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Thayusky da Penha Correa

# Distribuição, uso do habitat e estimativas populacionais dos golfinhos-pintados (*Stenella attenuata* e *Stenella frontalis*) na Bacia de Santos, Oceano Atlântico Sudoeste

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Tese apresentada ao Programa de Pós-Graduação em Ecologia da Universidade Federal de Santa Catarina, para a obtenção de título de Doutora em Ecologia.

Orientadora: Marta Jussara Cremer, Dra.
Coorientador: Leonardo Liberali Wedekin, Dr.

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Prof. Dr. Rodrigo Hipolito Tardin Oliveira
Universidade Federal do Rio de Janeiro

Prof. Dr. Paulo Cesar de Azevedo Simões-Lopes
Universidade Federal de Santa Catarina

Profa. Dra. Liliane Ferreira Lodi
Instituto Mar Adentro

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Orientadora

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*Eu dedico esta tese à Regina, minha mãe, que, com muita coragem e trabalho braçal, permitiu-me alcançar o mais alto título acadêmico que um indivíduo pode receber*

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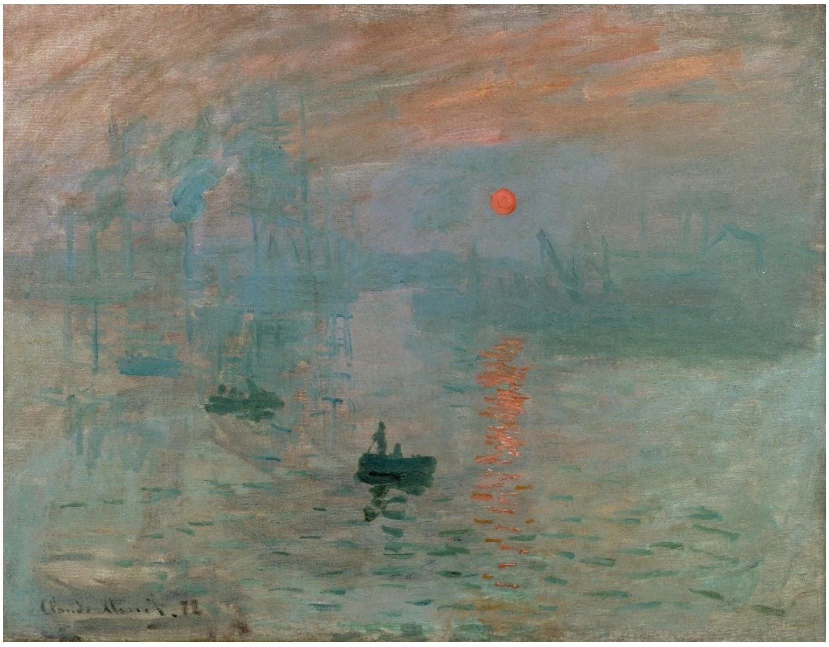

*Impression, soleil levant, 1874*
*(Claude Monet)*

"Fomos, durante muito tempo, embalados com a história de que somos a humanidade. Enquanto isso – enquanto seu lobo não vem – , fomos nos alienando desse organismo de que somos parte, a Terra, e passamos a pensar que ele é uma coisa e nós, outra: A Terra e a humanidade. Eu não percebo onde tem alguma coisa que não seja natureza. Tudo é natureza. O cosmos é natureza. Tudo em que eu consigo pensar é natureza."

Ailton Krenak (2020, p. 16-17)

**RESUMO**

Os golfinhos-pintados do gênero *Stenella* são amplamente distribuídos, ocorrendo de regiões tropicais a temperadas. O golfinho-pintado-pantropical (*Stenella attenuata*) habita águas do Atlântico, Pacífico e Índico, enquanto a ocorrência do golfinho-pintado-do-Atlântico (*Stenella frontalis*) está restrita às águas do oceano Atlântico. Embora ocorram em águas jurisdicionais brasileiras, o conhecimento sobre a ecologia de suas populações ainda é escasso. Dessa forma, a presente tese teve como objetivo geral investigar a distribuição, uso do habitat e estimativas populacionais de *S. attenuata e S. frontalis* na Bacia de Santos, área localizada na porção sudoeste do Oceano Atlântico entre 23°S e 27°S. De novembro de 2015 a março de 2021, um total de 25 cruzeiros embarcados monitoraram sistematicamente a bacia, registrando 40 grupos de golfinho-pintado-pantropical e 125 grupos de golfinho-pintado-do-Atlântico. Com base nesses dados, no primeiro capítulo, foram caracterizadas a distribuição e o uso do habitat do golfinho-pintado-pantropical. Os resultados revelaram que essa espécie ocorre consistentemente na Bacia de Santos, com exceção do período do inverno austral. Os registros dos grupos ocorreram em regiões de profundidades superiores a 200 metros e temperaturas superficiais médias da água em torno de 25,8°C. No segundo capítulo, estimaram-se a densidade e abundância do golfinho-pintado-do-Atlântico durante dois períodos sazonais por meio do método de transecções lineares com amostragem de distâncias. Esse trabalho resultou na primeira estimativa populacional do golfinho-pintado-do-Atlântico no oceano Atlântico Sudoeste. Foram observadas variações significativas nas estimativas populacionais, tanto entre as diferentes regiões da bacia quanto entre os dois períodos. Estimaram-se 8,692 indivíduos (CV = 0,27) durante a estação fria e 19,762 indivíduos (CV = 0,18) na estação quente. No terceiro capítulo, foi utilizada a abordagem de modelagem de densidade de superfície, com o objetivo de investigar as relações entre a densidade do golfinho-pintado-do-Atlântico, as características do habitat e feições oceanográficas. Os resultados indicaram que tanto a profundidade média quanto a temperatura da superfície do mar foram importantes preditores ecológicos para a espécie. Ainda, a abundância variou entre as feições oceanográficas avaliadas. Portanto, diante da crescente presença de estruturas e atividades antrópicas potencialmente prejudiciais a esses animais na área de estudo, esta tese fornece informações essenciais para subsidiar futuras discussões sobre estratégias de conservação das duas espécies de *Stenella* registradas na região mais desenvolvida do país.



**Palavras-chave**: amostragem por distâncias; cetáceos; ecologia de populações; Embaiamento Sul Brasileiro

# ABSTRACT

Spotted dolphins of the genus *Stenella* are widely distributed across tropical to temperate regions. The pantropical spotted dolphin (*Stenella attenuata*) inhabits the Atlantic, Pacific, and Indian Oceans, while the Atlantic spotted dolphin (*Stenella frontalis*) is restricted to the waters of the Atlantic Ocean. Although both species occur in Brazilian waters, knowledge of their population ecology remains scarce. Therefore, the main goal of this thesis was to investigate the distribution, habitat use, and provide population estimates of *S. attenuata* and *S. frontalis* in the Santos Basin, a region in the southwestern portion of the Atlantic Ocean between 23°S and 27°S. From November 2015 to March 2021, a total of 25 shipboard surveys systematically monitored the basin and recorded 40 groups of pantropical spotted dolphins and 125 groups of Atlantic spotted dolphins. Based on these dataset, the first chapter characterized the distribution and habitat use of the pantropical spotted dolphin. The results revealed that this species occurs consistently in the Santos Basin, except during the austral winter. Sightings were recorded in areas with depths greater than 200 meters and mean sea surface temperatures around 25.8°C. In the second chapter, density and abundance estimates of the Atlantic spotted dolphin were obtained for two seasonal periods using line transect sampling. This effort resulted in the first population estimate of the Atlantic spotted dolphin in the southwestern Atlantic Ocean. Significant variations in population estimates were observed both among different regions of the basin and the two seasons. An estimation of 8,692 individuals (CV = 0.27) were found during the cold season and 19,762 individuals (CV = 0.18) during the warm season. In the third chapter, a density surface modelling approach was applied to investigate the relationships between Atlantic spotted dolphin density, habitat characteristics, and oceanographic features. The results indicated that both mean depth and sea surface temperature were important ecological predictors for the species. Moreover, dolphin densities varied in response to the presence of specific oceanographic features. Due the increasing presence of offshore structures and anthropogenic activities potentially harmful to these animals, this thesis provides relevant information that can support future discussions on conservation strategies for both *Stenella* species recorded in the most industrially developed region of the country.



**Keywords**: distance sampling; cetaceans; population ecology; South Brazil Bight

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# 1 INTRODUÇÃO GERAL

Os cetáceos ocupam uma ampla variedade de habitats e desempenham papéis fundamentais nos ecossistemas aquáticos, atuando na ciclagem de nutrientes, em interações cooperativas com outras espécies e na dinâmica trófica (BOWEN, 1997; ESTES *et al*., 2011; JEFFERSON *et al*., 2015). A distribuição desses vertebrados marinhos não ocorre de forma aleatória, sendo influenciada por diversos fatores. Um dos mais consistentemente estudados diz respeito à associação com a distribuição de suas presas, uma vez que os cetáceos ocupam níveis elevados na teia trófica marinha (AMARAL *et al*., 2012; HENDERSON *et al*., 2014; NEUMANN, 2001). Além disso, esses animais ocorrem exclusivamente, ou preferencialmente, em áreas com características específicas de profundidade, temperatura da água e/ou processos oceanográficos. Tais atributos oceanográficos definem o habitat dos cetáceos, especialmente quando a distribuição direta de suas presas não pode ser avaliada. Assim, as características físicas do fundo do oceano influenciam diretamente a presença ou ausência de peixes bentônicos ou demersais. Já os organismos pelágicos, que habitam a coluna d'água, como peixes e cefalópodes, são influenciados indiretamente pela fisiografia por meio de mecanismos como o afloramento de nutrientes, que impulsiona a produção de algas e fitoplâncton. Esse aumento na produção primária resulta na agregação de zooplâncton e, por sua vez, de outros representantes da cadeia trófica, até chegar aos cetáceos (CAÑADAS; SAGARMINAGA; GARCÍA-TISCAR, 2002; DE OLIVEIRA SANTOS *et al*., 2002; MILMANN *et al*., 2016; PAULY; CHRISTENSEN, 1995).

Múltiplos fatores interligados influenciam a abundância e a distribuição de cetáceos, desde sua história evolutiva até características intrínsecas de cada espécie e do ambiente em que vivem (FORCADA *et al*., 2008). Os aspectos ecológicos (como distribuição de presas, predadores e competidores) de cada espécie englobam muitos outros fatores. Dentre esses, destacam-se: fatores demográficos (abundância, idade e ciclo de vida dos indivíduos), fatores evolutivos (morfologia e fisiologia), fatores ambientais (profundidade, temperatura da água, salinidade e tipo de substrato) e fatores antrópicos (degradação do habitat, capturas incidentais e efeito de mudanças climáticas). Geralmente, as espécies de cetáceos exibem padrões de distribuição bem definidos, indicando que sua ocorrência em determinadas regiões não é aleatória, mas atribuída a fenômenos de grande escala, como, por exemplo, estruturas oceanográficas (DO AMARAL *et al*., 2018; KANAJI *et al*., 2016). No entanto, é importante ressaltar que uma mesma espécie pode apresentar comportamentos e uso de áreas distintos nos diferentes locais onde ocorre (PERRIN; AKIN; KASHIWADA, 1991). Por isso, há algumas regiões em que o conhecimento da ecologia de certas espécies ainda é fragmentado ou até inexistente.

Nos últimos anos, o desenvolvimento e o avanço de métodos de modelagem espacial, sistemas de informação geográfica (GIS) e sensoriamento remoto possibilitaram o acesso a dados ambientais em diferentes escalas e até em áreas remotas (BOYD; FOODY, 2011). Uma vez obtidas as informações quantitativas sobre a ocorrência de uma espécie e seus preditores ambientais em um determinado espaço-tempo, os modelos estatísticos puderam ser utilizados para identificar padrões e processos ecológicos mais complexos (FLETCHER; FORTIN, 2018; FORTIN *et al.*, 2012). Essa abordagem permitiu reunir teorias ecológicas e modelagem de dados para elucidar como os organismos, por exemplo, utilizam o espaço e como esse uso pode estar relacionado, ou não, aos atributos incluídos dentro dos modelos (MASSOL *et al.*, 2011). Isso, por sua vez, tem permitido descrever e quantificar os fatores que determinam a distribuição e abundância das espécies (GUISAN; ZIMMERMANN, 2000; REDFERN *et al.*, 2006), questões centrais da ecologia. Portanto, com base nessas ferramentas, os estudos com cetáceos têm avançado anualmente na identificação de habitats essenciais (CAÑADAS *et al.*, 2005), predições de flutuações populacionais (BECKER *et al.*, 2019), na criação de novas áreas marinhas protegidas (EMBLING *et al.*, 2010) e no manejo de áreas já existentes (AZZELLINO *et al.*, 2012).

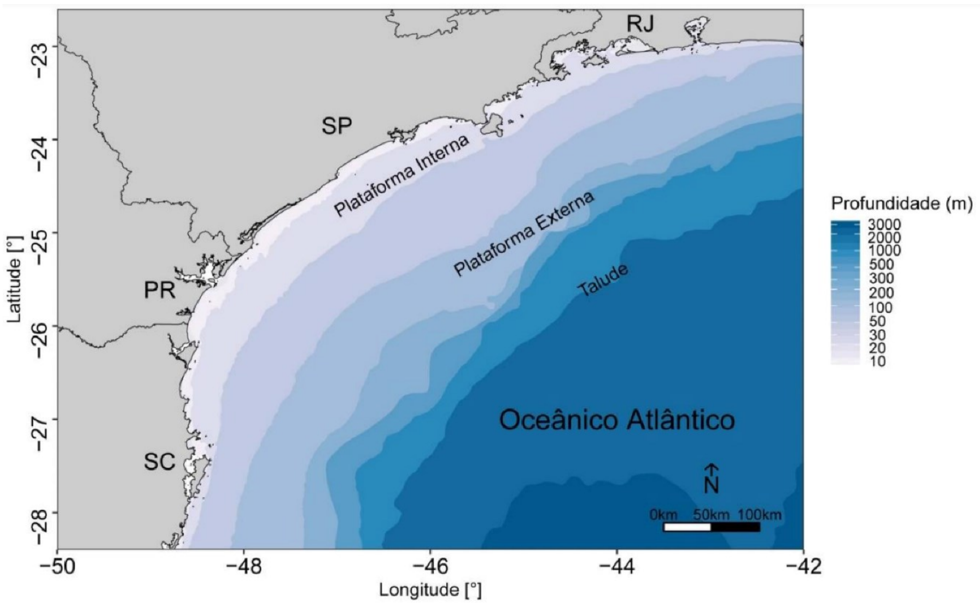
As condições ambientais influenciam não apenas a distribuição, mas também a densidade e a abundância das espécies, que tendem a variar de um local para outro. No contexto da ecologia, a definição mais pragmática de abundância vem de KREBS (2014), que define como o "número, ou biomassa, de organismos de uma espécie em uma área geral”. Embora a contagem direta de todos os indivíduos em uma população seja um método convencional para determinar abundância, essa abordagem não costuma ser viável, especialmente para organismos móveis. Quantificar cetáceos apresenta limitações no que diz respeito ao acesso ao ambiente marinho, à logística associada à coleta de dados, às particularidades do comportamento dos animais (EVANS; HAMMOND, 2004), e outros. Portanto, para aumentar a confiabilidade do número total de indivíduos presentes em uma população, o mais indicado é trabalhar com estimativas, ou seja, estimar o número de indivíduos presentes em uma área específica durante um período de tempo definido (e.g., BUCKLAND *et al.*, 2001). Como essas estimativas acabam se referindo à “população” de uma área, e não a uma população biológica mais ampla, torna-se crucial definir a qual população se refere a medida. Isso assegura sua precisão e relevância para comparações com outros estudos e para o direcionamento de esforços de conservação. Há uma variedade de metodologias, ferramentas e abordagens analíticas amplamente utilizadas para estimar o tamanho de populações de cetáceos (KASCHNER *et al.*, 2012). Entre elas: o reconhecimento individual por meio de fotografias (FRUET *et al.*, 2015), extrapolação para regiões pouco estudadas (MANNOCCI *et al.*, 2015), o uso de diferentes plataformas de coleta, como navios e aeronaves (HAMMOND *et al.*, 2013), e até mesmo o uso de imagens de satélite e veículos aéreos não tripulados (STEWART *et al.*, 2024). A escolha é ponderada pelos objetivos, as características comportamentais da espécie-alvo, a disponibilidade de recursos, assim como o uso dessa informação por formuladores de políticas ambientais (DAWSON *et al.*, 2008; THOMAS; WILLIAMS; SANDILANDS, 2007).

O monitoramento biológico de cetáceos, que resulta em estimativas populacionais, tende a enfrentar dois principais desafios: a variação espacial e a detectabilidade imperfeita. Isso ocorre porque as espécies podem ocupar grandes extensões de área, tornando inviável percorrê-las, e devido à incapacidade de detectar todos os indivíduos (BUCKLAND *et al.*, 2001; YOCCOZ *et al.*, 2001), uma vez que os indivíduos só são detectados quando estão na superfície. Portanto, os métodos que contabilizam adequadamente a probabilidade de detecção, como, por exemplo, a amostragem de distâncias, têm sido um dos mais recomendados para estimar o tamanho populacional de espécies de cetáceos em larga escala (BUCKLAND *et al.*, 2001). Esse método realiza levantamentos ao longo de linhas de transecção pré-definidas por meio de embarcações ou aeronaves (HAMMOND *et al.*, 2013; KASCHNER *et al.*, 2012; ROBERTS *et al.*, 2016). Primeiramente, estima-se a densidade de animais por unidade de área e depois extrapola-se a densidade para toda a área levantada, usando modelos estatísticos probabilísticos (BUCKLAND *et al.*, 2001; HAMMOND *et al.*, 2002). Recentemente, modelos preditivos que relacionam a densidade e abundância dos indivíduos às características do ambiente também se consolidaram como uma ferramenta robusta para analisar dados coletados por meio de amostragem de distâncias (GILLES *et al.*, 2016; PANIGADA *et al.*, 2017; ROGAN *et al.*, 2017). Essa técnica analítica envolve a modelagem da densidade populacional observada ao longo dos transectos em função de covariáveis ambientais referenciadas espacial e temporalmente (HEDLEY; BUCKLAND, 2004; MILLER *et al.*, 2013). Porém, a qualidade e confiabilidade dessas estimativas dependem do modelo ajustado aos dados, assim como das covariáveis inseridas (GILLES *et al.*, 2016; SIGOURNEY *et al.*, 2020). Os modelos de densidade de superfície (DSMs) têm sido utilizados para orientar a designação de áreas marinhas protegidas (CAÑADAS; VÁZQUEZ, 2014), avaliar os impactos de atividades humanas sobre mamíferos marinhos em alto-mar (MANNOCCI *et al.*, 2017), e ainda prever a dinâmica populacional de cetáceos diante de eventos climáticos extremos (BECKER *et al*., 2019). Apesar do número crescente de pesquisas que empregam essa abordagem, no Brasil sua aplicação ainda é incipiente (BORTOLOTTO *et al*., 2017).

## 1.1 EMBAIAMENTO SUL BRASILEIRO

Uma área particularmente importante para os cetáceos no Sul e Sudeste do Brasil é denominada, na literatura oceanográfica, como Embaiamento Sul Brasileiro (ESB), ou, em inglês, "South Brazil Bight", uma área de aproximadamente 150.000 km² situada entre Cabo Frio (23ºS) e o Cabo de Santa Marta (28ºS) (EMÍLSSON, 1961, Figura 1). Hidrologicamente, o ESB é principalmente influenciado pela Corrente do Brasil (CB), que se origina da divisão da Corrente Sul Equatorial e se desloca ao longo da plataforma continental em direção à região Sul, carregando a chamada Água Tropical, uma massa de água oligotrófica e quente (SILVEIRA *et al*., 2000). À medida que a CB se desloca, ela perde calor para a atmosfera e se mistura com águas de baixa salinidade e temperatura, originando, assim, a Água Subtropical, que faz parte da Água Central do Atlântico Sul (ACAS), uma massa de água com temperaturas entre 6ºC e 20ºC e salinidade entre 34,6 e 36 ppm (EMÍLSSON, 1961; SILVEIRA *et al*., 2000).

Figura 1- Mapa do Embaiamento Sul Brasileiro




Fonte: Adaptado de BUENO *et al*. (2018)

Uma das características oceanográficas mais marcantes do ESB é a presença sazonal da ACAS na região interior da plataforma continental, que flui para o norte em camadas profundas, podendo alcançar, inclusive, a margem continental (SILVEIRA *et al*., 2000). No verão, regiões de ressurgência da ACAS — fenômeno oceanográfico em que águas profundas e ricas em nutrientes sobem para a superfície — aumentam a produtividade primária, principalmente no litoral do Rio de Janeiro. Já no inverno, a ACAS retrai-se em direção ao limite da plataforma continental, e a Corrente das Malvinas, uma corrente de contorno oeste subpolar, exerce maior influência sobre o ESB (SILVEIRA *et al*., 2000).

Em relação ao relevo, ao longo da costa brasileira, a plataforma continental apresenta variações e características específicas em cada região. Entre 5° e 23°S, a plataforma é bastante estreita, e entre 16° e 20°S ocorre uma expansão correspondente ao Banco de Abrolhos (MAHIQUES *et al*., 2010). A partir de Cabo Frio (23°S), região da ESB, a plataforma alcança sua maior largura, especialmente na porção central, com aproximadamente 230 km, enquanto os extremos norte e sul são as partes mais estreitas, variando entre 50 e 70 km de largura, respectivamente (MAHIQUES *et al*., 2010). Assim, cada região da plataforma continental apresenta características singulares em termos de topografia, correntes marítimas, massas d'água e outras feições oceanográficas (CAMPOS; GONÇALVES; IKEDA, 1995).

## 1.2 A COMUNIDADE DE CETÁCEOS DO BRASIL

Para enfrentar questões ambientais e orientar políticas de manejo e conservação, primariamente, deve-se compreender a ecologia das espécies em discussão (HAMMOND *et al*., 2013; HUNT *et al*., 2020; JAUREGUIBERRY *et al*., 2022; KASCHNER *et al*., 2012; SORENSEN *et al*., 1984). Os esforços de conservação em países em desenvolvimento, como os da América Latina, são urgentes, mas enfrentam limitações, especialmente relacionadas à escassez de recursos financeiros e humanos. Essas restrições comprometem a ampliação do conhecimento ecológico e tornam desafiadora a obtenção de dados fundamentais para a produção científica e para a formulação de políticas ambientais eficazes (ARAGONES; JEFFERSON; MARSH, 1997; GOLDENBERG *et al*., 2022; KASCHNER *et al*., 2012; NELMS *et al*., 2021). Assim, para preencher lacunas e disseminar conhecimento sobre espécies animais que exibem movimentos transfronteiriços em áreas logisticamente desafiadoras, a alternativa é utilizar dados já coletados, provenientes de fontes como pesquisas sísmicas, dados históricos e outros bancos de dados públicos (e.g., BRAULIK *et al*., 2018; DALPAZ *et al*., 2021; HOLST *et al*., 2017).

O Projeto de Monitoramento de Cetáceos na Bacia de Santos (PMC-BS), em vigor desde 2015, avalia diferentes aspectos da ecologia de baleias e golfinhos, bem como os potenciais impactos das atividades de produção de petróleo e gás natural da empresa Petrobras na região (PETROBRAS, 2015). A atuação do projeto é uma medida de compensação exigida pelo processo de licenciamento ambiental federal, conduzido pelo Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA). O PMC-BS utiliza uma abordagem multimétodos para investigar a comunidade de cetáceos nessa região, e a amostragem da bacia ocorre por meio de plataformas embarcadas e aéreas. Até o momento, o projeto identificou 27 espécies de cetáceos, sendo 19 odontocetos e 8 misticetos (PETROBRAS, 2023). Os dados coletados pelo PMC-BS se consolidam como um dos mais relevantes da costa brasileira, impulsionando avanços e descobertas sobre a biologia, genética e ecologia dos cetáceos (e.g., MARTINS *et al*., 2023). Esse banco de dados também comprova a importância da bacia como local de reprodução, alimentação, socialização e descanso de várias espécies (e.g., DALPAZ *et al*., 2023; WEIR *et al*., 2020), assim como registros ocasionais e raros de outras espécies que também utilizam essa região (PETROBRAS, 2023). Isso reforça o potencial do projeto em fornecer dados fundamentais sobre a ecologia, estratégias de história de vida e áreas de distribuição, os quais serão essenciais para abordar os fatores e pressões atuais e potenciais que afetam esses animais.

### 1.2.1 Os modelos biológicos: *Stenella attenuata* e *Stenella frontalis*

Este estudo toma por foco duas espécies do gênero *Stenella*, pertencentes à ordem Artiodactyla, infraordem Cetacea, família Delphinidae. Ambas as espécies apresentam padrões de distribuição específicos ao longo da costa brasileira em resposta às condições hidográficas e topográficas (DO AMARAL *et al*., 2015), sendo elas: o golfinho-pintado-pantropical (*Stenella attenuata* Gray, 1846) e o golfinho-pintado-do-Atlântico (*Stenella frontalis* Cuvier, 1829). A primeira espécie é um golfinho com distribuição global, habitando regiões oceânicas desde os trópicos até zonas temperadas, embora também ocupe zonas costeiras com águas profundas adjacentes, como ilhas oceânicas (MORENO *et al*., 2005; PERRIN; THEWISSEN; WÜRSIG, 2009). Já a segunda espécie apresenta uma distribuição restrita ao Oceano Atlântico, principalmente sobre a plataforma continental, com registros esporádicos em regiões com até 1.000 m de profundidade (MORENO *et al*., 2005; PERRIN; THEWISSEN; WÜRSIG, 2009).

Embora presentes na Bacia de Santos, ambas as espécies ocupam nichos ecológicos distintos em diferentes regiões oceanográficas (DO AMARAL *et al*., 2015) e exibem diferenças no uso do habitat. A seguir, será apresentada uma breve descrição das duas espécies, assim como os hiatos existentes na literatura:

*1.2.1.1 Golfinho-pintado-pantropical – Stenella attenuata (Gray 1846)*

O golfinho-pintado-pantropical é assim denominado devido à presença de "pintas" (ou manchas) em sua pele, um de seus aspectos diagnósticos. Ao nascimento, esses golfinhos não apresentam pintas, mas, à medida que se desenvolvem, adquirem graus variados de pintas brancas na capa dorsal escura. Essa capa apresenta uma coloração escurecida e larga no dorso, que se acentua na região medial do corpo, estreitando-se em direção ao pedúnculo caudal, onde se torna cinza-claro (LODI; BOROBIA, 2013) (Figura 2). Sabe-se, ainda, que o grau de intensidade de pintas é leve em animais de mar aberto e elevado em indivíduos costeiros, a ponto de obliterar a capa (JEFFERSON *et al*., 2015).

Figura 2 - Fotografia de um golfinho-pintado-pantropical saltando para a superfície. A imagem mostra o rostro alongado, a capa dorsal escura contínua e o padrão de pintas em um indivíduo subadulto.

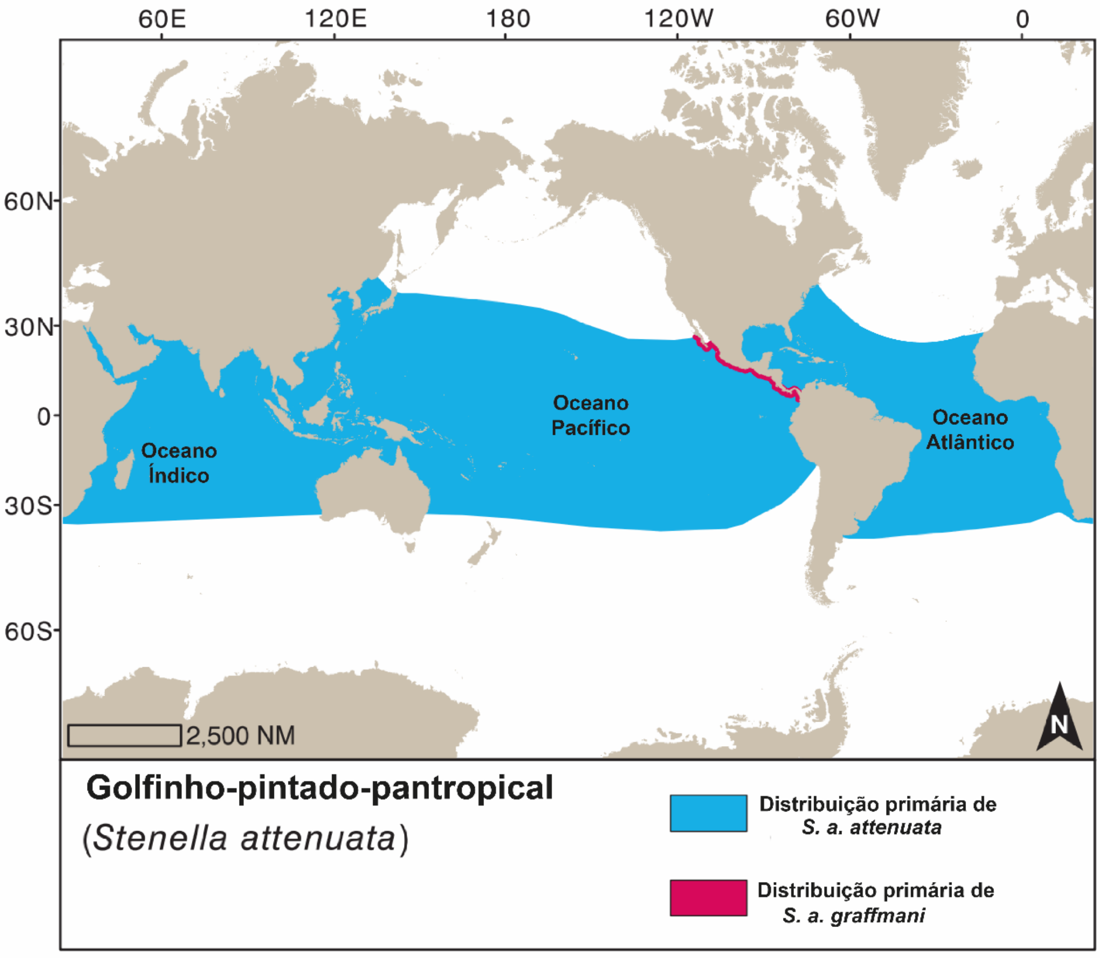
Fonte: PMC-BS

Essa espécie apresenta um corpo delgado e hidrodinâmico, sendo que os animais costeiros encontrados no Pacífico Tropical Oriental possuem um corpo moderadamente robusto

(JEFFERSON *et al*., 2015). Em termos de tamanho, os neonatos medem entre 80 e 85 cm de comprimento, enquanto os adultos variam: as fêmeas medem entre 1,6 e 2,4 metros, e os machos entre 1,6 e 2,6 metros (LODI; BOROBIA, 2013; JEFFERSON *et al*., 2015). O rostro (bico) é relativamente comprido e estreito, bem demarcado em relação ao melão. A extremidade do rostro e os lábios são brancos. A nadadeira dorsal é estreita, falcada e moderadamente pontiaguda; as nadadeiras peitorais são delgadas e recurvadas, enquanto a nadadeira caudal possui uma pequena reentrância medial , comum em membros da família *Delphinidae*, e extremidade pontiaguda (LODI; BOROBIA, 2013).

O golfinho-pintado-pantropical possui uma faixa de distribuição que se estende aproximadamente de 30°N a 40°N até 20°S a 40°S, abrangendo águas tropicais e subtropicais (PERRIN; THEWISSEN; WÜRSIG, 2009). Esses animais são encontrados principalmente em regiões distantes da costa, embora também possam circundar ilhas oceânicas e outras linhas costeiras onde haja águas profundas nas proximidades , como na América Central, Caribe, México, Ilhas Havaianas, Taiwan e Filipinas (JEFFERSON *et al*., 2015). No Oceano Pacífico Tropical, a espécie apresenta variações nas medições cranianas e pós-cranianas, no tamanho e na coloração do corpo, relacionadas à distribuição geográfica , diferenças essas confirmadas inclusive por dados genéticos (ESCORZA-TREVINO *et al*., 2005; LESLIE; ARCHER; MORIN, 2019). Portanto, há registro de ocorrência de duas subespécies: *S. a. attenuata* e *S. a. graffmani*, sendo esta última endêmica da costa do Pacífico Leste (Figura 3; PERRIN, 1975). Neste trabalho, será considerada apenas a subespécie *S. a. attenuata*, referida como *S. attenuata.*

Figura 3 - Mapa da distribuição global de *Stenella attenuata*, destacando as duas formas geográficas: em azul, a forma oceânica (*S. a. attenuata*), e em rosa, a distribuição da forma costeira (*S. a. graffmani*) no leste do Pacífico.




Fonte: Adaptado de JEFFERSON *et al.* (2015)

No Oceano Atlântico, essa espécie é encontrada predominantemente em regiões distantes da costa, em águas profundas e ao redor de ilhas oceânicas (PERRIN; THEWISSEN; WÜRSIG, 2009). No lado ocidental do Oceano Atlântico Sul, a distribuição da espécie se estende aproximadamente da latitude 02°40'S até 22°42'S (GURJÃO, 2020; MORENO *et al*., 2005). Em águas jurisdicionais brasileiras, os registros concentram-se em latitudes mais baixas, especialmente na região Nordeste, com poucos registros documentados nas regiões Sudeste e Sul do país (DI TULLIO *et al*., 2016; DO AMARAL *et al*., 2015; MORENO *et al*., 2005). Segundo Do Amaral *et al*. (2015), as condições ambientais ideais para a ocorrência da espécie incluem profundidades superiores a 1.000 metros, elevadas temperaturas da superfície do mar (>27 °C) e baixa variação térmica (cerca de 2,5 °C). Os golfinhos-pintados-pantropicais geralmente formam grupos com menos de 100 indivíduos, embora, no Brasil, tenham sido observados agrupamentos variando entre 3 e 250 indivíduos (JEFFERSON *et al*., 2015; MORENO *et al*., 2005). É comum o registro dessa espécie em grupos mistos com outras que habitam águas quentes e profundas, como *Stenella longirostris*, possivelmente como estratégia de proteção contra predadores (e.g., DE LIMA *et al*., 2023). Em relação aos hábitos alimentares, por se tratar de uma espécie pelágica, sua dieta ainda é pouco conhecida. No entanto, sabe-se que as formas oceânicas alimentam-se principalmente de pequenos peixes epi- e mesopelágicos (como *Benthosema panamense* e *Hyporhamphus naos*), além de lulas e crustáceos (ENRÍQUEZ-GARCÍA *et al*., 2022; JEFFERSON *et al*., 2015).

Apesar de apresentar uma ampla distribuição e ser uma das espécies mais abundantes, grande parte dos estudos com o golfinho-pintado-pantropical está concentrada no Oceano Pacífico (e.g., QUINTANA-RIZZO *et al*., 2021; TORRES *et al*., 2022). A dificuldade de realizar esforços sistemáticos em regiões oceânicas pode explicar, em parte, a escassez de registros e, consequentemente, de estudos em regiões como o Brasil. Portanto, ainda há a necessidade não apenas de realizar monitoramentos contínuos em áreas mais afastadas da costa onde a espécie ocorre, mas também de conduzir pesquisas sobre o uso de habitats e tamanhos populacionais do golfinho-pintado-pantropical no sul global.

Atualmente, o seu status de conservação é considerado "Pouco Preocupante", e uma das principais ameaças reconhecidas à espécie é a mortalidade ocasionada por capturas incidentais em áreas de pesca, como no Oceano Pacífico Oriental, relacionada à pesca do albacora (*Thunnus albacares*)**,** popularmente conhecido (BALLANCE *et al*., 2021; PERRIN, 2009; KISZKA; BRAULIK, 2018). No Brasil, a espécie não consta na atualização da Lista Nacional de Espécies Ameaçadas de Extinção (BRASIL, 2022), e os estudos sobre as ameaças ainda são escassos, o que indica a necessidade de diagnósticos de encalhes e capturas incidentais ao longo de sua distribuição (e.g., COSTA *et al*., 2017; ICMBIO, 2018), entre outras avaliações.

#### *1.2.1.2 Golfinho-pintado-do-Atlântico – Stenella frontalis (Cuvier 1829)*

O golfinho-pintado-do-Atlântico compartilha um padrão de coloração semelhante ao do golfinho-pintado-pantropical, assim como a presença de pintas em sua pele. Os filhotes nascem sem pintas e, à medida que se desenvolvem, adquirem graus variados de intensidade, apresentando pintas maiores na região do dorso e do ventre conforme envelhecem (LODI; BOROBIA, 2013; JEFFERSON *et al*., 2015). Alguns indivíduos podem apresentar um padrão de pintas tão intenso que a margem da capa e a chama ficam totalmente obliteradas. Além disso, em algumas populações, há indivíduos menores e menos pintados que habitam águas pelágicas (PERRIN; THEWISSEN; WÜRSIG, 2009). Uma característica diagnóstica e única dessa espécie está localizada abaixo da nadadeira dorsal e assemelha-se a uma intrusão na capa dorsal em forma de chama (conhecida em inglês como "spinal blaze"), apresentando variações em forma e intensidade (Figura 4, LODI; BOROBIA, 2013).

Figura 4 - Fotografia de dois indivíduos de golfinho-pintado-do-Atlântico em diferentes estágios de desenvolvimento: filhote e adulto. A imagem mostra a chama (“spinal blaze”) evidente no indivíduo adulto, a coloração típica da espécie e o estágio de desenvolvimento.

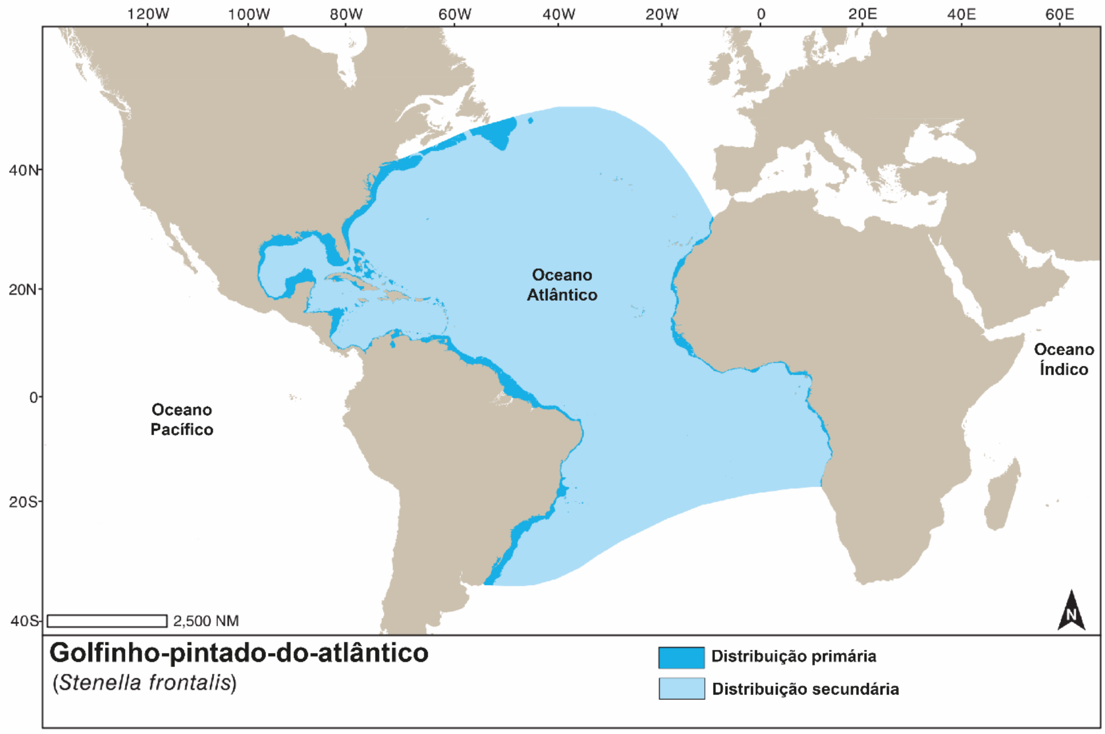
Fonte: PMC-BS

O corpo dos indivíduos apresenta formato robusto, e o rostro é moderadamente longo, com uma dobra distinta entre o melão e a base do rostro. A nadadeira dorsal é alta, com base larga e extremidade falcada, localizada no centro do dorso. As nadadeiras peitorais são recurvadas, delgadas e compridas. Os golfinhos-pintados-do-Atlântico recém-nascidos medem entre 0,8 e 1,2 metros de comprimento, enquanto os adultos podem atingir até 2,3 metros de comprimento (LODI; BOROBIA, 2013; JEFFERSON *et al.*, 2015).

O golfinho-pintado-do-Atlântico ocorre exclusivamente no Oceano Atlântico, em uma faixa de distribuição que se estende aproximadamente de 50°N a 30°S, em águas rasas da plataforma continental (JEFFERSON *et al.*, 2015; PERRIN; THEWISSEN; WÜRSIG, 2009; Figura 5). Embora seja encontrado principalmente em regiões com profundidades inferiores a

200m, também é registrado esporadicamente em áreas de águas mais profundas (BAUMGARTNER *et al*., 2001; DAVIS *et al*., 2002; SILVA *et al*., 2003; WEIR, 2011).

Figura 5 - Mapa da distribuição de *Stenella frontalis* destacado em tons de azul, sendo o tom mais escuro indicativo das principais áreas de ocorrência da espécie.




Fonte: Adaptado de JEFFERSON *et al.* (2015)

Estudos genéticos baseados em marcadores mitocondriais e nucleares identificaram dois "clusters" correspondentes aos que foram previamente descritos como os morfotipos costeiros e oceânicos ao longo do oeste do Atlântico Norte e Golfo do México. Além disso, o "cluster" costeiro parece estar sub-estruturado em três grupos que parecem estar correlacionados com distintos requerimentos ambientais (VIRICEL; ROSEL, 2014).

O golfinho-pintado-do-Atlântico é uma das espécies mais avistadas em diferentes áreas do Oceano Atlântico (por exemplo, no norte do Mar do Caribe, RODEN; MULLIN, 2000; Arquipélago dos Açores, SILVA *et al*., 2003; Golfo da Guiné e Angola, WEIR, 2011; Laje de Santos, SANTOS; FIGUEIREDO; BRESSEM, 2017; Golfo do México, ROBERTS *et al*., 2016). No entanto, as estimativas populacionais são notavelmente limitadas, com estudos realizados principalmente no Atlântico Norte (e.g., no Golfo do México, ROBERTS *et al*., 2016).

No Oceano Atlântico Sul Ocidental, a espécie é comumente avistada, principalmente em águas da plataforma continental e esporadicamente até o talude, com registros limitados pela isóbata dos 1.000 m (MORENO *et al*., 2005; PEREIRA *et al*., 2022; SANTOS; FIGUEIREDO; BRESSEM, 2017; ZERBINI *et al*., 2004). Apesar disso, até o momento, outras informações ecológicas da população que ocupa essa região são desconhecidas. Além disso, embora estudos como o de MORENO *et al*. (2005) indicassem que a costa do Rio de Janeiro seria a única área de sobreposição entre o golfinho-pintado-pantropical e o golfinho-pintado-do-Atlântico, pesquisas recentes provenientes de levantamentos embarcados na região do talude continental do Sudeste e Sul do Brasil sinalizaram uma co-ocorrência latitudinal das duas espécies em áreas mais ao sul (DI TULLIO *et al*., 2016). Isso indica que a dificuldade de acesso, assim como o uso de metodologias amostrais sistemáticas em ambientes oceânicos, é uma das principais causas das lacunas de conhecimento sobre essa espécie. Ademais, a baixa amostragem genética entre as regiões de ocorrência da espécie limita a confiabilidade das conclusões que inferem haver duas populações no Oceano Atlântico Sul (e.g., MORENO *et al*., 2005; CABALLERO *et al*., 2013).

Em relação ao habitat, DO AMARAL *et al*. (2015) demonstraram que áreas com alta adequabilidade ambiental são encontradas entre as latitudes 23°S e 27°S, principalmente na plataforma continental, sob temperaturas da superfície do mar em torno de 23 °C e com alta variação térmica (aproximadamente 5 °C). Entre as cinco espécies do gênero *Stenella* presentes no sudoeste do Oceano Atlântico, apenas o golfinho-pintado-do-Atlântico ocorre em ambientes de pouca profundidade e próximos à costa. Portanto, a partição de nicho e a segregação espacial tendem a ser mais acentuadas entre essa espécie e as demais do gênero, devido às variações nas características ambientais e nas preferências alimentares (DAVIS *et al*., 2002; MORENO *et al*., 2005).

O golfinho-pintado-do-Atlântico geralmente forma grupos com menos de 50 indivíduos, predominantemente entre 1 e 15, em áreas costeiras (JEFFERSON *et al*., 2015; MORENO *et al*., 2005). Contudo, esse padrão pode variar em algumas regiões. Por exemplo, em águas costeiras do sudeste do Brasil, na Baía de Ilha Grande, foram frequentemente observados grupos com mais de 100 golfinhos, com uma média de 80 indivíduos por grupo (PEREIRA *et al*., 2022). Essa área é utilizada pelos indivíduos como local de alimentação, e alguns demonstram fidelidade (PEREIRA *et al*., 2022). Um estudo recente realizado nessa mesma baía revelou uma alta diversidade trófica e uma ampla área de nicho isotópico para o golfinho-pintado-do-Atlântico (NEVES *et al*., 2023). Isso pode ser atribuído à exploração de uma vasta gama de presas e nichos pelos indivíduos dessa área. Embora outros trabalhos já tenham indicado que a espécie explora uma diversidade de cefalópodes e peixes, ela apresenta um hábito predominantemente teutófago, sendo a lula *Doryteuthis plei* uma das presas mais consumidas por essa espécie (JEFFERSON *et al*., 2015; LOPES *et al*., 2012).

Atualmente, o golfinho-pintado-do-Atlântico encontra-se com o status de "Pouco Preocupante", e a maior ameaça à espécie é a captura incidental ao longo de sua distribuição (BRAULIK & JEFFERSON, 2018). No Brasil, a espécie também não consta na Lista Nacional de Espécies Ameaçadas de Extinção (BRASIL, 2022); no entanto, estudos recentes apontaram altos níveis de poluição química em amostras de animais provenientes do litoral de São Paulo e Rio de Janeiro (e.g., OLIVEIRA-FERREIRA *et al*., 2024; MÉNDEZ-FERNANDEZ *et al*., 2018), indicando que esta é uma ameaça crescente à espécie.

## 1.3 OBJETIVOS

### 1.3.1 OBJETIVO GERAL E HIPÓTESES

O objetivo geral desta tese é investigar, ao longo de três capítulos, aspectos ecológicos, como distribuição, uso do habitat e estimativas populacionais, de duas espécies: *Stenella attenuata* e *S. frontalis*, presentes em uma bacia sedimentar no Brasil, a Bacia de Santos (Figura 6). Isso se deve ao fato de que informações sobre abundância e uso de habitat dessas espécies ainda são pouco compreendidas. Considerando a distribuição não homogênea dos grupos e a influência das características ambientais na distribuição espacial, densidade e abundância, espera-se que os padrões observados estejam correlacionados com as principais características hidrográficas e fisiográficas da Bacia de Santos. Além disso, dado que *S. frontalis* é descrita na literatura como relativamente abundante, prevê-se um tamanho populacional condizente com a área de estudo.

### 1.3.2 OBJETIVOS ESPECÍFICOS

Para alcançar o objetivo principal, a tese ramifica-se nos seguintes objetivos específicos:

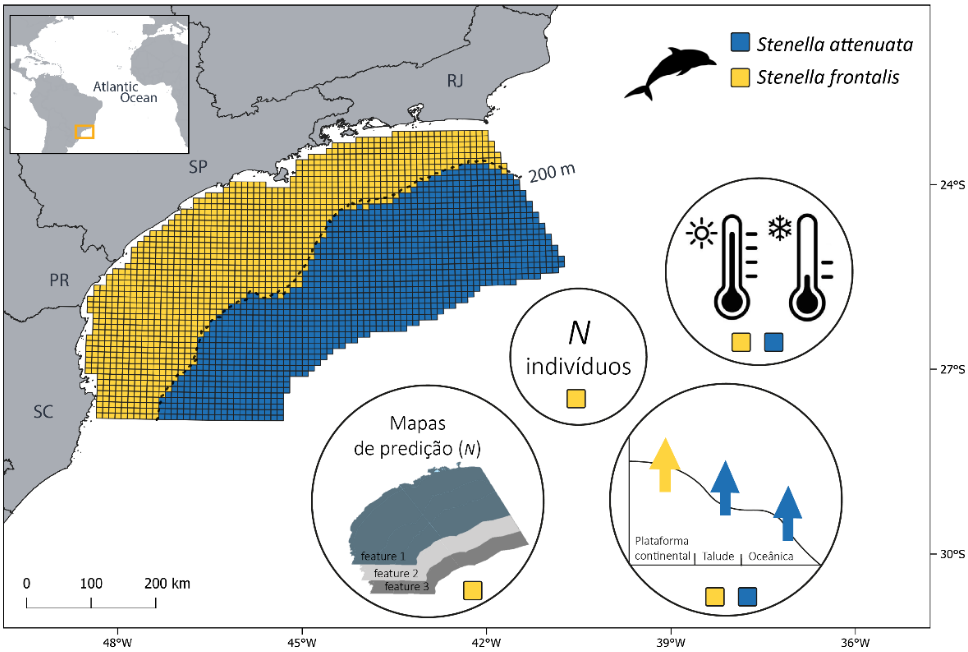
1.3.2.1 Caracterizar a distribuição e o uso do habitat de *Stenella attenuata* na Bacia de Santos (Capítulo I);

1.3.2.2 Estimar sazonalmente a densidade e abundância de *Stenella frontalis* na Bacia de Santos (Capítulo II);

1.3.2.3 Caracterizar o habitat de *Stenella frontalis* e considerar essas informações à estimativa populacional (Capítulo III);

1.3.2.4 Prever a densidade e abundância de *S. frontalis,* considerando as principais feições oceanográficas recorrentes na região da bacia (Capítulo III).

Figura 6 - Figura conceitual representando os manuscritos desenvolvidos nesta tese sobre o golfinho-pintado-Pantropical (*Stenella attenuata*) e golfinho-pintado-do-Atlântico (*S. frontalis*) na Bacia de Santos, Brasil.




Fonte: Autor

## 1.4 ESTRUTURA DA TESE

Esta tese será apresentada em forma de capítulos, sendo que cada um contém um manuscrito científico já publicado, submetido ou a ser submetido a revistas científicas. Todos os dados utilizados na elaboração desta tese foram coletados entre novembro de 2015 e março de 2021, durante os cruzeiros embarcados do Projeto de Monitoramento de Cetáceos da Bacia de Santos (processo n°02001.114279/2017-80, ACCTMB no. 657/2015). A seção intitulada "Introdução Geral" apresenta os principais referenciais teóricos, problemas e lacunas de conhecimentos ecológicos que motivaram a elaboração da tese, juntamente com o objetivo geral, as hipóteses e os objetivos específicos. Após essa seção, são apresentados os capítulos, cujos títulos estão em inglês: I) "Occurrence and habitat use of pantropical spotted dolphins (*Stenella attenuata*) at the edge of their distribution in the southwestern Atlantic Ocean"; II)

"Seasonal abundance and distribution of Atlantic spotted dolphins (*Stenella frontalis*) in the southwestern Atlantic Ocean"; e III) "Oceanographic features affect density and abundance of Atlantic spotted dolphins (*Stenella frontalis*) in the South Brazil Bight". Por fim, a seção intitulada "Conclusão" visa sintetizar os principais resultados obtidos nesta tese, que utilizou um banco de dados inédito proveniente de um programa de monitoramento associado ao licenciamento ambiental, trazendo, portanto, diversas contribuições para a gestão ambiental de uma região marinha onde as atividades antrópicas se sobrepõem à distribuição das espécies investigadas.

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# 2 CAPÍTULO I

Occurrence and habitat use of Pantropical spotted dolphin (*Stenella attenuata*) at the edge of their distribution in the Southwestern Atlantic Ocean

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**Occurrence and habitat use of Pantropical spotted dolphin (*Stenella attenuata*) at the edge of their distribution in the Southwestern Atlantic Ocean**

Thayusky P. Correa[1,3], Leonardo L. Wedekin[2], Marta J. Cremer[1,3]

[1] Laboratório de Mamíferos Aquáticos, Programa de Pós-Graduação em Ecologia, Departamento de Ecologia e Zoologia, Universidade Federal de Santa Catarina, Florianópolis, Santa Catarina, Brazil

[2] Socioambiental Consultores Associados, Florianópolis, Santa Catarina, Brazil

[3] Laboratório de Ecologia e Conservação de Tetrápodes Marinhos e Costeiros - TetraMar, Universidade da Região de Joinville, São Francisco do Sul, Santa Catarina, Brazil

Correspondence:

Thayusky da Penha Correa, Laboratório de Mamíferos Aquáticos (LAMAQ), Departamento de Ecologia e Zoologia, Centro de Ciências Biológicas, Universidade Federal de Santa Catarina, Trindade, Caixa Postal 5102, CEP, 88040- 970, Florianópolis, SC, Brazil

Email: thayusky@gmail.com

Pantropical spotted dolphins, *Stenella attenuata* (Gray, 1946), occur in all tropical and some subtropical waters from roughly 30°N–40°N to 20°S–40°S (Perrin, 2009). They are mostly found in deep offshore waters, although they can also surround oceanic islands, and other coastlines where there is deep water nearby (e.g., Central America, Caribe and Mexico, the Hawaiian Islands, Taiwan, and the Philippines; Jefferson et al., 2015; Perrin, 2009). Despite being widely distributed, the ecology of the species in the Southwestern Atlantic Ocean (SWA) is not well known (e.g., Do Amaral et al., 2015; Moreno et al., 2005). Previous studies in the SWA indicated that the northern limit of its distribution is in oceanic tropical waters (02°04'S), whereas the southern limit is 22°42'S (Gurjão, 2020; Moreno et al., 2005). Most sightings have been documented at lower latitudes in association with deep tropical warm waters (Di Tullio et al., 2016; Do Amaral et al., 2015; Moreno et al., 2005). Recent records in Southeastern and Southern Brazil(Di Tullio et al., 2016) have raised doubts about the species' distribution in their southern limits. In this work, we aimed to provide new information on the habitat use regarding water depth and sea surface temperature (SST) of the pantropical spotted dolphins at the southernmost limit of its range in the Southwestern Atlantic Ocean.

Surveys were carried out in the Santos Basin (SB), an area about 350,000 $km^2$ which extends from Cabo Frio, Rio de Janeiro state, to the Island of Santa Catarina, Florianópolis, Santa Catarina state, in Southeastern and South Brazil, respectively (23°S–28°S and 47°W–41°W, Figure 1). Data were collected during ship-based surveys, by the Cetacean Monitoring Project of the Santos Basin (PMC-BS), carried out by PETROBRAS as environmental licensing procedures required by Brazil's federal environmental agency, IBAMA, to produce and transport oil at the Santos Basin (process no. 02001.114279/2017-80). These surveys had two different aims, called herein as (1) systematic surveys (using line transect sampling for population estimates), and (2) telemetry surveys, to sample higher cetacean density areas for satellite tags deployments.

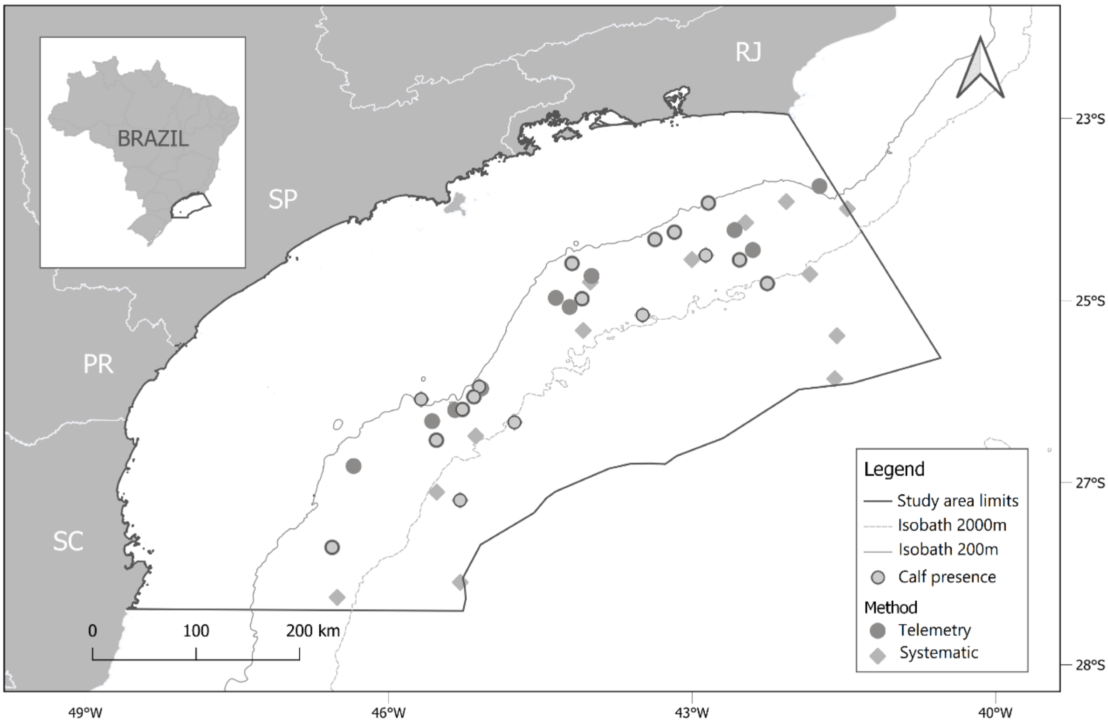


**FIGURE 1** Study area of Santos Basin, Southeastern Brazil, and pantropical spotted dolphin sightings recorded between 2015-2021. Acronyms represent the Brazilian states of Santa Catarina (SC), Paraná (PR), São Paulo (SP), and Rio de Janeiro (RJ).

To describe habitat, we defined regions of our study area (SB) as continental shelf (<200 m depth), continental slope (depth ranges from 200 to 2,000 m), and oceanic region (depths above 2,000 m). Sea surface temperature (SST) values were obtained by remote sensed data from Terra/Aqua satellite platform using moderate-resolution imaging spectroradiometer (MODIS) sensor. The spatial resolution was 1 km and the image acquisition was every 1-2 days. The data were extracted from Google Earth Engine (GEE) using Level 3 Standard Mapped Image (L3SMI) product (https://oceancolor.gsfc.nasa.gov/resources/docs/product-levels/). SST values were calculated for the specific geographic position of the sighting with a 3 km spatial buffer and filtered on a 10-day scale (5 days before and 5 days after each sighting date). Four austral seasons were considered in this study: summer (December – February), fall (March – May), winter (June – August), and spring (September – November). If there was overlap in seasons, we set the survey's season according to the longest period sampled. We defined group as two or more dolphins aggregated in the same area whether their behavior was coordinated or not. Calves were identified as two-tone (dark gray above, white below), not spotted, and about 1/3 to 3/4 adult size (Jefferson et al., 2015). We conducted tests to evaluate the normality and homogeneity of variance in our data set. We employed the Levene test to assess homogeneity of variance for both depth and SSTs across different seasons. The outcomes of both tests revealed that no significant differences were present, and we opted to perform a one-way analysis of variance (ANOVA), a parametric method, followed by pairwise multiple comparison tests using Tukey's honestly significant difference (HSD) method to further explore potential differences. In addition, boxplots were employed to illustrate differences in the means of depth and SST between the distinct seasons.

A total of 25 surveys were conducted between November 2015 and March 2021, totaling 5,189.8 hr and 36,196 nautical miles of systematic sampling effort and 3,231.7 hr and 19,576 nautical miles of telemetry effort (Table 1).

**TABLE 1** Summary of survey effort in the Santos Basin (Southwestern Atlantic Ocean) conducted between 2015 and 2021 and sightings of pantropical spotted dolphins, *Stenella atenuatta*. Survey type and number, year, months of effort, season, number of days of survey and hours sampling, and survey effort in nautical miles (nmi) for each cruise. Also provided the number of sightings (n), group size, and depth range for each survey. S = systematic surveys and T = telemetry surveys.

| Survey type | Survey number (Year) | Dates | Season | Duration (Days) | Hours | Effort (nmi) | Sigthings (*n*) | Group Size range (min - max) | Depth range (min -max) |
|---|---|---|---|---|---|---|---|---|---|
| S | 1 (2015) | Nov – Jan | Summer | 40 | 389.9 | 2,665.80 | 2 | 4–20 | 526–2,560 |
| T | 1 (2016) | Feb – Mar | Summer | 25 | 246.3 | 1,579.30 | 4 | 3–125 | 237–1,036 |
| S | 2 (2016) | May – Jun | Fall | 42 | 410.9 | 2,949.50 | 2 | 06–50 | 1,169–1,881 |
| T | 2 (2016) | Ago – Sep | Fall | 25 | 248.2 | 1,405.60 | 0 | 0 | 0 |
| S | 3 (2016) | Sep – Nov | Spring | 41 | 420.1 | 2,969.90 | 2 | 15–19 | 2,095–2,118 |
| T | 3 (2017) | Jan – Feb | Summer | 25 | 288.4 | 1,826.30 | 2 | 30–40 | 141–709 |
| S | 4 (2017) | Mar – Apr | Fall | 42 | 434.9 | 2,992.40 | 0 | 0 | 0 |
| T | 4 (2017) | Jul – Jul | Winter | 27 | 329.7 | 1,828.80 | 0 | 0 | 0 |
| S | 5 (2017) | Ago - Oct | Spring | 44 | 435.7 | 3,015.50 | 1 | 100 | 172 |
| T | 5 (2017) | Oct - Nov | Spring | 25 | 269.2 | 1,818.70 | 2 | 100–130 | 414–476 |
| S | 6 (2018) | Jan - Feb | Summer | 40 | 444.3 | 3,166.10 | 0 | 0 | 0 |
| T | 6 (2018) | Mar - Apr | Fall | 25 | 261.6 | 1,686.30 | 5 | 10–300 | 448–1,985 |
| S | 7 (2018) | Sep - Oct | Spring | 50 | 477.3 | 3,202.20 | 3 | 5–15 | 1,256–2,677 |
| T | 7 (2018) | Jul - Ago | Fall | 25 | 239.9 | 1,272.70 | 0 | 0 | 0 |
| S | 8 (2019) | Mar - Apr | Fall | 45 | 425.5 | 2,964.60 | 4 | 8–80 | 660–2,204 |
| T | 8 (2019) | Jan - Feb | Summer | 25 | 298.2 | 1,652.50 | 4 | 5–30 | 485–1,104 |
| S | 9 (2019) | Ago - Oct | Spring | 51 | 463.1 | 3,094.00 | 1 | 20 | 2,160 |
| T | 9 (2019) | Jul - Ago | Winter | 25 | 234.3 | 1,342.70 | 0 | 0 | 0 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| S | 10 (2020) | Mar - Mar | Fall | 23 | 235.8 | 1,687.00 | 0 | 0 | 0 |
| T | 10 (2020) | Jan - Feb | Summer | 25 | 279.1 | 1,811.10 | 3 | 12–60 | 433–556 |
| S | 11 (2020) | Ago - Oct | Spring | 47 | 424.7 | 2,983 | 0 | 0 | 0 |
| T | 11 (2020) | Jul - Ago | Fall | 25 | 242.9 | 1,546 | 0 | 0 | 0 |
| S | 12 (2020) | Oct – Nov | Spring | 20 | 224.3 | 1,660 | 2 | 10–15 | 844–2,628 |
| T | 12 (2021) | Nov - Dez | Spring | 24 | 293.9 | 1,806 | 1 | 15 | 742 |
| S | 13 (2021) | Jan –Feb | Summer | 41 | 398.4 | 2,845.3 | 2 | 10–15 | 872–1,920 |
| Total | | | | 827 | 8,416.6 | 55,771.3 | 40 | | |

Forty groups of pantropical spotted dolphins were recorded in three austral seasons (summer, fall, and spring), and in all the six years of sampling considered here from 2015 to 2021. No records occurred during winter months. Group size ranged from 3 to 300 individuals, with a mean overall group size of 42 individuals (*SD* = 55, median = 20, mode = 20). Calves were observed in 17 groups (Figure 1), corresponding to 41.4% of the total sightings, during the fall (*n* = 8), summer (*n* = 7), and spring (*n* = 2) seasons. Sightings occurred from latitude 23°40’03’’S to 27°44’02’’S and longitude 41°27’51’’W to 47°07’53’’W (Figure 1). The southernmost observed sighting was a group of five pantropical spotted dolphins (27°44’02’’S and 46°30’36’’W) on September 2018 on the continental slope (1,590 m) near the southern limit of our study area, where the mean SST was 21.6°C. To date, this is the southernmost sighting of this species in the SWA.

Groups of dolphins were observed in waters of depths that varied from 141 to 2,677 m (*M* = 1,181, *SD* = 730, mode = 526) and most sightings (75.6%) were obtained on the continental slope. Among the records corresponding to the seasons of summer (*n* = 14), fall (*n* = 15), and spring (*n* = 11), the observed SSTs values exhibited a range from 21.6°C to 29.2°C (*M* = 25.8°C, *SD* = 2.0, mode = 24.0°C, Figure 2). Depths where dolphins occurred did not change significantly between seasons (*n* = 40, ANOVA: *df* = 2, *F* = 2.56, *p* = 0.0912), in contrast to sea surface temperatures (SST), which exhibited a significant difference among the three sampled seasons (*n* = 40, ANOVA: *df* = 2, *F* = 44.87, $p < 0.0001$). In terms of SST, groups experienced significantly low mean temperatures during spring compared to summer and fall records (Tukey's HSD test: $p_{\text{spring-fall}} < 0.05$, $p_{\text{summer-fall}} = 0.68$, $p_{\text{summer-spring}} < 0.05$).

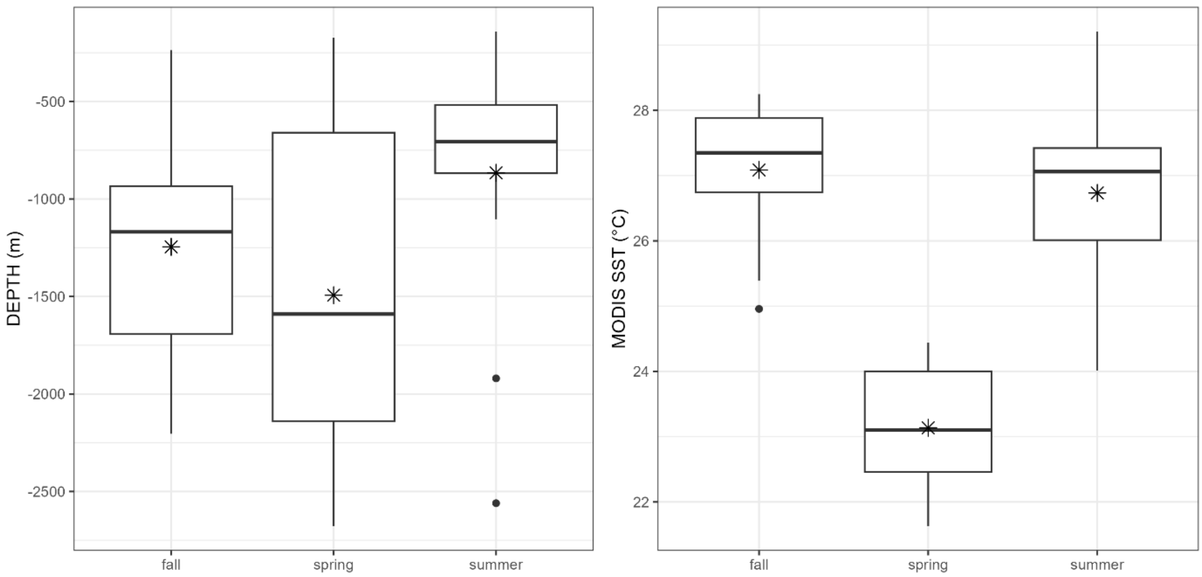


**FIGURE 2** Depth and temperature of records of the pantropical spotted dolphin in Santos Basin according to seasons. Box represent the first and third quartiles of observed values; whiskers represent up to 1.5 times the interquartile range; solid black lines represent up to 1.5 times the interquartile range; solid black lines represent the median and asterisks the mean.

In this work, we provide a relatively large set of *S. attenuata* records from the Southwestern Atlantic Ocean, in the region considered so far to be the southern limit of distribution of this species, bringing new insights on its distribution south of latitude 22ºS. Species' sightings were scarce south of this latitude, suggesting a low density and a borderline distribution in this region (see Di Tullio et al., 2016). Our observations, extending beyond the 200 m and up to the 1,000 m isobath, indicate that *S. attenuata* can occurs at higher latitudes and occupy shallower waters than previously proposed. According to Do Amaral et al. (2015), the established environmental conditions for pantropical spotted dolphins, tend to diminish around latitude 20°S, where the SST typically ranges from 25°C to 28.5°C (Moreno et al., 2005). However, it is necessary to consider that the modeling was based on the data available at that time. The sightings reported in our study, which occured further south of their predicted suitable habitat, can be explained by two hypotheses. First, the large and long-term systematic effort in the area, which has enabled us to identify a much larger range of SST within which the species can occur, spanning 7.6°C. This is a very plausible hypothesis, considering that in this region there were no field efforts in mangnitude like this one. The occurrence of this species is closely associated with the warm Tropical water carried by the Brazil Current southwards, and occasionally to upwelling sites of the South Atlantic Central

Water (Stramma & England, 1999). The lower temperatures observed for the species during the spring suggest a preference for these upwelling sites. Interestingly, the absence of sightings in the winter months may be related to seasonal movements beyond the limits of our study area, especially to the north, in response to the seasonal modulation of the Brazil Current (Campos et al., 1995). Also, it would not be surprising to find other borderline sightings of pantropical spotted dolphins further south of our study area. Another hypothesis worth considering is that the recent data showing a broader distribution may be attributed to the potential effects of climate change, including both direct and indirect factors, such as change in sea surface temperature and/or on prey distribution (Learmonth et al., 2006; MacLeod et al., 2005). For instance, some studies have established a connection between the gradual warming of water temperatures and a shift in the distribution of certain cetacean species, supported by an increase in strandings, sightings, and the presence of species typically associated with warmer waters (MacLeod et al., 2005).

The large number of sightings and widespread distribution along the shelf-break suggest that the Santos Basin is an important area for the species that primarily occupy slope waters. Upon reviewing observations from prior studies (see Moreno et al., 2005), our records indicate a much larger overlap area between *S. frontalis* and *S. attenuata*. The distribution of both spotted dolphins in SWA waters was seen until then with minimal spatial overlap (Do Amaral et al., 2015; Moreno et al., 2005). In contrast to Pantropical spotted dolphins, Atlantic spotted dolphins are typically found between 23°S and 27°S along the SWA in coastal waters on the continental shelf, with the southernmost record in Uruguay (Moreno et al., 2005; Paro et al., 2014). Combining the findings from existing literature and our work, it becomes evident that both species of spotted dolphins coexist within the Santos Basin, albeit in distinct habitats.

Pantropical spotted dolphin group size ranges from a few individuals to a thousand and can be segregated by age, sex or both (Perrin, 2001). In SWA, most observed groups range from 3 to 25 individuals, although groups up to 250 animals were also recorded (Moreno et al., 2005). Similar to previous studies, our records did not show much variability in group size (between 3 and 20 individuals), or in the maximum size of groups (300 individuals). The frequent presence of calves in groups throughout the basin indicates that it might be an important calving ground for this offshore species. This is the first to study to document substantial numbers of pantropical spotted dolphin calves in the SWA waters, predominantly during the austral summer and fall seasons. In the Eastern Tropical Pacific, *S. attenuata* stocks show seasonal patterns in their reproduction, with one or more calving peaks per year (Barlow, 1984). In SB, the distribution of groups with calves seems to be associated with high

productivity areas in the slope region (Campos et al., 2000). In the Eastern Tropical Pacific waters pregnant and lactating females were observed moving to high productivity areas to find appropriate nutritional habitats (Kellar et al., 2013).
Future research should investigate abundance and density patterns of *S. attenuata*, enhance predictions about the species' suitability for habitats in the Southwestern Atlantic Ocean, and even more effectively address the possible range shifts in distribution due to climate change.

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# 3 CAPÍTULO II

Seasonal abundance and distribution of Atlantic spotted dolphins (*Stenella frontalis*) in the southwestern Atlantic Ocean

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**Seasonal abundance and distribution of Atlantic spotted dolphins (*Stenella frontalis*) in the southwestern Atlantic Ocean**

Thayusky P. Correa[1,2], Guilherme A. Bortolotto[3,4], Leonardo L. Wedekin[5], Marta J. Cremer[1,2]

1 Programa de Pós-Graduação em Ecologia, Departamento de Ecologia e Zoologia, Universidade Federal de Santa Catarina, Florianópolis, Santa Catarina, Brazil
2 Laboratório de Ecologia e Conservação de Tetrápodes Marinhos e Costeiros – TetraMar, Universidade da Região de Joinville, São Francisco do Sul, Santa Catarina, Brazil
3 Department of Life Sciences, Aberystwyth University, Aberystwyth, Ceredigion, United Kingdom
4 Sea Mammal Research Unit, Scottish Oceans Institute, University of St Andrews, St Andrews, Fife, United Kingdom
5 Socioambiental Consultores Associados, Florianópolis, Santa Catarina, Brazil

Correspondence
Thayusky da Penha Correa, Laboratório de Ecologia e Conservação de Tetrápodes Marinhos e Costeiros (TetraMar), Departamento de Ecologia e Zoologia, Centro de Ciências Biologicas, Universidade Federal de Santa Catarina, Trindade, C.P. 5102, CEP 88040-970, Florianópolis, SC, Brazil.

Email: thayusky@gmail.com

**Abstract**

Little is known of the Atlantic spotted dolphin (*Stenella frontalis*) population size and distribution patterns in the southwestern Atlantic Ocean. Here, we assessed the spatial and seasonal abundance and distribution of Atlantic spotted dolphins in the Santos Basin, in the southwestern Atlantic Ocean (27º S - 23º S/ 41º W - 48º W). From November 2015 to March 2021, dolphin sightings were recorded during vessel-based line transect surveys. The analysis considered eight geographic strata and two seasonal periods (cold and warm). We estimated that on average 8,692 Atlantic spotted dolphins (*CV* = 0.27; *SE* = 2,400; 95% CI [5,100–14,815]) were present in the area in cold periods, and 19,762 (*CV* = 0.18; *SE* = 3,706; 95% CI [13,709–28,487]) in the warm periods. Estimated abundances were higher in the shelf stratum, during both seasonal periods. Our results revealed that the continental shelf is a core region for the Santos Basin population of Atlantic spotted dolphins, indicating high concentration of dolphins in areas characterized by intense human activities. That highlights the importance to implement strategies that ensure the conservation of this population and its ecosystem.

**KEYWORDS:** Cetacean, Delphinidae, density, distance sampling, population ecology, South Brazil Bight

## 1 | INTRODUCTION

Atlantic spotted dolphins (ASDs, *Stenella frontalis* Cuvier, 1829) inhabit tropical, subtropical, and warm temperate waters of the Atlantic Ocean, from 50°N to 30°S (Jefferson et al., 2015; Perrin, 2002). Although usually found in continental shelf waters influenced by both warm currents and upwellings (Moreno et al., 2005), ASDs are have also been observed in offshore waters (e.g., Baumgartner et al., 2001; Moreno et al., 2005; Silva et al., 2003; Viricel & Rosel, 2014; Weir, 2011). ASD is one of the predominant dolphin species in different areas in the Atlantic Ocean (e.g., northern Caribbean Sea, Roden & Mullin, 2000; Laje de Santos, in Brazil, Santos et al., 2017; Azores Archipelago, Silva et al., 2003; Gulf of Guinea and Angola, Weir, 2011; U.S. eastern Atlantic, Garrison et al., 2010; U.S. Gulf of Mexico, Fulling et al., 2003). However, comprehensive abundance estimates are notably limited, with available data primarily restricted to western North Atlantic including the northern Gulf of Mexico (e.g., Roberts et al., 2016).

Specifically for the Southwestern Atlantic Ocean (SWA), previous studies suggest that at least two distinct populations are present (Moreno et al., 2005): one in the northern and northeastern coasts of Brazil, to the north of 6°S (Paraíba state, Brazil; Do Amaral et al., 2015), and another between 18°S and 35°S (from Abrolhos Bank, in Brazil, to Uruguay; Danilewicz et al., 2013; Paro et al., 2014). In Brazilian waters, ASDs are predominantly found between 22°S and 30°S (e.g., Di Tullio et al., 2016; Pereira et al., 2022; Santos et al., 2017), including the sedimentary basin situated off the south and southeast coast, the Santos Basin. Although the southern population extends south to Uruguay (Moreno et al., 2005), we herein refer to ASDs found within the basin region as the “Santos Basin population”.

The current global conservation status of the ASD is “Least Concern” (IUCN; Braulik & Jefferson, 2018), meaning that no evidence of significant threats and population decline exist at present. However, information on population size for the South Atlantic Ocean is still scarce and systematic survey approaches are rarely implemented (e.g., Di Tullio et al., 2016). In general, ecological studies addressing the occurrence, distribution, and habitat use of ASDs rely on opportunistic records or are spatially restricted (e.g., Danilewicz et al., 2013; Do Amaral et al., 2015; Moreno et al., 2005; Pereira et al., 2022). ASDs inhabiting the Santos Basin are primarily found in coastal and shelf environments (Moreno et al., 2005; Pereira et al., 2022). The presence of potentially harmful anthropogenic activities for the species in this basin includes bycatch, chemical pollution, and intense vessel traffic (e.g., Bittencourt et al., 2020; Domiciano et al., 2016; Marega-Imamura et al., 2020; Méndez-Fernandez et al., 2018;

Zerbini & Kotas, 1998).

Since 2015, the Cetacean Monitoring Project in Santos Basin (in Portuguese “Projeto de Monitoramento de Cetáceos na Bacia de Santos”, PMC-BS) has been enforced by the Brazilian federal environmental agency (IBAMA). The aim of PMC-BS is to investigate the effects of oil and gas exploration activities on the cetacean community of the Santos Basin. PMC-BS comprises a multi-method approach, including aerial and vessel-based line transect surveys, acoustic and telemetry surveys (e.g., Dalpaz et al., 2023). Based on this unprecedented dataset ranging over six years, we analyzed Atlantic spotted dolphin' visual data obtained along transect lines to investigate the species’ population ecology within the basin. We aimed to (i) assess density and abundance of ASDs across different portions of the Santos Basin and to (ii) identify ASDs distribution through seasonal and geographic strata in the area.

## 2 | METHODS

### 2.1 | Study area and survey design

Santos Basin (SB) is located in southeastern Brazil, from Cabo Frio, Rio de Janeiro state, to Florianópolis, Santa Catarina state (23°S–28°S, Figure 1). The area designated for survey activities extends from the shoreline to the boundary of the Brazilian Exclusive Economic Zone, covering 272,567 $km^2$.

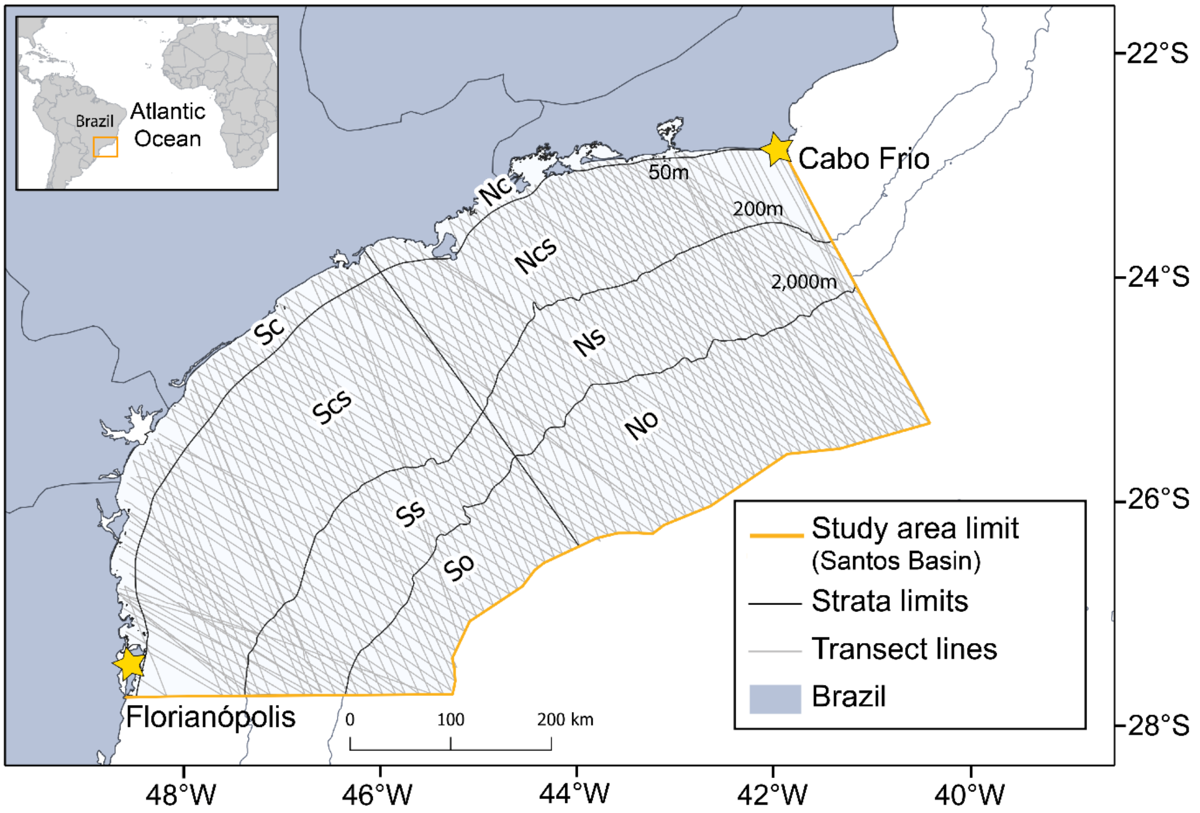


**FIGURE 1** Map of the study area in Santos Basin with line-transect survey tracks and the limits of eight strata. The eight geographic strata used in the analyses were: (Nc) North coastal, (Sc) South coastal, (Ncs) North continental shelf, (Scs) South continental shelf, (Ns) North slope, (Ss) South slope, (No) North oceanic and (So) South oceanic. Yellow stars indicate bordering coastal cities at the extreme north and south of the study area (23°S–27°S), namely Cabo Frio (Rio de Janeiro state) and Florianópolis (Santa Catarina state).

Ocean circulation over the basin is influenced by the Brazil Current, a tropical current that transports warm and oligotrophic waters to the region, especially on austral summer and autumn seasons. Particularly on austral summer and spring, wind-driven upwelling brings cold and nutrient-rich waters to the surface layers, which promotes high productivity in certain regions of the basin (Palma & Matano, 2009). Additionally, the shelf is seasonally influenced by freshwater discharges, which promote the cooling and freshening of the upper layers (Piola et al., 2008). As a result, the basin presents an interannual sea surface temperature variability, driven by changes in wind regimes, ocean circulation, and mesoscale processes (Palma & Matano, 2009). Consequently, the highly dynamic environment influences the continental shelf and slope ecosystems (Brandini et al., 2018). In regard to morphology, the SB shelf has a wider central portion (200 km) and narrows sections at its northern and southern ends (<70 km). Moreover, the basin presents a depth gradient, with the shelf break occurring at approximately 200 meters (Mahiques et al., 2010).

During warmer sea surface temperature (SST) periods, a combination of steep shelf break topography and the intensity and direction of winds promotes upwelling events in some portions of the basin (i. e., Cabo Frio upwelling). In contrast, during austral spring and winter (herein referred to as the colder seasons), upwelling events depend on the position of the main flow of the Brazil Current and are primarily driven by its meanders, which induce shelf-break upwellings (Campos et al., 2000). Please note that the limited number of sightings per survey prevents a more detailed abundance analysis, as recommended (i.e., per survey). Details of preliminary attempts at finer-scale analyses are provided in the supplementary material (Table S2).

To assess spatial variation in ASDs distribution and abundance, we geographically stratified Santos Basin into eight regions. The stratification process was based on four classes of depth: coastal, from 0 to 50 m, continental shelf, from 51 to 200 m, continental slope, from 201 to 2,000 m, and oceanic, for depths beyond 2,000 meters; and also considered a North and South division (Figure 1). The North-South division was based on clear differences of meteoceanographic processes, morphology, shoreline orientation and shelf width between these regions (Figueiredo Jr et al., 2023): the North shelf is narrower, deeper and with a steeper slope; while the South region has a wider continental shelf, relatively shallow depths and smoother slope. These differences reflect on distinct oceanographic regimes, with more influence of upwelling water masses in the North and coastal waters in the South region.

From November 2015 to March 2021, SB was systematically surveyed following line-transect distance sampling methodology (Buckland et al., 2001) (Figure 1). Surveys were carried out aboard the *RV Sea Route* (23.7 m long) and started in November 2015. The project objective was to survey the SB area at least twice a year, targeting the periods when SST variability should be well defined. In 2020, due to COVID-19 pandemic restrictions, some surveys were disrupted.

Zigzag lines were designed to be near-to-perpendicular to the coast and roughly perpendicular to the bathymetric gradient (i.e., oriented from the coast to oceanic regions; Figure 1). Surveys always started in the southern limit of the area, traveling northward, and returning to the south after reaching the northern limit, each lasting about 45 days to be completed: a survey here is considered one entire south-north-south cycle. Nevertheless, in

2020, some surveys were disrupted and did not have the standard structure. To avoid complete overlap with already sampled lines between surveys, transect lines planned in subsequent surveys were randomly shifted between 60 and 90 km apart in a North-South direction.

### 2.2 | Visual search effort

Survey lines were travelled at an average speed of 7 knots, during daylight hours (i.e., from 6 AM to 7 PM), and in adequate weather conditions (i.e., sea state below 5 in the Beaufort scale, and in the absence of rain or fog). Environmental and visibility (see Table 1, section 2.3 Detection function modelling) conditions were recorded at the beginning of survey effort and updated if changed. Experienced and qualified observers (i.e., Marine Mammal Observers, MMOs) continuously searched for cetaceans from an elevated point on the vessel, at 7 m above the water. Five MMOs rotated through three positions (port, starboard and bow) every 40 minutes and with at least 1 hr 20 min of rest between rotation cycles. The observer positioned at the center covered 20° on each side of the bow, while those at port and starboard covered from the bow to 90° on their respective side. Scans were carried out by the naked eye, using 7x50 reticulated binoculars or 15x50 binoculars with digital stabilization. When an animal or group was detected, the coordinates of the boat (via hand-held GPS), time, detection method (naked eye or type of binocular), detection cue and environmental conditions (see Table 1, 2.3 Detection function modelling) were recorded. Perpendicular distances between dolphin groups (or single individuals) and the transect line were obtained from bearing and binocular reticle readings, which were collected by the observer who first made the detection. The bearing, i.e., the angle between the sighting and the survey line, was measured using an angle board. Information about group size and number of calves were also recorded, both estimated through consensus among on-effort observers. We defined a dolphin group as individuals observed together in the same area and exhibiting apparent association, such as heading in the same direction when traveling and/or engaged in similar behaviors (e.g., Elliser, & Herzing, 2014; Shane, 1990). MMOs continuously communicated with each other to ensure that dolphin groups were recorded only once, avoiding double counting.

## 2.3 | Detection function modelling

We assumed the probability to detect ASDs over transect lines to be equal to one (i.e., $g(0) = 1$; Buckland et al., 2001) during the entire study period. To maximize meeting that assumption, we ensured that the number of observers in each survey, their level of experience, as well as the rotation cycles between them and the sea conditions were adequate. That was made to reduce risks associated with perception bias, and the low speed at which transects were traveled to reduce availability bias during surveys. Although some transects were traversed under suboptimal conditions, these instances were rare and were excluded from further analyses if present. We do however, recognize that visibility bias (i.e., perception and availability; Marsh & Sinclair, 1989) potentially deem these analyses conservative and address that in detail. We used the *Distance* package (v1.0.8, Miller et al., 2019) in software R (v4.1.3, R Core Team, 2023), for detection function modelling. Conventional distance sampling and multiple-covariate distance sampling (MCDS, Buckland et al., 2001, 2015) were tested. The detection function modelling included two key functions (half-normal and hazard-rate), with no adjustment terms applied. We considered the following covariates in MCDS models (see Table 1): sea state (Beaufort), group size, weather, detection method, cue, visibility, and glare.

**TABLE 1** Environmental and biological variables tested as covariates in candidate detection function models for the Atlantic spotted dolphins in Santos Basin.

| Covariate | Factor/numeric | Levels/range |
|---|---|---|
| Sea state | Factor | Calm (0–3) and moderate (4–5) |
| Group size | Numeric | 1–300 |
| Weather | Factor | Good, partly cloudy, cloudy without rain, and rainy |

| | | |
|---|---|---|
| Detection method | Factor | Naked eye, 7x50 binoculars and 15x50 binoculars |
| Cue | Factor | Leaping, blow, body and fin |
| Visibility | Factor | Excellent, good, bad and terrible |
| Glare | Factor | No reflection, low (as 5–10%), medium (as 15-20%) and high (as 30-50%) |

Preliminary visual inspection of perpendicular distances and the considered covariates were conducted using histograms, *QQ*-plots, box-plots and scatterplots to identify potential outliers and guide further decisions (Appendix Figure S2, Buckland et al., 2001). The examination of the distances indicated that it was appropriate to right-truncate the 10% largest distances (i.e., distances at the tail of the distribution and therefore with very low detection probability), to increase model fitting (Buckland et al., 2001; Thomas et al., 2010).

Forward stepwise selection was conducted and subsequently ranked using the Akaike Information Criterion (AIC, Burnham & Anderson, 2002). To compensate for the size bias effect ( i.e., small dolphin groups missed at large distances, see Fig S2), we decided to include group size as a primary covariate in the candidate detection function models and then add the following covariates. The model used to compute density and abundance was selected based on the lowest AIC score. However, if two competing models showed AIC scores under 2 units apart, the model was selected based on fewer degrees of freedom, since it was considered as the simpler model. The Cramer-von-Mises and the Kolmogorov-Smirnov goodness-of-fit tests were used to evaluate adequate model fit (Buckland et al. 2015).

**2.4 | Density and abundance estimates analysis**

Density and abundance of ASDs were estimated across two distinct seasonal periods: warm (December-May) and cold (June-November). Specifically, austral summer and autumn were grouped under the warm seasonal period, while austral winter and spring were grouped in the cold seasonal period. That is consistent with the fact that due to logistical constraints and migration patterns of other target species such as baleen whales, surveys occurred mainly during two different periods of the year. Although these periods were not strictly fixed, they typically aligned with the austral summer and spring months. Therefore, a broad categorization was adopted for the analysis.

The two seasonal periods were defined based on previous knowledge of the observed within-year variability of SST, that are associated with variations in ocean circulation, particularly in the middle and inner shelf. Austral cold seasonal period was characterized by the minimum SSTs, typical during August-September, while austral warm seasonal period by the maximum SSTs, typical in February-March (Chen et al., 2019). Additionally, to ensure more reliable estimates, we also employed a geographic stratification of the study area (see 2.1 study area and survey design section), considering the spatial heterogeneity of the region, and the possible concentration of animals in sub-areas.

A single detection function was fitted for both seasons and strata due the small sample size. We estimated the average density and abundance within each stratum and season using the Horvitz-Thompson estimator (Miller et al., 2019). A non-parametric bootstrap method was used to assess uncertainty in abundance and density estimates across different strata within seasons (Miller et al., 2019).

## 3 | RESULTS

From November 2015 to March 2021, 13 boat surveys were carried out totaling 526 days of effort, with 571 transects covered in a search effort of 66,939 km (Table 2; Table S3). In total, 125 ASD groups were sighted and the mean group size was 34.5 (range = 299, Table 2).

**TABLE 2** Summary of survey effort and sightings in the Santos Basin survey area, between November 2015 and March 2021. Survey ID and year, dates (range), austral seasons (warm or cold), total number of days and hours of sampling, survey effort (km), number of group sightings (*N*), and the mean and range of group size are shown.

| Survey (Year) | Dates | Season | Days | Hours | Effort (km) | *N* | Group size mean | Group size range |
|---|---|---|---|---|---|---|---|---|
| 1 (2015) | 20 Nov–05 Jan | Warm | 40 | 389.9 | 4,937.1 | 7 | 14.4 | 3–50 |
| 2 (2016) | 10 May–20 Jun | Warm | 42 | 410.9 | 5,462.5 | 10 | 52.5 | 10–150 |
| 3 (2016) | 27 Sep–06 Nov | Cold | 41 | 420.1 | 5,500.3 | 6 | 13.5 | 5–30 |
| 4 (2017) | 08 Mar–18 Apr | Warm | 42 | 434.9 | 5,541.9 | 16 | 32.1 | 1–100 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| 5 (2017) | 25 Aug–07 Oct | Cold | 44 | 435.7 | 5,584.7 | 8 | 29 | 7–80 |
| 6 (2018) | 12 Jan–20 Feb | Warm | 40 | 449.4 | 5,863.6 | 23 | 27 | 4–200 |
| 7 (2018) | 01 Sep–20 Oct | Cold | 50 | 477.3 | 5,930.5 | 3 | 118 | 4–300 |
| 8 (2019) | 13 Mar–26 Apr | Warm | 45 | 425.5 | 5,490.4 | 15 | 23.2 | 2–100 |
| 9 (2019) | 24 Aug–13 Oct | Cold | 51 | 463.1 | 5,730.1 | 4 | 42.2 | 2–100 |
| 10 (2020) | 04 Mar–27 Mar | Warm | 23 | 235.8 | 3,124.3 | 13 | 29.9 | 1–120 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| 11 (2020) | 28 Aug–07 Oct | Cold | 47 | 424.7 | 5,416.2 | 3 | 38.3 | 15–60 |
| 12 (2020) | 28 Oct–16 Nov | Cold | 20 | 224.3 | 3,093.4 | 5 | 9.4 | 2–30 |
| 13 (2021) | 16 Jan–25 Feb | Warm | 41 | 398.6 | 5,264.4 | 12 | 18.9 | 3–35 |
| Total | - | - | 526 | 5,190.2 | 66,939.40 | 125 | 34.5 | 1–300 |

After right truncation of detection distances (1,075 m), a total of 112 detections (89.6% of the original total) were retained for detection function modeling (the largest perpendicular distance was 3,107 m in the original dataset) (Figure 2). A total of 28 detection function models were fitted. A hazard-rate function with group size (log-transformed) and detection method as covariates was chosen as the best model (Figure 2; Table S1).

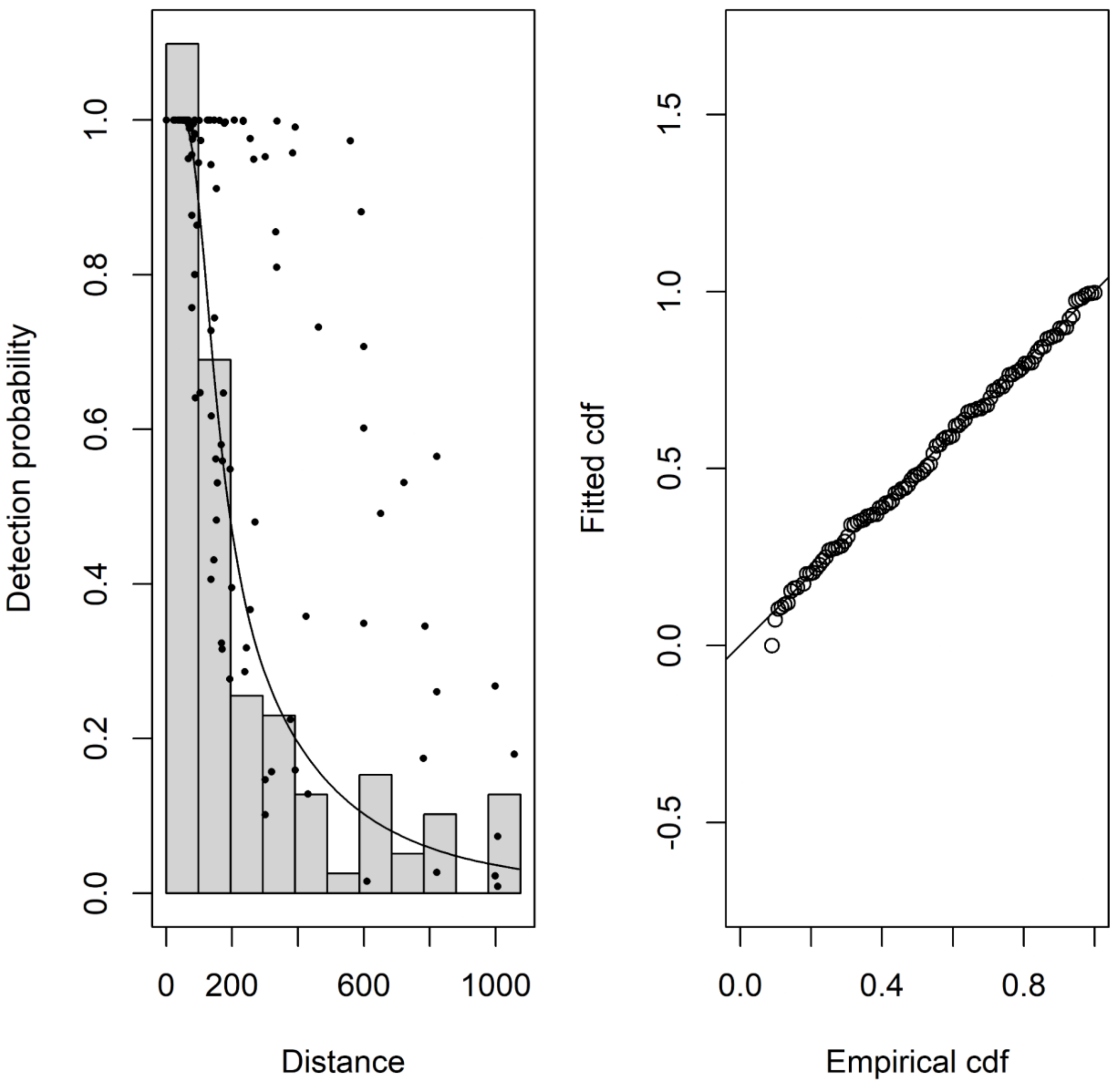


**FIGURE 2** (A) Plot of the fitted detection function onto the observed distances for the final model (a hazard-rate model with detection method and group size as covariates). A black line represents the average detection probability and circles represent the probability of detection of each sighting per detection distance, given its detection method and group size; (B) Q-Q plot of fitted cumulative distribution function (cdf) and empirical cumulative distribution

function for the final detection function model, showing “goodness-of-fit”.

Our findings revealed a clear pattern throughout the Santos Basin, evident in both population estimates and spatial distribution. We present the results from strata-seasons here (Table 3), while estimates per survey are provided in the Supplementary Material (Table S3). Group size varied between cold (*M*= 30.1; range= 298) and warm seasonal periods (*M*= 22.1; range = 199). Abundance and density estimates presented notable variability across different strata and seasons, and were higher in shelf strata during both austral seasons (Table 3). Based on data collected from November 2015 to March 2021, the abundance estimated for the warm seasonal periods was of 19,762 individuals (*CV* = 18%; 95% CI [13,709–28,487]), and of 8,692 individuals for the cold periods (*CV* = 27%; 95% CI [5,100–14,815]) (Table 3, Figure 4). During warm seasons, the “South continental shelf” (Scs) stratum presented the highest abundance, with 9,351 individuals (*CV*=24%; 95% CI [5,789–15,106]), and the “North continental shelf” (Ncs) stratum, the highest density with 0.15 individuals/km$^2$ (*CV* = 28%; 95% CI [0.091– 0.279]). Density was greatest in both Scs and Ncs strata during the warm seasonal periods (0.13 and 0.159 individuals/km$^2$, respectively). The lowest estimates were found in the “South oceanic” (So) stratum in the cold periods, with 126 individuals estimated (*CV* >100%; 95% CI [23–679]). There were three strata for which the abundance and density estimates were not possible to be calculated because there were no sightings: two during the cold period (“North slope”, Ns, and “South slope”, Ss) and one on the warm (So; Figure 4, Table 3).

**TABLE 3** Density and abundance estimation of Atlantic spotted dolphin in the period of November 2015 to March 2021 in Santos Basin region, Southwestern Atlantic. Data are presented by seasons, strata, the mean ± the standard error, coefficient of variance (*CV*), and 95% confidence interval (*CI*). The acronyms of eight strata represent: (Nc) North coastal; (Sc) South coastal; (Ncs) North continental shelf; (Scs) South continental shelf; (Ns) North slope; (Ss) South slope; (No) North oceanic and (So) South oceanic.

| **Seasons** | **Strata** | **Abundance** | **CI** | **Density (ind./km$^2$)** | **CI** | ***CV*** | **Seasons** | **Strata** | **Abundance** | **CI** | **Density (ind./km$^2$)** | **CI** | ***CV*** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Colder** | **Nc** | – | – | – | – | – | **Warmer** | **Nc** | 303 ± 211 | 84–1,088 | 0.042 ± 0.029 | 0.011–0.15 | 0.69 |
| | **Sc** | 987 ± 635 | 303–3,211 | 0.064 ± 0.041 | 0.019–0.208 | 0.64 | | **Sc** | 984 ± 746 | 247–3,913 | 0.063 ± 0.049 | 0.016–0.25 | 0.77 |
| | **Ncs** | 3,593 ± 1,326 | 1,770–7,295 | 0.081 ± 0.030 | 0.040–0.165 | 0.36 | | **Ncs** | 7,051± 2,037 | 4,030–12,338 | 0.159± 0.046 | 0.091–0.279 | 0.28 |
| | **Scs** | 3,572± 1,709 | 1,454–8,774 | 0.051 ± 0.024 | 0.020–0.125 | 0.47 | | **Scs** | 9,351 ± 2,301 | 5,789–15,106 | 0.13 ± 0.033 | 0.083–0.216 | 0.24 |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **Ns** | 220 ± 180 | 53–916 | 0.006 ± 0.005 | 0.001–0.025 | 0.82 | | **Ns** | 414 ± 322 | 105–1,627 | 0.011 ± 0.009 | 0.002–0.046 | 0.77 |
| | **Ss** | – | – | – | – | – | | **Ss** | 1,333 ± 605 | 561–3167 | 0.045 ± 0.020 | 0.019–0.108 | 0.45 |
| | **No** | 191 ± 150 | 48–756 | 0.003 ± 0.002 | 0.0009 – 0.014 | 0.78 | | **No** | 323 ± 329 | 60–1,722 | 0.006 ± 0.006 | 0.001–0.033 | 1.01 |
| | **So** | 126 ± 127 | 23–679 | 0.006 ± 0.006 | 0.001–0.032 | 1.006 | | **So** | – | – | – | – | – |
| | **Total** | 8,692 ± 2,400 | 5,100–14,815 | 0.032 ± 0.008 | 0.018–0.054 | 0.27 | | **Total** | 19,762 ± 3,706 | 13,709 – 28,487 | 0.072 ± 0.013 | 0.050–0.104 | 0.18 |

Abundance of ASDs in the Santos Basin varied between the austral warmer and colder seasons (Figure 3); animals were particularly more abundant in the continental shelf (NCs and SCs strata). The highest uncertainties (CV) were found in the slope and oceanic strata, as expected due to the low number of sightings. Conversely, the continental shelf strata presented the most precise estimates (Figure 3) and the confidence intervals for all strata within seasons consistently overlapped (Figure 4).

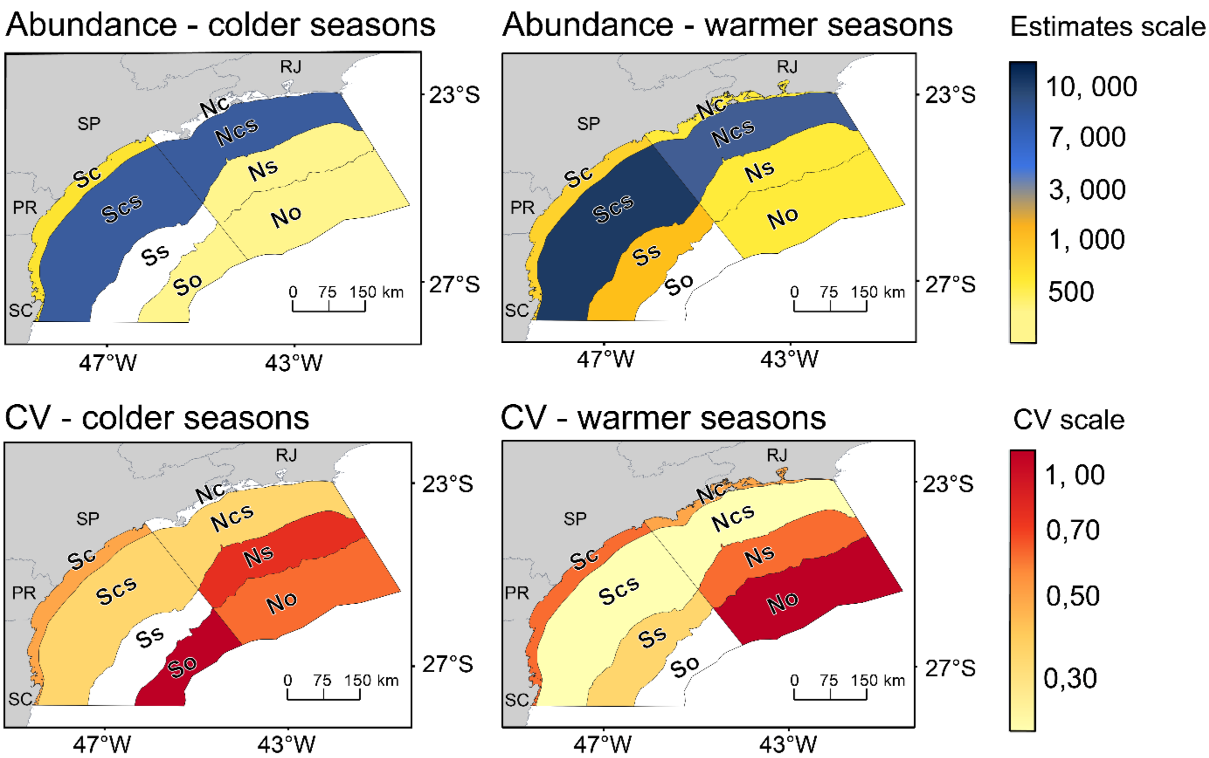


**FIGURE 3** Estimated abundance (top panel) of Atlantic spotted dolphins, and coefficient of variation in abundance estimates (bottom panel), for both austral cold and warm seasons in the Santos Basin. The acronyms on the map denote: Rio de Janeiro (RJ), São Paulo (SP), Paraná (PR), Santa Catarina (SC), North coastal (Nc), South coastal (Sc), North continental shelf (Ncs), South continental shelf (Scs), North slope (Ns), South slope (Ss), North oceanic (No) and the South oceanic (So).

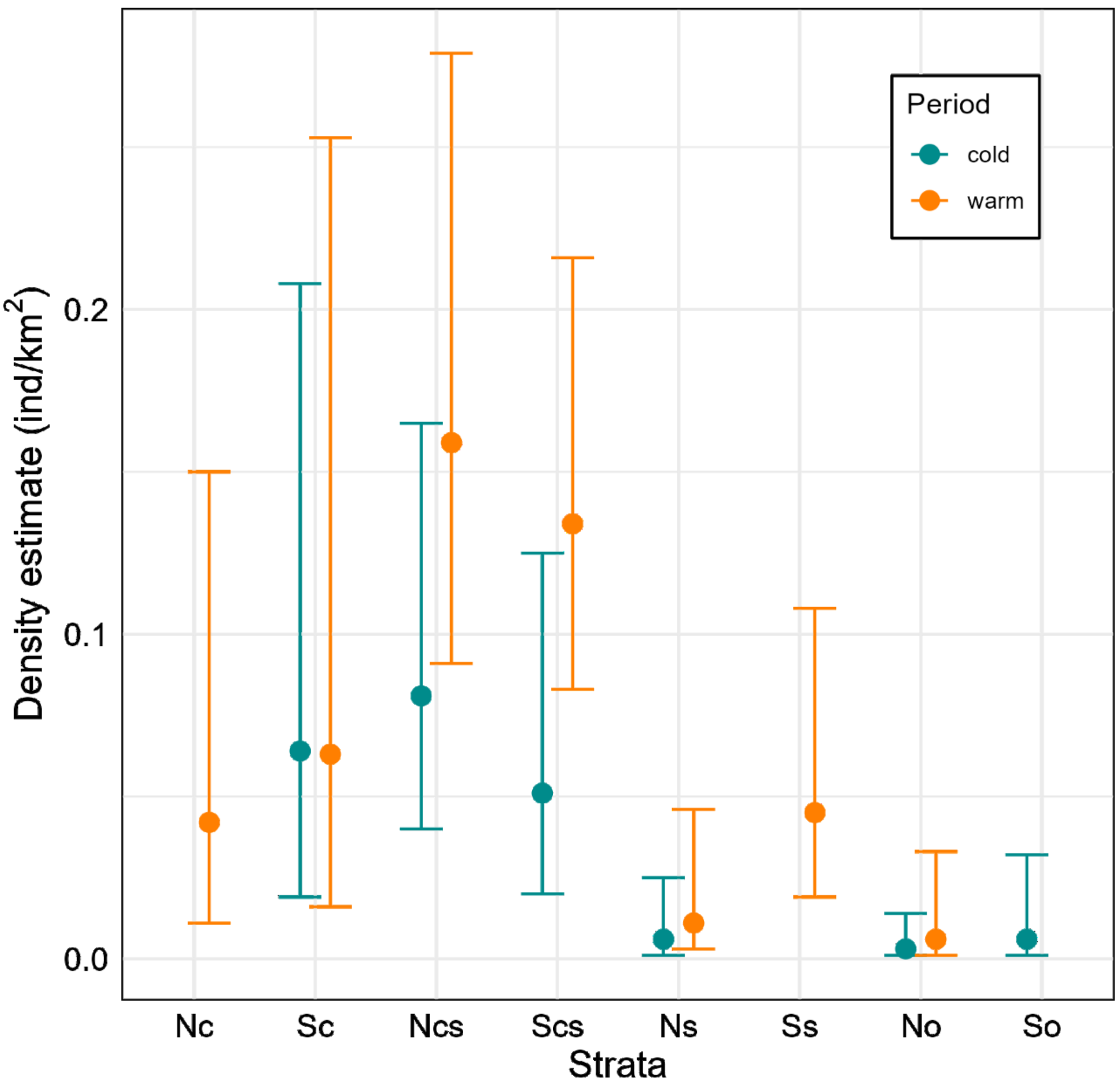


**FIGURE 4** Density estimates (y-axis) across different strata (x-axis) during warm and cold seasons (orange and blue respectively). The confidence interval provided a visual representation of the range of uncertainty associated with each density estimate. The strata include the North coastal (Nc), South coastal (Sc), North continental shelf (Ncs), South continental shelf (Scs), North slope (Ns), South slope (Ss), North oceanic (No) and the South oceanic (So).

## 4 | DISCUSSION

Here we presented the first large scale abundance and density estimates for *Stenella frontalis* in the Southwestern Atlantic Ocean waters. These estimates were the result of an extensive monitoring program using line transect with distance sampling methodology. The sampled area within the Santos Basin encompasses a significant portion of the known habitats of the

South–Southwest Atlantic population (Do Amaral et al., 2021). Our findings indicate that the species uses the shelf to oceanic regions of this basin, whereas it is concentrated in the shelf especially during periods characterized by the presence of relatively warmer waters.

## 4.1 | Density and abundance

The two continental shelf strata (Ncs and Scs) showed noticeably higher densities in both cold and warm seasonal periods. In contrast, the more coastal and deeper regions within Santos Basin presented lower dolphin densities, with high uncertainty ($CV > 0.5$, Nc, Sc, Ns, No and So; Table 3). Comparable assessments of ASD abundance are only available for the North Atlantic (i. e., Fulling et al., 2003; Garrison et al., 2010; Griffin & Griffin, 2003; 2004). The most recent estimates using aerial and ship surveys, spanning a period of 23 years, revealed relatively high abundance of ASDs in the mid and outer shelf off eastern U.S. and northern Gulf of Mexico, where the species is among the most abundant in both regions ($N = 55{,}436$, $CV = 0.32$ and $N = 47{,}488$, $CV = 0.13$ respectively; Roberts et al., 2016). In the Santos Basin, our results suggest that ASDs is among the most common delphinids in this basin (Martins et al., 2023). Also we identified the basin as another area of ecological importance for the species worldwide.

Recently, an abundance estimate of 397 ASDs (95% CI [389-406], for the period of 2017 to 2020) was assessed using mark-recapture methods in the inshore waters of Ilha Grande Bay (Rio de Janeiro, 22°50'S-23°20'S; Pereira et al., 2022), an area not encompassed by our surveys since did not include enclosed bays. In the North coastal stratum, which is contiguous to Ilha Grande Bay, we estimated 303 individuals ($CV = 0.69$; $SE = 211$; 95% CI [84-1,088]) in the austral warm months. This suggests that the ASDs that inhabit Ilha Grande bay are part of a larger population. However, further studies are needed to investigate the connectivity between distinct habitats occupied by the species (from coastal sites to shelf and offshore), which may be impacted by age-class composition, behavior, habitat characteristics, and seasonal patterns. This demonstrates that, while only our results corroborate that ASDs concentrate in shelf waters, they may approach inshore environments depending on habitat characteristics and seasonal periods.

## 4.2 | Detection function

Significant effort was made to maximize precision in the estimates by following the main assumptions of a widely used abundance estimation method (Buckland et al., 2001). Here, we assumed a perfect detectability within the transect lines, *g* (0) = 1, and it can provide underestimate abundance estimates. However, due the sampling protocols, which included low vessel speed and experienced observers onboard, adequate environmental conditions and the short dive time of the species, we believe bias is minimal and we were able to provide the most accurate estimates possible with this dataset (Thomas et al., 2010). However, certain considerations and cautions must be detailed when interpreting the data.

The primary source of high uncertainty in some strata was the variability in encounter rates. This could be dealt with by explicitly modelling encounter rates as a function of spatial variability, for which methods derived from Distance Sampling would be useful (e.g., "Density Surface Modelling"; Miller et al., 2022). Another important aspect of our detection function modelling was the variability in group sizes. Group size is one of the most common covariates that influence the detectability of dolphins in line transect surveys (Barlow et al., 2001). In our dataset, 45% of the sightings were for groups of less than 10 individuals, which indicates that smaller group sizes were not significantly missed. By incorporating group size in the detection function we reduced the positive size bias within this data set. Therefore, a significant bias related to it is not expected.

An issue that requires careful consideration is the risk of responsive movement of animals toward the vessel, which can be a source of bias in detections (Glennie et al., 2015). ASDs are known to be attracted to the boat prior to detection to bow-ride (e.g., 81% of the sightings in Griffin & Griffin, 2003). The information on responsive movement was not available to account for it in our analysis. Consequently, we recognize that the abundance and density estimates presented in this study might be overestimated. Despite this, the bias may not be substantial due to the implementation of effective survey protocols and the low vessel speed. Nonetheless, we recommend that future efforts mitigate potential movement effects and/or collect animal orientation data to apply as correction factors (Glennie et al., 2021; Palka & Hammond, 2001).

### 4.3 | Distribution

Atlantic spotted dolphins are well-documented to inhabit shallow coastal waters (e.g., Perrin, 2002). In the north-central and northwestern regions of Gulf of Mexico, aerial line-transect surveys revealed the species mainly occur in mid-shelf habitats while opportunistically occupying deeper waters (76–546 m, Mullin et al., 2004). Due the complexity of the physiography and ocean circulation, for example where warm-temperate water influence north and tropical water the south, different studies have been revealing the influence of oceanographic characteristics (e.g., bathymetry and ocean dynamics) on the distribution and abundance of cetaceans in this enclosed area (Baumgartner et al., 2001; Ramírez-León et al. 2021). In the SWA, among the five species of the genus *Stenella,* only ASDs use shallow continental shelf as their primary habitat (Moreno et al., 2005). In contrast, Pantropical spotted dolphins (*S. atenuatta*), spinner dolphin (*S. longirostris*), Clymene´s dolphin (*S. clymene*) and striped dolphin (*S. coeruleoalba*) exhibit broad environmental suitability to offshore waters, displaying a significant overlap in their distributional ranges along the Brazilian coast (Correa et al., 2023; Do Amaral et al., 2015). That may suggest niche partitioning and spatial segregation, which can be expected to be more pronounced among ASDs and other *Stenella* species due to variations in prey distribution, feeding preferences and environmental characteristics (Davis et al., 1998; Do Amaral et al., 2015). However, distributional overlap between these species seems to occur primarily in the Santos Basin. The basin shelf is an important habitat also for other cetacean species, including small dolphins as *Tursiops truncatus*, *Sotalia guianensis* and baleen whales as *Megaptera novaeangliae* and *Balaenoptera brydei* (Dalpaz et al., 2023; Martins et al., 2023). Consistent with previous studies, our findings indicate that ASD is widely observed and abundant on the Santos Basin shelf, with groups primarily occupying waters with depths ranging from 50 to 200 m (shelf strata, Ncs and Scs). Moreover, sightings exhibit both spatial and seasonal variation (Figure S1). Di Tullio et al. (2016) and Pereira et al. (2022) findings have already demonstrated seasonal patterns in the outer continental shelf (~150m), slope (1500m) and in bays off southeastern Brazil. Both studies recorded an increase in the use of the Santos Basin portions, particularly during the austral autumn months, but also during winter months in Ilha Grande Bay. Our findings are consistent with theirs and indicate that species' habitats may vary seasonally.

In southeastern Brazil, ASDs were found to feed on different demersal and pelagic preys (Lopes et al., 2012; Melo et al., 2010). Among the most present organisms are the squid species *Doryteuthis plei* and the fish *Porichthys porosissimus*, both widely distributed in the SWA (Haimovici & Perez,1991; Vianna & Verani, 2000). The feeding habits revealed through stable isotope analyses indicated that ASDs' prey distribution is linked to the South Atlantic Central Water (Bisi et al., 2013), a water mass that emerges through seasonal upwelling events which contribute to local productivity in continental shelf and slope regions.

As shown here, the high concentration of ASDs on the northern shelf strata during austral warm seasons may be linked to oceanographic processes which may increase prey availability and indirectly influence dolphins' distribution (e.g., Cabo Frio upwelling, Acha et al., 2004). Other studies also indicated a strong association of higher productivity regions and their occurrence (Bisi et al., 2013; Di Tullio et al., 2016; Pereira et al., 2022). According to that hypothesis, individuals may also use outer continental shelf regions by taking advantage of shelf-break upwellings associated with intense "vortical structures" during both austral cold and warm months (e.g., meanders, vortices and eddies, Campos et al., 2000).

Along the Santos Basin, seasonal abundance fluctuations across strata may be due to physical characteristics of each stratum and the hydro-geomorphological features. Reinforcing that, factors such as bathymetry, chlorophyll concentrations, and the presence of oceanic fronts have already been indicated as important predictors of ASD habitat (e.g., Barragán-Barrera et al., 2019; Do Amaral et al., 2015; Griffin & Griffin, 2003; 2004). Sea water temperature is a crucial variable for discerning seasonality and exhibits a clear correlation with ASD densities variations across temporal and spatial scales. In the north Atlantic, previous studies observed seasonality in ASDs' densities, suggesting movements alongshore toward warmer waters and from inshore to offshore waters (Griffin & Griffin, 2004).

In SWA, warmer waters also determine their habitat, which typically range from 19°C to 29ºC (Moreno et al., 2005; Santos et al., 2017). Thus, it is plausible to consider the hypothesis that some individuals migrate north during austral cold months avoiding colder surface waters coming from south. For example, results from boat surveys conducted in southeastern and southern Brazil (22.9°S - 33.7°S) indicated higher frequencies of ASD groups towards north of 31°S, along with seasonal patterns (Di Tullio et al., 2016). However, to gain a deeper understanding of those animals' movements, it is necessary to collect data from additional locations and monitor animal movements (i.e., employing satellite tags or using photoidentification data) to investigate it on a broader scale (Moore et al., 2024).

### 4.4 | Conservation considerations and future research

Our work provides essential baseline information for future assessments and monitoring regarding distribution, density, and abundance of the *Stenella frontalis* population in the Santos Basin. Caution must be exercised when extrapolating our findings beyond our study area or time periods, since we did not cover the entire population in the South-Southeast Brazil.

Our results represent the expected average abundance of Atlantic spotted dolphins across the two seasonal periods and within each portion of Santos Basin. The Santos Basin encompasses Brazil's largest reserves of oil and natural gas (Bruhn et al., 2017), and intense anthropogenic activities such as port operations and fisheries. Furthermore, high concentration of contaminants was recorded in individuals sampled in São Paulo state (Méndez-Fernandez et al., 2018). It is a critical concern for top predators that are susceptible to high concentrations of contaminants through bioaccumulation (Tovar et al., 2023). Thus, animals that occupy Santos Basin area seem to be exposed to a range of threats (Marega-Imamura et al., 2020). However, comprehensive threat assessment focusing on this population and in this basin is still necessary. The research efforts we report here are part of the wider PMC-BS, which largely aims to assess those threats to not only dolphins, but all cetacean species in the area.

To complement the understanding of the species' ecology and evaluate the need for conservation efforts, there is a need for research on the environmental drivers that influence species' habitat (e.g., Ramírez-León et al., 2021), and consequently the estimates. That may allow identifying more specific regions within the basin and to comprehend movement patterns exhibited in dynamic environments. Additionally, to obtain a more comprehensive picture of the distribution and the dynamics of ASDs population in SWA, future studies should incorporate systematic surveys over a wider geographic area towards the north and the south of Santos Basin, with a special focus on the continental shelf habitat. Furthermore, biopsy sampling and genetic analyses would significantly narrow the knowledge gap regarding the discussions of different populations across their distribution. Specifically, there is a need for samples and studies to bring clarity to the hypothesis of the existence of an isolated population in southeastern Brazil (Caballero et al., 2013; Do Amaral et al., 2021).It could elucidate the connectivity between basins and habitats, which is crucial for designing effective conservation strategies for this species.

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**Appendix S1** Supplementary Information

To

**Seasonal abundance and distribution of Atlantic spotted dolphins (*Stenella frontalis*) in the southwestern Atlantic Ocean**

Thayusky P. Correa, Guilherme A. Bortolotto, Leonardo L. Wedekin, Marta J. Cremer

*Marine Mammal Science*

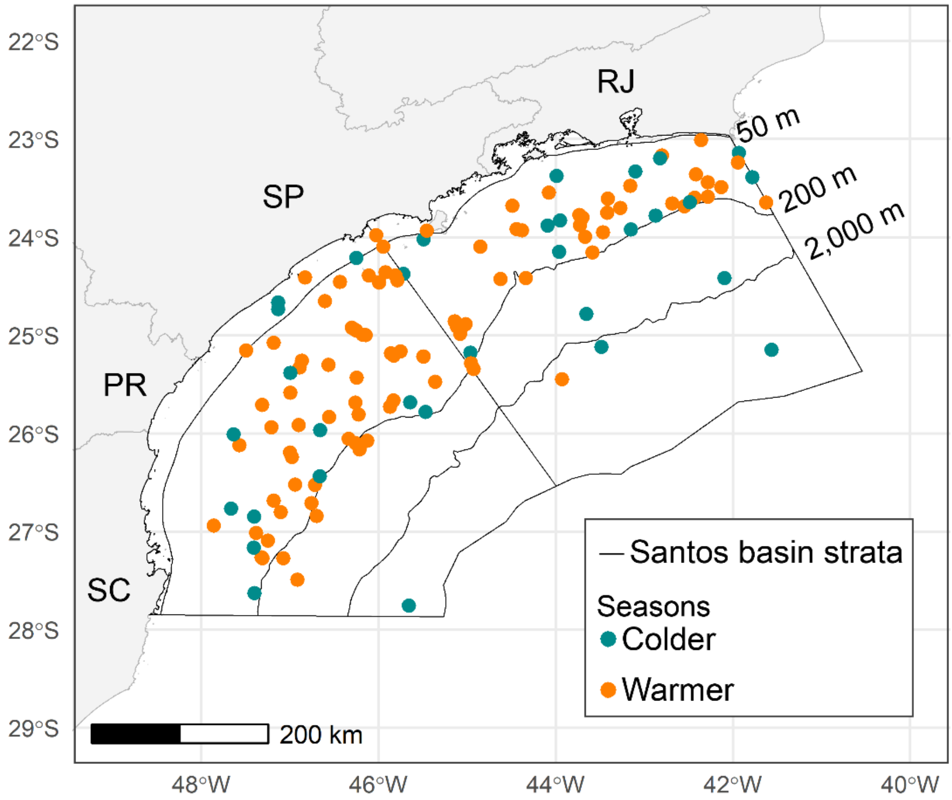
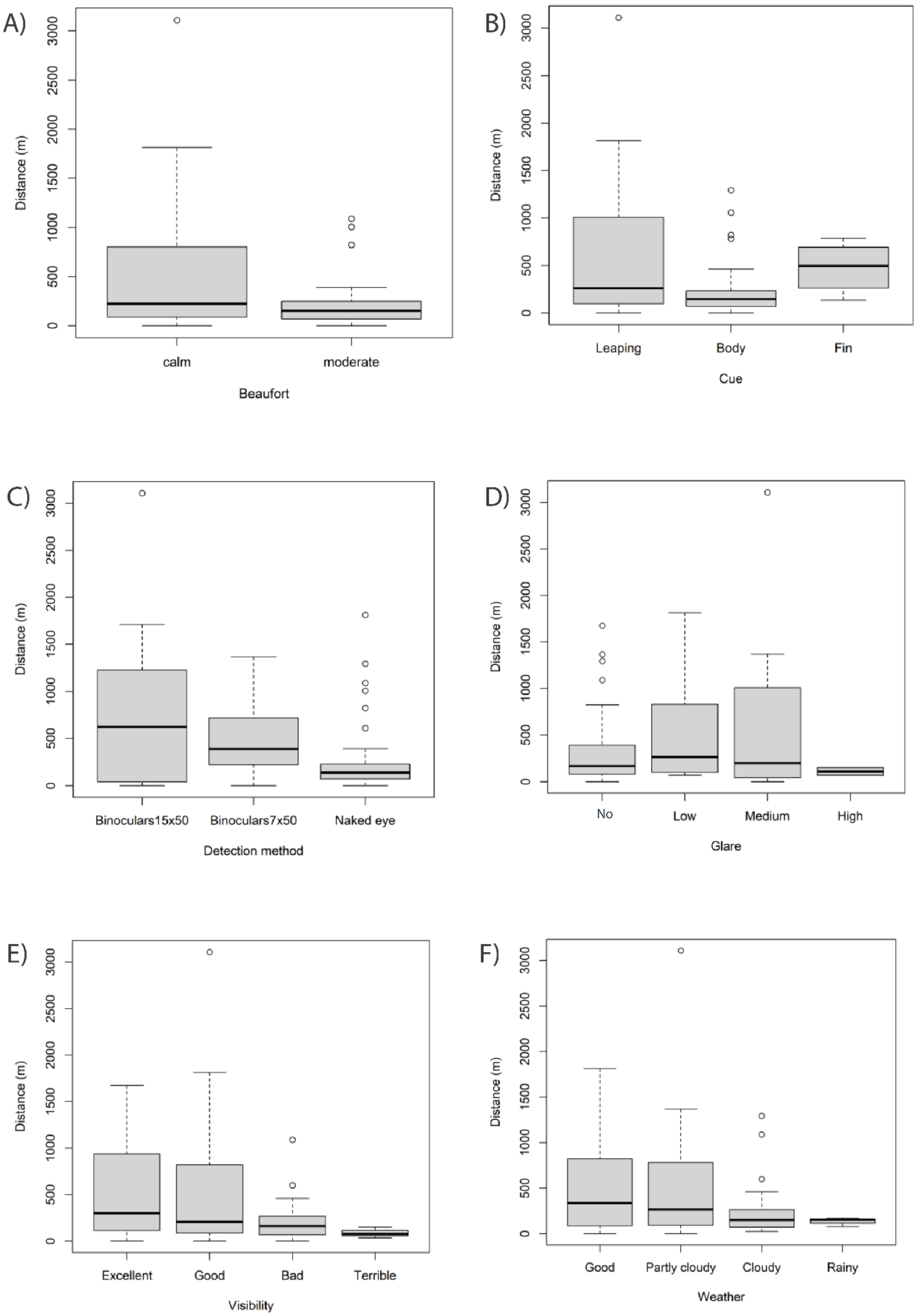



**FIGURE S1** Sightings of *Stenella frontalis* from November 2015 to March 2021 in the Santos Basin. The acronyms on the map denote: Rio de Janeiro (RJ), São Paulo (SP), Paraná (PR), and Santa Catarina (SC) states.


A)
Distance (m)
0
500
1000
1500
2000
2500
3000
calm
moderate
Beaufort
B)
Distance (m)
Leaping
Body
Fin
Cue
C)
Distance (m)
Binoculars15x50
Binoculars7x50
Naked eye
Detection method
D)
Distance (m)
No
Low
Medium
High
Glare
E)
Distance (m)
Excellent
Good
Bad
Terrible
Visibility
F)
Distance (m)
Good
Partly cloudy
Cloudy
Rainy
Weather

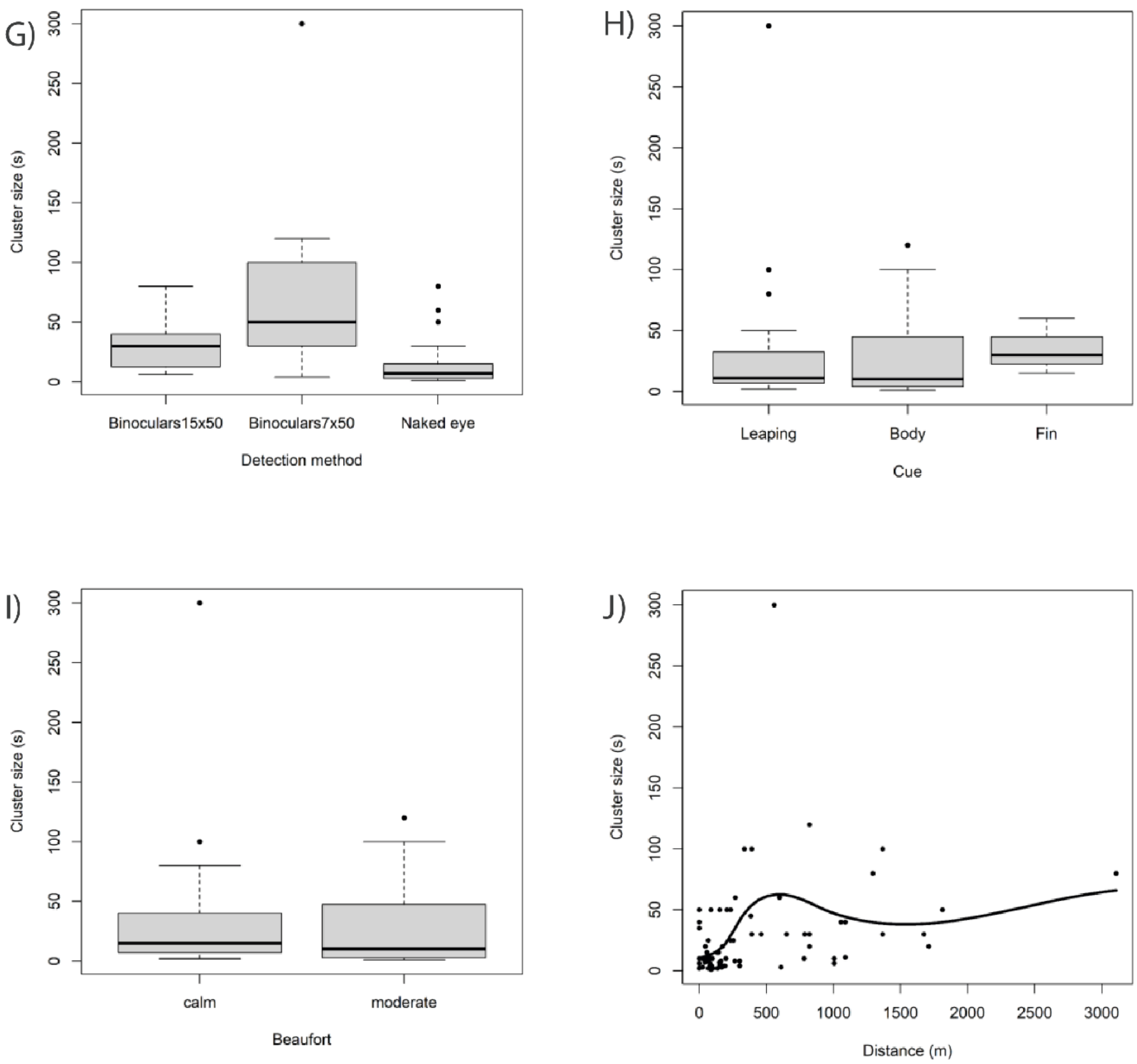



**FIGURE S2** Exploratory analysis of the effects of covariates on distances and cluster size (number of individuals) at which *Stenella frontalis* were detected in the Santos Basin. Plots of the covariates considered in the detection function modeling, presented from panels A to J. Panels A to I: boxplots of each covariate by distance (m) and cluster size where the thick black lines represent the medians, the boxes encompass the 25th and 75th percentiles, the whiskers extend to the most extreme data points within 1.5 times the interquartile range from the box, and the circles indicate data points beyond the whiskers. Panel J: scatterplot of cluster size as a function of distance (m). The solid line represents the fitted regression line, illustrating the relationship between distance and size.

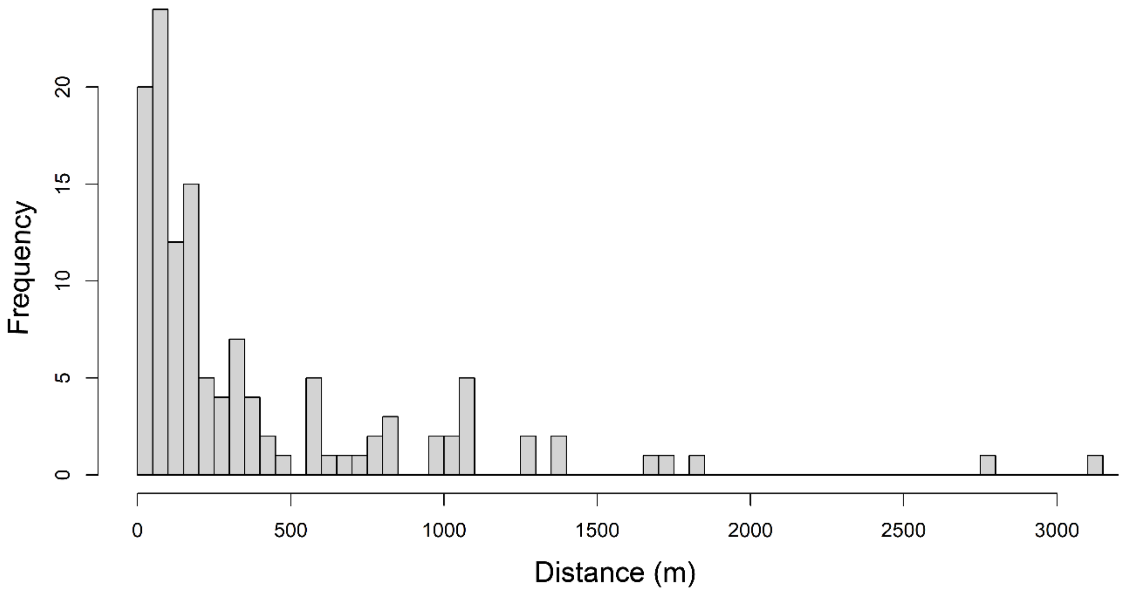



**FIGURE S3** Frequency distributions of perpendicular distances of sightings of *Stenella frontalis* groups during line transect surveys in Santos Basin from November 2015 to March 2021.

**TABLE S1** Summary of detection function models fitted. Two key functions were considered (hazard rate and the half-normal). Group size (size), detection method (detecFactor), glare (glareFactor), visibility (visibilityFactor), cue (cueFactor), weather (weatherFactor) and sea state (beaufortFactor) were tested for inclusion as covariates.The acronyms represent: Cramer-von Mises values (*CvM*), Standard Error (*SE*), and Akaike's information criterion (AIC).

| | Model | Key function | Formula | *CvM* | Average detectability | *SE* (Average detectability) | Delta AIC |
|---|---|---|---|---|---|---|---|
| 1 | df_hr_logsize_detec | Hazard-rate | ~detecFactor + log(size) | 0.917359022 | 0.260131506 | 0.032325456 | 0 |
| 2 | df_hr_detec | Hazard-rate | ~detecFactor | 0.683419395 | 0.243383326 | 0.033374616 | 2.500773862 |
| 3 | df_hr_logsize_glare | Hazard-rate | ~glareFactor + log(size) | 0.779373729 | 0.247950433 | 0.035522523 | 6.810833178 |
| 4 | df_hr_logsize_cue | Hazard-rate | ~cueFactor + log(size) | 0.633747118 | 0.268695256 | 1.397839184 | 7.963283926 |
| 5 | df_hn_logsize_vis | Half-normal | ~visibilityFactor + log(size) | 0.107377414 | 0.287617984 | 0.031973357 | 8.850340158 |
| 6 | df_hr_logsize_beau | Hazard-rate | ~beaufortFactor + log(size) | 0.648404777 | 0.274687145 | 0.034707829 | 9.408071262 |
| 7 | df_hr_logsize_vis | Hazard-rate | ~visibilityFactor + log(size) | 0.517785542 | 0.282293799 | 0.036055065 | 9.632560509 |
| 8 | df_hr_size | Hazard-rate | ~log(size) | 0.719915087 | 0.27397249 | 0.036200494 | 11.83591476 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| 9 | df_hr_cue | Hazard-rate | ~cueFactor | 0.849953393 | 0.245006286 | 4.413946129 | 18.00368374 |
| 10 | df_hr_beau | Hazard-rate | ~beaufortFactor | 0.913029947 | 0.234614668 | 0.037484341 | 21.10850437 |
| 11 | df_sf_hr | Hazard-rate | ~1 | 0.775288588 | 0.233458147 | 0.038366149 | 22.11018689 |
| 12 | df_hn_logsize_detec | Half-normal | ~detecFactor + log(size) | 0.012749092 | 0.33329204 | 0.019010473 | 22.44736644 |
| 13 | df_hn_logsize_glare | Half-normal | ~glareFactor + log(size) | 0.007773116 | 0.320710292 | 0.024452006 | 22.60771859 |
| 14 | df_hr_logsize_weather | Half-normal | ~weatherFactor + log(size) | 0.029030854 | 0.323923572 | 0.029139653 | 22.88007082 |
| 15 | df_hn_logsize_weather | Half-normal | ~weatherFactor + log(size) | 0.029030854 | 0.323923572 | 0.029139653 | 22.88007082 |
| 16 | df_hn_logsize_cue | Half-normal | ~cueFactor + log(size) | 0.013163074 | 0.318408046 | 0.025384771 | 23.07919441 |
| 17 | df_hr_glare | Hazard-rate | ~glareFactor | 0.789938919 | 0.203247607 | 0.03777709 | 23.36638926 |
| 18 | df_hr_vis | Hazard-rate | ~visibilityFactor | 0.83299522 | 0.233076013 | 0.03758262 | 23.72319269 |
| 19 | df_hr_weather | Hazard-rate | ~weatherFactor | 0.838452894 | 0.238675953 | 0.038868291 | 27.36945548 |
| 20 | df_hn_vis | Half-normal | ~visibilityFactor | 0.00510827 | 0.329825027 | 0.03455883 | 28.65615064 |
| 21 | df_hn_logsize_beau | Half-normal | ~beaufortFactor + log(size) | 0.00309106 | 0.35901002 | 0.019195561 | 32.78843121 |
| 22 | df_hn_detec | Half-normal | ~detecFactor | 0.00050531 | 0.371804044 | 0.017813109 | 35.0045034 |
| 23 | df_hn_size | Half-normal | ~log(size) | 0.001170474 | 0.369643136 | 0.019167565 | 35.27294275 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| 24 | df_hn_weather | Half-normal | ~weatherFactor | 0.001295031 | 0.374228015 | 0.039223372 | 44.73808008 |
| 25 | df_hn_glare | Half-normal | ~glareFactor | 0.000193769 | 0.361523657 | 0.038625699 | 47.06219534 |
| 26 | df_hn_beau | Half-normal | ~beaufortFactor | 0.00013963 | 0.401965585 | 0.020082364 | 48.93751148 |
| 27 | df_hn_cue | Half-normal | ~cueFactor | 0.000106518 | 0.404340516 | 0.019866155 | 52.30843182 |
| 28 | df_sf_hn | Half-normal | ~1 | 1.58851E-05 | 0.426817628 | 0.02110216 | 56.70776021 |

**TABLE S2** Abundance and density estimations produced by surveys (austral seasons and year) of Atlantic spotted dolphins in the period of November 2015 to March 2021 in the Santos Basin region, Southwestern Atlantic. The acronyms represent: Standard Error (*SE*), Lower Confidence Limit (*LCL*), Upper Confidence Limit (*UCL*), and Coefficient of variation (*CV*).

| Survey | Season (Year) | Abundance | | | | Density | | | | *CV* |
|---|---|---|---|---|---|---|---|---|---|---|
| | | **Estimate** | ***SE*** | ***LCL*** | ***UCL*** | **Estimate** | ***SE*** | ***LCL*** | ***UCL*** | |
| 1 | Summer (2015) | 9991.992 | 5416.358 | 3651.448 | 27342.55 | 0.036659 | 0.019872 | 0.013397 | 0.100315 | 0.54207 |
| 2 | Autumn (2016) | 17732.29 | 8653.481 | 7097.788 | 44300.3 | 0.065057 | 0.031748 | 0.026041 | 0.16253 | 0.488007 |
| 3 | Spring (2016) | 6453.045 | 2961.685 | 2710.653 | 15362.27 | 0.023675 | 0.010866 | 0.009945 | 0.056361 | 0.458959 |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| 4 | Autumn (2017) | 31386.56 | 11050.23 | 15971.2 | 61680.77 | 0.115152 | 0.040541 | 0.058596 | 0.226296 | 0.352069 |
| 5 | Spring (2017) | 8768.156 | 3779.621 | 3866.396 | 19884.29 | 0.032169 | 0.013867 | 0.014185 | 0.072952 | 0.431062 |
| 6 | Summer (2018) | 31104.58 | 11181.03 | 15604.71 | 62000.2 | 0.114117 | 0.041021 | 0.057251 | 0.227468 | 0.359466 |
| 7 | Spring (2018) | 10824.35 | 8694.216 | 2669.19 | 43895.93 | 0.039713 | 0.031898 | 0.009793 | 0.161046 | 0.803209 |
| 8 | Autumn (2019) | 12675.69 | 5390.685 | 5644.369 | 28466.07 | 0.046505 | 0.019777 | 0.020708 | 0.104437 | 0.425278 |
| 9 | Spring (2019) | 9307.579 | 6704.343 | 2584.082 | 33524.88 | 0.034148 | 0.024597 | 0.009481 | 0.122997 | 0.72031 |
| 10 | Autumn (2020) | 27027.13 | 10002.63 | 13202.7 | 55327 | 0.099158 | 0.036698 | 0.048438 | 0.202985 | 0.370096 |
| 11 | Winter (2020) | 4367.84 | 2735.161 | 1395.281 | 13673.24 | 0.016025 | 0.010035 | 0.005119 | 0.050165 | 0.626205 |
| 12 | Spring (2020) | 9239.011 | 5977.012 | 2812.406 | 30350.99 | 0.033896 | 0.021929 | 0.010318 | 0.111352 | 0.646932 |
| 13 | Summer (2021) | 8569.162 | 3242.091 | 4149.575 | 17695.92 | 0.031439 | 0.011895 | 0.015224 | 0.064923 | 0.378344 |

**TABLE S3** Summary of survey effort by strata-season conducted between November 2015 and March 2021. Information about area, covered area, survey effort, number of transects (k), mean and amplitude of group size (*s*) for each stratum in both seasons is provided. The acronyms strata represent: (Nc) North coastal; (Sc) South coastal; (Ncs) North continental shelf; (Scs) South continental shelf; (Ns) North slope; (Ss) South slope; (No) North oceanic and (So) South oceanic.

| Strata | Area (Km) | Season | Covered Area (Km) | Effort (Km) | k | *s* mean | *s* amplitude | Season | Covered Area (Km) | Effort (Km) | K | *s* mean | *s* amplitude |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Nc | 7,215 | **Cold** | 510.1142 | 237.0745 | 17 | 0 | 0 | **Warm** | 807.113 | 375.1041 | 33 | 6 | 2–10 |
| Sc | 15,417 | | 2,911.4486 | 1,353.0897 | 53 | 27.7 | 3–60 | | 2,490.637 | 1,157.5185 | 48 | 14 | 5–30 |
| NCs | 44,145 | | 11,611.2051 | 5,396.2835 | 90 | 35.6 | 2–100 | | 13,699.601 | 6,366.8612 | 97 | 43.2 | 3–200 |
| SCs | 69,677 | | 16,976.8685 | 7,889.9645 | 112 | 52.2 | 10–300 | | 14,767.569 | 6,863.1972 | 97 | 20 | 1–120 |
| Ns | 35,302 | | 10,074.2474 | 4,681.9856 | 88 | 6 | 2–10 | | 9,218.080 | 4,284.0834 | 89 | 35 | 20–50 |
| Ss | 29,199 | | 6,862.6121 | 3,189.3848 | 61 | 80 | 0 | | 7,182.006 | 3,337.8226 | 58 | 16.7 | 4–40 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| No | 50,905 | 13,596.7094 | 6,319.0425 | 97 | 4.5 | 2–7 | 13,259.981 | 6,162.5485 | 97 | 20 | 0 |
| So | 20,925 | 4,717.8291 | 2,192.6013 | 47 | 5 | 0 | 5,115.089 | 2,377.2272 | 51 | 0 | 0 |
| Total | 272,785 | 67,261.0344 | 31,259.4265 | 565 | 30.1 | 2–300 | 123,232.221 | 57,271.9196 | 570 | 22.1 | 1–200 |

# 4 CAPÍTULO III

Oceanographic features affect density and abundance of Atlantic spotted dolphins (*Stenella frontalis*) in the South Brazil Bight

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(A ser submetido à revista científica *Deep Sea Research Part II: Topical Studies in Oceanography*)

Formatado de acordo com os moldes da revista

Correa, T.P., Wedekin, L.L., Bortolotto, G.A., Cremer, M.J. Oceanographic features affect density and abundance of Atlantic spotted dolphins (*Stenella frontalis*) in the South Brazil Bight

**Oceanographic features affect density and abundance of Atlantic spotted dolphins (*Stenella frontalis*) in the South Brazil Bight**

Thayusky P. Correa[1,2], Leonardo L. Wedekin[3], Guilherme A. Bortolotto [4,5,] Marta J. Cremer[1,2]

[1] Programa de Pós-Graduação em Ecologia, Departamento de Ecologia e Zoologia, Universidade Federal de Santa Catarina, Florianópolis, Santa Catarina, Brazil

[2] Laboratório de Ecologia e Conservação de Tetrápodes Marinhos e Costeiros – TetraMar, Universidade da Região de Joinville, São Francisco do Sul, Santa Catarina, Brazil

[3] Socioambiental Consultores Associados, Florianópolis, Santa Catarina, Brazil

[4] Department of Life Sciences, Aberystwyth University, Aberystwyth, Ceredigion, United Kingdom

[5] Sea Mammal Research Unit, Scottish Oceans Institute, University of St Andrews, St Andrews, Fife, United Kingdom

Corresponding author

Thayusky da Penha Correa, Laboratório de Ecologia e Conservação de Tetrápodes Marinhos e Costeiros (TetraMar), Departamento de Ecologia e Zoologia, Centro de Ciências Biologicas, Universidade Federal de Santa Catarina, Trindade, C.P. 5102, CEP 88040-970, Florianópolis, SC, Brazil.

E-mail address: thayusky@gmail.com

## Abstract

The distribution and abundance of Atlantic spotted dolphins (ASDs, *Stenella frontalis*) on the South Brazil Bight area presented notable seasonality. The environmental factors behind such variations have not been well investigated, but dynamic oceanographic features in the area must be related. To address this ecological question, we analyzed the spatial densities of ASDs within Santos Basin, a large ocean area in the south and southeastern coast of Brazil. We applied density surface models in a generalized additive modeling framework to predict dolphin density and abundance considering three mesoscale oceanographic features: (1) Cabo Frio upwelling, (2) Subtropical Shelf front, and (3) Brazil Current meandering and eddies. Dolphin sightings were collected during dedicated boat surveys from November 2015 to March 2021, with over 65 thousand kilometers of line-transect effort. The best-fitted model included mean water depth and monthly sea surface temperature as important ecological predictors of ASDs. Prediction maps were generated for each of the oceanographic features, which we argue are proxies for the seasonal ASD density patterns in the area. Our findings show the role of bathymetry and sea water temperature in providing suitable habitats for this species. The results indicate a link between the densities of ASDs and ecosystem dynamics, particularly to mesoscale oceanographic features that enhance biological productivity, such as upwelling and ocean fronts. We also highlight that the two hotspots in the South Brazil Bight are overlapped to areas of intense offshore human activities.

**Keywords:** Density Surface Modelling; Line transect sampling, Santos Basin, Upwelling, Habitat

## 1. Introduction

Cetacean density and distribution are typically linked to prey-rich areas driven by dynamic oceanographic features which presumably enhance foraging opportunities (Morato et al., 2008; Mannocci et al., 2014). Consequently, different studies have identified important predictors of cetacean presence, including water depth, seafloor slope, sea surface temperature, salinity, prey distribution, and proximity to features as eddies, upwellings, and seamounts (Cañadas et al., 2002; Azzellino et al., 2012; Hann et al., 2016, Palacios et al., 2023). A set of habitat characteristics for predicting cetacean presence vary depending on the size of the study area, sample size, data resolution and the species of interest (Redfern et al., 2006). Also, the frequency, duration, and seasonality features can significantly influence the productivity and community composition from lower to top trophic level vertebrates (Gill, 2002; Mannocci et al., 2017a).

The Atlantic spotted dolphin (ASD, *Stenella frontalis*) is only found within the Atlantic Ocean, inhabiting tropical, subtropical, and warm temperate waters (Perrin, 2009; Do Amaral et al., 2021). In the southwestern Atlantic Ocean (SWAO), the ASDs is one of the most sighted species, primarily on the continental shelf waters and eventually occuring on inshore environments to the slope, with a depth limit around 1,000 meters (Moreno et al., 2005; Santos et al., 2017; Pereira et al., 2022). Recent work on the South Brazil Bight (SBB, 23°S–28°S) reveals seasonal variations in ASDs distribution and abundance (Correa et al., *in preparation*) showing higher densities mainly on continental shelf waters with variations depending on the season and regions. The ecological drivers of such variation, however, have not yet been fully understood. Enviromental factors linked to how this species use their habitats in the SWAO included bathymetry (<1,000 m), sea surface salinity (35 – 36.5 psu), annual mean chlorophyll A (0.15 – 0.25 $mg^3$), sea surface temperature (around 23°C), and closer distances to the shore (Do Amaral et al., 2015).

The SBB is a large semi-enclosed marine ecosystem characterized by a wide continental shelf on the southeast and south Brazilian coast, bordering the states of Rio de Janeiro, São Paulo, Paraná and Santa Catarina (23°S–27°S, Castro and Miranda, 1998). The SBB is a moderate to high productive region shaped by temporal and spatial variability (Ekau and Knoppers, 1999; Castro et al., 2006; Brandini et al., 2018). This region contains Brazil's largest offshore sedimentary basin, the Santos Basin, where intense oil and gas production activities takes place (Modica and Brush, 2004; Castro et al., 2006; Souza and Chaves-Sgarbi, 2019). Remarkably, it exhibits significant biological diversity and, particularly on cetacean species, has one of the highest ecological richness in the world (Tittensor et al., 2010; Martins et al., 2023). Recent findings suggest that ASDs in this region may track the southward displacement of the tropical waters of the Brazil Current during warm seasons, and upwelling events (Bisi et al., 2013; Di Tullio, 2016).

To gain a deeper ecological understanding and, ultimately, help on conservation and management procedures, spatial models is a useful tool. Density surface modeling (DSM) is a spatial modeling technique for line transect data that offers an effective framework to estimate spatially explicit densities (Miller et al., 2013). In a DSM, a set of oceanographic features can be included to explore density estimates and trends in cetacean populations (Becker et al., 2014; Mannocci et al., 2017b). The spatial model can provide more reliable estimates for wildlife conservation and management by accounting for uncertain detection using distance sampling methods alongside identifying oceanographic features that trigger cetacean habitat use (Tynan et al., 2005; Miller et al., 2013).

Then here, we sought to investigate density patterns, environmental and oceanographic features for ASDs in the Santos Basin using the DSM approach. We first investigated which habitat covariates may be linked to their densities, then we created spatial predictions maps for three distinct oceanographic mesoscale features in the South Brazil Bight. We hypothesize that the density of ASDs in the basin may be influenced by specific environmental and oceanographic characteristics. In particular, we expect that mesoscale oceanographic features presence, such as eddies, fronts, and upwelling zones, play a role in shaping their spatial distribution and density. Furthermore, we anticipate that areas with higher primary productivity (serving as proxies for prey availability) will be associated to greater densities of spotted dolphins.

## 2. Material and Methods

### *2.1 Study Area*

This study was undertaken in the South Brazil Bight, focused in the Santos Basin area (SB, 272,567 km$^2$) located off the south and southeast of the Brazilian coast, between 23°S to 27°S latitude and 48°W to 41°W longitude (Fig. 1).

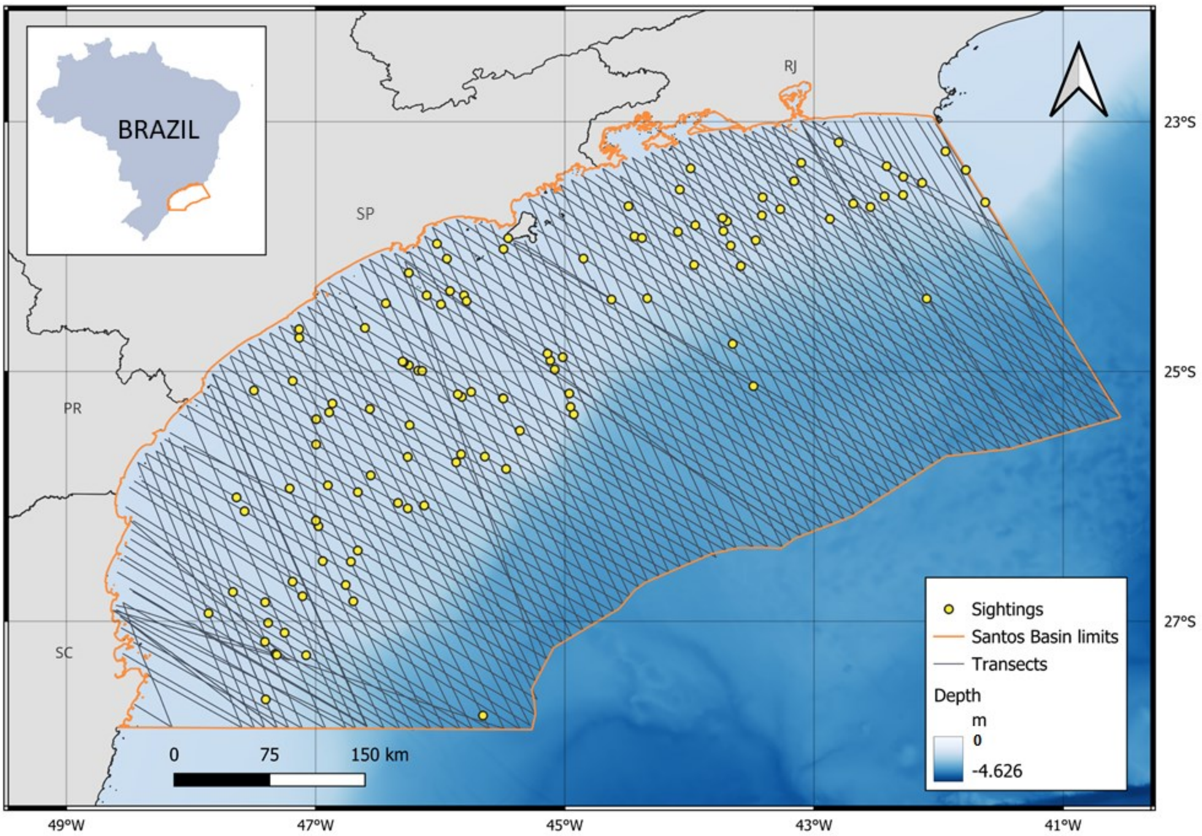


**Fig. 1** Ship-based survey lines and sighting locations of Atlantic spotted dolphins, *Stenella frontalis*, in Santos Basin between 2015–2021. Acronyms represent the Brazilian states of Santa Catarina (SC); Paraná (PR); São Paulo (SP) and Rio de Janeiro (RJ).

In the northernmost part of the basin, the Cabo Frio region exhibits an abrupt northeast to southwest (NE-SW) and east to west (E-W) coastline shift accompanied by a progressively widening continental shelf reaching up to 200 km offshore in some locations (Modica and Brush, 2004; Castro et al., 2006). The thermodynamic state and circulation patterns show the influence of two major ocean currents: the Brazil Current (BC) and the Malvinas/Falkland Current (Matano et al., 2010). The area is primarily defined by the BC, which flows southward along the shelf break and into deeper waters which can create intense meso-scale activity along the BC flow (Campos et al., 1995; Silveira et al., 2000). The composition of water mass mainly includes: (1) Tropical water in the upper layer (0-200 m) with warm (>20°C) and salty characteristics (>36,4 ps), (2) South Atlantic Central Water (SACW) in the lower layer (200-500 m) with cold (<20°C) and less salty characteristics (<36,4 ps), and (3) the Coastal Water which is a result of a mixture of different shelf waters and local freshwater discharge from several estuarine systems (Castro and Miranda, 1998). The sudden change in coastline orientation creates favorable conditions for the interaction between eddy-induced upwelling and wind-generated Ekman transport which leads to the intrusion of the nutrient-rich SACW onto the shelf-break (Lima et al., 1996). During the summer, wind-driven upwelling of cold nutrient-rich waters occurs in the region, resulting in the increase of biological productivity (Silveira et al., 2000).

*2.2. Oceanographic features in the South Brazil Bight*

In the SBB, oceanographic features were identified based on ensembles of satellite derived products from the period of each survey of various parameters, including sea surface temperature (SST), salinity, chlorophyll "a," and the direction and intensity of currents. SST data was obtained from two distinct sources: (1) produced at the Oceanographic Modeling and Observation Network (REMO) of the Applied Meteorology Laboratory at the Federal University of Rio de Janeiro (LMA/UFRJ) and archived at http://podaac.jpl.nasa.gov/dataset/REMO_OI_SST_5km-UFRJ-L4-SAMERICAv1.0; and (2) products produced by the Danish Meteorological Institute (DMI) using an optimal interpolation (OI) approach on a global 0.05 degree grid archived at https://podaac.jpl.nasa.gov/dataset/DMI_OI-DMI-L4-GLOB-v1.0. Ocean current data was derived from the Ocean Surface Current Analyses - Real Time (OSCAR) project and was extracted from the website https://www.esr.org/data-products/. Chlorophyll-a concentration data was sourced from the NASA GSFC OceanColor Group, which provides climatological data in raster format for a Level 3 Standard Image (L3SI) product and we obtained from NASA's Ocean Color website (https://oceancolor.gsfc.nasa.gov/atbd/chlor_a/). Finally, surface water salinity data was obtained from the Hybrid Coordinate Ocean Model (HYCOM) and by the National Centers for Environmental Prediction (NCEP) Climate Forecast System Reanalysis (CFSR) sources (https://rda.ucar.edu/datasets/ds093.1/). The data were interpolated onto a 1/25° grid (GOMu0.04), converted to NetCDF format, and interpolated onto 40 levels. Based on the resulting images, three prominent oceanographic features were identified in the study area and data was grouped accordingly (Table 1): (1) the Cabo Frio upwelling (CFU), (2) the Subtropical Shelf front (STSF), and (3) the Brazil Current meanders and eddies (BCME). Such features are related to intense mesoscale activity and present a high spatiotemporal variability. On certain surveys, two features were identified simultaneously and, thus, these surveys were excluded from the final prediction analysis to ease the interpretation of the distribution and density patterns observed.

**Table 1** Description of each oceanographic feature included in the predicted analysis.

| Oceanographic features | Description | References |
|---|---|---|
| **Cabo Frio upwelling** | In the northernmost part of the Santos Basin, particularly during the austral summer/spring, this system is primarily driven by prevailing northeasterly winds. These winds, aligning with the coastline direction, induce Ekman transport, a process that brings nutrient-rich deep waters to the surface. During stronger upwelling events, the Brazil Current advects along the shelf break, the nutrient-rich South Atlantic Central Water to the surface. This water mass contrasts sharply with the Tropical Water also present in the region. This cooler water then propagates southwestward along the coast of Rio de Janeiro state. The Cabo Frio Eddy could also facilitate and intensify this upwelling process. Depending on the period, the waters may exhibit a phytoplankton growth before being effectively transported by the Brazil Current. In this case, there is advection of colder waters, but with low nutrient value and/or production. | Campos et al., (1996); Franchito et al. (2008); Coelho-Souza et al. (2012); |
| **Subtropical Shelf front** | In the southernmost region of the basin, a cold water tongue moves from south to north over the continental shelf of Uruguay and the South and Southeast regions of Brazil during austral winter. Two distinct advection processes contribute to it: (1) the coastal water transports continental and coastal input, primarily freshwater and nutrients, from sources such as the Rio de la Plata and other coastal rivers; (2) the Brazil Current advects Tropical Water, characterized by higher salinity and lower nutrient concentrations, in the shelf. This front formation is particularly prevalent during the occurrence of cold fronts, when the southward movement of air masses intensifies the plume of coastal waters. Additionally, variations in Ekman transport, wind-driven movement of surface waters can also | Möller et al. (2008); Piola et al. (2000); Brandini, et al. (2018) |

| | | |
|---|---|---|
| | influence the strength and location of the tongue. Then, the nutrient input increases phytoplankton growth and disperse over the vast continental shelf of the southern Santos Basin. | |
| **Brazil Current meanders and eddies** | The prominent mesoscale features that significantly influence the region, depending on the period, include the Brazil Current meanders and the Cabo Frio Eddy which exhibit complex interactions that shape the distribution of chlorophyll-a and water temperature gradients. Brazil Current develops intense mesoscale activity and large meanders sometimes can enclose eddies. The meanders and eddies can also induce shelf break upwelling events. For example, the Cabo Frio Eddy is a persistent cyclonic eddy that traps nutrient-rich waters and promotes phytoplankton blooms, contributing significantly to the region's high productivity. | Campos et al. (2000); Silveira et al. (2023) |

*2.3. Survey data and field methodology*

Visual survey data was obtained during a large scale monitoring program, which was demanded by the Brazilian federal environmental agency (IBAMA) as a condition in the environmental licensing process for oil extraction and production in the SB (process no. 02001.114279/2017-80). The Cetacean Monitoring Project of the Santos Basin (PMC-BS) monitors the cetacean community since 2015, using different types of methodologies to assess possible impacts of oil activities and gas on these animals. Vessel-based visual surveys followed the line-transect methods (Fig. 1) between November 2015–February 2021 (Buckland et al., 2001). Here, we employed the same data sources and data collection protocols that are well-described in Correa et al. (*in preparation*).

*2.4 Spatial data preparation*

Segment lengths were used as an offset in spatial models (Miller et al., 2013). We segmented traversed transect lines into 10 km segments using QGIS software (QGIS. 3.32.2, QGIS Development Team 2023, Open Source Geospatial Foundation). That length was sufficiently short to capture the spatial resolution of environmental covariates, while long enough to minimize issues related to zero-inflation which can be caused by the typical clustered distribution of cetaceans (i.e., if too many segments have no animal records; see Modelling framework section, Rhodes, 2015). Segments shorter than the target length (10 km) but longer than 5 km were considered as an independent segment; segments less than 5 km long were combined with the previous segment. That procedure resulted in a few segments between 10 and 15 km long, and another few between 5 and 10 km long.

*2.5 Environmental data*

The candidate set of habitat variables were selected based on environmental data availability and previous ecological knowledge on the distribution of ASDs (e.g.: Do Amaral et al., 2015; Correa et al. *in preparation*). Environmental covariates were obtained at the geographic coordinates (latitude and longitude) of the center point of each segment or within a 5 km buffer, primarily for dynamic covariates. We derived covariate values directly from remotely sensed data and specific R packages, using either the segment midpoint or the buffer. A total of 8 covariates were considered as candidate explanatory variables in the statistical models (Table 2):

**Table 2** Explanatory variables used in the Generalized Additive Modeling (GAM) framework for spatial modeling of the distribution of *Stenella frontalis* dolphins in the South Brazil Bight region.

| Variable | Abbreviation | Source | Unit | Spatial Resolution |
|---|---|---|---|---|
| **Average depth** | Depth_mean | GEBCO | meter | 1/30 arc |
| **Depth range** | depth_range | GEBCO | meter | 1/30 arc |
| **Depth sd** | depth_sd | GEBCO | meter | 1/30 arc |
| **Distance from shore** | dist | GIS calculations | kilometer | - |
| **Monthly average sea surface temperature** | sst_month | Aqua/ MODIS (NASA) | ºc | 4 km |
| **Monthly average of Chlorophyll concentration** | chla_month | Aqua/ MODIS (NASA) | mg/m3 | 4 km |
| **Easting** | x | - | UTM (m) | - |
| **Northing** | y | - | UTM (m) | - |

The dynamic covariates, SST and chlorophyll concentration were obtained by remote sensed data from Terra/Aqua satellite platform using moderate-resolution imaging spectroradiometer (MODIS) sensor. The data were extracted from Google Earth Engine using a Level 3 Standard Mapped Image (L3SMI) product with 4 km spatial resolution (https://oceancolor.gsfc.nasa.gov/products/). Both values were calculated for the specific geographic position of the sighting with a 5 km spatial buffer and filtered on a monthly scale. Physical static features (distance to coast and depth values) were obtained using R software. Distance from shore was the shortest distance between the segment midpoint and the coastline feature extracted by *getNOAA.bathy* function using the *marmap* package which downloads data directly from NOAA servers (ETOPO1 dataset, Amante and Eakins, 2009; Pante and Simon-

Bouhet, 2013). All water depth values were obtained from the General Bathymetric Chart of the Oceans (GEBCO) 2022, 30 arc-second gridded bathymetry (equivalent to a spatial resolution of nearly 0.9 km; Weatherall et al., 2015). We used the zonal statistical analyses tool in QGis to calculate  mean, standard deviation and range of depth values within 5 km buffers.

*2.6 Modeling framework*

To model density using distance sampling data, a two-stage approach was implemented (Miller et al., 2013). First, detectability was modeled with a detection function fitted to distance sampling data. Secondly, counts on sampling locations were modeled as a function of spatially explicit predictors. These stages are described in more detail in the following sections.

*2.6.1 Stage 1. Detection probability estimation*

We fitted the ASDs detection probability from the line transect data using 'Distance' package version 1.0.8 (Miller et al., 2022a) in R (version 4.3.1). We used the same detection function model provided in Correa et al. (*in preparation*). Multiple Covariate Distance Sampling (Marques et al., 2007) concepts were applied to the left-truncated data (at 15% for the farthest observations, i.e., distances at the tail of the distribution and therefore with very low detection probability; Buckland et al., 2001; Thomas et al., 2010).  More details on the detection function model selection are provided elsewhere in Correa et al. (*in preparation*).

*2.6.2 Stage 2. Density surface modeling*

After fitting the detection function, we used the number of groups per segment as the response variable in a Generalized Additive Modeling (GAM) approach. This was implemented using *dsm* package version 2.3.3 (http://github.com/DistanceDevelopment/dsm, Miller et al., 2022). To guide covariate inclusion in candidate models, correlation matrices for explanatory variables were used to identify if any covariate pair presented high correlation (i.e., Pearson's correlation coefficient greater than 0.7; Zuur et al., 2007), If it was the case, the two were not included in the same model at the same time . Therefore, if one covariate was selected at a model selection

step, those correlated were not considered in subsequent steps of model selection.
The quasi-Poisson, negative binomial and Tweedie distributions were tested for the response variable distribution. Segment length was used as an offset of the response and smooth functions were fitted to candidate covariates.
We conducted model selection adding one variable at a time, starting with a set of models of a single candidate explanatory variable (Table S3). The model selected at each step was chosen by looking for an improvement in the REML score (Miller et al., 2013). The basis dimension parameter $k$ (<10) for each covariate was set to capture non-linear relationships, however, it was restricted to avoid overfitting. A decision was made for basis dimensions by comparing the effective degree of freedom and random patterns in residuals for each smoother (Wood, 2017). As part of model diagnostics we also tested for spatial autocorrelation in the residuals (ordered by the time of data collection, for each survey) using the *acf* function (*stats* R package). Model adequacy was assessed with model diagnostic plots (Normal Q-Q-plot, function *gam.check*, *mgcv* R package).

*2.7 Density prediction and variance estimation*

The response distribution obtained by DSM was then used to predict density over the whole study area for each oceanographic feature. Prediction maps were built by creating a grid of 10 km² squares over the shapefile of the study area using the *create grid* tool in QGIS software. The resolution of prediction grid cells was chosen to match that of the segments. The covariate values were extracted for the midpoint of the grid, using 5 km buffers when appropriate, similar to that described for segments.
Predictions were made for each cell based on predictor variables that fit the model and summed over all grid cells to obtain an overall model-based density estimate on each oceanographic feature described above (in section Study area). To estimate coefficient of variation (CV), we used the delta method, which combines the variance from the detection function and the spatial models by using the *dsm.var* function of the *dsm* R package (Seber, 1992; Miller et al., 2013, 2022b). We then plotted the CV to detect spatial patterns of uncertainty, elucidating the total uncertainty surrounding our abundance estimates. Maps showing patterns of distribution (density surface) and uncertainty in model predictions (CV) were created using QGIS software.

**3. Results**

From November 2015 to March 2021 data were collected in 13 boat surveys totaling 526 days of field in a search effort of 66,939 km and 571 transects lines. A total of 125 groups were identified, encompassing an estimated 3,772 individuals.

*3.1 Detection function*

We decided to right-truncate perpendicular distances to reduce bias in our results, setting the distance to 1,075 m based on previous graphical analysis. This removed 16 (out of 111) detections from the detection function analysis. We used a hazard rate model with the covariates detection method and sea conditions (Fig. S2, Table S2). Here, the average probability of detection ($p$) was estimated as 0.29 (SE = 0.03, CV = 0.12) and the goodness of fit tests showed a good fit (Cramer-von Mises test statistic = 0.04, p = 0.87).

*3.2 Spatio-temporal distribution and response to habitat variable*

We built models to investigate the influence of environmental variables in the distribution of dolphins (e.g., Table S3). Model diagnostics showed that Quasi-Poisson and negative-binomial produced poor-quality residuals (due to the lack of fit) and indicated the Tweedie distribution was more adequate to deal with zero inflation in our dataset (Fig. S3). Therefore, the selected DSM included the spatial component (Easting, Northing), mean depth and monthly SST covariates, which explained 26% of deviance (Table 3).

**Table 3** Model parameters of habitat covariates using Generalized Additive Modeling applied to spatial data of *Stenella frontalis*. (x, y = easting and northing coordinates; depth_mean = average depth; sst_month = monthly average sea surface temperature; df = degrees of freedom; F = F distribution value) *Significant at α = 0.05.

| | **Estimate** | **Std. Error** | ***p*-value** |
|---|---|---|---|
| **Intercept** | -18.2539 | 0.2424 | <2e-16*** |
| Approximate significance of smooth terms: | | | |

| | Smooth terms | Effective df | Reference df | F | p-value |
|---|---|---|---|---|---|
| **1** | s(x,y) | 8.481 | 11.584 | 1.176 | 0.306 |
| **2** | s(depth_mean) | 2.276 | 2.796 | 7.147 | <0.01 |
| **3** | s(sst_month) | 4.411 | 4.844 | 4.028 | <0.01 |

The spatial component of the selected model had the greatest contribution in explaining the variation in ASDs densities, and habitat covariates (monthly SST and mean depth) provided some additional explanation. ASDs densities were related to monthly SST and showed two peaks, one around 20°C and other around 26°C (Fig. 2), while the density of dolphins decreases as depth increases.

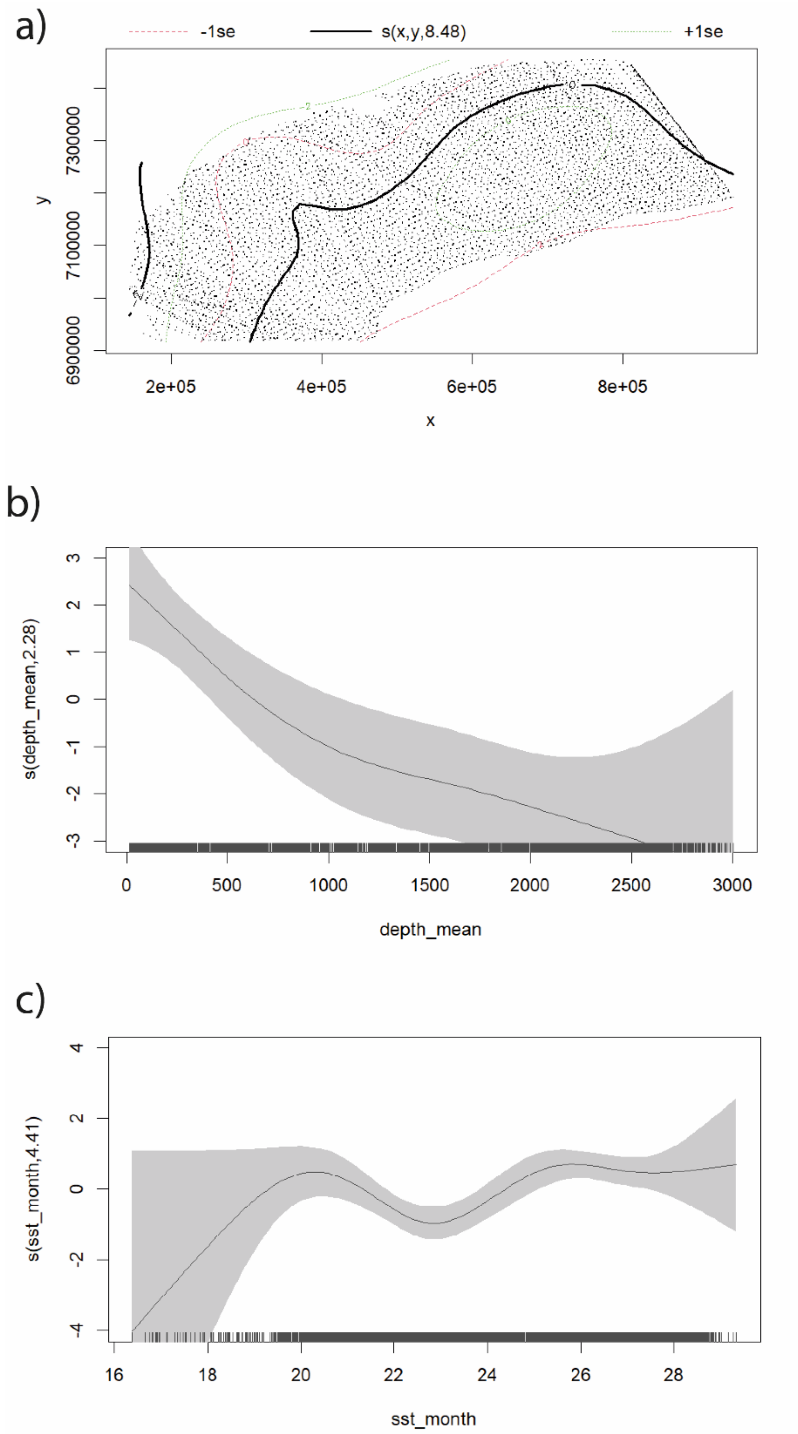


**Fig. 2** Fitted smooth terms of habitat covariates: 2a) Easting and northing coordinates (x, y), 2b) average depth (depth_mean), and 2c) monthly average sea surface temperature (sst_month). Gray shades represent 95% confidence intervals. The y-axis denotes the scale of the log link function, while the x-axis indicates the range of environmental parameters.

*3.3 Oceanographic feature predictions*

In general, predicted densities ranged from 0.01 to 23 individuals on each grid cell. Predicted density maps showed higher values in two regions of the basin, well pronounced in the BCME feature map (Fig. 3). Abundance was higher in the BCME feature, with 15,972 individuals estimated; and lower in STSF feature with 3,694 individuals (Table 4).

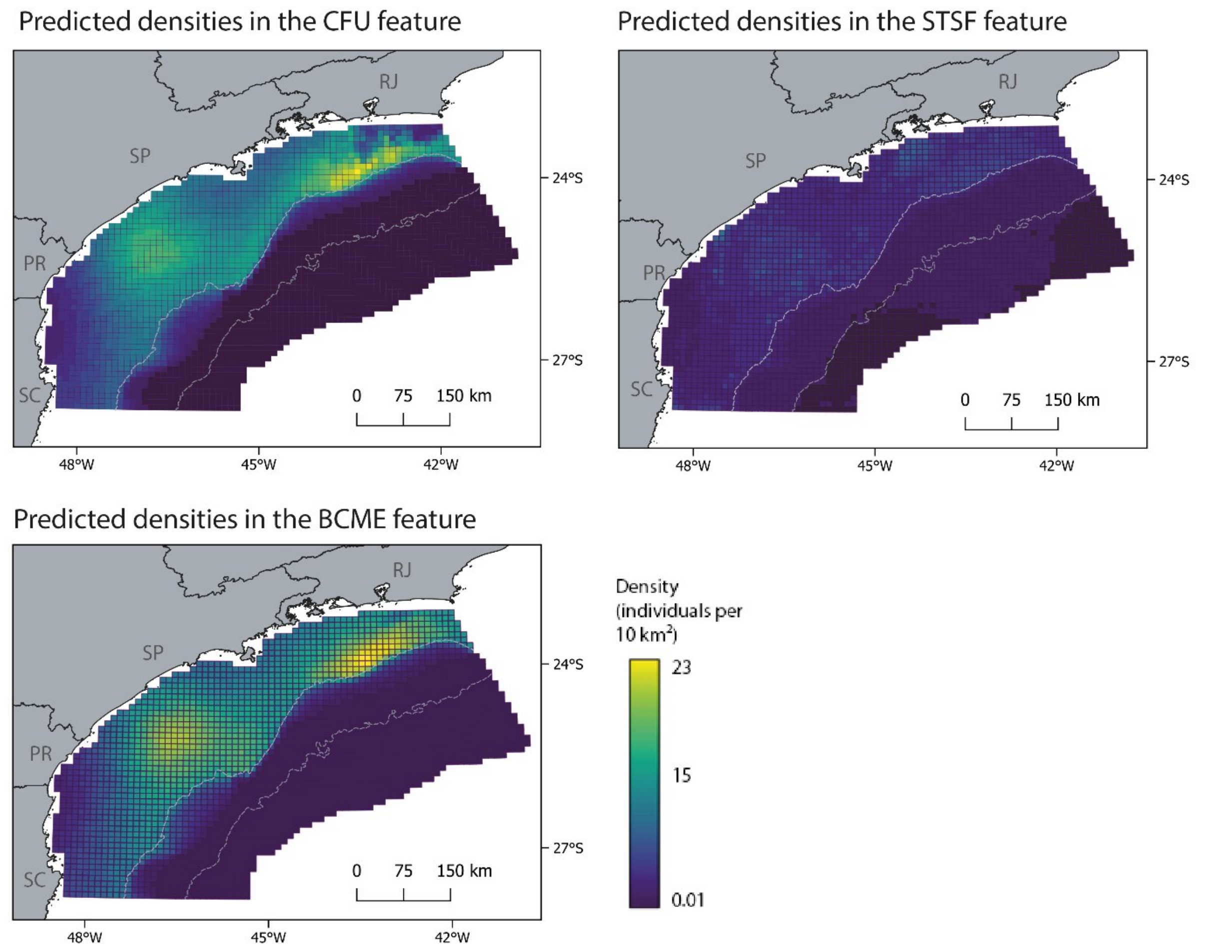


**Fig. 3** Map of the predicted densities (individuals per 10 km$^2$) calculated from both detection function and GAM parameters of the density model for the three oceanographic features: Cabo Frio Upwelling (CFU), Subtropical Shelf Front (STSF), and, the Brazil Current meanders and eddies (BCME). The acronyms on the map denote the Santa Catarina (SC), Paraná (PR), São Paulo (SP), and Rio de Janeiro (RJ) states. Dotted blue line represents bathymetry at 200 and 2,000 meters.

Dolphin densities were predicted to arrise at two distinct SST values, with higher densities observed away from oceanic features linked to lower SST (< 20°), as illustrated by the CFU predicted map in the northern region of the basin. Overall, our results showed variation in predicted abundance across the three features (Table 4). The lowest abundance of ASDs was predicted in the STSF feature, whereas the highest was observed in the BCME feature. This spatial pattern is clear in the prediction maps (Fig. 3). Uncertainty was higher in the offshore and some coastal areas of the basin where sightings were less frequent. We observed CVs > 0.5 in most of its distributional ranges except in the São Paulo and Rio de Janeiro mid shelf in the CFU and BCME features, where CVs were <0.3.

**Table 4** Summary of abundance estimates and their uncertainty in the Density Surface Modeling, calculated analytically for Generalized Additive Models (GAM) with the delta method applied for each oceanographic feature. Abundance estimates for each feature are presented as the mean, 25th, and 97.5th percentiles of a posterior distribution. (CFU = Cabo Frio Upwelling, STSF = Subtropical Shelf Front, BCME = Brazil Current meanders and eddies, CV = coefficient of variation)

| **Abundance estimate in the CFU feature** | | | **Abundance estimate in the STSF feature** | | | **Abundance estimate in the BCME feature** | | |
|---|---|---|---|---|---|---|---|---|
| **25%** | **Mean** | **97.5%** | **25%** | **Mean** | **97.5 %** | **25%** | **Mean** | **97.5%** |
| 7,709 | 13,92 4 | 25,149 | 2,001 | 3,694 | 6,817 | 10,371 | 15,972 | 24,598 |
| **Point estimate** | | 13,924 | **Point estimate** | | 3,964 | **Point estimate** | | 15,972 |
| **CV of detection function** | | 0.12 | **CV of detection function** | | 0.12 | **CV of detection function** | | 0.12 |
| **CV from GAM** | | 0.28 | **CV from GAM** | | 0.29 | **CV from GAM** | | 0.18 |
| **Total standard error** | | 4,297 | **Total standard error** | | 1,183 | **Total standard error** | | 3,562 |
| **Total CV** | | 0.30 | **Total CV** | | 0.32 | **Total CV** | | 0.22 |

The model predicted high densities in the continental shelf in CFU and BCME features periods; the hotspots were prominent at São Paulo and Rio de Janeiro mid shelf. The distribution of the dolphins was not heterogeneous in the STSF feature and areas with higher densities were predicted mainly close to the coast (Fig. 3).

## 4. Discussion

This study is the first attempt to predict the density of the *Stenella frontalis* in the South Brazil Bight onsidering some environmental variables and oceanographic features known to influence the cetacean' distribution. By using this approach, we estimated abundance at a higher resolution, uncovering spatio-temporal density patterns within a highly dynamic habitat.

### *4.1 Abundance Estimates*

Our predicted abundance estimates using DSM (3,694-15,972 individuals, depending on the predicted oceanographic feature) were consistent with previously described seasonal patterns using DS (8,692 individuals [CV = 0.27] in the cold period and 19,762 [CV = 0.18] in the warm, Correa et al., *work in preparation*). By employing a novel approach that considers the Santos Basin's main oceanographic features, our analyses confirm that the continental shelf serves as critical habitat for ASDs within the basin. Environmental variability induces changes in distribution of forage resources for predators, and as a consequence, predators exhibit clear responses to those changes (Fleming et al., 2016). *S. frontalis* is a wide-ranging species that exhibits a non-homogeneous distribution within the Santos Basin due to bathymetric factors (Moreno et al., 2005). Seasonal patterns were observed in some Atlantic Ocean regions driven by a complex interplay of environmental factors with a increased abundance in mid-shelf regions during warm seasons (e.g., Griffin and Griffin, 2004; Weir, 2011; Simard et al., 2015). The models predicted ASD distribution primarily on the mid-shelf of São Paulo state (~24°S) and the mid to outer shelf of Rio de Janeiro state (~23°S), with notable high-density regions, particularly within the CFU and BCME features. During late austral summer, the Brazil Current reaches its southernmost limit which clearly aligns with the patterns observed in the predicted maps reflecting large-scale changes in the distribution (Stramma and Peterson, 1990). Interestingly, our study revealed that densities decrease during the STSF feature, where some dolphins conversely can concentrate in other regions, as bays (Pereira et al., 2022). Our hypothesis suggests that seasonal shifts in environmental conditions may also influence prey availability. For example, one of the main prey species for ASDs, the squid *Doryteuthis plei*, is a warm-water species abundant during the warmer season along the southern coast of Brazil (Dos Santos & Haimovici, 2001; Lopes et al., 2012). ASDs displacements associated with decreases in sea surface temperature and chlorophyll “a” concentration have been also observed in the Bahamas were is linked to prey availability (Herzing et al., 2017).

Beyond longitudinal movements, we hypothesize that groups of ASDs might also exhibit latitudinal movements northward during the STSF feature, because it brings colder waters from the south into the basin during the austral cold seasons and directs them to suitable areas (Piola et al., 2000). Species distributions reflect a complex interplay of factors, which can be challenging to measure directly. The chosen model selected only one physiographic and dynamic variable, which may insufficiently capture the complexity of the oceanographic features considered in our analysis. Data limitations often direct the use of indirect and easier measurements which provide a less comprehensive picture of cetacean distribution (Austin, 2002). However, even these approaches can still offer valuable insights. While our findings identified some key habitat conditions, the predicted densities needs interpretation cautious due to their dependence on the included habitat variables. Our findings support previous studies on the importance of bathymetry as a predictor of ASDs (Do Amaral et al., 2015; Barragán-Barrera et al., 2019). The inclusion of sea surface temperature as a covariate linked to climate variability effectively captured the seasonal variations observed in previous studies (e.g., Correa et al., *in preparation*). Driven by basin-scale ocean dynamics, and the ongoing effects of climate change, future studies should integrate additional habitat features and covariates into their models to elucidate the ecosystem's response to abiotic changes (e.g., sea surface temperature) under different scenarios.

The model’s explanatory power, as indicated by the percentage of deviance explained, was relatively low (26%), suggesting that additional, unmeasured factors may influence the species’ distribution. For example, the spatial and temporal resolution of the environmental covariates may not have captured fine-scale habitat variability, or key ecological drivers may have been overlooked (Becker et al., 2010; Mannocci et al., 2017a). GAMs may fail to capture the real-time environmental conditions to which dolphins’ groups respond, largely due to their highly mobile behavior and the limited availability of high-resolution, real-time oceanographic data.

Also, given the species' coexistence with various anthropogenic activities in the region, further investigation is needed to evaluate the potential effects of human structures and operations on its ecological patterns. Furthermore, as small cetaceans function as both predators and prey (e.g., for sharks), their distributional dynamics are also likely shaped by biotic interactions, which needs an analytical framework that has not yet been applied to this species in this region (e.g., Benoit-Bird and Au, 2003). To improve model accuracy and ecological relevance, targeted investigations are needed to determine the optimal temporal and spatial resolution of environmental covariates that best align with dolphin movement, population dynamics and habitat use. A Bayesian hierarchical framework could be an alternative approach because it quantifies uncertainty across multiple levels and accounts for processes operating at different spatial and temporal scales, providing a more realistic representation in complex marine environments (Pardo et al., 2015; Kanaji and Gerrodette, 2020).

### *4.2 Oceanographic features in South Brazil Bight*

At the shelf-ocean interface, the SBB is mostly influenced by the Brazil Current and by year-round presence of upwelling regimes (Silveira et al. 2000; Palma and Matano 2009). During austral summer/spring seasons, some areas are dominated by bottom intrusions driven by a strong vertical thermal stratification that brings the cold and nutrient-rich SACW to the surface layers (Campos et al., 2000). Consequently, these events may lead to an increase in nutrient availability by enhancing concentration of inorganic nutrients, which increase the local biological productivity (Brandini et al., 2014). Upwelling features occur in the coastal areas of Rio de Janeiro, between Cabo Frio and São Sebastião Island, but also in the shelf break regions further offshore (Campos and Silveira, 2000; Palma and Matano, 2009). During winter, cold frontal systems invert the wind stress from northeast to southwest and the SACW retreats toward the slope leading to a homogenization of the water column properties (Campos et al., 1995; Castro and Miranda, 1998). Also the increased frequency and strength of southwest winds transport substantial nutrients from the La Plata River and Patos Lagoon plumes on the continental shelf towards the shelf break and slope of Santos Basin (Ciotti et al., 2014). Previous work on isotopic signatures have found that during summer in coastal areas of Ilha Grande Bay (Rio de Janeiro) ASDs occur in proximity to upwelling zones (Castro et al., 2008; Bisi et al., 2013). However, our results suggest that ASD density may not be directly linked to upwelling zones due to the cold water temperatures as demonstrated in the CFU feature.

Conversely, the seasonal variability of the BC, driven by mesoscale processes such as meanders and eddies, seems to be linked to their distribution and density as well demonstrated in the BCME feature map. The transition between water masses, characterized by strong temperature and salinity gradients, forms ocean fronts that have the potential to create feeding grounds for these dolphins (Cascão et al., 2020). Therefore, we expect to find higher densities of ASDs in these upwelling zones for feeding, as it can stimulate local prey abundance. While this link could not be definitively investigated in our study, future research should analyze the role of ocean fronts (e.g., distance to fronts) in determining the distribution and abundance of this species within the Santos Basin and forcing model predictions to directly assess the effect of their prey distributions.

As high trophic level predators, they are known to consume a wide variety of demersal and pelagic fish and cephalopod species (Di Beneditto et al., 2001, Melo et al., 2010; Lopes et al., 2012). For example, near Cananéia, São Paulo, the Atlantic cutlassfish, *Trichiurus leptrurus*, was identified as the most important fish species in their diet, while *Doryteuthis plei* was the dominant cephalopod species (Lopes et al., 2012). This squid is abundant along southeastern Brazil, especially in warmer waters (Araujo and Gasalla, 2018). Among the environmental factors in the ocean, temperature is often assumed to have the most important effect on fish and cephalopods. This influences their physiological capabilities (e.g., Clarke, 1996) and then leads to changes in their spatial distribution, which can also indirectly affect the distribution of their predators. Covariates within density surface modeling are generally seen as proxies for the underlying features that truly drive cetacean distribution (Becker et al., 2010). In our model, the spatial smooth accounted for the majority of deviance explained and the geographic habitat covariates accounted for 19% of additional explanatory power. Spatial covariates help account for distribution patterns caused by unmeasured processes for which the other covariates are not good proxies; however, it can not explain the habitat needs of these small cetaceans. The habitat covariate that was best supported for inclusion in our model was mean depth, followed by monthly sea surface temperature. Other studies have suggested that both covariates are among the most important predictors of ASDs habitat (Davis et al., 1998; Do Amaral et al., 2015; Barragán-Barrera et al., 2019). Here, our model detected a negative linear correlation pattern between depth and dolphin density, confirming their occurrence on shelf areas up to 500 meters deep (Di Tullio et al., 2016). Regarding monthly SST, we observed two intervals with a positive influence which could be linked to instances where groups were near features like the SFST during colder periods or proximity to SACW present during certain seasons. Furthermore, we can hypothesize the existence of a relationship between both predictors to prey availability. Supporting this, seasonal variations in water temperature and stratification of the water column influence the distribution and feeding behavior of one of their main prey, the squid *Doryteuthis plei* (Gasalla et al., 2010). This squid displays a diurnal and seasonal inshore-offshore migration pattern, inhabiting both shallow waters less than 30 meters deep and deeper waters between 30 and 100 meters (Gasalla et al., 2010). Additionally, the demersal-pelagic fish, *T.lepturus*, inhabits the entire shelf and shelf break, primarily on the mid-shelf, strongly related to SACW (Martins and Haimovici, 1997; Contente and Rossi-Wongtschowski, 2016). Therefore, oceanographic features clearly play a significant role in structuring the trophic interactions and shaping the distribution and density patterns of ASDs within the South Brazil Bight ecosystem. This aligns with the hydrographically complex structure that varies across seasons and generates spatial variations in temperature and salinity (Möller et al.,2008). For example, cyclonic eddies and meanders of the Brazil Current are stronger in the spring and summer as we tried to predict in the BCME feature (Campos et al., 1995). Also during these seasons, prevailing northeast winds and the higher frequency of cyclonic meanders favor cross-shelf SACW intrusions toward the coast as demonstrated in the CFU feature (Ciotti et al., 2014). Given the future challenges presented by climate change, climate variability, and the increase of human structures and activies in marine habitats as in the Santos Basin (Souza et al., 2020), future studies should focus on improving our predictive capabilities to detect changes in distribution and abundance to inform effectively marine mammal management.

## 5. Conclusion

In the Global South, few studies have provided long-term assessments of cetacean populations across extensive areas. Identifying environmental conditions at a fine scale is crucial for understanding animal distribution patterns within ecosystems, especially in regions affected by significant anthropogenic activities. Our research can contribute to environmental management in Brazil by offering a novel overview of the distribution and population estimates of Atlantic spotted dolphins in the South Brazil Bight. These findings elucidate some points of the relationship between ocean dynamics and the density patterns of these dolphins, underscoring the importance of integrating ecological research into conservation strategies.

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**Appendix S1** Supplementary Information

To

**Oceanographic features affect density and abundance of Atlantic spotted dolphins (*Stenella frontalis*) in the South Brazil Bight**

Thayusky P. Correa, Leonardo L. Wedekin, Guilherme A. Bortolotto, Marta J. Cremer

**Table S1** Summary of survey effort in the Santos Basin between November 2015 and March 2021. Survey number (year), dates (range), number of days and hours of sampling, survey effort (km) for each survey, number of group sightings (N) and each oceanographic feature are shown. Cabo Frio upwelling = CFU, Subtropical Shelf Front= STSF, Brazil Current meandering and eddies= BCME

| Survey (Year) | Dates | Feature | Days | Hours | Effort (km) | *N* |
|---|---|---|---|---|---|---|
| 1 (2015) | 20 Nov–05 Jan | CFU | 40 | 389.9 | 4,937.1 | 7 |
| 2 (2016) | 10 May–20 Jun | STSF | 42 | 410.9 | 5,462.5 | 10 |
| 3 (2016) | 27 Sep–06 Nov | STSF | 41 | 420.1 | 5,500.3 | 6 |
| 4 (2017) | 08 Mar–18 Apr | BCME | 42 | 434.9 | 5,541.9 | 16 |
| 5 (2017) | 25 Ago–07 Oct | CFU+ STSF | 44 | 435.7 | 5,584.7 | 8 |
| 6 (2018) | 12 Jan–20 Feb | CFU | 40 | 449.4 | 5,863.6 | 23 |
| 7 (2018) | 01 Sep–20 Oct | STSF+ BCME | 50 | 477.3 | 5,930.5 | 3 |
| 8 (2019) | 13 Mar–26 Apr | STSF | 45 | 425.5 | 5,490.4 | 15 |
| 9 (2019) | 24 Ago–13 Oct | STSF | 51 | 463.1 | 5,730.1 | 4 |
| 10 (2020) | 04 Mar–27 Mar | BCME | 23 | 235.8 | 3,124.3 | 13 |
| 11 (2020) | 28 Ago–07 Oct | CFU | 47 | 424.7 | 5,416.2 | 3 |

| | | | | | | |
|---|---|---|---|---|---|---|
| 12 (2020) | 28 Oct–16 Nov | CFU+ STSF | 20 | 224.3 | 3,093.4 | 5 |
| **13 (2021)** | 16 Jan–25 Feb | CFU | 41 | 398.6 | 5,264.4 | 12 |
| **Total** | - | - | 526 | 5,190.2 | 66,939.40 | 125 |

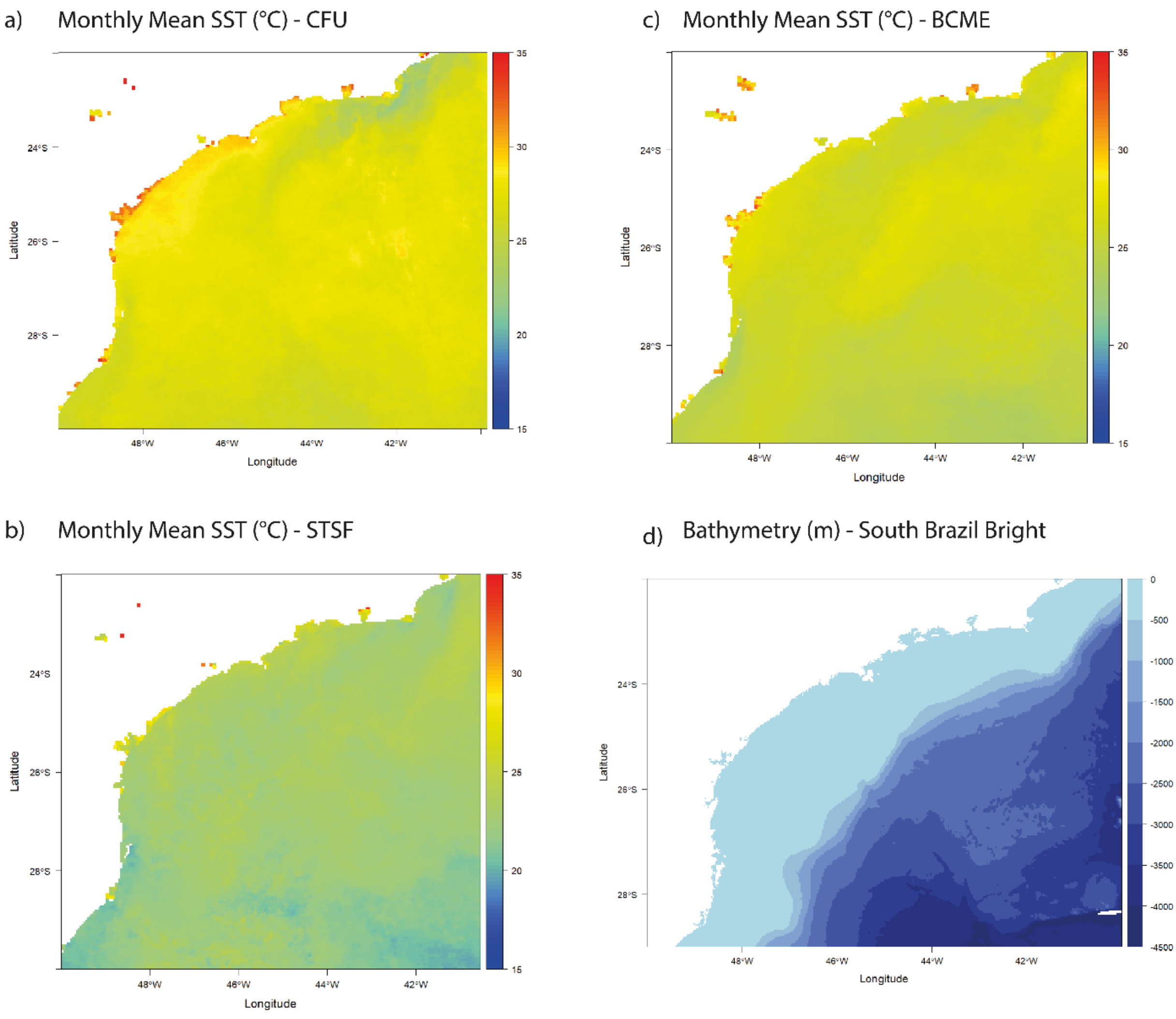


**Fig. S1** Spatial distribution of the predictor variables in the study area used for each feature. From a) to c): average sea surface temperature (SST) values for a) Cabo Frio Upwelling (CFU), b) Subtropical Shelf Front (STSF), and c) Brazil Current Meandering and Eddies (BCME), respectively; and d) shows the bathymetry of the South Brazil Bight.

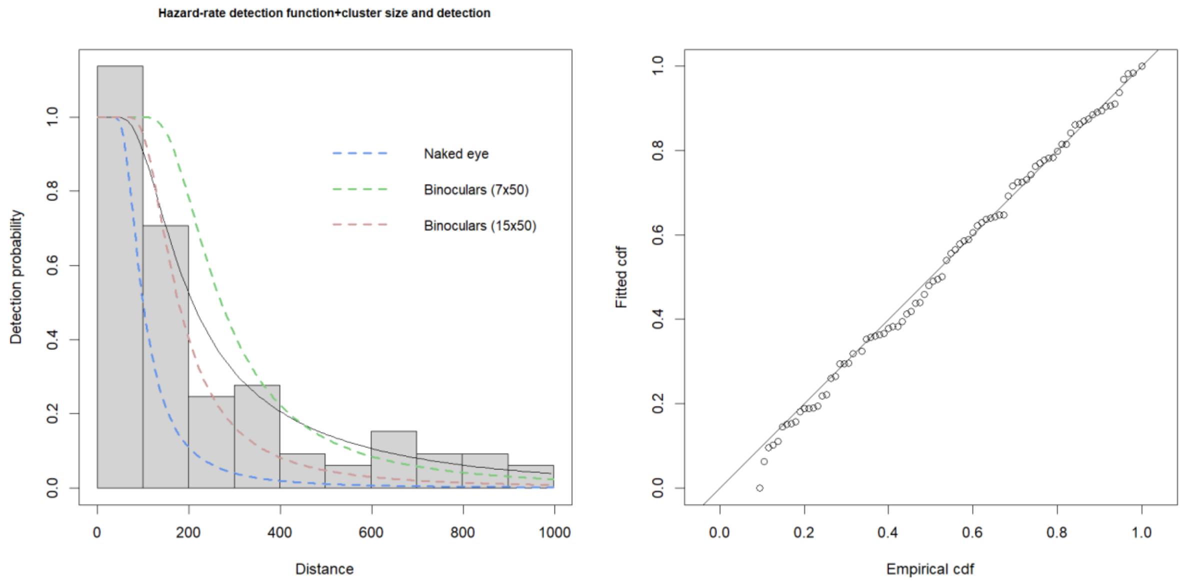


**Fig. S2** A) Plot of the fitted detection function onto the observed distances for the final model (a hazard-rate model with detection method and cluster size as covariates). A black line represents the average detection probability; (B) Q-Q plot of fitted cumulative distribution function (cdf) and empirical cumulative distribution function for the final detection function model

**Table S2** Detection function model selection for Atlantic spotted dolphin between 2015 and 2021 in Santos Basin. *SE* = standard error, *CVM* = Cramer-von Mises and AIC= Akaike Information Criterion.

| | Model | Key function | Formula | *CVM* p-value | Average detectability | *SE* (Average detectability) | AIC | Delta AIC |
|---|---|---|---|---|---|---|---|---|
| **1** | df_hr_logsize_beau_detec | Hazard-rate | ~beaufortFactor + detecFactor + log(size) | 0.917 | 0.260 | 0.032 | 1.425.566 | 0.000 |
| **2** | df_hr_logsize_detec | Hazard-rate | ~detecFactor + log(size) | 0.878 | 0.29 | 0.045 | 1.426.667 | 1.101 |
| **3** | df_hr_detec | Hazard-rate | ~detecFactor | 0.684 | 0.243 | 0.033 | 1.429.168 | 3.602 |
| **4** | df_hr_logsize_beau_whether_detec | Hazard-rate | ~beaufortFactor + weatherFactor + log(size) + detecFactor | 0.718 | 0.276 | 0.031 | 1.429.680 | 4.114 |
| **5** | df_hr_logsize_beau_whether_reflex | Hazard-rate | ~beaufortFactor + reflexFactor + weatherFactor + log(size) | 0.818 | 0.259 | 0.032 | 1.432.115 | 6.549 |
| **6** | df_hr_logsize_reflex | Hazard-rate | ~reflexFactor + log(size) | 0.779 | 0.248 | 0.035 | 1.433.478 | 7.912 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| **7** | df_hr_logsize_beau_reflex | Hazard-rate | ~beaufortFactor + reflexFactor + log(size) | 0.722 | 0.250 | 0.034 | 1.433.865 | 8.298 |
| **8** | df_hr_logsize_cue | Hazard-rate | ~cueFactor + log(size) | 0.634 | 0.269 | 0.337 | 1.434.631 | 9.064 |
| **10** | df_hr_logsize_beau_cue | Hazard-rate | ~beaufortFactor + cueFactor + log(size) | 0.673 | 0.269 | 0.309 | 1.435.978 | 10.411 |
| **11** | df_hr_logsize_vis | Hazard-rate | ~visibilityFactor + log(size) | 0.518 | 0.282 | 0.036 | 1.436.300 | 10.734 |
| **13** | df_hr_logsize_weather | Hazard-rate | ~weatherFactor + log(size) | 0.792 | 0.273 | 0.035 | 1.437.259 | 11.693 |
| **15** | df_hr_logsize_beau | Hazard-rate | ~beaufortFactor + log(size) | 0.641 | 0.275 | 0.035 | 1.438.072 | 12.505 |
| **16** | df_hr_logsize_beau_whether | Hazard-rate | ~beaufortFactor + weatherFactor + log(size) | 0.707 | 0.281 | 0.034 | 1.438.327 | 12.761 |
| **17** | df_sf_hr_logsize | Hazard-rate | ~log(size) | 0.720 | 0.274 | 0.036 | 1.438.503 | 12.937 |
| **19** | df_hr_logsize_beau_visi | Hazard-rate | ~beaufortFactor + visibilityFactor + log(size) | 0.420 | 0.285 | 0.036 | 1.439.604 | 14.038 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| **21** | df_hr_cue | Hazard-rate | ~cueFactor | 0.850 | 0.245 | 0.358 | 1.444.671 | 19.105 |
| **24** | df_hr_reflex | Hazard-rate | ~reflexFactor | 0.761 | 0.079 | 0.028 | 1.447.998 | 22.432 |
| **25** | df_sf_hr | Hazard-rate | ~1 | 0.775 | 0.233 | 0.038 | 1.448.778 | 23.211 |
| **29** | df_sf_hr_beau | Hazard-rate | ~beaufortFactor | 0.918 | 0.234 | 0.037 | 1.449.739 | 24.173 |
| **31** | df_hr_vis | Hazard-rate | ~visibilityFactor | 0.833 | 0.233 | 0.038 | 1.450.391 | 24.824 |
| **32** | df_hr_weather | Hazard-rate | ~weatherFactor | 0.838 | 0.239 | 0.039 | 1.454.037 | 28.471 |

**Table S3** Description of Generalized Additive Model statistics applied to investigate the influence of explanatory variables in densities of ASDs in SBB (df = degrees of freedom, F = F distribution value). Explanatory variables were depth (depth_mean), depth variation (depth_range), Easting, Northing (x,y), distance from the coast (dist_coast_km), average chlorophyll a (chla_month), and average SST (sst_month).
*Significant at α = 0.05

| | Model | Effective df | Reference df | F | p-value | Deviance explained | REML |
|---|---|---|---|---|---|---|---|
| **1** | s(depth_mean)+ offset(off.set) | 1.015 | 1.029 | 46.62 | <2e-16 *** | 17.20% | 892.26 |
| **2** | s(x,y) + offset(off.set) | 14.74 | 19.09 | 3.316 | 1.75e-06 *** | 21.20% | 901.51 |
| **3** | s(dist_coast_km)+ offset(off.set) | 3.523 | 4.391 | 9.559 | <2e-16 *** | 14.40% | 903.04 |
| **4** | s(depth_sd)+ offset(off.set) | 3.275 | 4.049 | 10.59 | <2e-16 *** | 12.50% | 907.48 |
| **5** | s(sst_moth)+ offset(off.set) | 6.346 | 7.509 | 4.481 | 4.2e-05 *** | 9.45% | 921.29 |
| **6** | s(log(chla_month))+ offset(off.set) | 4.078 | 5.075 | 3.811 | 0.00199 ** | 5.44% | 925.14 |

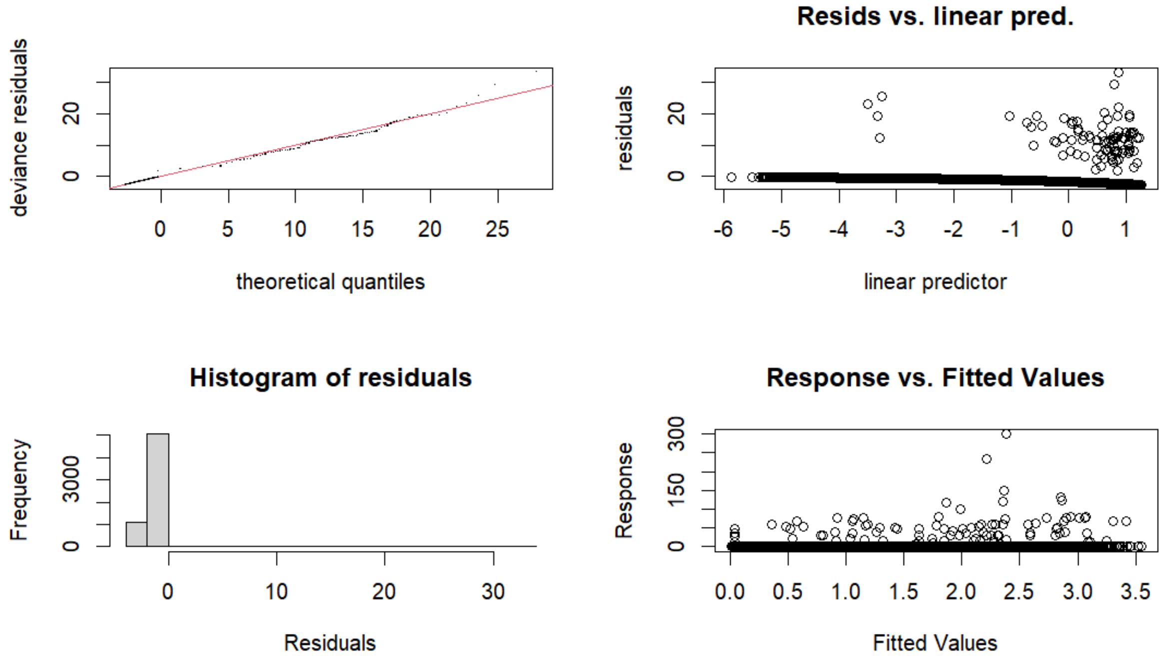


**Fig. S3** Density Surface Model diagnostic plots generated by the rgam.check function and auto-correlation in the residuals (ordered by the time of the dateset) plotted using the acf function

# 5 CONCLUSÃO GERAL

Os resultados desta tese demonstraram que as duas espécies de golfinhos pintados do gênero *Stenella* (*S. attenuata* e *S. frontalis*) se distribuem ao longo da Bacia de Santos em diferentes regiões e em concordância com a heterogeneidade ambiental dessa área. Os dados utilizados derivam de um programa de monitoramento de longo prazo, associado ao licenciamento ambiental, que desde 2015 realiza esforços sistemáticos desde a costa até regiões distantes, obtendo dados valiosos da comunidade de cetáceos da região. É precisamente por isso que foi possível trazer novos saberes sobre distribuições, uso do habitat e estimativas populacionais de espécies pouco conhecidas em território brasileiro. Acessar e divulgar esse conhecimento ecológico básico é de grande importância para poder avaliar o estado de conservação das espécies e guiar estratégias de manejo ambiental de forma efetiva.

No Capítulo 1, utilizando a combinação de avistagens obtidas durante diferentes cruzeiros embarcados, identificamos que *S. attenuata* ocorre de forma consistente na Bacia de Santos durante a maior parte do ano, com exceção do inverno austral. Esse resultado foi possível através dos esforços de monitoramento sistemático e de longo prazo, que permitiram expandir a fronteira do conhecimento sobre a distribuição dessa espécie no Oceano Atlântico Sul Ocidental, incluindo seu possível limite latitudinal. Além disso, este capítulo também fortaleceu a evidência de que a bacia é uma área crucial para a espécie, evidenciada pela presença de filhotes em grupos, indicando haver possíveis áreas de berçários na bacia. Observamos que os golfinhos-pintados-pantropical são encontrados nessa área principalmente em águas quentes e profundas, com alguns registros em uma faixa de temperatura que vai além do intervalo previamente conhecido para a espécie. Apesar de não termos investigado essa premissa a fundo, os resultados nos direcionaram à hipótese de que essa população é vulnerável a mudanças das condições ambientais e climáticas futuras.

No Capítulo 2, ao utilizar exclusivamente os dados coletados em cruzeiros embarcados com amostragem de distância em linhas de transecção, fornecemos a primeira estimativa populacional de *S. frontalis* para o Oceano Atlântico Sul Ocidental em dois períodos sazonais. Essa informação é crucial para uma avaliação populacional e para guiar precisamente as ações de manejo e conservação nessa bacia. Nossos resultados indicaram a existência de um padrão sazonal na abundância e densidade de *S. frontalis*: menores estimativas durante o período frio, provavelmente devido à tolerância a temperaturas baixas e, ainda, possível efeito associado à distribuição de suas presas. A sazonalidade é bem presente na bacia e fortemente relacionada à

Corrente do Brasil, que predomina na região ocupando grande parte da plataforma continental, principalmente durante o período sazonal quente. Adicionalmente, observamos que as maiores estimativas de abundância, em ambos os períodos, ocorreram na plataforma continental, o que nos leva a concluir que, além da temperatura da água do mar, a profundidade é outro fator central para determinar o habitat dessa espécie. Por meio deste estudo, enfatizamos a importância do monitoramento de longo prazo no fornecimento de informações essenciais para gerar estimativas populacionais de uma espécie pouco conhecida, e destacamos que as características regionais ambientais devem ser consideradas ao investigar padrões populacionais. Ainda, apesar de não haver estimativas de outras espécies para comparação na região, os valores indicam que *S. frontalis* pode ser uma das espécies de golfinhos mais abundantes na bacia.

Por consequência, no Capítulo 3, investigamos o uso de habitat e os efeitos de características oceanográficas na densidade e abundância de *S. frontalis*. Assim, estimamos esses aspectos populacionais considerando as características do habitat e três feições oceanográficas de mesoescala recorrentes na Bacia de Santos. Os resultados da modelagem indicaram que a profundidade e a temperatura superficial da água do mar médias são importantes preditores ecológicos para o golfinho-pintado-do-Atlântico. Os valores das estimativas foram distintos na presença de cada feição oceanográfica, e, junto dos mapas de predição, indicaram maiores densidades previstas principalmente em duas regiões da plataforma continental, localizadas nos estados de São Paulo e Rio de Janeiro. Portanto, nossos resultados sugerem uma correlação entre os sistemas frontais e a dinâmica do ecossistema marinho com níveis elevados da cadeia trófica marinha, como os cetáceos. A nossa principal conclusão é que as flutuações das estimativas populacionais entre diferentes períodos e regiões da bacia possuem relação com as diferentes características do ambiente marinho nessa área de estudo.

Por fim, embora esta tese não explore as ameaças em detalhes, diferentes populações podem estar expostas a diferentes condições e pressões. A concentração significativa desses golfinhos na região da plataforma continental e talude nos estados do Rio de Janeiro e São Paulo coincide com os principais portos do país, rotas de cabotagem, áreas importantes para o setor da pesca e de exploração de óleo e gás natural. Isso indica um risco de interações negativas entre essas espécies e atividades antrópicas presentes na área. Dentre as principais ameaças já presentes na literatura científica, destacamos a contaminação por poluentes como PCBs (bifenilas policloradas), que afetam o sistema imunológico e, consequentemente, aumentam a suscetibilidade a doenças e reduzem a sobrevivência dos indivíduos. A colisão com embarcações também é uma potencial ameaça, pois é comum alguns indivíduos se aproximarem de embarcações para a prática do comportamento de "bowriding". Ainda, ruídos provenientes do tráfego de embarcações e empreendimentos propagam efeitos nas atividades comportamentais dessas espécies, como forrageio e comunicação entre os indivíduos.

A Bacia de Santos abriga pelo menos 27 espécies de cetáceos documentadas em águas brasileiras, que compartilham essa área com diversas atividades humanas. Uma estratégia globalmente adotada para promover a conservação da natureza é a criação de áreas protegidas. No Brasil, uma das principais estratégias de gestão e conservação da biodiversidade são as Unidades de Conservação (Ucs), que abrangem diferentes possibilidades de preservação da natureza, como a criação de áreas que conciliam a conservação com o uso sustentável dos recursos naturais. Apesar da existência de Ucs com diferentes objetivos em várias partes da bacia, elas estão concentradas principalmente em regiões costeiras. Embora haja registros de grupos próximos à costa e até mesmo dentro de baías, como a Baía de Ilha Grande, no estado do Rio de Janeiro, nossos resultados indicam que grande parte da população na bacia pode não se beneficiar plenamente dessas áreas protegidas. Além disso, a região é de grande relevância para o contexto econômico do país, e a potencial expansão das atividades existentes, assim como o surgimento de novas, intensificarão a competição por espaço nessa área. Portanto, é fundamental encontrar um equilíbrio entre o uso e a proteção do ambiente, considerando de forma integrada os aspectos ambientais, econômicos e sociais, utilizando ferramentas como o Planejamento Espacial Marinho (PEM). Os resultados de nossos estudos, combinados com informações sobre a distribuição e intensidade das atividades antrópicas, podem apoiar decisões de gestão e medidas de conservação no contexto do PEM. Para isso, será essencial continuar os esforços de monitoramento, investigar as ameaças às espécies nessa área e promover discussões sobre as medidas de mitigação adotadas pelas atividades antrópicas. Por fim, acreditamos que outra estratégia-chave inclui o fomento a pesquisas que promovam soluções integradas entre os setores ambiental, econômico, tecnológico e social, visando avaliar melhor os riscos às populações selvagens presentes em áreas de múltiplos interesses.