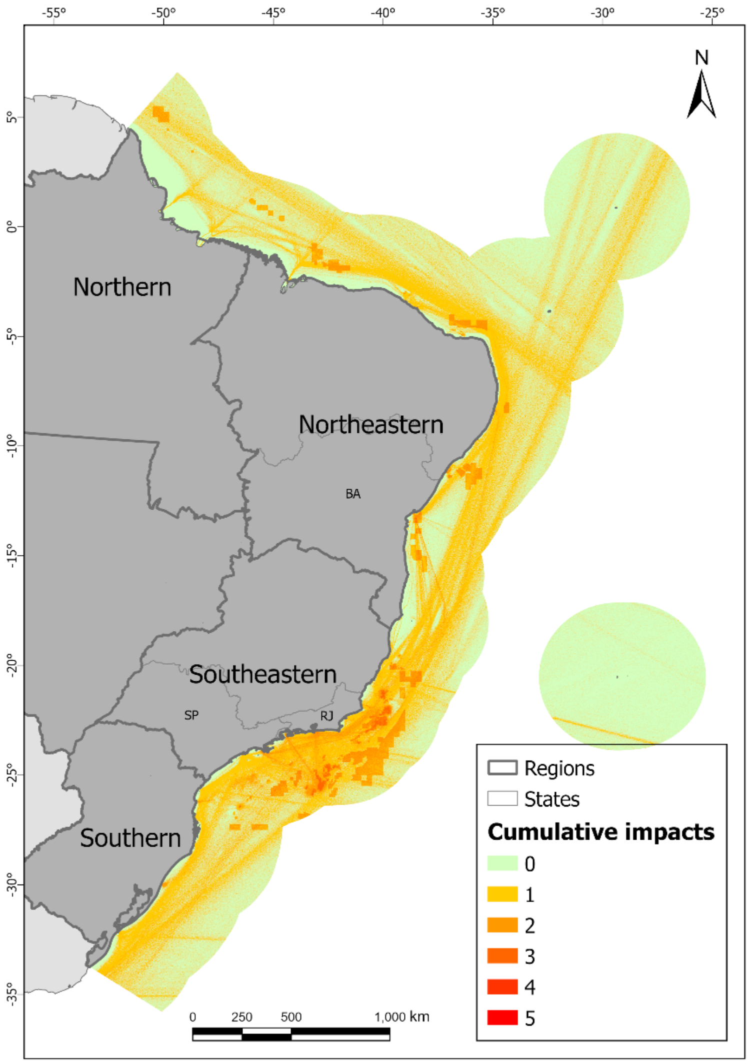
Figure 5 – Spatial distribution of the 188 Marine Protected Areas in Brazil and their respective categories in the MPA Guide (https://mpatlas.org/mpaguide).



2.2.3 Cumulative human activities

A high concentration of cumulative human activities can be observed both at the inner and outer shelf of the Exclusive Economic Zone of Brazil. Multiple activities could be found, especially, in Northeast and Southeast (Figure 6).

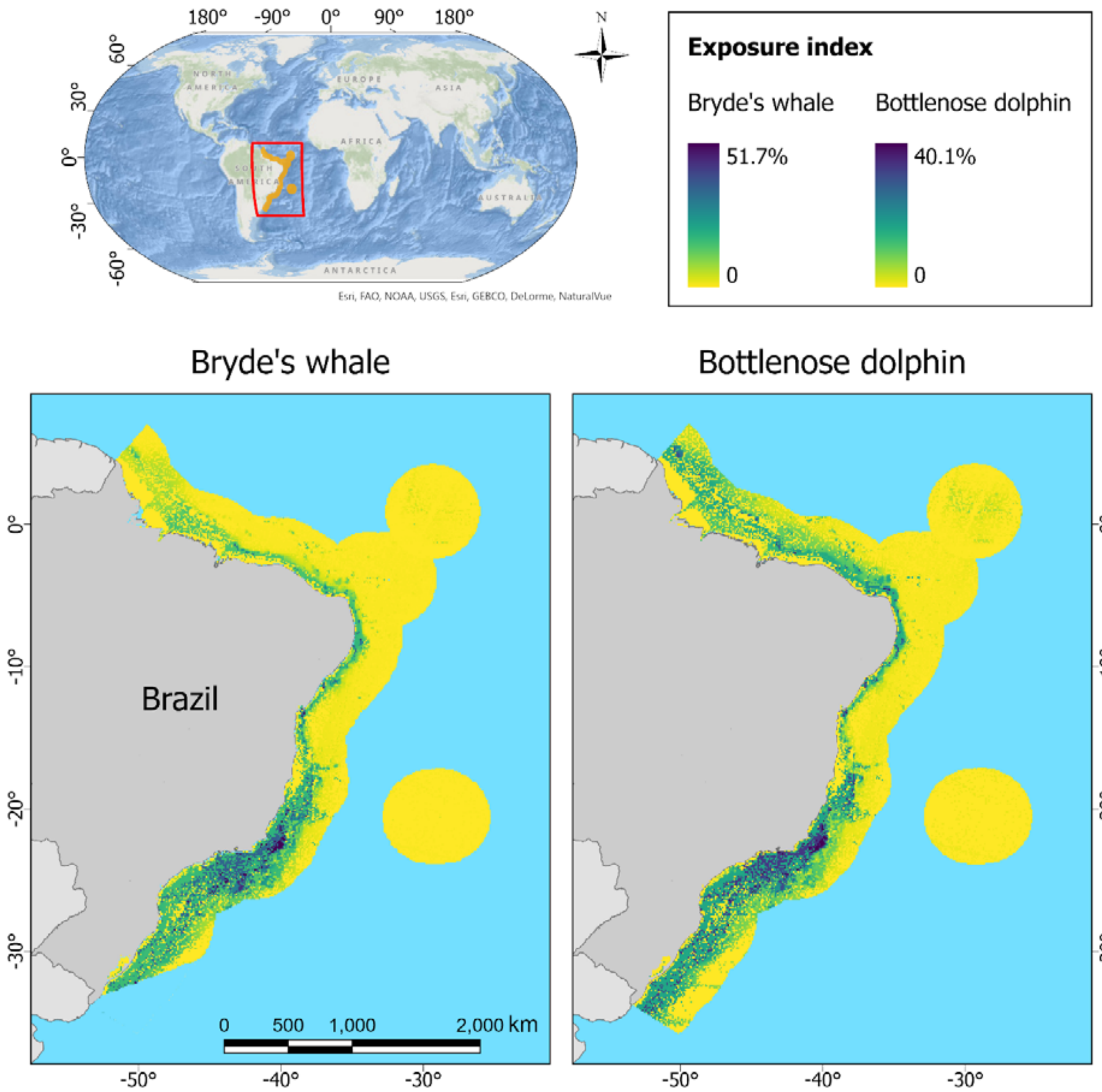
Figure 6 – Cumulative human activities in Brazil caused by port complexes, vessel traffic, and oil and gas activities. It was calculated by overlapping the number of activities through their binary values (i.e., presence or absence).



2.2.4 Exposure index

The index showed that Bryde's whale and bottlenose dolphin are exposed in both coastal and oceanic waters from the South and primarily Southeast. In the Northeast, both species are more exposed in coastal regions, while the bottlenose dolphin is exposed in oceanic waters in the North (Figure 7).

Figure 7 – Exposure index of Bryde's whale, *Balaenoptera brydei*, (left) and bottlenose dolphin, *Tursiops truncatus*, (right) considering Marine Protected Areas and cumulative impacts in Brazil.



2.3 Discussion

We showed that the most suitable areas for the occurrence of Bryde's whales and bottlenose dolphins are primarily located in Southeastern Brazil, which also exhibits a higher concentration of cumulative human activities. The Southeastern region also harbors the largest number of highly and fully protected MPAs, although the majority are situated along the coastal regions, not encompassing the oceanic areas where there is a high exposure to cumulative impacts.

Shallower waters were more suitable for Bryde's whales and bottlenose dolphins. Shallow waters receive more sunlight, allowing greater photosynthetic activity and primary productivity (Sigman & Hain, 2012). Coastal waters also benefit from nutrient-rich runoff from land, including nitrogen and phosphorus, which stimulate production in these areas, and remain well-mixed and oxygenated (Webb, 2021). These factors contribute to the coastal waters' greater nutritional richness compared to the open ocean, thereby explaining the enhanced habitat suitability of Bryde's whales and bottlenose dolphins in regions characterized by higher primary productivity values. Primary productivity is also associated with colder temperatures and steeper seabed, which were more suitable to target species. This is often linked to upwelling and water mixing processes (Sigman & Hain, 2012). To our surprise, however, primary productivity was not important to the final ensemble model. One possible explanation is that many regions with high primary productivity are associated with eutrophicated bays and estuaries (Castelo et al., 2021), which may not necessarily reflect prey abundance and availability. For bottlenose dolphins, the low degree of importance of primary productivity may be associated with potential competition with Guiana dolphins (*Sotalia guianensis*), which are known to occur in these areas (Ribeiro-Campos et al., 2021). For Bryde's whales, no evidence of competition is reported, but many of the high primary productivity areas are very shallow and may present maneuverability difficulties for the individuals.

In the Brazilian coast, the states of Rio de Janeiro, São Paulo (Southeast), and Bahia (Northeast) accounted for nearly half (44.7%) of the MPAs. In general, the Southeastern region has a higher proportional investment in environmental and sustainability initiatives (CLP, 2022). However, this does not necessarily mean that these areas are more protected. Studies report a lack of political will and financial resources for effective management of Brazilian MPAs. Funds scarcity, conflicts with local enterprises and activities, poor management, and lack of support from decision-makers are some of the problems that make it difficult to achieve the expected conservation results from an MPA (Borges et al., 2020; Gerhardinger et al., 2011; Mills et al., 2020).

The majority of MPAs are in coastal regions. The presence of MPAs in coastal areas is associated with accessibility, which is directly related to higher human activities as well as scientific knowledge, two key factors for MPA establishment (Ceccarelli et al., 2021; Schéré et al., 2021). Although there are four MPAs in oceanic regions, they are considered ineffective for conservation purposes (Magris & Pressey, 2018). In fact, for the target species of this study, these MPAs are not efficient as they are located away from suitable areas for Bryde’s whales and bottlenose dolphins.

Our findings indicate that Bryde’s whales and bottlenose dolphins are exposed to cumulative impacts along the entire Brazilian coast, except offshore regions in the Northeast. However, there is a higher exposure in oceanic regions of the Southeast. The Southeast harbors two of Brazil's most important sedimentary basins for oil and gas exploration, and it also has the highest population density, making it more vulnerable to species. A study identifying key regions for maintaining marine biodiversity and achieving global conservation goals reveals that the majority of top priority areas are in the Southeast (Magris et al., 2021), which aligns with our findings. As an economically significant region for Brazil with increasing human activities, it is expected that conflicts with biodiversity will become more common unless more attention is given to mitigation measures.

The most suitable areas for Bryde’s whales and bottlenose dolphins overlap with areas of higher cumulative human activities. These impacts can affect both species in various ways. One of the most well-reported is vessel collisions (Schoeman et al., 2020; Van Waerebeek et al., 2007). As whales and dolphins must surface to breathe, they are vulnerable to being struck by vessels, which can result in injuries and even mortality (e.g., Dwyer et al., 2014; Félix & Van Waerebeek, 2005). Studies conducted in New Zealand and Gulf of Mexico revealed that Bryde’s whales spend a significant amount of time in shallow depths, making them vulnerable to vessel strikes (Constantine et al., 2015; Soldevilla et al., 2017). In Ecuador, it was reported that there has been a five-fold increase in bottlenose dolphins with scars from vessel collisions over a 25-year period (Félix et al., 2018). The establishment of restricted navigation zones for dolphins (Baş et al., 2015; La Manna et al., 2020) and the reduction of vessel speeds for whales (Constantine et al., 2015; Ebdon et al., 2020; Redfern et al., 2019) can be effective measures to mitigate vessel collisions.

Acoustic impact on behavior is also reported, particularly in areas with high vessel traffic and oil and gas exploration. This impact can have negative effects on marine mammals, including disturbance of behavior, changes in communication, physiological stress, and even physical harm (Erbe et al., 2019). In Australia, bottlenose dolphins exhibited an increased average swimming speed during high maritime traffic and allocated more time to traveling while reducing their resting and socializing activities (Marley et al., 2017). In Italy, the presence of fast boats caused dolphins to interrupt their normal behavior and actively avoid the area. Additionally, dolphin sightings were less frequent when there was a higher concentration of vessels nearby (Papale et al., 2012). A slight reduction in vessel speed can significantly decrease the acoustic impact on marine mammals (Findlay et al., 2023).

Maritime activities are also associated with other types of operations, such as dredging, rock blasting, and pile driving. In Scotland, bottlenose dolphins are less frequently sighted during pile driving activities associated with harbor construction. Auditory injuries are also observed within a 100 m radius, and behavioral changes may occur up to 50 km away (Bailey et al., 2010; Graham et al., 2017). Furthermore, the presence of ports and vessels can also lead to pollution and an increased risk of contamination caused by oil spills and other harmful substances, which can also alter habitat quality (Sèbe et al., 2019; Soldevilla et al., 2017). In Brazil, studies conducted on rough-toothed dolphins (*Steno bredanensis*) reveals that individuals collected in Southeastern Brazil exhibit the highest levels of contaminants (Oliveira-Ferreira et al., 2021, 2023). Exposure to contaminants can affect the immune system of whales and dolphins, rendering them even more susceptible to cumulative impacts (Fair et al., 2013; Schwacke et al., 2012).

Many whales and dolphins can become entangled in fishing nets, leading to injuries, traumas, and even death (e.g., Cassoff et al., 2011; Segre et al., 2022). In Southeastern Brazil, ethnobiological data reveal an overlap between the distribution of bottlenose dolphins and fishing areas, potentially leading to an increased frequency of bycatch (Zappes et al., 2016). In South Africa, most bycatches involve females and calves, raising concerns regarding potential long-term effects on population demography (Plön et al., 2020). Some studies indicate that establishing more rigorous laws and a fishing exclusion area, and utilizing acoustic deterrents can be effective in preventing entanglement of small cetaceans, yet there is still no efficient system for large whales (Di Tullio et al., 2015; Hamilton & Baker, 2019; Zappes et al., 2016).

In conclusion, our study demonstrated that the most suitable areas for Bryde's whales and bottlenose dolphins in Brazil are primarily located in the Southeastern region, which also experiences higher cumulative impacts. These impacts pose various threats to both species, including vessel collisions, acoustic disturbances from maritime traffic and oil and gas exploration, as well as the potential for entanglement in fishing nets. The establishment of restricted navigation zones and reduced vessel speeds can help mitigate vessel collisions, while slight reductions in vessel speed can significantly decrease acoustic impacts on marine mammals. Measures such as fishing exclusion areas and the use of acoustic deterrents may help prevent the entanglement of small cetaceans, however, more effective solutions are needed for the protection of large whales. Furthermore, the presence of ports and maritime activities can lead to pollution and contamination risks, which can further degrade habitat quality and affect the immune systems of whales and dolphins. Given the economic significance of the Southeastern region and the increasing human activities in the area, it is crucial to prioritize conservation efforts (such as the creation or expansion of MPAs) and implement mitigation measures to reduce the conflicts between biodiversity conservation and human activities.

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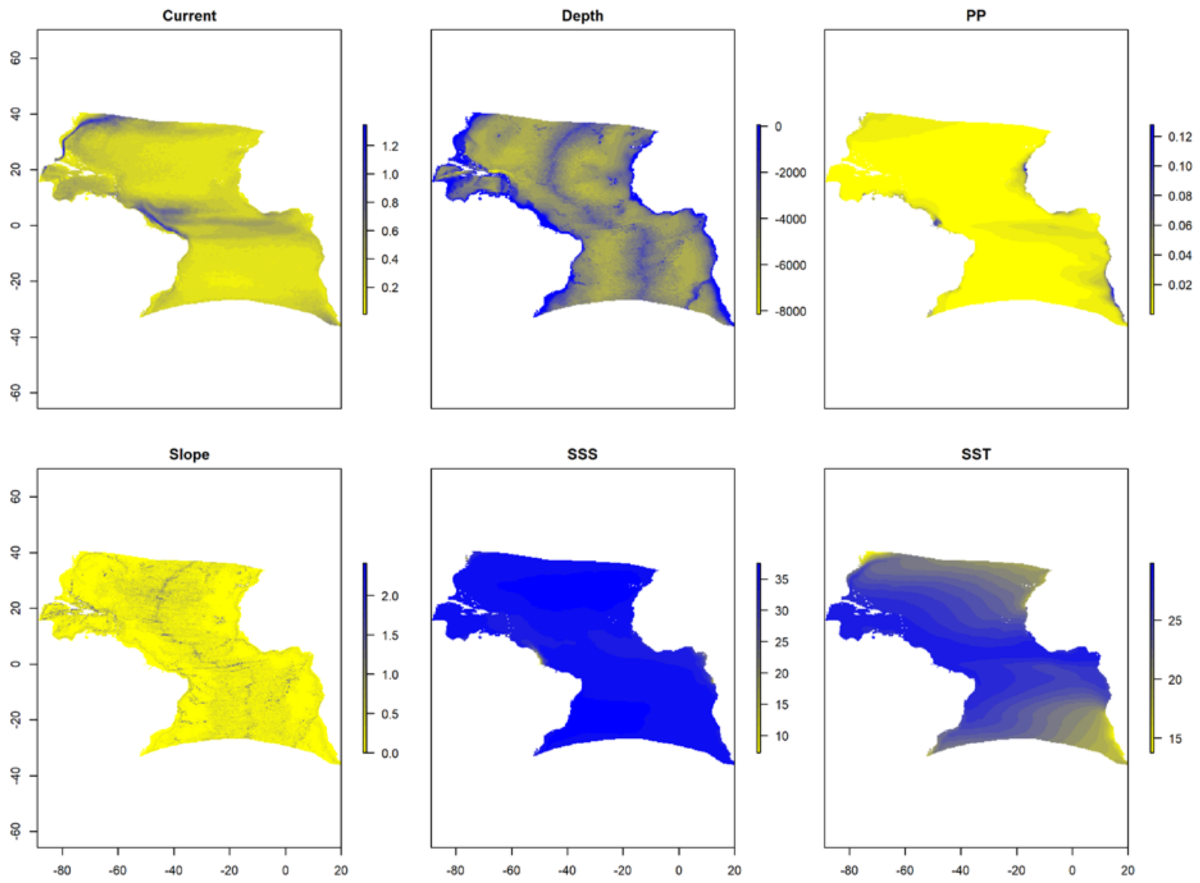
Supplementary material

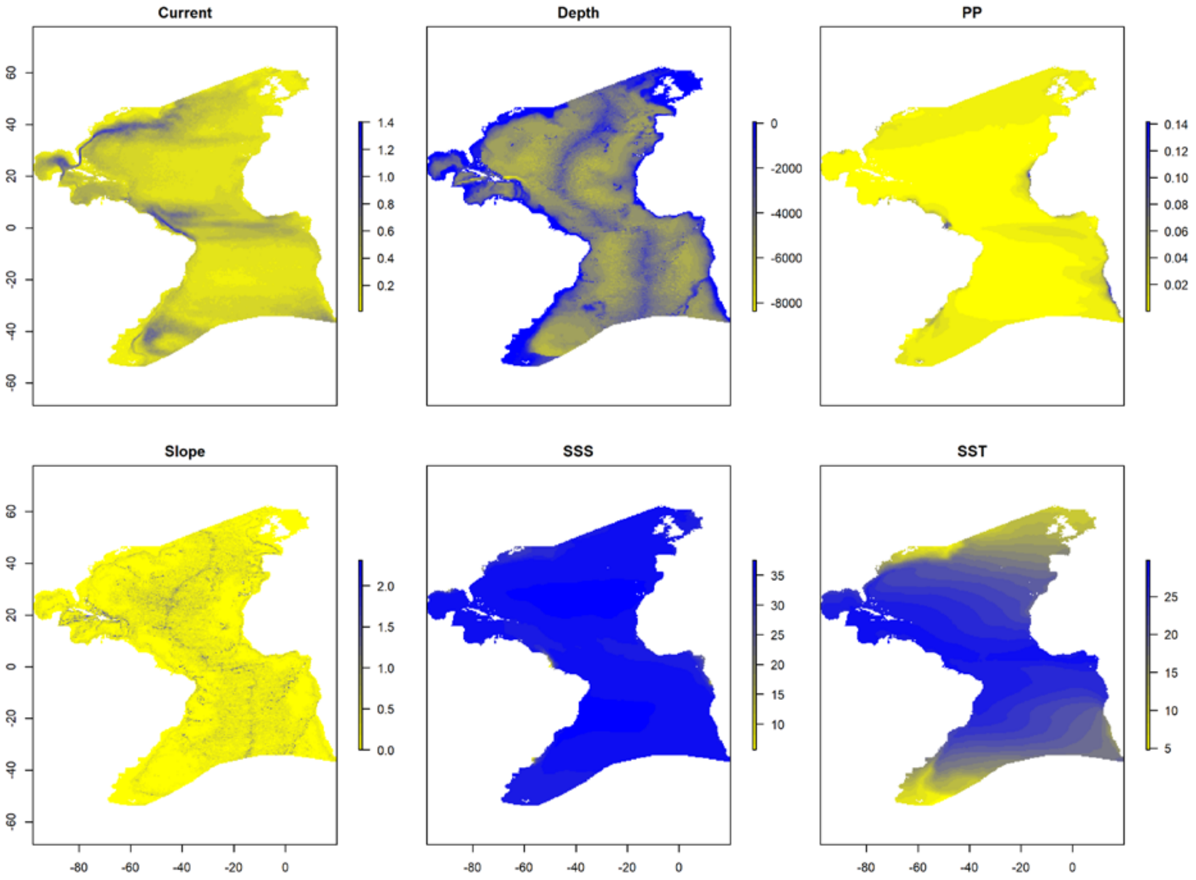
Supplementary Table 1 – Sources of the occurrence data of the Bryde's whale (*Balaenoptera brydei*) and the bottlenose dolphin (*Tursiops truncatus*) used in the habitat suitability modeling analysis.

Source	Available on
ENGEO Soluções Integradas	-
Global Biodiversity Information Facility – GBIF	https://www.gbif.org
Instituto Baleia Jubarte	-
Lodi et al. (2016)	https://doi.org/10.5597/lajam00214
Lucas Milmann, Dr.	-
Marine Ecology and Conservation Laboratory – ECoMAR / UFRJ	-
Ocean Biodiversity Information System – OBIS	https://obis.org
Projeto Baleias & Golfinhos do Rio	-
Projeto Coral Vivo	-
Projeto de Monitoramento de Cetáceos na Bacia de Santos – PMC-BS	https://sispmcprd.petrobras.com.br/sispmc
Sistema de Apoio ao Monitoramento de Mamíferos Marinhos – SIMMAM	http://simmam.acad.univali.br/sistema
Sistema de Avaliação do Risco de Extinção da Biodiversidade – SALVE	https://salve.icmbio.gov.br

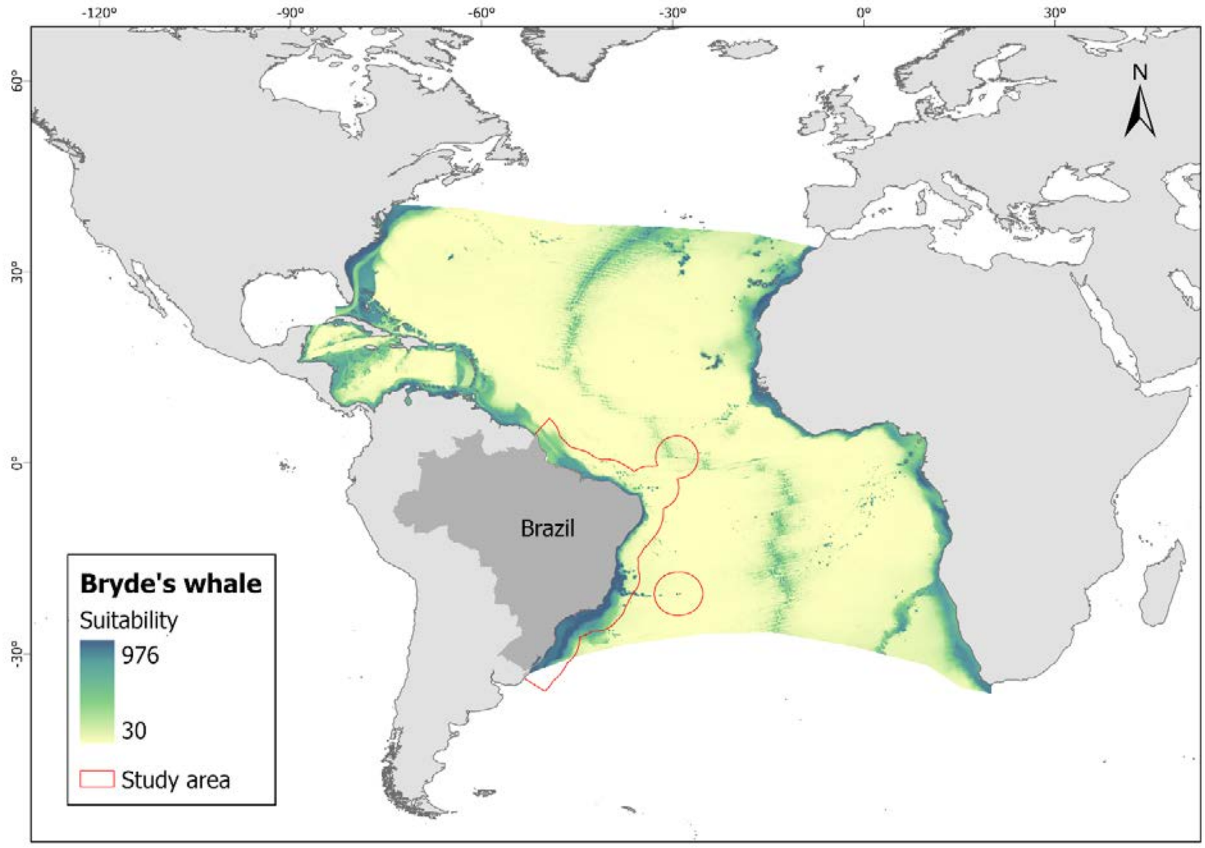
Supplementary Figure 1 – Environmental layers used as explanatory variables to model the habitat suitability of the Bryde's whale (*Balaenoptera brydei*) in the Atlantic Ocean. Current = current velocity; PP = primary productivity; Slope = seabed slope; SSS = sea surface salinity; SST = sea surface temperature.



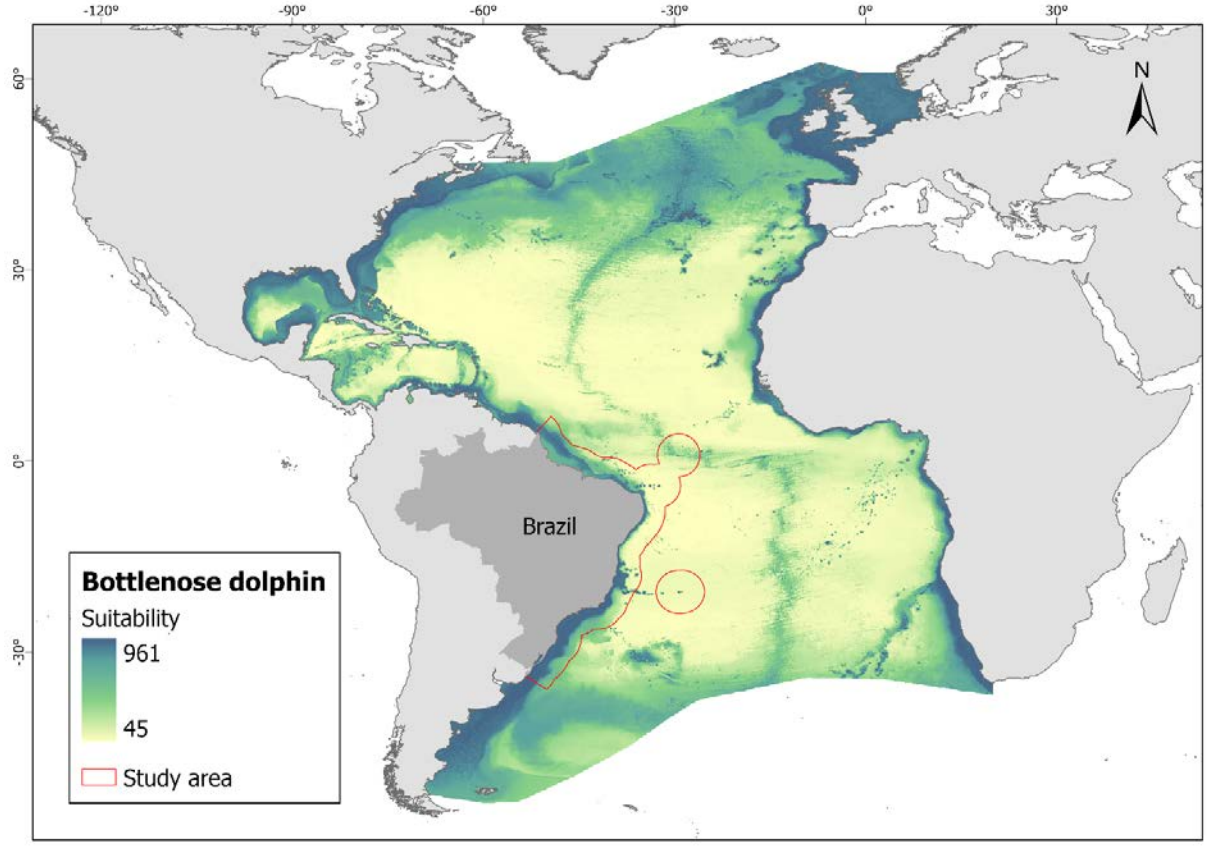
Supplementary Figure 2 – Environmental layers used as explanatory variables to model the habitat suitability of the bottlenose dolphin (*Tursiops truncatus*) in the Atlantic Ocean. Current = current velocity; PP = primary productivity; Slope = seabed slope; SSS = sea surface salinity; SST = sea surface temperature.



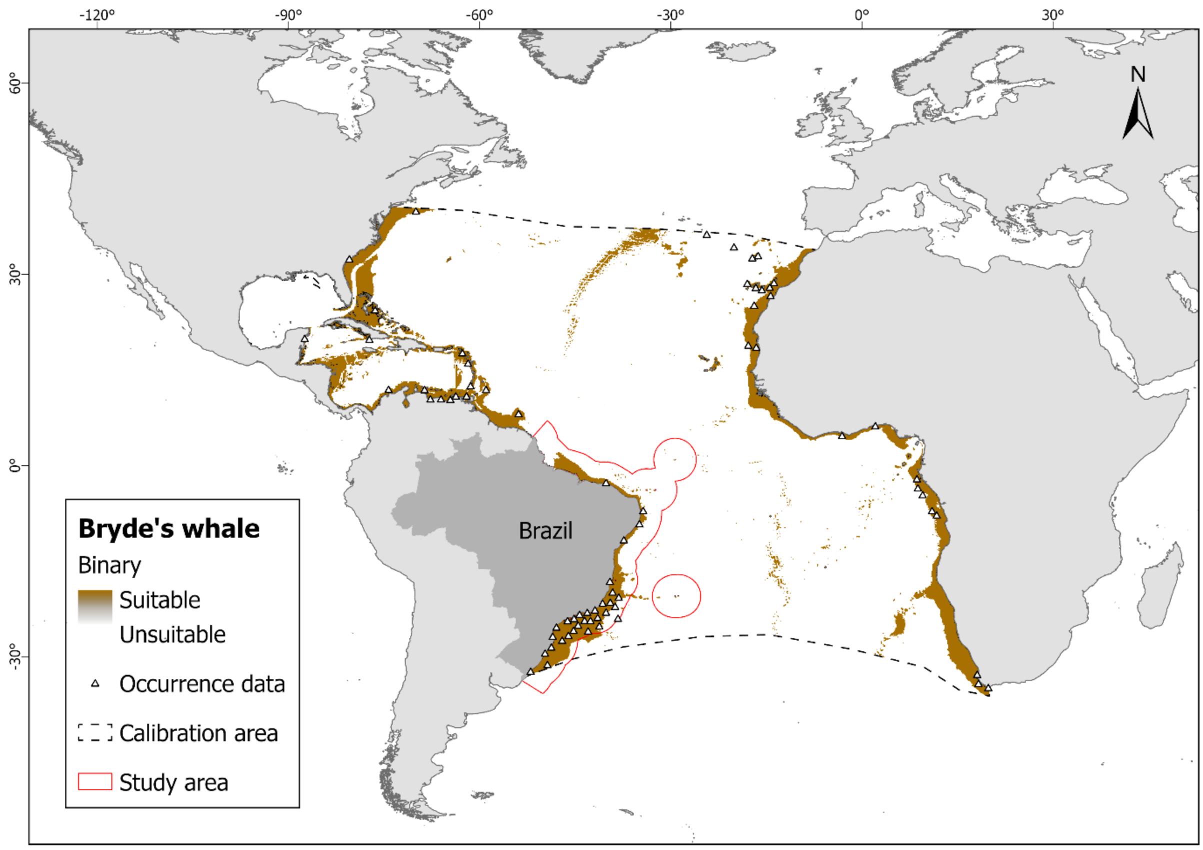
Supplementary Figure 3 – Habitat suitability of the Bryde’s whale (*Balaenoptera brydei*) in the Atlantic Ocean.



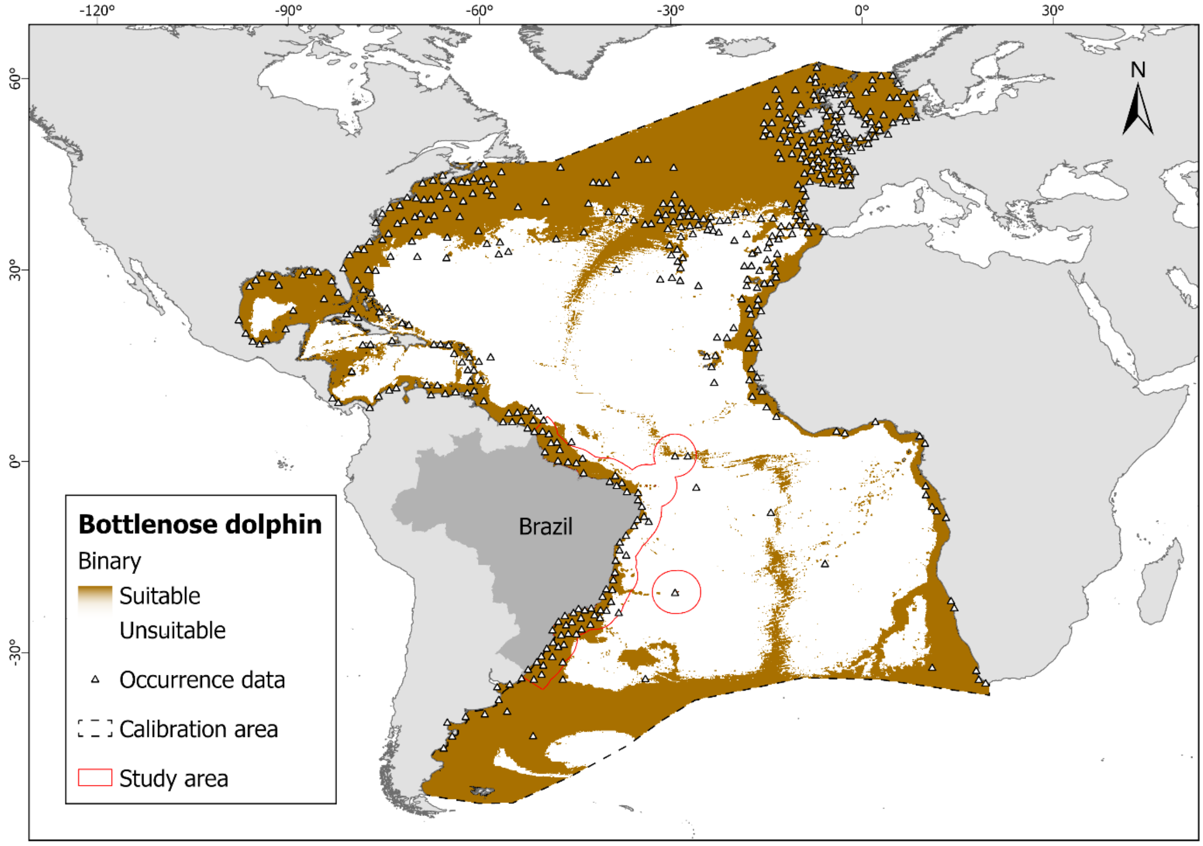
Supplementary Figure 4 – Habitat suitability of the bottlenose dolphin (*Tursiops truncatus*) in the Atlantic Ocean.



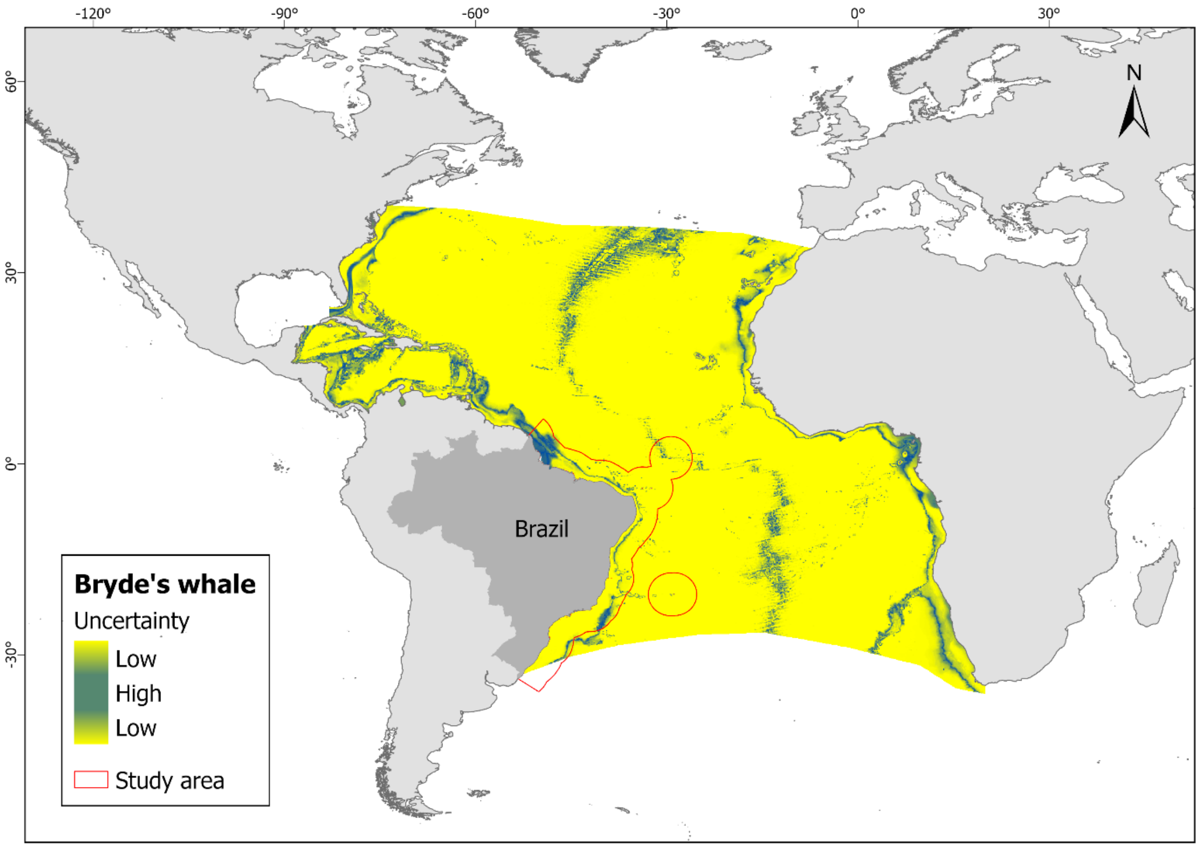
Supplementary Figure 5 – Suitable and unsuitable areas (binary values) for habitat suitability of the Bryde's whale (*Balaenoptera brydei*) in Brazil.



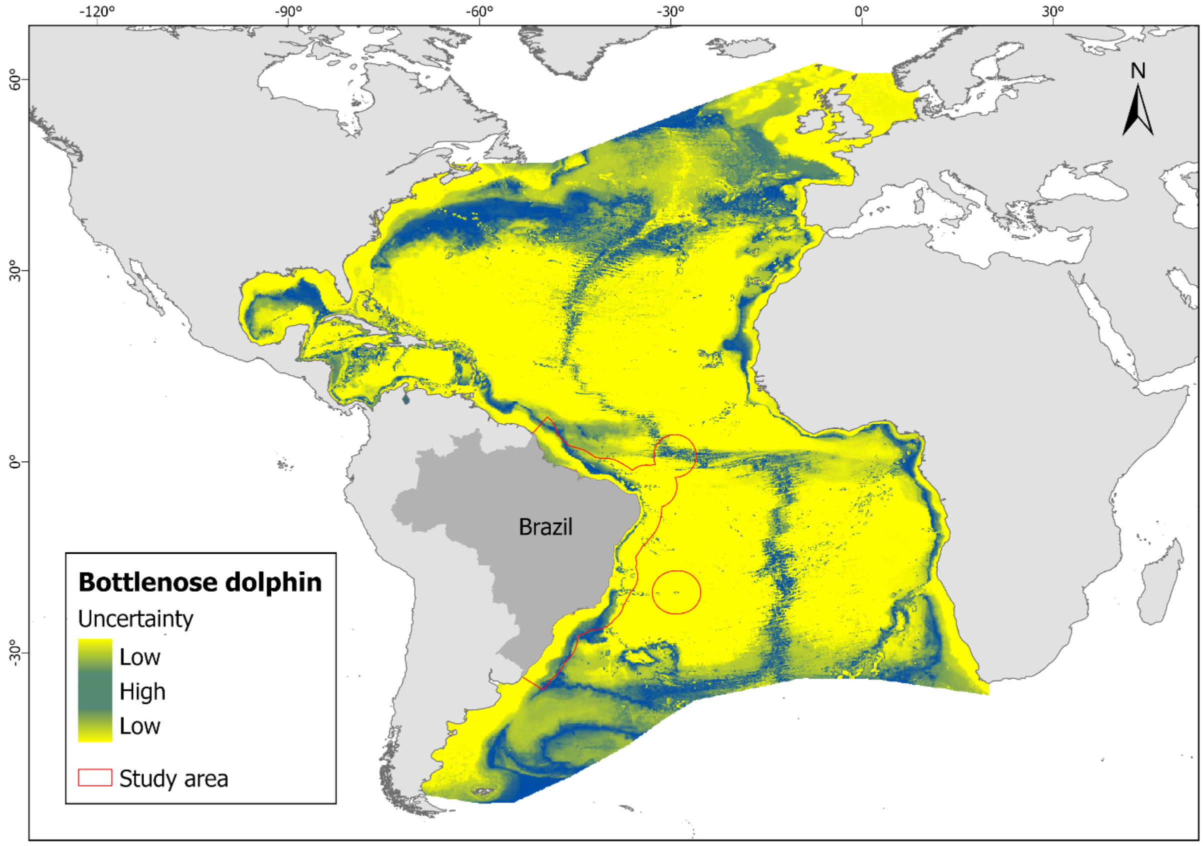
Supplementary Figure 6 – Suitable and unsuitable areas (binary values) for habitat suitability of the bottlenose dolphin (*Tursiops truncatus*) in Brazil.



Supplementary Figure 7 – Uncertainty in habitat suitability for the Bryde's whale (*Balaenoptera brydei*) calculated using the committee average, where the median values (Low) mean a non-agreement of the individual models regarding whether the area is suitable or not.



Supplementary Figure 8 – Uncertainty in habitat suitability for the bottlenose dolphin (*Tursiops truncatus*) calculated using the committee average, where the median values (Low) mean a non-agreement of the individual models regarding whether the area is suitable or not.



3 MARINE PROTECTED AREAS ARE NOT EFFECTIVE FOR AN ENDANGERED DOLPHIN WHEN FEEDING IN SOUTHEASTERN BRAZIL

Abstract: Feeding is crucial for obtaining the nutrients and energy necessary for growth, reproduction, and survival. Understanding feeding behavior and variables associated with its occurrence is important to direct conservation actions. Although dolphins perform coordinated feeding tactics, their knowledge is still incipient since there are few places where we can note it frequently. The objective of this study was to understand the environmental factors influencing the Guiana dolphin's (*Sotalia guianensis*) feeding behavior and coordinated feeding tactics and to evaluate the effectiveness of local MPAs for its conservation. The Guiana dolphin is a small and endangered dolphin species, found in bays and estuaries of Latin America. Suitability modeling was used to predict suitable feeding areas based on environmental variables. The study area, Ilha Grande Bay, Southeastern Brazil, is characterized by high human activity, including fishing, tourism, and port complexes. The results showed that chlorophyll concentration, depth, and vessel traffic were significant factors influencing the suitability of areas for feeding behavior. Suitable areas were in regions with higher chlorophyll values, closer to islands, and with lower vessel traffic. During the rainy season, suitable feeding areas were shallower compared to the dry season. The study also revealed a high overlap between suitable feeding areas and fishing gear, highlighting the risk of bycatch and the ineffectiveness of local MPAs in addressing this issue. Depth and seabed slope were important variables in explaining coordinated feeding tactics. Shallow waters and flatter regions were more suitable for performing feeding tactics. However, the most suitable areas overlapped with noisy regions, raising concerns about the impact of underwater noise on dolphin communication to coordinate tactics. Our findings suggest the need for improved management strategies to reduce bycatch and enhance the effectiveness of MPAs. Additionally, mitigating the negative effects of underwater noise on dolphin behavior is crucial. This study provides valuable insights into the ecological aspects of feeding and conservation challenges of the Guiana dolphin population in Ilha Grande Bay, emphasizing the importance of considering temporal dynamics and implementing targeted conservation measures in the region.

Keywords: Atlantic Ocean. Coastal management. Environmental impacts. Marine conservation. Species distribution models.

Resumo: A alimentação é crucial para obter os nutrientes e energia necessários para o crescimento, reprodução e sobrevivência. Compreender o comportamento alimentar e as variáveis associadas à sua ocorrência é importante para direcionar ações de conservação. Embora os golfinhos realizem táticas coordenadas de pesca, o conhecimento ainda é incipiente, pois existem poucos lugares onde podemos observá-las com frequência. O objetivo deste estudo foi entender os fatores ambientais que influenciam o comportamento alimentar e as táticas coordenadas de alimentação do boto-cinza (*Sotalia guianensis*) e avaliar a eficácia de Áreas Marinhas Protegidas (AMPs) locais para sua conservação. O boto-cinza é uma espécie de golfinho pequena e ameaçada, encontrada em baías e estuários da América Latina. A modelagem de adequabilidade foi usada para prever áreas adequadas para alimentação com base em variáveis ambientais. A área de estudo, Baía da Ilha Grande, no Sudeste do Brasil, é caracterizada por alta atividade humana, incluindo pesca, turismo e portos. Os resultados mostraram que a concentração de clorofila, profundidade e tráfego de embarcações foram fatores significativos que influenciaram a adequabilidade do comportamento alimentar. As áreas adequadas estavam em regiões com valores mais altos de clorofila, mais próximas de ilhas e com menor tráfego de embarcações. Durante a estação chuvosa, as áreas adequadas para alimentação eram mais rasas em comparação com a estação seca. O estudo também revelou uma sobreposição significativa entre as áreas adequadas para alimentação e as redes de pesca, destacando o risco de captura incidental e a ineficácia das AMPs locais para abordar essa questão. A profundidade e a declive do relevo submarino foram variáveis importantes para explicar as táticas coordenadas de pesca. Águas rasas e regiões mais planas foram mais adequadas para realizar essas táticas. No entanto, as áreas mais adequadas se sobrepuseram a regiões com ruído, levantando preocupações sobre o impacto do ruído subaquático na comunicação dos golfinhos para coordenar suas táticas. Nossos resultados sugerem a necessidade de estratégias de gestão aprimoradas para reduzir a captura acidental e aumentar a eficácia das AMPs. Além disso, mitigar os efeitos negativos do ruído subaquático no comportamento dos golfinhos é crucial. Este estudo fornece informações valiosas sobre os aspectos ecológicos da alimentação e os desafios de conservação da população de botos-cinza na Baía da Ilha Grande, enfatizando a importância de considerar dinâmicas temporais e implementar medidas de conservação direcionadas na região.

Palavras-chave: Oceano Atlântico. Gerenciamento costeiro. Impactos ambientais. Conservação marinha. Modelos de distribuição de espécie.

Introduction

Understanding feeding behavior and variables associated to its occurrence is important to direct conservation actions. Among the various aspects of behavior, feeding behavior stands out as an important factor affecting species' survival and their ecological role (Stander 1992; Lachat and Haag-Wackernagel 2016; Mills et al. 2018). Different species exhibit specific feeding strategies tailored to their ecological niche and prey availability. For instance, predatory species, such as lions (*Panthera leo*), hunt in coordinated groups, utilizing stealth and communication to encircle and capture their prey. This collaborative behavior ensures a more efficient acquisition of food and the survival of pride (Stander 1992). Another example occurs with peregrine falcons (*Falco peregrinus*), engaging in aerial attacks, stooping at high speed to catch their prey (Mills et al. 2018). Meanwhile, creatures like the Bobbit worm (*Eunice aphroditois*), hide under sand or mud, waiting for unsuspecting prey to pass by before ambushing them swiftly (Lachat and Haag-Wackernagel 2016).

However, many species face reduced food resources due to human-induced changes in the environment, like habitat loss and overexploitation of prey. In such cases, they may struggle to find alternative strategies to feed, which can lead to reduced reproductive success and population declines (Newton 2004; Collister and Wilson 2007; Grames et al. 2023). Therefore, it is crucial to develop conservation strategies that address the specific feeding requirements and challenges of different species to ensure their survival and additionally that contribute to overall biodiversity conservation efforts.

The environment plays a pivotal role in shaping feeding behavior, as the availability of food resources can vary significantly across regions and seasons. Consequently, species exhibit behavioral plasticity, adapting their feeding strategies in response to environmental conditions (Heithaus et al., 2018). Optimization of prey capture is paramount for enhancing individual energy gain, often requiring the development of specialized tactics to surpass prey antipredator strategies (MacArthur & Pianka, 1966; Naruei et al., 2022). Understanding the interplay between feeding behavior and habitat suitability holds implications for marine ecology and conservation. This knowledge can subsidize more effective management and conservation strategies, ensuring the sustainability of resource extraction and the conservation of marine biodiversity amid environmental challenges and human activities (Almenar et al., 2009; Milmann et al., 2016).

Dolphins are gregarious animals and renowned for displaying intricate social organization. They can perform multiple strategies to catch their prey and rarely exhibit this behavior individually (Methion & López, 2019). The Guiana dolphin (*Sotalia guianensis*) is one of the smallest dolphin species, with its distribution limited between Southern Brazil to Honduras. It is a coastal species, primarily found in bays, estuaries, and coves (Carvalho and Meirelles, 2020). This characteristic exposes it to various human activities, including port areas, fishing activities, and pollution from the coast, resulting in habitat loss and degradation (Tardin et al., 2011; Tardin et al., 2020; Ribeiro-Campos et al., 2021; Maciel et al., 2023). While it is classified as “Near Threatened” by the IUCN, in Brazil, where the largest portion of its distribution is found, the species is considered “Vulnerable”.

One of the largest populations of Guiana dolphins can be found in Ilha Grande Bay, Southeastern Brazil (Espécie, 2011). More than 70% of individuals are resident in the region, which is considered preserved and a priority for biodiversity conservation (Espécie et al., 2010; MMA, 2018). It is common to observe dolphins engaging in vital activities for species maintenance, such as feeding and breeding (Tardin et al., 2014). While feeding, individuals display a diverse repertoire of coordinated feeding tactics to pursue and capture their prey. For example, dolphins tend to overcome prey defenses by trapping them among each other or against a natural barrier (e.g., seabed slope and water surface) (Heithaus et al., 2018). The Ilha Grande region also harbors protected areas and is surrounded by traditional communities engaged in fishing, tourism activities, and port complexes (Junior et al., 2002; Creed et al., 2007; Cordeiro et al., 2020; de Freitas et al., 2020).

Although the feeding success is intricately shaped by their surrounding environment, human activities within these habitats can influence these behaviors, altering ecological dynamics (Motta et al., 2021). Marine Protected Areas (MPAs) have emerged as valuable tools for biodiversity conservation, offering the potential to ensure abundant resources for predators, which may lead to increased utilization of these protected areas as primary feeding grounds (Claudet et al., 2011). Understanding the complex relationship between predators and MPAs holds implications for effective conservation strategies aimed at preserving marine ecosystems and their ecological balance (Hooker et al., 2011). By investigating how MPAs can favor feeding behavior and strategies, we gain insights into the role of MPAs in supporting predator populations and enhancing overall conservation in the marine ecosystem (Clemente et al., 2011).

Considering multiple overlapping human activities affecting a resident population of a threatened species, the Guiana dolphin, this study aimed to achieve two objectives. The first was to map and understand how the most suitable feeding areas for Guiana dolphins and their coordinated feeding tactics are influenced by the environment. Considering that environmental factors influence the presence of prey for this dolphin, we hypothesized that these factors would also influence the suitability of feeding areas for the species. We predicted that dolphins' habitat suitability would be influenced by chemical variables, as they can affect the distribution of prey, and by physical variables, as dolphins may utilize them as barriers to facilitate prey capture. Second was to evaluate the effectiveness of protected areas as a preferentially suitable area for Guiana dolphins when feeding. Tardin et al. (2020) showed no overlap between the habitat of Guiana dolphins and local protected areas, however these authors did not evaluate it, specifically, during this dolphin’s feeding behavior. Based on these authors study, we hypothesized that the most suitable feeding areas for Guiana dolphins are not within the boundaries of protected areas.

3.1 Methods

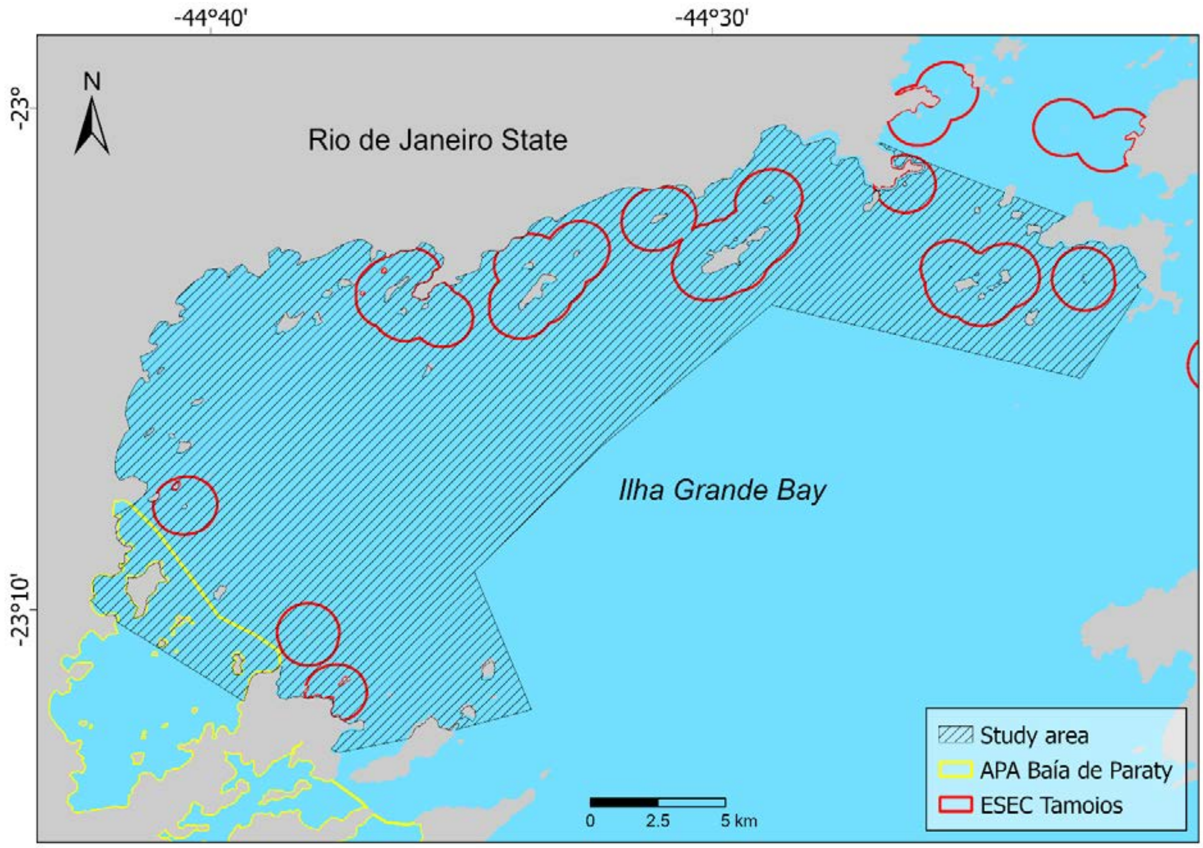
3.1.1 Study area

Ilha Grande Bay (IGB), located in the Southeastern Brazil, serves as a biodiversity hotspot situated between two major Brazilian metropolitan areas, Rio de Janeiro and São Paulo (Figure 1). The region’s richness and marine species diversity can be attributed to its unique geographic, hydrographic, and oceanographic characteristics, coupled with factors such as the diversity and connectivity of coastal systems, the input of organic matter from rivers, and variation in physical and chemical oceanographic factors (Creed et al., 2007). Additionally, the region benefits from nutrient enrichment through the influx of South Atlantic Central Waters (SACW) during the summer, influencing the abundance, diversity, and richness of marine organisms (Palma and Matano, 2009; Kjerfve et al., 2021). In 2007, the Brazilian government recognized the region’s significance for biodiversity conservation, reaffirming its importance in an update in 2018, by designating the area as of extremely high biological importance and a priority for action (MMA, 2018).

Figure 1 – Map of the study area (Ilha Grande Bay) located in SE Brazil. RJ = Rio de Janeiro State, SP = São Paulo State.

Due to its conservation significance and scenic beauty, the region harbors 11 protected areas. This study focuses on the western portion of IGB, where two marine protected areas are present: *Estação Ecológica de Tamoios* (Ecological Station, IUCN category Ia), hereafter ESEC Tamoios, and *Área de Proteção Ambiental da Baía de Paraty* (Environmental Protection Area, IUCN category V), hereafter APA Baía de Paraty (Figure 2). The establishment of ESEC Tamoios in 1990 was a compensation measure for implementing two nuclear power plants in the region, aiming to preserve the local ecosystem and monitor its environmental quality. APA Baía de Paraty was created in 1984 with the objective of protecting breeding areas for marine organisms. The purpose of these protected areas goes beyond the nuclear power plants, as the region is also subject to other human activities that may impact biodiversity.

Figure 2 – Map of Ilha Grande Bay showing the study area and local Marine Protected Areas: *Área de Proteção Ambiental da Baía de Paraty* (APA Paraty) and *Estação Ecológica de Tamoios* (ESEC Tamoios).



Nuclear power plants have the potential to alter local environmental characteristics primarily through thermal discharges, which lead to changes in water temperature, chlorine levels, and current velocity. These alterations, particularly the temperature increase, can negatively impact the richness and diversity of fish assemblages and benthic communities, such as sponges (Vilanova et al., 2004; Teixeira et al., 2009). The region is also home to port complexes (PMTE-BS, 2021), which consequently increase vessel traffic and pose risks to biodiversity. These risks include increased underwater noise, alterations in current dynamics caused by port and marina construction and dredging activities, oil spills, contamination from anti-fouling paint compounds, and exposure to invasive species through ballast water and hull fouling (Junior et al., 2002; Madeira et al., 2020; Kjerfve et al., 2021; Mangelli et al., 2021).

Fishing activities are also commonplace in the region, particularly artisanal fishing using purse seine nets and trawling, although industrial fishing also contributes to discharge (PMAP-BS, 2022). Due to the scenic attractiveness of the region, tourism and nautical leisure activities are also prominent (Mangelli et al., 2021). Consequently, the coastal region experiences real estate projects that result in deforestation and pollution of coastal waters through the occupation of slopes, riverbanks, islands, and mangrove areas (Creed et al., 2007; de Freitas et al., 2020). These cumulative impacts combined with the ecological importance make the Ilha Grande Bay a priority area for conservation actions.

3.1.2 Data collection and definition

We collected data in 2007, 2008, and from 2019 to 2022, throughout dry and rainy seasons, along systematic routes in the western portion of IGB to sample the entire study area equally. Dry season was defined as April to September, and rainy season as October to March according to precipitation data in the region (Soares et al., 2014). The season can influence environmental characteristics, such as nutrient input, temperature, and salinity.

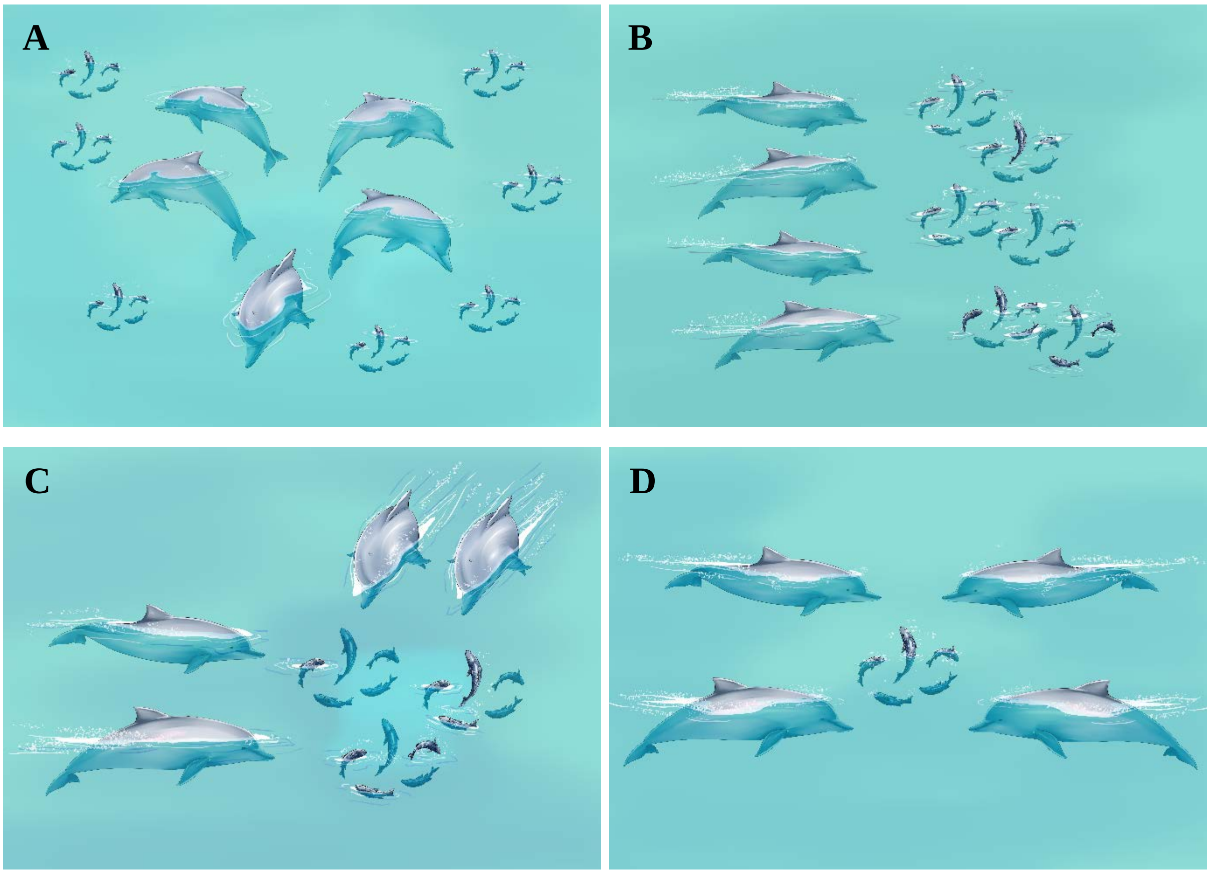
Guiana dolphins' occurrence data were obtained using a handheld GPS every 10 minutes, or 500 meters traveled from the last coordinate, while feeding behavior and coordinated feeding tactics data were collected using a spreadsheet. We wrote feeding behavior and coordinated feeding tactics down only once regardless of how many times they occurred within that specific timeframe. One researcher observed the animals and verbally communicated each tactic performed, while a second researcher took note of the tactics. We used four coordinated feeding tactics: kettle, line abreast, perpendicular feeding, and wall formation (Table 1 and Figure 3).

Fishing activity data was also collected during the same fieldwork from 2019 onwards. Fishing gear was identified whenever possible and with the assistance of local fishermen.

Table 1 – Description of the coordinated feeding tactics performed by the Guiana dolphin (*Sotalia guianensis*) in Ilha Grande Bay, SE Brazil.

Coordinated feeding tactic	**Description**
Kettle	Animals dive under a school of fish, forcing it to the surface, emerging from several directions (Bel'kovich, 1991)
Line abreast	Animals form a tight line, swimming side-by-side, separated by no more than one dolphin-body width (Neumann & Orams, 2003)
Perpendicular feeding	A group of dolphins split into two subgroups which join in perpendicular directions (Tardin et al., 2011)
Wall formation	A group of dolphins split into two subgroups which join in opposite directions (Bel'kovich, 1991)

Figure 3 – Coordinated feeding tactics performed by the Guiana dolphin, *Sotalia guianensis*, in Ilha Grande Bay, SE Brazil. Kettle (A), line abreast (B), perpendicular feeding (C), and wall formation (D). Made by Gabriel Melo-Santos.



The explanatory variables were obtained from different sources. Chlorophyll and particulate organic carbon were obtained from the Giovanni database at a resolution of 4 × 4 km (NASA, 2022). Depth and seabed slope were calculated using nautical chart No. 1633 from the Brazilian Navy in 1 × 1 km grids. Distance to islands was calculated in ArcGIS Pro using the Near tool also for 1 × 1 km grids. Shipping traffic was acquired through the Vessel Traffic Monitoring Project in the Santos Basin (PMTE-BS, 2021). Underwater noise was calculated using field-collected data from 2019 onwards. The study area was divided into 23 grids of 5 × 5 km each. We recorded for 10 minutes at the centroid of each grid using a SoundTrap with a sampling rate of 192 kHz/16 bits. To calculate the average Sound Pressure Levels (SPL) in each grid, we ran the PAMGuide in MATLAB. For the models of coordinated feeding tactics, we included only variables that we deemed important for explaining the occurrence of tactics: depth, distance to islands, seabed slope, and underwater noise.

3.1.3 Data analysis

We created two sets of models to investigate suitable areas for dolphins during their feeding behavior: i) a set of models combining all feeding tactics, and ii) a set of models specific to each tactic. For both sets, the modeling procedures were similar, as described below. We ran suitability models using the biomod2 package (Thuiller et al., 2023) in the R environment (R Core Team, 2023). All explanatory variables were standardized at a resolution of 1 × 1 km, and we checked for potential multicollinearity issues using the usdm package (Naimi et al., 2014). To avoid spatial autocorrelation, we thinned the points within a 1 km radius using spThin package (Aiello-Lammens et al., 2015), matching the resolution of the explanatory variables.

We generated 10 sets of pseudo-absences with 50 records each using the disk strategy, ensuring that no records were created within a 2.5 km radius of occurrence points. We employed six algorithms based on different techniques: regression (Generalized Linear Model - GLM and Generalized Additive Model - GAM), boosting (Generalized Boosting Model - GBM and Random Forest - RF), discriminant (Flexible Discriminant Analysis - FDA), and presence-background (Maximum Entropy - MaxEnt) (see Guisan et al., 2017 for more details). To calibrate the models, we used 70% of the presence records for training and 30% for testing (Guisan et al., 2017), and each algorithm was run 10 times. After evaluating the performance of each model, we selected those with the Area Under the Curve (AUC) from the Receiver Operating Characteristic (ROC) weighted mean values > 0.7 to make an ensemble model (Araújo and New, 2007; Guisan et al., 2017) and calculated the importance of the variables and their response curves.

Spatial overlap analyses were conducted using ArcGIS Pro. Binary values (0 - unsuitable and 1 - suitable) from the ensemble models were utilized, and the number of pixels (1 × 1 km grids) within and outside the MPA boundaries was summed to calculate the percentage of pixels within and outside the MPAs. To analyze the richness of coordinated feeding tactics, we overlaid the ensemble model of each tactic and summed the binary value for each grid. Fishing gear was plotted and percentage quantified based on the absolute number of gears in suitable and unsuitable areas for the Guiana dolphin’s feeding behavior.

3.2 Results

3.2.1 Feeding behavior suitability

A total of 276 occurrence records for the dry season and 173 for the rainy season were initially considered. After spatial rarefaction, 21 (dry) and 35 (rainy) records were used in the subsequent analyses. All seven explanatory variables were included since there were no issues of multicollinearity among them.

The ensemble model was generated based on 358 (dry) and 491 (rainy) individual models, out of a total of 600, after selecting only the models with an AUC value > 0.7. In general, MaxEnt exhibited the highest AUC values and the largest number of individual models within the ensemble model, whereas GAM demonstrated the lowest values and a smaller number of models within the ensemble. However, all algorithms yielded satisfactory results with a substantial number of individual models in the ensemble model (Table 2).

Table 2 – Mean, standard deviation (SD), and number of individual models within the ensemble model (Ensemble) for each algorithm used to model the suitability of Guiana dolphin's, *Sotalia guianensis*, feeding behavior in Ilha Grande Bay, SE Brazil.

Season	Algorithm	Mean	SD	Ensemble
Dry	Generalized Linear Model – GLM	0.80	0.07	68
	Generalized Additive Model – GAM	0.80	0.07	48
	Generalized Boosting Model – GBM	0.80	0.06	55
	Random Forest – RF	0.79	0.06	63
	Flexible Discriminant Analysis – FDA	0.78	0.06	52
	Maximum Entropy – Maxent	0.80	0.06	72
Rainy	Generalized Linear Model – GLM	0.79	0.06	72
	Generalized Additive Model – GAM	0.81	0.07	63
	Generalized Boosting Model – GBM	0.81	0.06	92
	Random Forest – RF	0.84	0.07	88
	Flexible Discriminant Analysis – FDA	0.83	0.07	81
	Maximum Entropy – Maxent	0.85	0.06	95

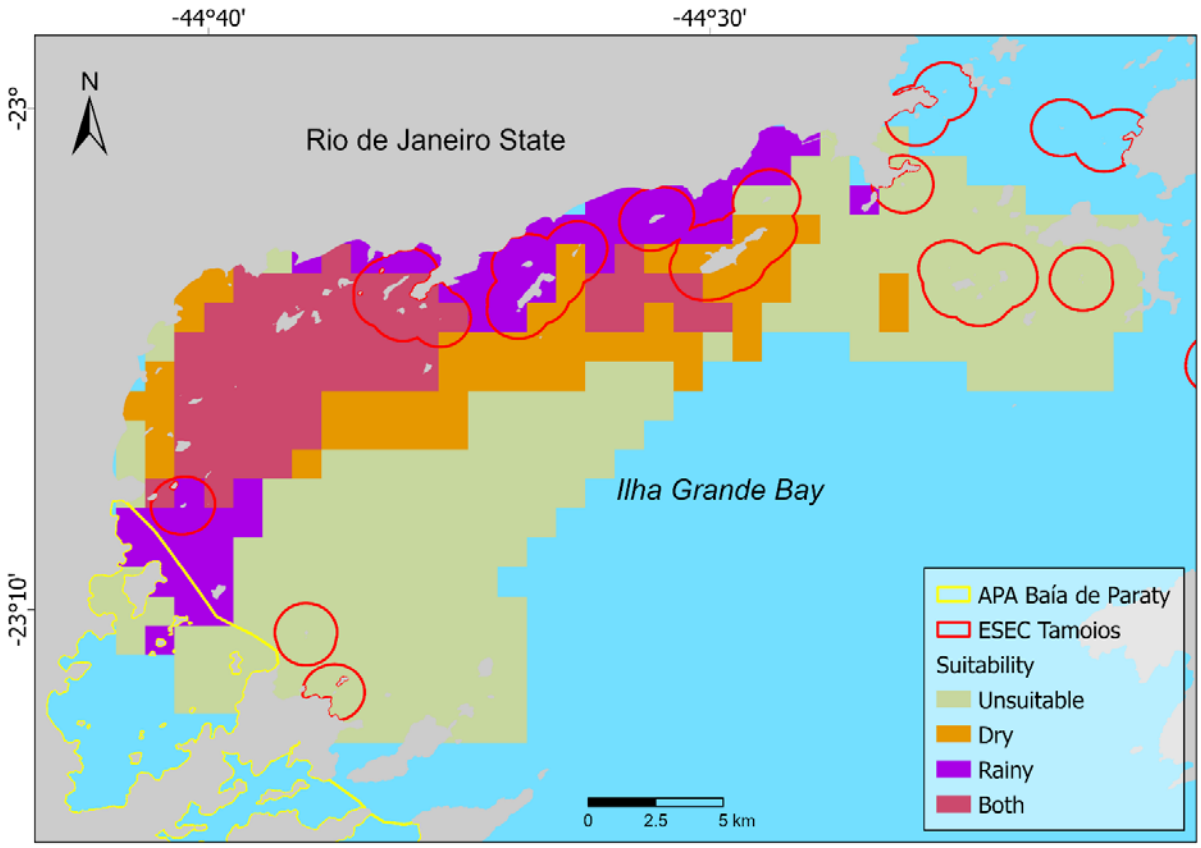
Chlorophyll was the most important variable in explaining the suitability of the Guiana dolphin's feeding behavior, regardless of the specific feeding tactics, during the dry season, whereas depth was the most important during the rainy season. Shipping traffic was also important in both seasons (Table 3). Higher suitability was observed in areas with higher chlorophyll values, closer to islands, and with lower vessel traffic, regardless of the season. The most suitable areas were also found in shallower waters during the rainy season, whereas the opposite was true during the dry season (Table 3). Maps of the explanatory variables during dry and rainy seasons can be found respectively in Supplementary Figures 1 and 2.

Table 3 – Importance of explanatory variables in explaining the suitability of Guiana dolphin's (*Sotalia guianensis*) feeding behavior in Ilha Grande Bay, SE Brazil. Values in bold represent the most important variables. ↗ = greater suitability in areas with higher values, → = greater suitability in areas with average values, ↘ = lower suitability in areas with higher values.

Variable	**Dry season**		**Rainy season**	
Chlorophyll	**0.40**	↗	0.14	↗
Depth	0.23	↗	**0.44**	↘
Distance to islands	0.13	↘	0.09	↘
Particulate organic carbon	0.16	↗	0.08	→
Seabed slope	0.10	↘	0.06	↗
Shipping traffic	0.30	↘	0.25	↘
Underwater noise	0.06	→	0.10	↘

In both seasons, the northwestern part of the study area exhibited higher suitability for the Guiana dolphin's feeding behavior. During the dry season, the most suitable areas were further from the coast compared to the rainy season (Figure 4).

Figure 4 – Suitability of Guiana dolphin's, *Sotalia guianensis*, feeding behavior during dry, rainy, and both seasons in Ilha Grande Bay, SE Brazil. APA Baía de Paraty = *Área de Proteção Ambiental da Baía de Paraty*, ESEC Tamoios = *Estação Ecológica de Tamoios*.



A total of 60 fishing nets was identified, with 21 during the dry season (six gillnets and 15 trawling) (Figure 5) and 39 during the rainy season (32 gillnets and seven trawling) (Figure 6). There was a greater overlap of suitable areas with MPAs during the rainy season (27.3%) compared to the dry season (16.2%). However, there was also more overlap between suitable areas and fishing gear during the rainy season (Table 4).

Figure 5 – Overlap between Marine Protected Areas (APA Baía de Paraty and ESEC Tamoios) and fishing gear (Gillnet and Trawling) with the suitable areas for Guiana dolphin's, *Sotalia guianensis*, feeding behavior during dry season in Ilha Grande Bay, SE Brazil. APA Baía de Paraty = *Área de Proteção Ambiental da Baía de Paraty*, ESEC Tamoios = *Estação Ecológica de Tamoios*.

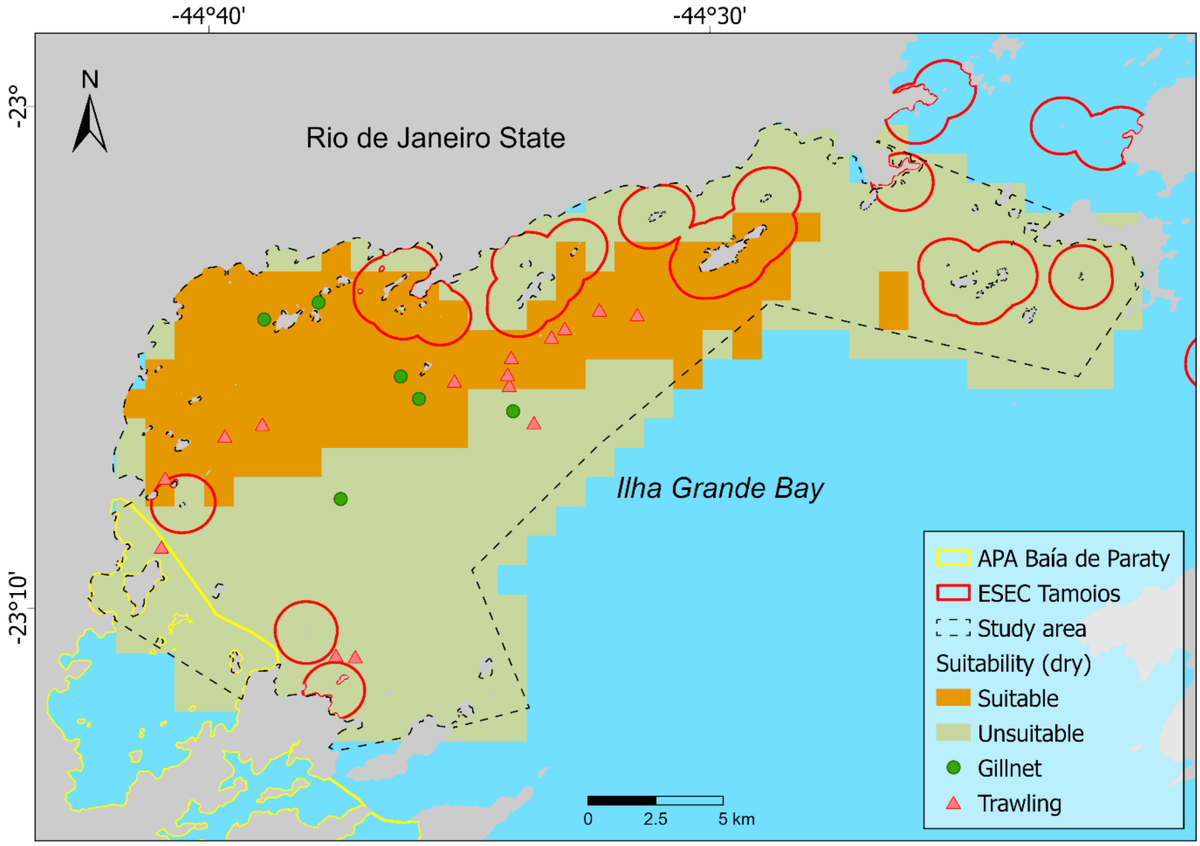


Figure 6 – Overlap between Marine Protected Areas (APA Baía de Paraty and ESEC Tamoios) and fishing gear (Gillnet and Trawling) with the suitable areas for Guiana dolphin's, *Sotalia guianensis*, feeding behavior during rainy season in Ilha Grande Bay, SE Brazil. APA Baía de Paraty = *Área de Proteção Ambiental da Baía de Paraty*, ESEC Tamoios = *Estação Ecológica de Tamoios*.

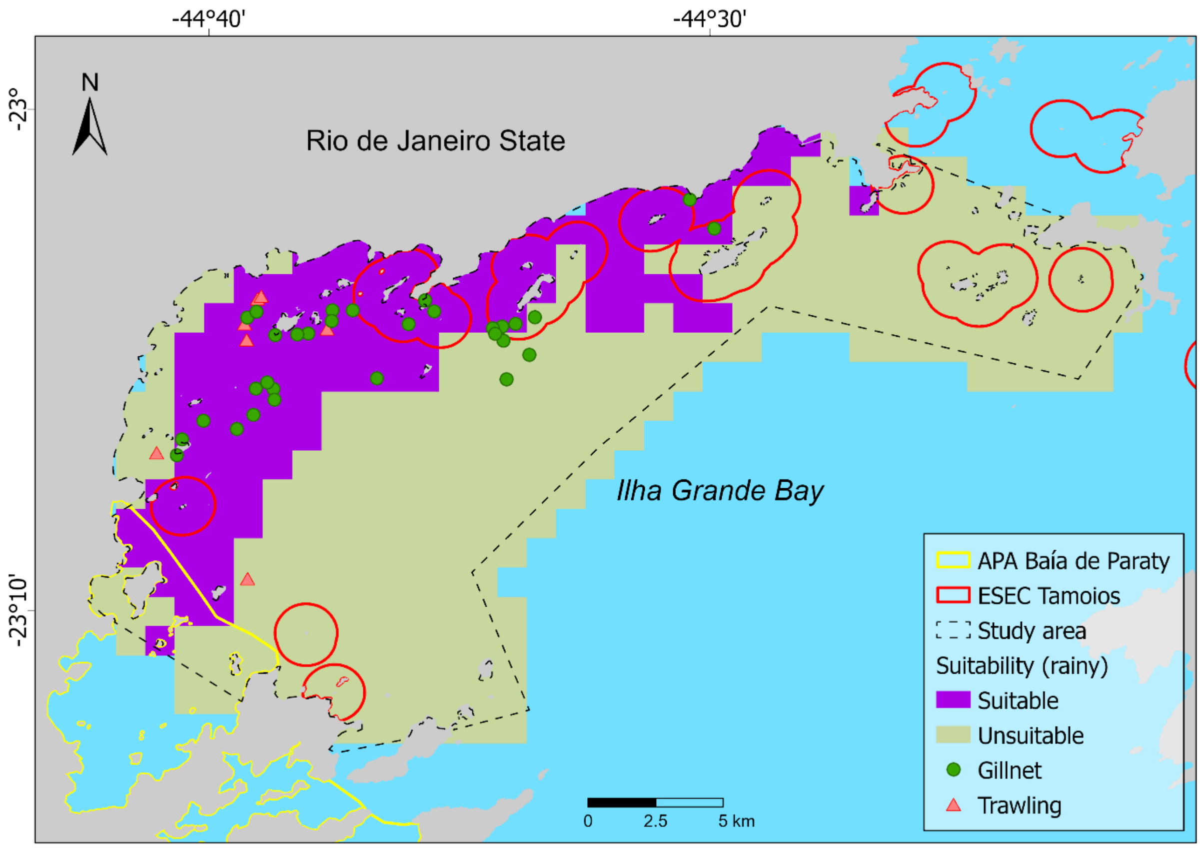


Table 4 – The percentage of overlap between Marine Protected Areas (MPAs) and fishing gear with the suitable areas for Guiana dolphin's, *Sotalia guianensis*, feeding behavior in Ilha Grande Bay, SE Brazil. APA Baía de Paraty = *Área de Proteção Ambiental da Baía de Paraty*, ESEC Tamoios = *Estação Ecológica de Tamoios*.

Season	**Dry**	**Rainy**
MPA		
APA Baía de Paraty	0.0%	5.1%
ESEC Tamoios	16.2%	22.2%
Fishing gear		
Gillnet	66.7%	84.4%
Trawling	73.3%	71.4%

3.2.2 Coordinated feeding tactics suitability

Wall formation was the coordinated feeding tactic with the highest number of records in both seasons, whereas there were only a few records for line abreast. After spatial rarefaction, the occurrence data ranged from seven to 30 (mean = 19, SD = 8) (Table 5).

Table 5 – Occurrence records before and after spatial rarefaction for coordinated feeding tactic models performed by Guiana dolphins, *Sotalia guianensis*, in Ilha Grande Bay, SE Brazil. Tactic = Coordinated feeding tactic, Perp. feeding = Perpendicular feeding.

Season	Tactic	Before	After
Dry	**Kettle**	34	12
	Line abreast	14	7
	Perp. feeding	41	14
	Wall formation	61	16
Rainy	**Kettle**	84	24
	Line abreast	50	24
	Perp. feeding	98	30
	Wall formation	106	28

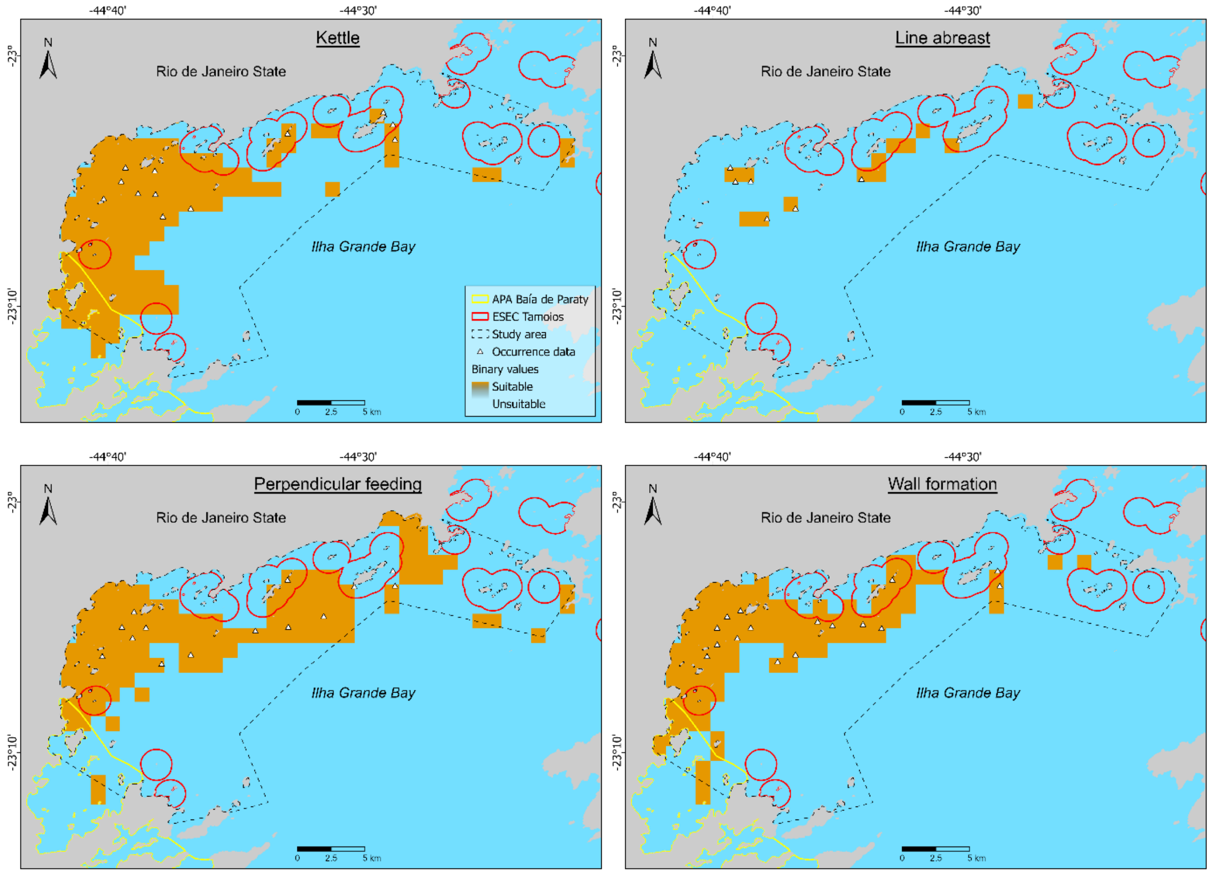
Overall, the seabed slope was the most important variable in explaining coordinated feeding tactics during the dry season, except for line abreast. Depth was the most important during the rainy season for all tactics (Table 6). The most suitable areas, regardless of the season and coordinated feeding tactic, were in shallower waters and a flatter seabed. Areas closer to islands exhibited higher suitability during the dry season compared to the rainy season. No discernible relationship was observed between underwater noise and suitable areas (Table 6). Supplementary Figures 1 and 2 contain the maps of the explanatory variables for the dry and rainy seasons, respectively.

Table 6 – Importance of explanatory variables in explaining and the relationship of each explanatory variable with the suitability of Guiana dolphin's, *Sotalia guianensis*, coordinated feeding tactics in Ilha Grande Bay, SE Brazil. Values in bold represent the most important variables. Tactic = Coordinated feeding tactic, Perp. feeding = Perpendicular feeding, Dist. islands = Distance to islands, Slope = Seabed slope, Noise = Underwater noise. ↗ = greater suitability in areas with higher values, → = greater suitability in areas with average values, ↘ = lower suitability in areas with higher values. Under. noise = underwater noise

Season	Tactic	Depth		Dist. islands		Seabed slope		Under. noise	
Dry	**Kettle**	0.31	↘	0.49	↘	**0.61**	↘	0.15	↘
	Line abreast	**0.46**	↘	0.26	↗	0.41	↘	0.33	↗
	Perp. feeding	0.15	↘	0.32	↘	**0.78**	↘	0.12	↗
	Wall formation	0.30	↘	0.26	↘	**0.59**	↘	0.24	→
Rainy	**Kettle**	**0.78**	↘	0.13	↗	0.16	↘	0.08	→
	Line abreast	**0.85**	↘	0.16	↗	0.08	↘	0.06	→
	Perp. feeding	**0.79**	↘	0.19	↗	0.14	↘	0.06	→
	Wall formation	**0.88**	↘	0.13	↗	0.06	↘	0.06	↗

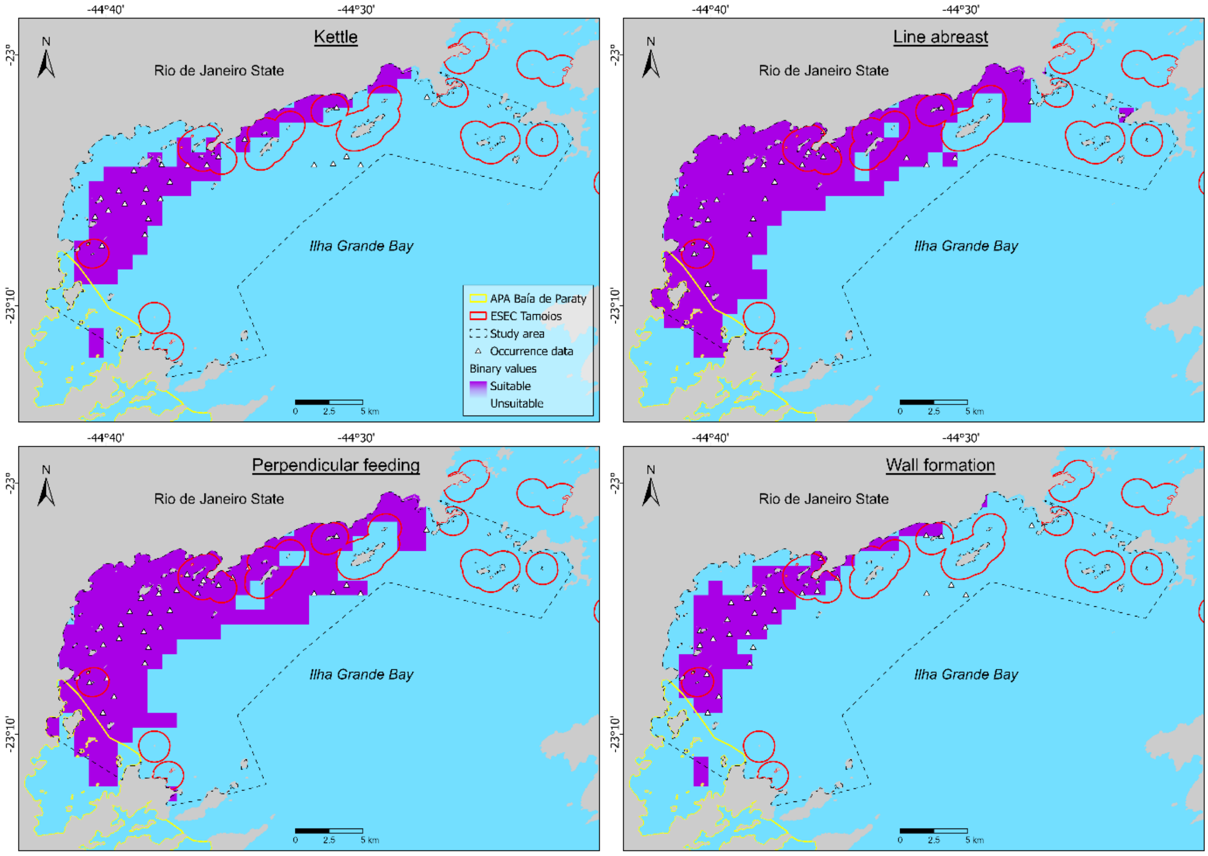
During the dry season, kettle, perpendicular feeding, and wall formation showed a large suitable area, and their patterns were similar. On the other hand, line abreast exhibited fewer suitable areas (Figure 7).

Figure 7 – Suitability of coordinated feeding tactics (kettle, line abreast, perpendicular feeding and wall formation) performed by Guiana dolphins, *Sotalia guianensis*, during the dry season in Ilha Grande Bay, SE Brazil. APA Baía de Paraty = *Área de Proteção Ambiental da Baía de Paraty*, ESEC Tamoios = *Estação Ecológica de Tamoios*.



During the rainy season, line abreast and perpendicular feeding exhibited larger and similarly patterned suitable areas. Kettle and wall formation showed smaller suitable areas, which were also like each other (Figure 8).

Figure 8 – Suitability of coordinated feeding tactics (kettle, line abreast, perpendicular feeding and wall formation) performed by Guiana dolphins, *Sotalia guianensis*, during the rainy season in Ilha Grande Bay, SE Brazil. APA Baía de Paraty = *Área de Proteção Ambiental da Baía de Paraty*, ESEC Tamoios = *Estação Ecológica de Tamoios*.



During the dry season, it was challenging to identify areas where there was congruence among all coordinated feedings tactics (Figure 9). On the other hand, there were many suitable areas for performing all tactics during the rainy season, particularly in the northwestern part of the study area (Figure 10).

Figure 9 – Map of richness showing the sum of coordinated feeding tactics (zero to four) performed by Guiana dolphins, *Sotalia guianensis*, during the dry season in Ilha Grande Bay, SE Brazil. APA Baía de Paraty = *Área de Proteção Ambiental da Baía de Paraty*, ESEC Tamoios = *Estação Ecológica de Tamoios*.

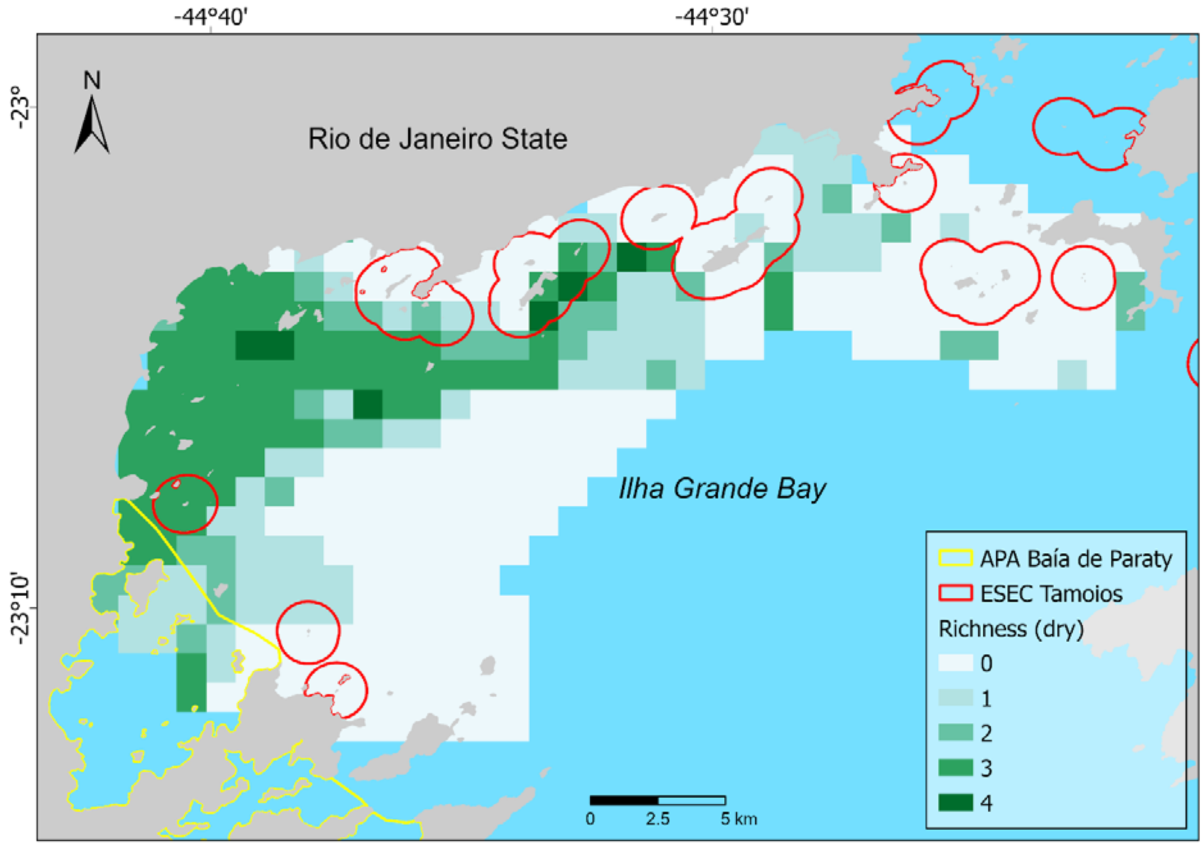
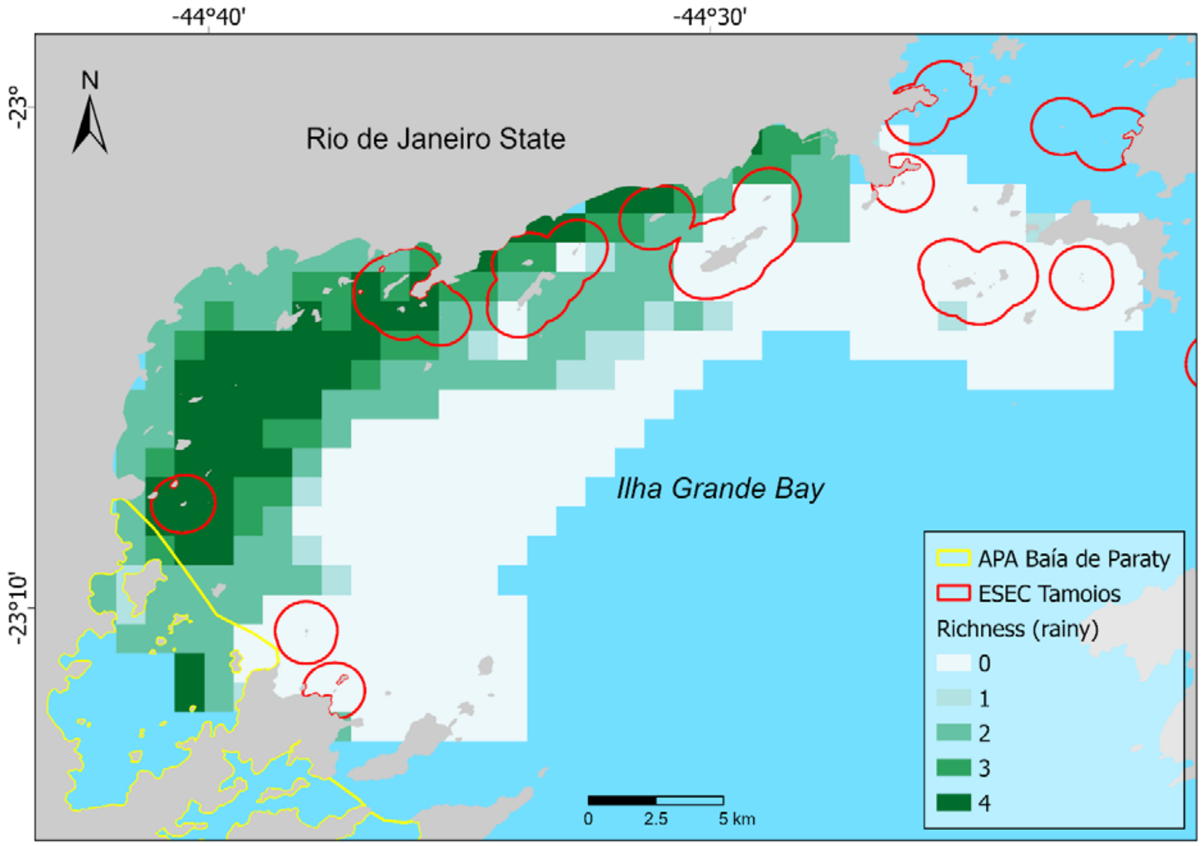


Figure 10 – Map of richness showing the sum of coordinated feeding tactics (zero to four) performed by Guiana dolphins, *Sotalia guianensis*, during the rainy season in Ilha Grande Bay, SE Brazil. APA Baía de Paraty = *Área de Proteção Ambiental da Baía de Paraty*, ESEC Tamoios = *Estação Ecológica de Tamoios*.



3.3 Discussion

We have provided the first maps of suitable areas used by dolphins when feeding, explicitly modeling in function of environmental and human activities. Studying a resident population in a small study area has allowed us to present refined results regarding the feeding behavior of a threatened species. Our findings showed that the factors influencing the suitability of feeding behavior and the performance of coordinated feeding tactics by Guiana dolphins can vary depending on the season. Furthermore, we have shown that local MPAs are not preferentially used for dolphins during their feeding behavior.

The most suitable areas were found in locations with higher chlorophyll values. The IGB receives inputs from several rivers, transporting nutrients from the land and leading to a high concentration of them into the bay (SEMADS, 2001). Chlorophyll levels are positively correlated with the abundance of zooplankton and fish (Duarte et al., 2014; Capuzzo et al., 2018), making the area suitable for their predators, such as the Guiana dolphin (Tardin et al., 2020). Depth was more important during the rainy season. Sardines are the primary fishery in IGB (Cordeiro et al., 2020), and during the rainy season, the greater influence of the SACW enables the occurrence of larger sardine schools (Paiva and Motta, 2000; Palma and Matano, 2009). Sardines are found in shallower waters in the region (Paiva and Motta, 2000), which may explain the higher suitability for feeding behavior of the Guiana dolphin at shallower depths.

During the performance of coordinated feeding tactics, depth and seabed slope were the most important variables in explaining suitable areas. Shallow waters were found to be more suitable, which can be related to a smaller water column for herding and capturing prey. Greater suitability may also be associated with the abundance and type of prey found in shallower waters (Heithaus and Dill, 2002; Cañadas and Hammond, 2008). The performance of feeding tactics was more suitable in flatter regions and further from islands. This could be attributed to bathymetry, as steeper regions tend to be deeper. A similar finding was also observed for the Franciscana dolphin (*Pontoporia blainvillei*), another coastal and resident species in bays and estuaries (Paitach et al., 2023). In the present study, the most suitable areas also overlapped with the noisiest ones, raising concerns about the potential negative impact of underwater noise on the communication of Guiana dolphins during their feeding.

Regarding coordinated feeding tactics, the seabed slope emerged as the most influential factor in explaining suitability during the dry season. Considering that mullets are larger and form smaller schools than sardines, two important prey of them, Guiana dolphins require flatter regions to have ample space for herding and capturing their prey effectively. In the rainy season, depth played a crucial role in determining suitable areas for coordinated feeding tactics. Shallower depths lead to the concentration of large fish schools, such as sardines, making them more exposed and easier for Guiana dolphins to capture. A study carried out on dusky dolphins (*Lagenorhynchus obscurus*) in New Zealand revealed that feeding tactics and location change intra-annually and according to the consumed prey, which varies in size and shape (Vaughn et al., 2007). Given the seasonality of the Guiana dolphin's prey in IGB, the changes in coordinated feeding tactics and where they occur may be linked to the type of prey consumed.

Finding areas of congruence between feeding tactics was easier during the rainy season than during the dry season. Although the length of the suitable feeding area was similar between seasons, the feeding tactics were more dispersed during the dry season. This could be related to the type of prey. The influence of the SACW on IBG during the rainy season brings large schools of sardines (Paiva & Motta, 2000). Sardines, for example, form large groups and have small body sizes, being agile and requiring Guiana dolphins to employ a broader repertoire of tactics to successfully capture them. During the dry season, mullet fish are more abundant in an adjacent bay to IGB (Silva & Araújo, 2000). Since mullets are larger and less agile than sardines, it is likely that Guiana dolphins may not need to employ as many tactics to catch them, optimizing the energetic cost. Our result corroborates with what was described by Tardin et al. (2020) for habitat use in the same study area.

The suitability was lower in regions with higher vessel traffic. Shipping traffic is commonly linked to increased noise, which was also negatively correlated with suitable areas. Given that dolphins tend to vocalize more while feeding (Acevedo-Gutiérrez and Stienessen, 2004), noisier regions may hinder vocalization and coordination of feeding tactics, making them unsuitable for such behavior. In Sepetiba Bay, an adjacent area, considering the increasing number of human activities, Guiana dolphins are spending less time feeding and vocalizing, and avoiding areas close to shipping routes and anchoring areas (Maciel et al., 2023).

The IGB encompasses multiple traditional communities whose main activity and source of income is fishing (Cordeiro et al., 2020). As expected, there was a high overlap between the suitable feeding areas for Guiana dolphins and fishing nets. Bycatch is one of the major causes of dolphin mortality (Van Waerebeek et al., 2007; Zappes et al., 2016; Schoeman et al., 2020), and there is a low overlap between local MPAs, which could mitigate this conflict, and the most suitable feeding areas for Guiana dolphins. Less than a quarter of the suitable areas are within MPAs' boundaries, indicating that the local MPAs are ineffective in addressing this issue.

Our study provides valuable insights into the suitability of the feeding behavior and coordinated feeding tactics for the Guiana dolphin population in IGB. We found that the factors influencing feeding behavior and coordinated feeding tactics vary with the season, emphasizing the importance of considering temporal dynamics in conservation efforts. The presence of high vessel traffic and associated noise negatively impacts the suitability of feeding areas, potentially affecting the communication and coordination of the dolphins during feeding. Furthermore, the overlap between suitable feeding areas and fishing nets highlights the risk of bycatch and the need for improved management strategies to mitigate this conflict.

Despite the existence of local MPAs, our findings indicate that currently they are not efficient for the Guiana dolphin conservation, emphasizing the importance of reassessing and strengthening conservation measures in the region. Recommendations include promoting sustainable fishing practices to minimize bycatch and enhancing the effectiveness of MPAs. Additionally, it will be important to further investigations to understand the specific impacts of underwater noise on dolphins’ communication and behavior during feeding events.

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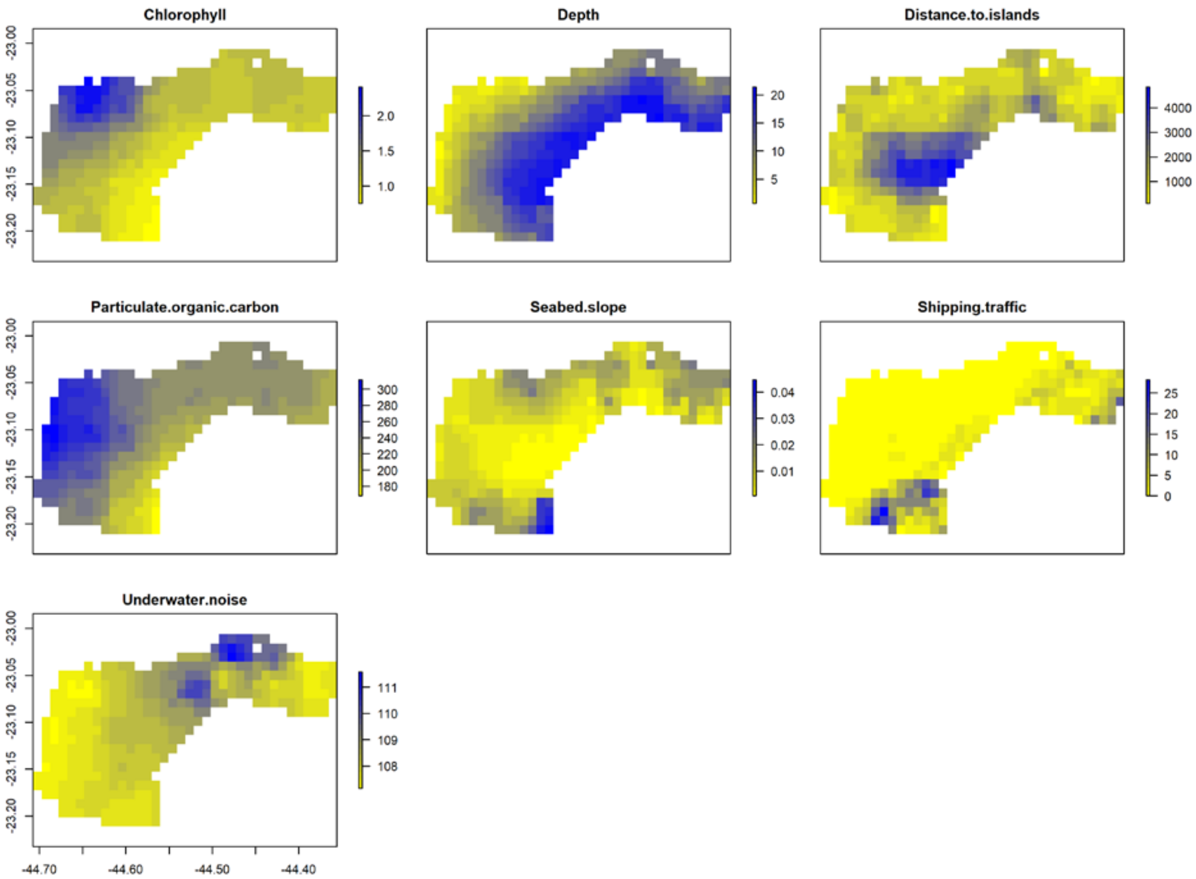
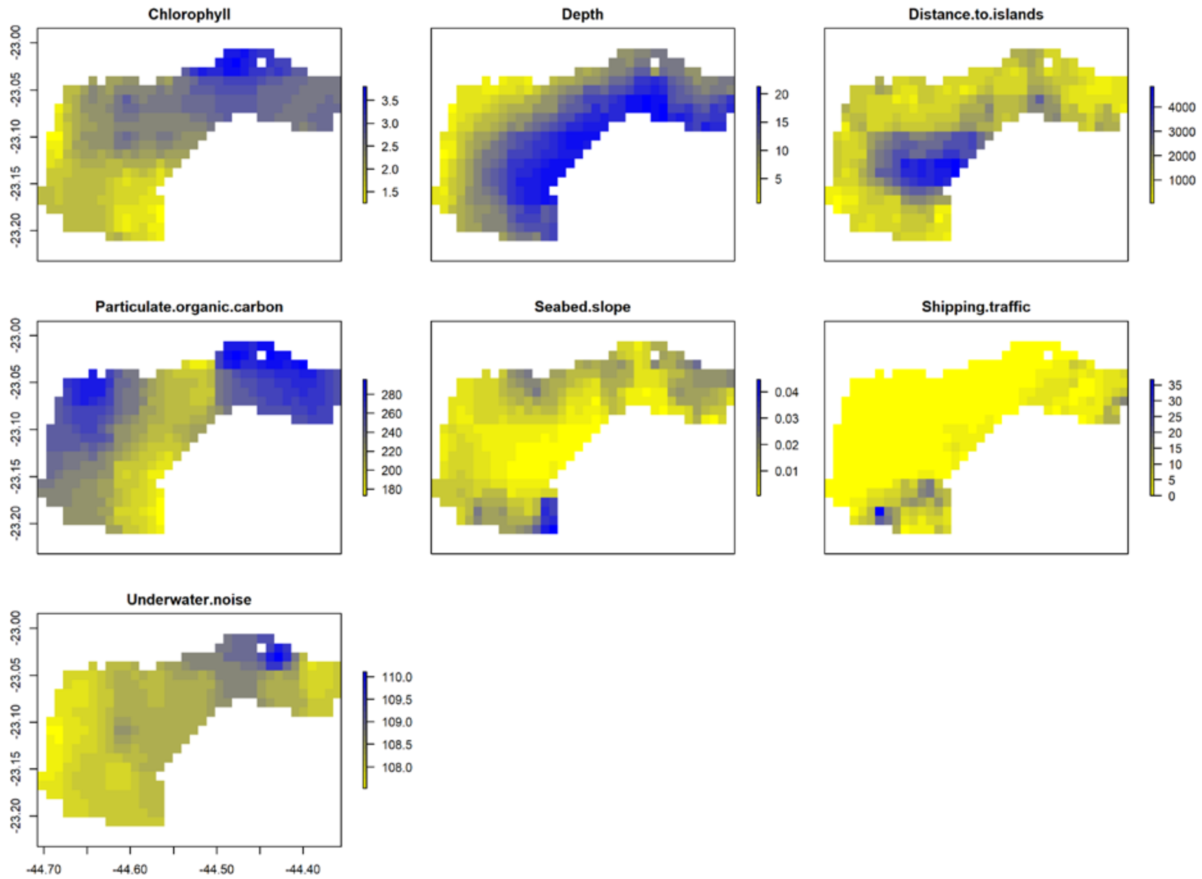
Supplementary material

Supplementary Figure 1 – Environmental layers used as explanatory variables to model the suitability of feeding behavior and coordinated feeding tactics performed by the Guiana dolphin, *Sotalia guianensis*, during the dry season in Ilha Grande Bay, SE Brazil. For the coordinated feeding tactics models, only the variables chlorophyll, depth, particulate organic carbon, and underwater noise were considered.



Supplementary Figure 2 – Environmental layers used as explanatory variables to model the suitability of feeding behavior and coordinated feeding tactics performed by the Guiana dolphin, *Sotalia guianensis*, during the rainy season in Ilha Grande Bay, SE Brazil. For the coordinated feeding tactics models, only the variables chlorophyll, depth, particulate organic carbon, and underwater noise were considered.



DISCUSSÃO

A conservação dos cetáceos é uma preocupação crescente em todo o mundo devido à sua importância ecológica e à sua vulnerabilidade a diversas ameaças. Neste tópico, abordaremos os principais pontos levantados nos três capítulos da tese, bem como suas implicações para a conservação dessas espécies e dos ecossistemas marinhos como um todo.

No primeiro capítulo, enfatizamos a importância de compreender os fatores que influenciam a distribuição das espécies, especialmente para a tomada de decisões assertivas em sua conservação. Nossa revisão sistemática mostrou que, embora as técnicas de modelagem de distribuição de espécies sejam amplamente utilizadas para prever a distribuição de diversas espécies, os estudos sobre baleias (Mysticeti) ainda carecem de um protocolo analítico bem estabelecido para garantir a replicabilidade das análises. Identificamos que fatores como a concentração de clorofila, profundidade, distância da costa, temperatura da superfície do mar e declive do relevo submarino são essenciais para explicar a distribuição dessas espécies. No entanto, a resposta da ocorrência das espécies a essas características depende do tipo de habitat (reprodução, alimentação e permanente) e da zona marítima (costeira e oceânica) das variáveis explicativas. Esses achados ressaltam a necessidade de considerar esses fatores de maneira cuidadosa e fundamentada para direcionar as medidas de conservação para baleias e golfinhos.

No segundo capítulo, focamos na importância das Áreas Marinhas Protegidas (AMPs) como ferramentas essenciais para enfrentar os desafios impostos pelas atividades humanas cumulativas sobre a biodiversidade marinha. Nossa pesquisa buscou identificar áreas prioritárias para a conservação das baleias-de-bryde (*Balaenoptera brydei*) e dos golfinhos-nariz-de-garrafa (*Tursiops truncatus*) ao longo da costa brasileira, considerando sua exposição às atividades humanas cumulativas e à sobreposição com as AMPs existentes. Utilizando modelagem de adequabilidade, identificamos áreas mais adequadas para essas espécies, principalmente na região Sudeste do Brasil, onde se concentra o maior número de atividades humanas. Águas mais rasas, com maior produtividade primária e riqueza de nutrientes, mostraram-se mais adequadas para ambas as espécies. No entanto, a região Sudeste também abriga o maior número de AMPs altamente e totalmente protegidas, embora muitas delas estejam situadas em regiões costeiras e não englobem áreas oceânicas com alta exposição às atividades humanas cumulativas. Nossos resultados enfatizam a necessidade de priorizar esforços de conservação e implementar medidas de mitigação para reduzir conflitos entre a proteção da biodiversidade e as atividades humanas nessa importante região econômica do país.

No terceiro capítulo, nossa pesquisa se voltou para o estudo do comportamento alimentar do boto-cinza (*Sotalia guianensis*) na Baía da Ilha Grande, Sudeste do Brasil. Essa espécie é considerada ameaçada e sua alimentação é crucial para seu crescimento, reprodução e sobrevivência. Utilizando a modelagem de adequabilidade, identificamos os fatores ambientais que influenciam o comportamento alimentar do boto-cinza e suas táticas coordenadas de alimentação. Descobrimos que a concentração de clorofila, profundidade e tráfego de embarcações foram fatores significativos que influenciaram a adequabilidade do comportamento alimentar. As áreas mais adequadas para alimentação ocorreram em regiões com maiores valores de clorofila, mais próximas das ilhas e com menor tráfego de embarcações. Essas descobertas nos alertam sobre a sobreposição dessas áreas com redes de pesca, aumentando o risco de captura incidental e mostrando a necessidade de medidas mais eficazes para reduzir esse conflito e melhorar a efetividade das AMPs locais. Além disso, nossos resultados também destacaram a importância de considerar os efeitos negativos do ruído submarino no comportamento dos botos-cinza e a implementação de estratégias de mitigação.

De forma geral, os resultados dos três capítulos mostraram abordagens de conservação focadas em baleias e golfinhos, que por serem espécies guarda-chuva podem trazer benefícios amplos para outras espécies que compartilham os mesmos habitats. Além disso, as abordagens feitas consideraram diferentes escalas espaciais e temporais e particularidades de cada espécie, o que importante para o direcionamento de estratégias de conservação eficazes e replicáveis.

Nesse sentido, a criação e o aprimoramento de AMPs devem ser uma prioridade para garantir a preservação das espécies de cetáceos e de seus habitats, reduzindo os impactos humanos sobre a biodiversidade marinha. Além disso, o entendimento detalhado do comportamento e das necessidades específicas dos cetáceos é crucial para a implementação de medidas de conservação efetivas e para a mitigação dos riscos impostos pelas atividades humanas, como a pesca e o tráfego de embarcações.

Por fim, é essencial que as decisões de conservação sejam fundamentadas em pesquisas científicas sólidas e replicáveis, para garantir a eficácia das medidas adotadas. A colaboração entre cientistas, gestores ambientais, governos e a sociedade civil é fundamental para enfrentar os desafios complexos da conservação da biodiversidade e para garantir o bom funcionamento dos ecossistemas marinhos.

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