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**Padrões de uso de habitat e comportamento de toninhas: abordagens acústicas para monitoramento e conservação de uma espécie ameaçada**

Florianópolis  
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Renan Lopes Paitach

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Dissertação/Tese submetida ao Programa de Pós-Graduação em Ecologia da Universidade Federal de Santa Catarina para a obtenção do título de Doutor em Ecologia

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

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

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Florianópolis, 2021.

Esse trabalho é dedicado (*in memoriam*)  
ao indivíduo Pb#17 e sua família.

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“Num país como o Brasil, manter a esperança viva é, em si, um ato revolucionário”

(Paulo Freire)

## RESUMO GERAL

A toninha (*Pontoporia blainvillei*) é um pequeno cetáceo criticamente ameaçado de extinção no Brasil, principalmente devido ao alto número de capturas incidentais em redes de pesca. Na Baía Babitonga, em Santa Catarina, existe uma população residente que está ameaçada pela degradação do habitat. O objetivo geral do estudo foi analisar a bioacústica, comportamento, distribuição, uso do habitat e avaliar a eficácia de um dispositivo acústico de dissuasão ("pinger") para toninhas, em diferentes escalas espaciais e temporais, por meio de dispositivos de monitoramento acústico passivo (MAP) denominados C-PODs (Chelonia Ltd., UK). O comportamento acústico foi analisado comparativamente em dois habitats: estuário (Baía Babitonga: BB) e mar aberto (Praia de Itapirubá: IB). Os parâmetros acústicos das cadeias de cliques foram analisados e o critério de intervalo mínimo entre cliques <10ms foi usado como proxy para o comportamento de forrageamento/alimentação. A principal diferença observada entre os habitats está relacionada ao espectro de frequência acústica, com largura de banda de 17kHz em BB e 10kHz em IB. Além disso, a taxa de repetição de cliques foi quase 20% maior no estuário. Ambos os habitats estudados apresentaram alta taxa de alimentação (BB = 68%; IB = 58%), maior em BB ( $p < 0,001$ ) e à noite ( $p < 0,001$ ), para ambos os habitats. Para analisar o uso de habitat e distribuição de toninhas na Baía Babitonga, 60 estações de MAP com C-PODs foram implementadas entre junho e dezembro de 2018. O modelo aditivo generalizado selecionado para descrever a relação entre a ocorrência de toninhas e diversas variáveis ambientais incorporou 51% da variação dos dados. Há um claro padrão diário, onde as toninhas permanecem nas áreas de alta ocorrência principalmente pela manhã. No resto do dia, a população se dispersa para outras áreas com padrões sazonais diferentes. As toninhas evitaram áreas nos períodos em que a presença de botos-cinza (*Sotalia guianensis*) é muito intensa e preferem áreas com fundo plano e substrato arenoso, mas durante a tarde e na madrugada vão também para áreas de fundo lamacento, predominantemente para fins de alimentação. A distribuição predominou na região mais interna do estuário, sem uso significativo do canal de entrada da baía. A distribuição é mais ampla no inverno do que na primavera. Toda a região central das ilhas, entre as margens norte e sul da baía, representa uma importante área de alimentação. Para testar o efeito dissuasor do Banana pinger (Fishtek Marine Ltd, UK), bem como os efeitos colaterais da habituação e exclusão de habitat, um experimento de exposição controlada foi realizado com 5 C-PODs posicionados a diferentes distâncias do pinger. Os dados indicam que o pinger efetivamente afasta as toninhas em até 100m, mas não 400m, e, portanto, tem potencial para reduzir as capturas incidentais. Nenhum efeito de habituação foi observado a qualquer distância. Houve uma diminuição gradual da presença de toninhas ao longo dos dias de experimento, possivelmente relacionado a variações sazonais no uso do habitat pela população, mas requer atenção em estudos futuros. Os C-PODs foram usados de forma inédita para o estudo de toninhas e mostraram grande potencial para estudos ecológicos da espécie. Os resultados apresentados são um importante subsídio para o manejo da população da Baía Babitonga e para a implementação de medidas de mitigação de capturas incidentais da espécie em geral.

**Palavras-chave:** Monitoramento acústico passivo. C-POD. Bioacústica. Ecologia comportamental. Habitat crítico. Captura incidental. Pingers. Cetáceos. *Pontoporia blainvillei*. Biologia da conservação.

## GENERAL ABSTRACT

**Habitat use and behavior patterns of franciscana dolphins: acoustic approaches for monitoring and conservation of threatened species.** The franciscana dolphin (*Pontoporia blainvillei*) is a small cetacean critically endangered in Brazil, mainly due to the high number of incidental captures in fishing nets (bycatch). In Babitonga Bay, Santa Catarina, there is a resident population which is threatened by habitat degradation. The general objective of the study was to analyze the bioacoustics, behavior, distribution, habitat use and evaluate the effectiveness of an acoustic deterrent device ("pinger") for franciscanas, at different spatial and temporal scales, by means of a passive acoustic monitoring (PAM) device called C-POD (Chelonia Ltd., UK). The acoustic behavior of franciscana was analyzed comparatively in two habitats: estuary (Babitonga Bay: BB) and open sea (Itapirubá Beach: IB). The acoustic parameters of the click trains were analyzed and the minimum inter-click interval criterion <10ms was used as a proxy for foraging/feeding behavior. The main acoustic difference observed between habitats was related to the frequency spectrum, with a bandwidth of 17kHz in BB and 10kHz in IB. Also, the click repetition rate was almost 20% higher in the estuary. Both habitats studied presented a high feeding rate (BB = 68%; IB = 58%), higher in BB ( $p < 0.001$ ) and at night ( $p < 0.001$ ), for both habitats. To analyze the habitat use and distribution of franciscanas in Babitonga Bay, sixty C-PODs stations were implemented between June and December 2018. The generalized additive model selected to describe the relationship between the occurrence of franciscanas and several environmental variables incorporated 51% of the data variation. There is a diel pattern, where franciscanas remain in the areas of high occurrence mainly in the morning. The rest of the day, the population dispersed to other areas with different seasonal patterns. Franciscana avoid areas in periods when the presence of Guiana dolphins (*Sotalia guianensis*) is very intense and prefer areas with a flat bottom and sandy substrate, but during the evening and dawn they goes into areas of muddy bottom predominantly for feeding. The distribution was predominant in the innermost region of the estuary, without significant use of the bay's inlet channel. The distribution was wider in winter than in spring. The entire central region of the islands, between the north and south margins of the bay, represents an important feeding area. To test the deterrent effect of Banana pinger (Fishtek Marine Ltd, UK), as well as side effects of habituation and habitat exclusion, an exposure-controlled experiment was carried out with 5 C-PODs positioned at different distances from the pinger. The data indicate that the pinger effectively withdraw the franciscanas up to 100m, but not 400m, and therefore has the potential to reduce bycatch. No habituation effects were observed at any distance. There was a gradual decrease in the presence of franciscanas over the days, probably due seasonal variations in the population's habitat use but requires attention in future studies. C-PODs were used in an unprecedented way for the study of franciscanas and showed great potential to monitor the occurrence, behavior, distribution, and habitat use of the species. The results representing an important subsidy for management of the Babitonga Bay population and for the implementation of bycatch mitigation measures for the species in general.

**Keywords:** Passive acoustic monitoring. C-POD. Bioacoustics. Behavioral ecology. Critical habitat. Bycatch. Pingers. Cetaceans. *Pontoporia blainvillei*. Conservation biology.

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## INTRODUÇÃO GERAL

### *Ecologia e conservação de cetáceos*

As populações de cetáceos estão globalmente impactadas pela ação humana. Os principais impactos são a captura incidental em redes de pesca, degradação de seus habitats, poluição química e acústica, sobre-exploração dos recursos pesqueiros, colisões com embarcações, além da captura intencional de algumas espécies (Harwood, 2001). Esse cenário de ameaças tem causado o declínio de diversas populações e, inclusive, a extinção recente de algumas espécies. Dois exemplos são o golfinho do rio Yangtze (*Lipotes vexillifer*), na China, que foi recentemente considerado extinto na natureza (Turvey et al., 2007), e a vaquita (*Phocoena sinus*), endêmica no Golfo do México, que segue pelo mesmo caminho (Jaramillo-Legorreta et al., 2017). Mitigar os impactos que ameaçam as espécies se faz urgentemente necessário.

O estudo da ecologia das espécies constitui um importante subsídio para a elaboração de estratégias voltadas a conservação *in situ* (Primack & Rodrigues, 2001). Medidas efetivas para o ordenamento das atividades humanas, com objetivo de minimizar impactos, devem considerar uma série de atributos ecológicos das espécies, como os padrões de uso do habitat e seus fatores (bióticos e abióticos) de influência (Hastie et al., 2004). Sobretudo, a proteção das áreas de alimentação e reprodução de mamíferos marinhos são essenciais para a conservação das espécies (Hoyt, 2012). No entanto, estudar estes aspectos ecológicos pode ser uma tarefa difícil, especialmente quando aplicado aos cetáceos, que vivem no ambiente aquático e ficam indisponíveis a maior parte do tempo para um observador à superfície. Assim, estudos baseados em observações visuais podem fornecer uma noção momentânea sobre a distribuição e uso de habitat da população estudada (Verfuß et al., 2007; Dede et al., 2013). Em contraposição, metodologias de monitoramento que permitem análises em diferentes escalas temporais podem ser muito úteis em estudos de espécies altamente móveis que exploram habitats dinâmicos, como os cetáceos (González-García et al., 2018).

### *Monitoramento acústico passivo*

Um método promissor é o monitoramento acústico passivo (MAP), que consiste no registro autônomo e contínuo dos sons subaquáticos. Houve um grande desenvolvimento na última década em termos de hardware e software utilizados para o MAP, permitindo ampliar o uso da bioacústica em pesquisas científicas e gestão ambiental (Van Parijs et al., 2009). Uma das principais vantagens do MAP em relação às técnicas convencionais de observação visual é a possibilidade de estudos de longa duração, mesmo em períodos de visibilidade limitada ou condições adversas (Mellinger et al., 2007; Van Parijs et al., 2009). O MAP é normalmente conduzido a partir de matrizes de hidrofones que podem ser fixados no ambiente ou em estruturas de interesse (e.g., redes de pesca, parques eólicos marinhos, plataformas de extração mineral), lançados à deriva das correntes, ou ainda rebocado por embarcações ou submarinos, tripulados ou autônomos (e.g., Carstensen et al., 2006; Van Parijs et al., 2009; Kimura et al., 2014; Bittencourt et al., 2018; Clay et al., 2018; Andriolo et al., 2018). Quando o dispositivo de MAP é rebocado, fornece dados para grandes áreas em curtos períodos (dias ou semanas), enquanto aparelhos fixos podem fornecer dados para pequenas áreas no decorrer de longos períodos (meses ou anos) (Mellinger et al., 2007; Van Parijs et al., 2009).

Os cetáceos produzem uma grande variedade de sinais acústicos, pois dependem do som para navegação, localização de presas e comunicação, de forma que variações nos padrões de emissão acústica possibilitam a identificação de comportamentos (Tyack & Clark, 2000). O uso do MAP é, portanto, uma estratégia altamente eficiente para investigar diversos aspectos ecológicos e comportamentais dos cetáceos, de forma não invasiva aos organismos (Batista & Gaunt, 1997). O método vem sendo utilizado e aprimorado em todo mundo para estudos de ocorrência, distribuição, comportamento, uso de habitat e estimativas populacionais de cetáceos (e.g., Mellinger et al., 2007; Van Parijs et al., 2009; Akamatsu et al., 2010; Gallus et al., 2012; Marques et al., 2013; Kimura et al., 2014; Jaramillo-Legorreta et al., 2017).

Para que se possa aplicar as técnicas de MAP é necessário o conhecimento prévio dos parâmetros do repertório acústico da espécie que se pretende estudar, possibilitando assim o seu reconhecimento acústico. As emissões acústicas de cetáceos odontocetos podem ser genericamente divididas em sinais tonais (assobios) e sinais pulsados (cliques de ecolocalização, “*burst-pulses*” e codas). Os sinais

pulsados podem diferir em relação ao espectro de frequência, e estudos sugerem que quatro tipos evoluíram de forma convergente entre os odontocetos (Au, 1993; Møhl et al., 2003; Zimmer et al., 2005; Kyhn et al., 2010; 2013): pulsos de banda larga, sinais de pulsação múltipla; pulsos modulados de longa frequência; e pulsos de banda estreita em alta frequência. Os sons de banda estreita em alta frequência (NBHF – *narrow band high frequency*) são emitidos exclusivamente pelas famílias Pontoporiidae, Kogiidae, Phocoenidae, e ao menos seis espécies da família Delphinidae (Kuroda et al., 2020).

Os clicks das espécies NBHF são estereotipados e semelhantes, fazendo com que estas espécies possam ser identificadas e monitoradas através dos mesmos sistemas de gravação e reconhecimento acústico (Kyhn et al., 2010; 2013). Um dispositivo de MAP projetado especificamente para a detecção de sons do tipo NBHF é o C-POD (Chelonia Limited, UK, Fig. 1). A natureza do registro de dados feito pelo C-POD o torna particularmente adequado para o estudo com espécies NBHF, uma vez que a taxa de amostragem necessária (>150 kHz) torna o registro de longo prazo quase impossível de outra forma. O C-POD pode operar continuamente por mais de quatro meses sem necessitar de troca de baterias. O processamento desse volume de dados é viabilizado por meio de um classificador automatizado que o dispositivo oferece, que economiza tempo e reduz o viés de subjetividade do pesquisador (Rayment et al, 2009).

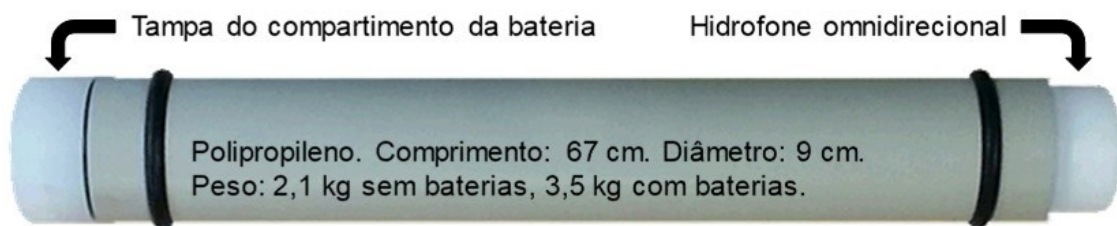


Figura 1: C-POD – Chelonia Limited, UK (<https://www.chelonia.co.uk/>).

### A toninha

*Pontoporia blainvillei* (Gervais & d'Orbigny, 1844), popularmente conhecida como toninha (em português) ou franciscana (em espanhol e inglês), é um pequeno cetáceo que produz sons pulsados do tipo NBHF (Von Fersen et al., 2000). Essa característica representa um forte potencial para o seu reconhecimento acústico, uma

vez que ela é a única espécie que produz clicks NBHF na maior parte de sua distribuição (Paitach et al., 2016). O MAP pode ser, portanto, uma ferramenta importante para o estudo da ecologia e comportamento das toninhas.

Até o momento, o conhecimento sobre o repertório comportamental da toninha é extremamente limitado, pois ela é considerada uma espécie discreta, com pouca exposição do corpo à superfície (Bordino et al., 1999). De acordo com Cremer & Simões-Lopes (2005), sua coloração críptica e tamanho pequeno, associado aos ambientes que normalmente ocupa, com águas turvas e baixa visibilidade, dificultam ainda mais o seu avistamento (Fig. 2). Isso faz com que estudo de distribuição e estimativas populacionais da espécie, que habitualmente são feitas por meio de observações visuais a partir de aeronaves, apresentem diversos vieses, além de serem altamente custosas (Danilewicz et al., 2010; Zerbini et al., 2011). A maior parte do que se conhece sobre a biologia e ecologia da toninha vem de indivíduos mortos, encalhados nas praias ou capturados acidentalmente em redes de pesca (Crespo et al., 2009).



Figura 2: Toninha, *Pontoporia blainvillei* (Gervais & D'Orbigny, 1844) (Pontoporiidae).

A toninha é considerada o pequeno cetáceo mais ameaçado de extinção no Oceano Atlântico Sul Ocidental devido a elevada taxa de capturas acidentais em redes de pesca (Secchi, 2010; Fig. 3). A espécie ocorre apenas entre o Estado do Espírito Santo, no Brasil, e a Província de Chubut, na Argentina (Crespo et al., 2009), com dois hiatos na distribuição (ver detalhes em: Amaral et al., 2018). O hábitat estritamente

costeiro, com distribuição predominante até os 30 metros de profundidade, torna a toninha especialmente vulnerável aos impactos antrópicos como a captura acidental e a degradação dos habitats (Danilewicz et al., 2009). As atividades humanas impactantes, somadas ao baixo potencial reprodutivo da toninha, representam um grande risco de extinção para a espécie (Secchi, 2010). A toninha é listada como “criticamente em perigo” no Livro Vermelho da Fauna Brasileira Ameaçada de Extinção e “vulnerável” na IUCN *Red List of Threatened Species* (MMA, 2014; Zerbini et al., 2017).



Figura 3: Toninhas capturadas acidentalmente em uma única rede de pesca de emalhe em Laguna, sul do Brasil, em 2019 (Imagem: PMP-BS/UDESC).

Na Baía Babitonga, sul do Brasil, existe a única população conhecida de toninhas que reside o ano todo em ambiente estuarino, com cerca de 50 indivíduos (Cremer & Simões-Lopes, 2005; 2008). Estudos de morfometria, genética e rastreamento de indivíduos por satélite sugerem que se trata de uma população isolada (Alves, 2013; Dias et al., 2013; Cremer et al. 2018). Portanto, para fins de conservação deve ser considerada como uma unidade de manejo demograficamente independente (sensu Moritz, 1994). Há indícios de que o uso de habitat desta população seja influenciado pelos ciclos sazonais, ciclo de maré e, potencialmente, ao ciclo nictemeral (Paitach et al., 2017). Porém esse conhecimento é limitado devido

aos métodos visuais utilizados. Também não está claro se o uso exclusivo do habitat estuarino pode ter ocasionado mudanças no repertório acústico e nos padrões comportamentais dessa população. Um aspecto relevante no uso de habitat das toninhas na Babitonga é a simpatria direta com o boto-cinza (*Sotalia guianensis*) (Cremer, 2007; Cremer et al., 2018). Espécies ecologicamente semelhantes compartilhando recursos limitados se afetam mutuamente, e as consequências disso para sua sobrevivência ainda são pouco compreendidas (Bearzi, 2005).

O futuro dessa população de toninhas está fortemente ameaçado pela degradação do habitat, que inclui a ocupação desordenada das margens, o despejo de efluentes domésticos e industriais, e a especulação de novos empreendimentos portuários, que acarretam intensas obras de dragagem e derrocagem (Cremer, 2007). A captura acidental em redes de pesca também é uma ameaça (Pinheiro & Cremer, 2003), que pode ser agravada ainda mais pela instalação de novos portos, que limitam as áreas de pesca artesanal ocasionando uma maior sobreposição com as áreas de ocorrência da toninha (Cremer et al., 2018; Paitach et al., 2019). É essencial o monitoramento desta população para a compreensão profunda sobre a sua distribuição e uso de habitat, permitindo verificar os efeitos de fatores ambientais e ecológicos, auxiliando na avaliação de impactos e construção das políticas públicas para conservação.

### *Políticas públicas*

Existem alguns regulamentos para a pesca com rede de emalhar no Brasil que podem auxiliar a redução de capturas incidentais, incluindo limitações no comprimento e altura das redes, restrições de áreas e períodos de pesca e mecanismos de monitoramento da frota pesqueira (e.g., IBAMA 166/2007; MPA/MMA 12/2012; MPA/MMA 16/2013). No entanto, a falta de fiscalização por parte das autoridades para avaliar o cumprimento desses regulamentos e a baixa participação das comunidades pesqueiras nos ambientes de gestão tornam tais regulamentos ineficazes para mitigação de capturas incidentais de toninhas (Di Tulio et al., 2020).

A discussão sobre a conservação da espécie vem sendo realizada em diferentes fóruns nacionais e internacionais, porém sem grades avanços práticos. No âmbito nacional, ganhou o respaldo do poder público a partir da publicação do 1º Plano de Ação Nacional (PAN) para a Conservação da Toninha (Rocha-Campos et al.

2010), revisado em 2019, com a publicação do 2º ciclo deste PAN (MMA/ICMBio 655/2019). Neste documento, as principais ameaças para a conservação da toninha são explicitas em seu objetivo principal: “Evitar o declínio populacional da toninha em todas as áreas de manejo, em especial por meio da redução das capturas incidentais e da proteção do habitat”. No âmbito internacional, em 2015 foi realizado o VIII Workshop para a Pesquisa e Conservação da Toninha, reunindo pesquisadores e gestores do Brasil, Uruguai e Argentina. O encontro resultou em um relatório que foi utilizado para propor junto a Comissão Internacional da Baleia (CIB) (na qual os três países citados são signatários) a criação de um Plano de Manejo e Conservação (*Conservation and Management Plan – CMP*), tendo sido aprovado em 2016. A necessidade de redução das capturas incidentais e a proteção de seus habitats foi ressaltada neste documento, com várias abordagens propostas, mas que ainda demandam de subsídios de pesquisa antes que possam ser colocadas em prática.

#### *Dispositivos de dissuasão acústica*

Uma possível abordagem para auxiliar na redução das capturas incidentais é a utilização de repelentes acústicos, ou “pingers”, que são pequenos dispositivos alimentados a bateria, projetados para serem presos às redes de pesca, transmitindo sons dissuasivos que mantêm os pequenos cetáceos afastados das redes, reduzindo assim o risco de emalhe (Dawson et al., 2013). Esta é uma das estratégias mais eficazes e adotadas mundialmente, principalmente porque, se comprovada a sua eficácia em mitigar a captura incidental da espécie-alvo, pode ter um efeito imediato na redução da mortalidade (e.g., Palka et al. 2008; Carretta & Barlow 2011). Os pingers são relativamente baratos e fáceis de implementar, mas evidências conclusivas de que funcionam para uma espécie-alvo, sem efeitos colaterais significativos, devem ser produzidas primeiro (FAO, 2021). O MAP possibilita a realização de testes de eficácia de pingers de forma experimental (e.g., Omeyer et al., 2020), sem nenhum risco de mortalidade aos animais, sendo adequado para testes preliminares antes da iniciação de testes diretamente em redes de pesca.

### *Estrutura da tese*

O objetivo geral desse trabalho foi analisar aspectos da bioacústica, comportamento e ecologia de toninhas, por meio de abordagens acústicas como o monitoramento acústico passivo e a utilização de repelentes acústicos. Os capítulos foram escritos no formato de manuscrito e estão pré-formatados para as revistas científicas em que serão submetidos. O primeiro capítulo buscou analisar diferenças na estrutura dos sons pulsados e nos padrões de comportamento acústico da toninha em diferentes habitats. No segundo capítulo foi aplicada uma abordagem de MAP a partir de um grid de monitoramento na Baía Babitonga, buscando identificar padrões espaço-temporais e as variáveis ambientais que afetam o uso de habitat da toninha, com ênfase para a influência que o boto-cinza exerce. Também buscou-se identificar as principais áreas de alimentação de toninhas na Babitonga. No terceiro capítulo foi testada a eficácia e os possíveis efeitos colaterais de um repelente acústico para toninhas, objetivando a redução das capturas incidentais. Ao longo de todos os capítulos é discutido o potencial e as limitações do método de MAP com C-PODs para o estudo de toninhas.

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## **CAPÍTULO 1 – Echolocation variability of franciscana dolphins (*Pontoporia blainvillei*) between estuarine and open-sea habitats, with insights into feeding behavior**

### **Abstract**

This study documents for the first time the use of a well-established passive acoustic monitoring device (C-POD) to log echolocation sounds and analyze the behavior of franciscana dolphins in different habitats: estuary (Babitonga Bay – BB) and open sea (Itapirubá Beach – IB). A total of 10,924 click trains were recorded in BB and 6,093 in IB. Click trains were automatically processed using the KERNO classifier (C.POD.exe) and 'Full Train Details' were extracted. An inter-click interval <10ms (so called "feeding buzzes") was used as a proxy for feeding activity. The main difference in the acoustic parameters between habitats was related to the frequency spectrum, with higher maximum and lower modal and minimum click frequencies in BB, and a train frequency range of 17kHz, against 10kHz in IB. Also, the click emission rate (clicks/s) was almost 20% higher in BB. Both studied habitats showed a high proportion of feeding buzzes (BB = 68%; IB = 58%), but with a higher probability of occurrence in BB ( $p < 0.001$ ) and at night period ( $p < 0.001$ ), for both habitats. The C-PODs showed great potential to monitor occurrence, bioacoustics parameters and echolocation behavior of franciscana dolphins. Longer-term temporal and spatial monitoring is necessary for elucidating several hypotheses raised in this study.

Keywords: C-POD; bioacoustics; behavioral ecology.

### **Introduction**

Cetaceans use a wide variety of acoustic signals to communicate, navigate and locate preys (Tyack and Clark, 2000). The pulsed sounds, commonly called "clicks", are exclusive to odontocetes (suborder Odontoceti) and are mainly associated with echolocation (biosonar), but are also used for social communication in some species (Blomqvist and Amundin, 2004; Clausen et al., 2010; Cremer et al, 2017; Martin et al., 2019). Clicks can vary intra- and interspecifically and the dolphins are able to modify acoustic parameters to increase the sensorial and communicational efficiency (Tyack and Clark, 2000; Ey and Fischer 2009). Environmental and ecological factors can trigger changes in the acoustic repertoire of dolphins, such as physical and structural variations in the habitat (May-Collado and Wartzok 2008; Leão et al., 2016), the need to overcome natural and anthropogenic noises (Parks et al. 2009, Pirodda et al., 2014a), or even the acoustic niche partitioning between ecologically similar species living in sympatry (Kyhn, et al., 2010; 2013).

Most odontocetes produce broadband clicks with peak frequency at 30–100 kHz (Kuroda et al., 2020), but the exceptions are four groups that share the same type of narrow-band high-frequency (NBHF) stereotyped clicks with a peak frequency at 130 kHz and no essential energy below 100 kHz (Madsen et al., 2005). They are the families Phocoenidae, Kogiidae, and Pontoporiidae, and at least six species of the family Delphinidae (von Fersen et al., 1997; Madsen et al., 2005; Kyhn et al., 2009; 2010; Tougaard and Kyhn, 2010; Kyhn et al., 2013; Reyes Reyes et al., 2018; Kuroda et al., 2020). Two main hypotheses try to answer why NBHF clicks evolved convergingly in these groups. The 'acoustic crypsis' hypothesis postulates that predation pressure is the evolutionary drive of this characteristic. Considering that the NBHF clicks are above the auditory range of potential predators such as the killer whales *Orcinus orca* (Szymanski et al., 1999) and the extinct raptorial sperm whale *Acrophyseter* sp., the NBHF species could echolocate without being heard by these predators (Andersen and Amundin, 1976; Madsen et al., 2005; Galatius et al., 2019). On the other hand, the 'environmental' hypothesis suggests that the natural noise in the ocean by wind-generated waves may also have been a selective driver. Galatius et al. (2019) showed that wind speeds of 4-9 m/s were constant during the periods in which the NBHF species lineages evolved, providing a minimum noise at 100-150 kHz window (Richardson et al., 1995), which favors the evolution of this particular frequency range in NBHF species. Possibly the combination of these hypotheses may be the best answer (Galatius et al., 2019).

The franciscana dolphin (*Pontoporia blainvillei*, Gervais and d'Orbigny, 1844), the only living species of the family Pontoporiidae, is considered the most endangered small cetacean in the Western South Atlantic Ocean due to the high bycatch levels in gillnets, being listed as "vulnerable" by the IUCN Red list of threatened species (Zerbini et al., 2017). The species uses both the open-sea environment of the continental shelf, up to the 50 m isobath (Danilewicz et al., 2009), as well as the estuarine environments in bays and river mouths, and in some cases can move between these different habitats (Bordino et al., 1999; Rodriguez et al., 2002; Failla et al., 2004; Zappes et al., 2016). However, in Brazil there is a resident population of franciscanas that occurs potentially restricted to an estuarine habitat, the Babitonga Bay, with an estimated abundance of 50 individuals (CV = 0.29) (Cremer and Simões-Lopes, 2005; 2008; Sartori et al., 2017). Babitonga Bay is a highly productive environment and free of

predators of the franciscana, which possibly contributed to the establishment of this extremely restricted home range of this population, varying between 3.7 and 14.1 km<sup>2</sup> (Fixed Kernel Density at 95%, Paitach, 2012). It is not clear yet, however, whether the exclusive use of the estuarine habitat may have driven changes in the species' acoustic repertoire.

Due to its small size, cryptic color, and inconspicuous behavior, the franciscana is one of the most difficult species to detect and study visually (Cremer and Simões-Lopes, 2005), and therefore information about the species in the wild is scarce, especially in the open sea where conditions for visual observations tend to be worse. There is no bioacoustics information about the franciscana for most of its distribution, which ranges from the State of Espírito Santo, in Brazil (18°25' S), to the Province of Chubut, in Argentina (42°35' S) (Crespo, 2009). Von Fersen et al. (1997) recorded clicks of an adult individual undergoing rehabilitation in Argentina and reported for the first time that the franciscana produces NBHF clicks. Echolocation signals were also recorded by Melcón et al. (2012), for the first time in the wild, in Argentina, confirming the NBHF characteristic of the species, with clicks of on average 139 kHz peak frequency, ranging from 130 to 149kHz. In the study of Tellechea and Norbis (2014), carried out with two franciscana calves in rehabilitation, both about one week old, it was observed that even young individuals are acoustically active. Melcón et al. (2016) analyzed the sounds of franciscana calves in the Rio Negro estuary, observing wider frequency range than in adults. The presence of whistles in the acoustic repertoire of species, although rare, was first reported by Cremer et al. (2017) in Babbitonga Bay. Recently, Barcellos and Santos (2021) analyzed franciscana-like clicks registered by autonomous devices (with recording frequency range limited to 144 kHz) and reported a peak frequency of 104 kHz. The characteristics and frequency of species' behaviors in nature are also poorly understood (e.g., Bordino et al., 1999; Cremer and Simões-Lopes, 2005).

Passive acoustic monitoring (PAM) has proven to be an alternative and promising method for collecting information on bioacoustics and behavior of free-living cetaceans (e.g., Rayment et al., 2009; Leeney et al 2011). The possibility to collect information continuously, in periods of reduced visibility and adverse climatic conditions, is one of the main PAM advantages in relation to methods that depend on visual detection (Mellinger et al., 2007; Van Parijs et al., 2009). Among PAM devices,



the C-POD—a porpoise click detector—is especially advantageous because it has an automated NBHF click detection system and an associated software for data classification and extraction. Dolphins usually echolocate more frequently than they produce other types of sounds (Jensen et al., 2012), possibly due to the need to survey the surroundings, in order to avoid colliding with obstacles and to find food, so an automated click detector can be extremely effective. The nature of the data recorded by the C-PODs makes it particularly suitable for the study of NBHF species, as the sampling rate required ( $> 150$  kHz) requires a lot of storage capacity and makes long-term, full bandwidth recordings challenging. The franciscana is the only NBHF species in most of its distribution range and, therefore, the C-POD is a promising tool for long-term passive acoustic monitoring of the species. This device can also be used to assess diel variations in echolocation activity, allowing inferences regarding the feeding behavior and ecology (e.g., Carlström, 2005; Nuutila et al., 2013; Pirodda, et al., 2014b; Schaffeld et al., 2016). It is widely recognized that during foraging, dolphins considerably increase the repetition rate of echolocation clicks within the train as they approach prey until they reach extremely fast rates (so called “feeding buzzes”) just before capture (Amundin, 1991; Koschinski et al., 2008; DeRuiter et al., 2009; Verfuß et al., 2009; Wisniewska et al., 2012, 2014).

The objective of the present study was for the first time to employ an established PAM device (C-POD) to log and characterize the pulsed sounds of free-ranging franciscana dolphins, and to compare selected acoustic parameters of the species living in two areas with different environmental and ecological pressures and conditions, one estuarine and one in the open sea. The hypothesis is that there are acoustic adaptations of the franciscanas echolocation in these habitats, such as increased click source level and/or repetition rate in the estuarine environment with its reduced visibility, as these parameters will determine the prey detectability. The diel and habitat-dependent variations in the occurrence of feeding buzzes were also studied, as an indication of the feeding activity of the species. In this case, we hypothesize that there is a diel pattern in the frequency of feeding, driven by the availability of the prey and that this can be different in each habitat. Obtaining information about the echolocation behavioral patterns of franciscanas using PAM can help to understand the habitat use of the species and the circumstances that affect the

risk of bycatch, contributing to conservation actions (Baptista and Gaunt, 1997; Frainer et al., 2015).

## Material and methods

### Study areas

The study was carried out in two distinct areas: at Babitonga Bay ( $26^{\circ} 15'30''\text{S}$ ,  $48^{\circ} 42'45''\text{O}$ ) and at Itapirubá Beach ( $28^{\circ} 19'35''\text{S}$ ,  $48^{\circ} 41'30''\text{O}$ ), both in the State of Santa Catarina, southern coast of Brazil. These areas represent two different habitats of franciscana dolphins, being the first an estuarine environment and the second an open sea environment (Fig. 1).

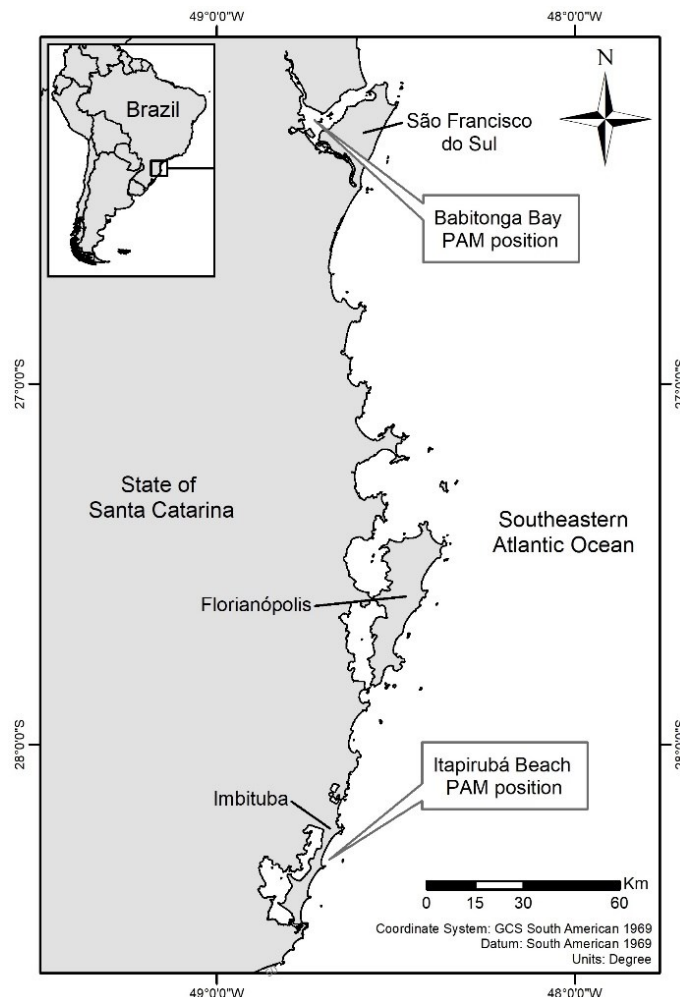


Figure 1: Positions of the passive acoustic monitoring (PAM) stations deployed in 2018 in southern Brazil, inside Babitonga Bay ( $26^{\circ}15'30''\text{S}$ ,  $48^{\circ}42'45''\text{O}$ ), from June 28 to July 23 and from September 22 to October 18, and in an open sea area close to Itapirubá Beach ( $28^{\circ}19'35''\text{S}$ ,  $48^{\circ}41'30''\text{O}$ ), from April 13 to June 20.

Babitonga Bay (BB) has about 160 km<sup>2</sup> of water surface, with an average depth of 6 meters and extensive very shallow areas that are exposed at low tide. Its hydrographic basin reaches over 1,560 km<sup>2</sup>, draining six municipalities in the surroundings and causing a high turbidity and, consequently, low visibility in the bay (Oliveira et al., 2006). Its margins hold approximately 6,200 ha of mangroves, the last major plant formation of this type in the south of the Americas, which contributes to high productivity and represents a great ecosystemic and socioeconomic importance (Cremer, 2006). Its outlet channel, in the northeast direction, is about 3.8 km wide and 28 meters deep, and the only connection between the bay and the open sea since the closure of the southern channel in 1937 for the construction of the access road to the island of São Francisco.

Itapirubá Beach (IB) is 12 km long and has dissipative morphodynamics. It belongs to the municipality of Imbituba and is inside a 156,000 ha Federal Marine Protected Area (Environmental Protection Area of the Right Whale), which extends over approximately 130 km of coastline. The region is characterized by an indented coast with many coves and small sandy beaches separated by rocky promontories (Carvalho and Rizzo, 1994; Silveira et al., 2011). An abundance of approximately 1,200 (CV: 0.47) franciscanas was estimated from aerial surveys in this protected area using the distance sampling method (D. Danilewicz, pers. comm. 2019).

### *Passive acoustic monitoring*

The C-POD (Chelonia Limited, UK) used in this study is an autonomous, battery-powered data logger, designed to log trains of tone-like pulses with a frequency spectrum between 20 and 160 kHz. The C-POD system uses click trains for species classification, which gives much lower false positive rates than can be achieved by identifying the characteristics of individual clicks (Dähne et al., 2013). The C-POD has an omni-directional hydrophone and an approximate detection range of 400 m on-axis (depending on the source level). It can operate continuously for more than four months using ten D-cell alkaline batteries, with data being stored on an SD card. The vertical angle of the device is recorded every minute, verifying if the C-POD was in the correct vertical orientation. This is important because if too much tilted, the omnidirectionality is impaired.

The C-PODs were mounted inside protective structures (“cages”) developed especially for preventing entanglement in drifting gillnets while causing the least possible interference of the acoustic recording (Fig. 2). The cages with the C-PODs in the center were placed on the bottom, with no surface marking buoys to prevent theft or collision by boats. Two 3 kg anchors were attached to the cage with 25 m ropes. During the deployment, the ropes were stretched as straight and tight as possible on the seabed before the anchors were dropped. The GPS coordinates of the cage and the two anchors were recorded. For the recovery, a four-arm grapple suspended in a rope was pulled along the seabed perpendicular to the ropes between the cage and the anchor in order to catch the rope. For deployment and recovery of the C-POD cages in Babitonga Bay a 6.5 m outboard rigid inflatable outboard boat was used, while in Itapirubá Beach this was carried out using a 12 m inboard fishing vessel.

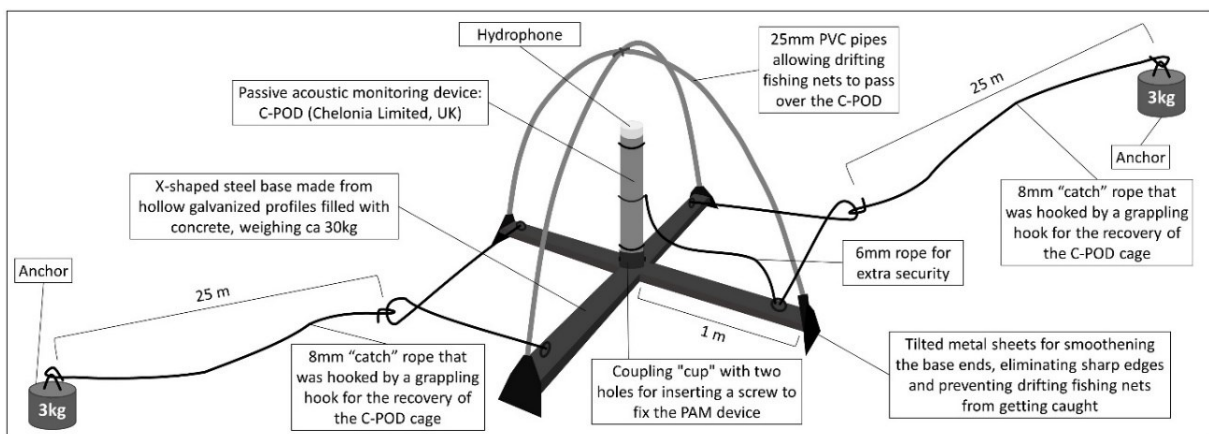


Figure 2: Schematic design of the "cage" developed for anchoring the C-POD and protecting it from being caught by drifting fishing nets during the passive acoustic monitoring. Components are out of scale.

The site sampled in BB is situated in the center of the core area of franciscana occurrence, previously known through photoidentification studies and distribution analyzes (Fig. 1; Cremer and Simões-Lopes, 2008; Paitach, 2012; Sartori et al., 2017). The C-POD cage was deployed at a depth of 7.5 m, in an area with a flat bottom and predominantly sandy sediment. Data was collected from June 28 to July 23 and from September 22 to October 18, 2018, totaling 53 days of monitoring.

At IB, the PAM position (Fig. 1) was chosen based on the indications of the artisanal fishermen in the region, who during earlier ethno-ecological surveys reported that it was a place of frequent franciscana observations (D.F. Herbst, pers. comm.

2018). The C-POD cage was deployed approximately 1.8 km off the coast, at a depth of 10 meters, in a flat bottom area with sandy sediment, and remained in operation from April 13 to June 20, 2018, totaling 65 days of logging.

#### *Data processing*

The data stored on the SD cards was uploaded to a computer using the C-POD.exe software (Chelonia Inc., version 2.044). All data collected was carefully checked visually through the program to ensure the quality of the logged click trains and the absence of excessive environmental noise, which may compromise the further analysis. Then, using the KERNO classifier, an advanced train detection and classification algorithm of the C-POD system, the franciscana sonar click trains (series of clicks) were identified and classified into four quality classes. Only click trains classified in the two higher classes, 'high' and 'moderate' probability of being generated by franciscanas, were included in the analysis, according to the manufacturer's recommendation. When this classification process was done, an export function was used to extract 'Full Train Details', which was then transferred to Excel (Microsoft® Excel for Office version 2103) for descriptive and graphical analysis. All statistical analyses were performed using the R software v.4.0.3 (R Core Team, 2020).

#### *Acoustic parameters analysis*

A total of 12 different acoustic parameters of the click trains logged by the C-PODs or obtained from calculations performed with the available information were investigated: 1) number of clicks in a train; 2) train duration (ms); 3) clicks per second in each train; 4) average, 5) minimum, and 6) maximum inter-click intervals – ICI (ms) - in each train; 7) modal, 8) minimum, and 9) maximum click frequencies (kHz) within a train; 10) frequency range (kHz) of the train; and 13) average and 14) maximum received sound pressure level – SPL (dB re 1 $\mu$ Pa) in a train. It is important to note that the click trains recorded by a static device usually represent only fragments of the total trains emitted by the animal which are captured when the narrow acoustic beam sweeps passed the hydrophone while the animal is scanning from side to side and sometimes also up and down. The duration of the click trains, therefore, is a measure of the speed of such scanning movements and does not represent the total duration of the generated train. The click rate was calculated by dividing number of clicks in train

minus 1 by click duration and the average ICI was obtained by dividing the duration of the train by number of clicks in the train minus 1. The frequency of the click is calculated from the timing of the zero crossings of the sine waves in the clicks. The modal frequency is the average of such click frequencies within the train. The frequency range was calculated as the maximum frequency minus the minimum frequency of clicks within each train, thus representing the whole train and not of isolated clicks. Received SPL is stored as calibrated Pascals and converted to dB re 1 $\mu$ Pa, and depends on the actual source level, the distance to the animal and how the sonar beam hits the C-POD.

The data from each area were analyzed separately using descriptive statistics and graphs. We chose not to describe the extreme values (minimum and maximum) recorded for each acoustic parameter to avoid giving undue importance to values that can be generated by possible false-positive identifications. Generalized Linear Models (GLM) (Zuur et al., 2009) were used to investigate whether the mean values of each acoustic parameter differed between the studied environments. All parameters consist of continuous variables and were modeled with a Gamma-type error distribution and log-link function. The adjustments of the models were evaluated graphically considering the residual errors and the variations between the areas were inferred considering the significance level of 0.01 (Zuur et al., 2009).

### *Feeding behavior inference and analysis*

Feeding buzzes were used as a proxy to identify feeding behavior based on the ICI criterion. As there are no specific data for the franciscana dolphin that describe an ICI cutoff value for feeding buzzes, the classification was based on studies carried out with another NBHF species, the harbor porpoise (*Phocoena phocoena*) (Carlström, 2005; DeRuiter et al., 2009; Todd et al., 2009; Verfuß et al., 2009; Nuuttila et al., 2013; Wisniewska et al., 2016); and the criterion adopted here for feeding buzzes was  $ICI < 10$ ms. Non-feeding trains then represent click trains of relatively slower and less variable click repetition rate and can be attributed to inspection of the environment during travelling, being considered in the 'traveling' category. Evidently, these behaviors can be complementary in the animals' routine, so that small displacements and events of approximation and prey capture can be interspersed and successively repeated, but this generic classification of behaviors fulfills the objective of the study,

which is to identify general patterns. We graphically analyzed the distribution values of average SPL between the feeding and traveling click trains as these variations may affect the potential for detecting the click trains.

To analyze differences in behavioral patterns between estuarine and open sea habitats, a probability of occurrence of feeding behavior was calculated for each diel period ('day' = 06:00–17:59; and 'night' = 18:00–05:59) for each monitoring day. Therefore, the number of feeding buzzes was counted and the proportion in relation to the total click trains detected in the period was calculated using the R software, assigning a weight of evidence according to the total number of observations per period. Binomial GLM with a logit link function (Zuur et al., 2009) was used to test whether there are variations in the probability of occurrence of feeding behavior in relation to the different habitats and diel periods, as well as the interaction between habitats and diel periods. The lowest AIC value (Akaike Information Criterion, Burnham and Anderson, 2002) was used to identify the most parsimonious model.

## **Results**

In BB, the 53 days of data collection resulted in a total of 1,263 hours of passive acoustic monitoring, 636 hours of which (50.4%) contained franciscana loggings. A total of 10,924 franciscana click trains were recorded, with a total duration of 72.8 min. In IB, the 65 days of data collection resulted in a total of 1,554 hours of passive acoustic monitoring, of which 514 hours (33.1%) contained franciscana loggings. A total of 6,093 franciscana click trains were recorded, with a total duration of 40.5 min. Combining all click trains from both areas, a total of 501,518 clicks were analyzed.

### *Acoustic parameters*

The click rate (clicks per second), maximum ICI, modal, minimum, and maximum click frequency in a train, train frequency range, average SPL, and maximum SPL differed significantly between the two locations (Table 1). There were no significant differences between the two locations in number of clicks per train, train duration, average ICI and minimum ICI (Table 1).

Franciscana dolphins in BB generated click trains with a faster repetition rate, reaching a mean of 169 ( $\pm 129$ ) clicks/s, which is almost 20% higher than in IB with a

mean of 143 ( $\pm 115$ ) clicks/s. Clicks/s histograms show that the peak in BB is at 40 clicks/s and at 60 clicks/s in IB (Fig 3). Also, there are substantially higher proportion of click trains with click rate above 100 clicks/s in BB (Fig. 3).

Table 1: Descriptive statistics of acoustic parameters of the franciscana dolphins (*Pontoporia blainvillei*) recorded in two different habitats in southern Brazil, Babitonga Bay (estuary) and Itapirubá Beach (open sea), and results of the generalized linear models (GLM) that tested the variation between locations. (n = number of click trains analyzed; SD = standard deviation; Q1 = first quartile; Q3 = third quartile; ICI = inter click interval; SPL = sound pressure level).

Acoustic parameters	Babitonga Bay (n = 10,924)				Itapirubá Beach (n = 6,093)				GLM	
	Mean	SD	Median	Q1–Q3	Mean	SD	Median	Q1–Q3	Estimate	p-value
Number of clicks	29.5	16.2	25.0	19–36	29.4	17.3	25.0	18–36	-0.004	0.673
Duration (ms)	399.8	534.6	190.7	83–513	398.8	486.2	232.5	100–518	-0.002	0.907
Clicks/s	169.1	128.5	137.2	61–242	143.1	114.8	100.6	60–193	-0.167	<b>&lt;0.001</b>
Average ICI (ms)	12.6	13.6	7.3	4–16	12.3	9.7	9.9	5–17	-0.019	0.222
Minimum ICI (ms)	10.0	10.8	5.9	4–13	10.2	7.6	8.5	5–14	0.017	0.264
Maximum ICI (ms)	21.2	23.7	12.4	7–27	22.6	19.4	17.6	9–31	0.063	<b>&lt;0.001</b>
Modal frequency (kHz)	128.7	4.6	129.0	125–132	129.9	3.2	130.0	128–132	0.009	<b>&lt;0.001</b>
Minimum frequency (kHz)	118.0	13.9	120.0	117–124	123.7	4.6	124.0	121–126	0.048	<b>&lt;0.001</b>
Maximum frequency (kHz)	135.1	5.7	135.0	131–139	134.2	4.0	134.0	132–136	-0.007	<b>&lt;0.001</b>
Bandwidth (kHz)	17.1	15.6	14.0	8–21	10.5	5.9	9.0	7–13	-0.491	<b>&lt;0.001</b>
Average SPL (dB)	151.8	5.2	151.1	148–155	151.3	5.8	150.1	147–155	-0.004	<b>&lt;0.001</b>
Maximum SPL (dB)	155.2	6.1	154.5	151–159	154.7	6.7	153.8	149–159	-0.003	<b>&lt;0.001</b>

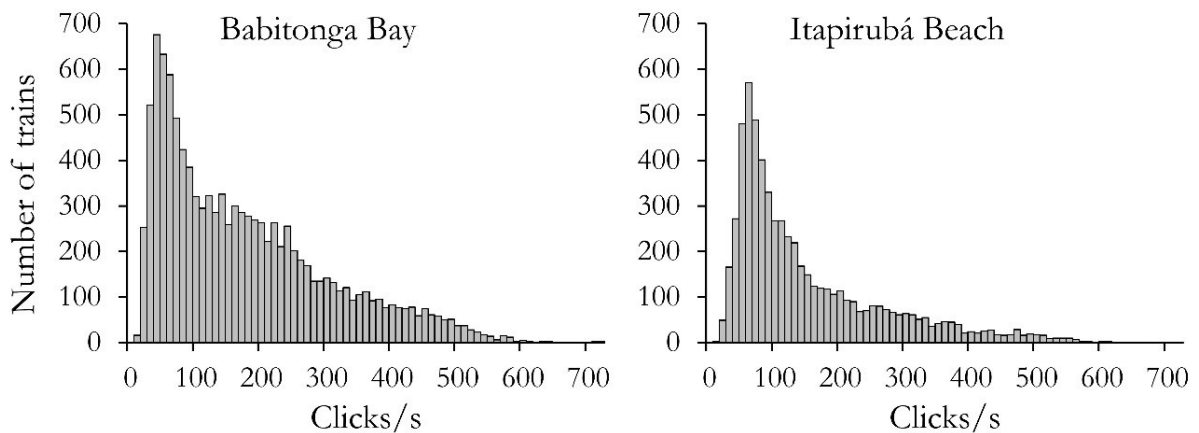


Figure 3: Distribution of the clicks/s values of the franciscana dolphins click trains recorded in estuarine (Babitonga Bay, n=10,924) and open sea (Itapirubá Beach, n=6,093) environments.



The maximum ICI was slightly different between areas, with a mean of 21 ( $\pm 23$ ) ms in BB, just 2 ms below the mean recorded in IB (23  $\pm 19$  ms) (Fig. 4). The franciscanas emitted clicks with modal frequencies of 129 ( $\pm 5$ ) kHz in BB, and 130 ( $\pm 3$ ) kHz in IB (Fig. 5). The mean minimum and maximum click frequency in BB were 118 ( $\pm 14$ ) and 135 ( $\pm 6$ ) kHz, respectively (Fig. 5). In IB the mean minimum and maximum frequency were 124 ( $\pm 5$ ) and 134 ( $\pm 4$ ) kHz, respectively (Fig. 5). The train frequency range was much higher at BB, reaching a mean of 17 ( $\pm 16$ ) kHz, while in IB it was 10 ( $\pm 6$ ) kHz, and this high difference is possibly associated with the variation observed in the minimum frequencies. In BB 458 (4.2%) click trains had minimum click frequencies below 100 kHz, ranging from 25 to 99 kHz, while in IB there were only 9 (0.15%) below 100 kHz. Looking closer to these <100 kHz minimum frequency trains of BB shows that they all had the modal and maximum frequencies >100 kHz, and only the minimum frequency standing out very much lower. Although significant differences in average and maximum SPL were identified between habitats, the variations were very subtle (Fig. 6).

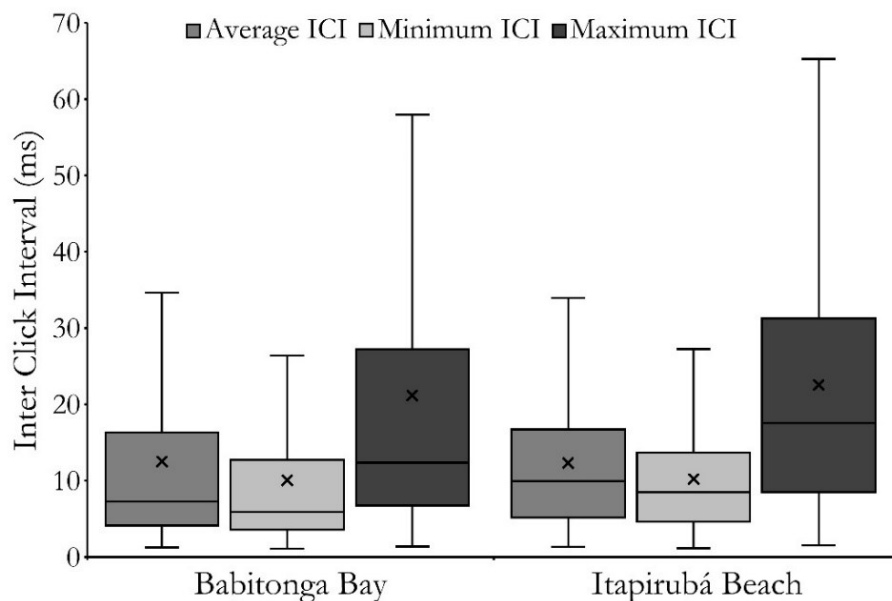


Figure 4: Inter Click Interval parameters of the click trains emitted by franciscana dolphins in Babitonga Bay (n=10,924) and Itapirubá Beach (n=6,093), in southern Brazil. (Box-plots values: upper whisker = maximum (no outliers); upper box line = third quartile; middle box line = median; bottom box line = first quartile; bottom whisker = minimum (no outliers); marker x = mean).

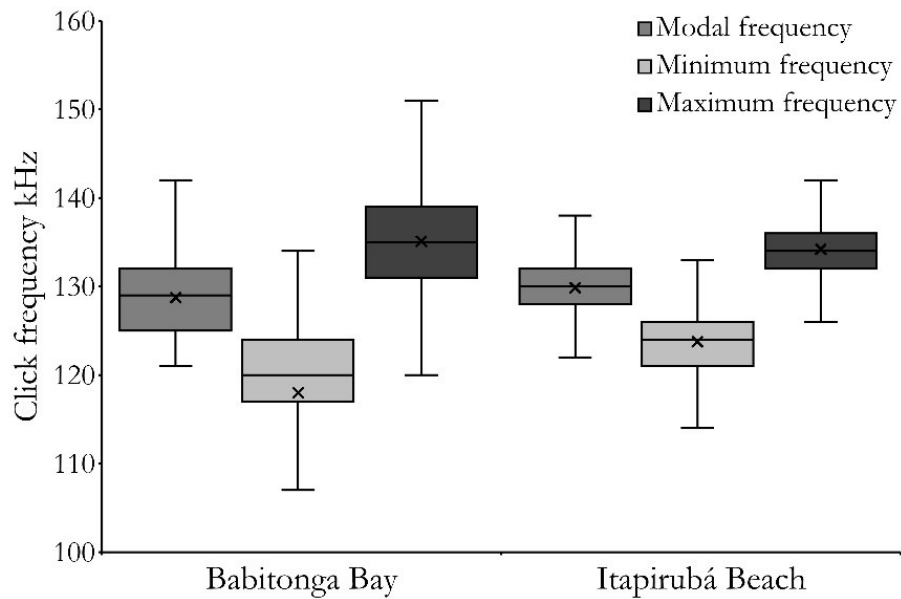


Figure 5: Frequency parameters of the click trains emitted by franciscana dolphins in Babitonga Bay (n=10,924) and Itapirubá Beach (n=6,093), in southern Brazil. (Box-plots values: upper whisker = maximum (no outliers); upper box line = third quartile; middle box line = median; bottom box line = first quartile; bottom whisker = minimum (no outliers); marker x = mean).

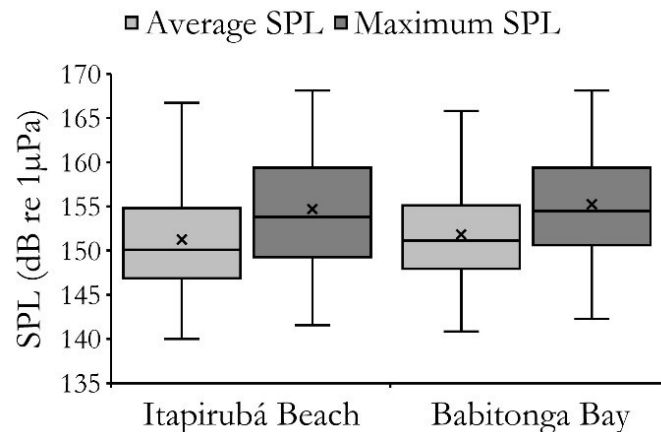


Figure 6: Sound Pressure Level (SPL) of the click trains emitted by franciscana dolphins in Babitonga Bay (n=10,924) and Itapirubá Beach (n=6,093), in southern Brazil. (Box-plots values: upper whisker = maximum (no outliers); upper box line = third quartile; middle box line = median; bottom box line = first quartile; bottom whisker = minimum (no outliers); marker x = mean).

### *Feeding behavior*

In BB, 7,416 (68%) of the click trains analyzed had a minimum ICI less than 10 ms and were thus categorized as feeding buzzes, while in IB this value was 3,554 (58.3%), demonstrating that both sampled areas were intensely used for feeding. The

average source level is reduced in feeding buzzes compared to regular click trains used for traveling, which is demonstrated by the frequency distribution of these categories in the received SPL values (Fig. 7).

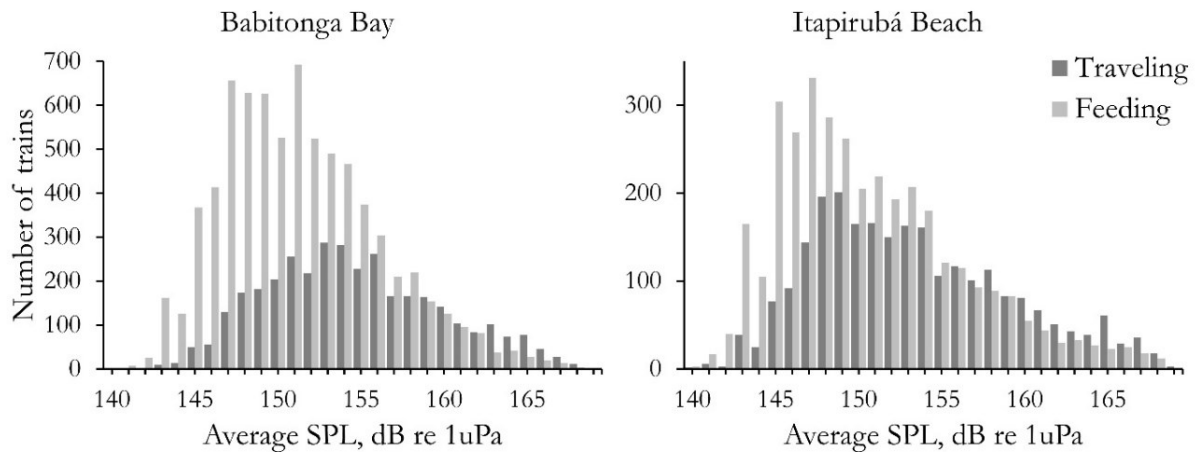


Figure 7: Distribution of the received average SPL values of the feeding buzzes and traveling click trains of franciscana dolphins in Babitonga Bay ( $n=10,924$ ) and Itapirubá Beach ( $n=6,093$ ). Note that the Y-axes differ in BB and IB because of the different sample sizes.

The most parsimonious model that describes the probability of feeding buzzes included location and diel periods as predictive variables, but without interaction between these factors. The place sampled in IB had a lower probability of occurrence of feeding buzzes (estimate =  $-0.419$ ;  $p$ -value  $<0.001$ ), with almost the same proportion as for traveling, in comparison with the place sampled in BB, where the probability of feeding compared to traveling was almost the double (Fig. 8). In both habitats, the night was the period of the day when franciscanas were most involved in feeding (estimate =  $0.255$ ;  $p$ -value  $<0.001$ ) (Fig. 8).

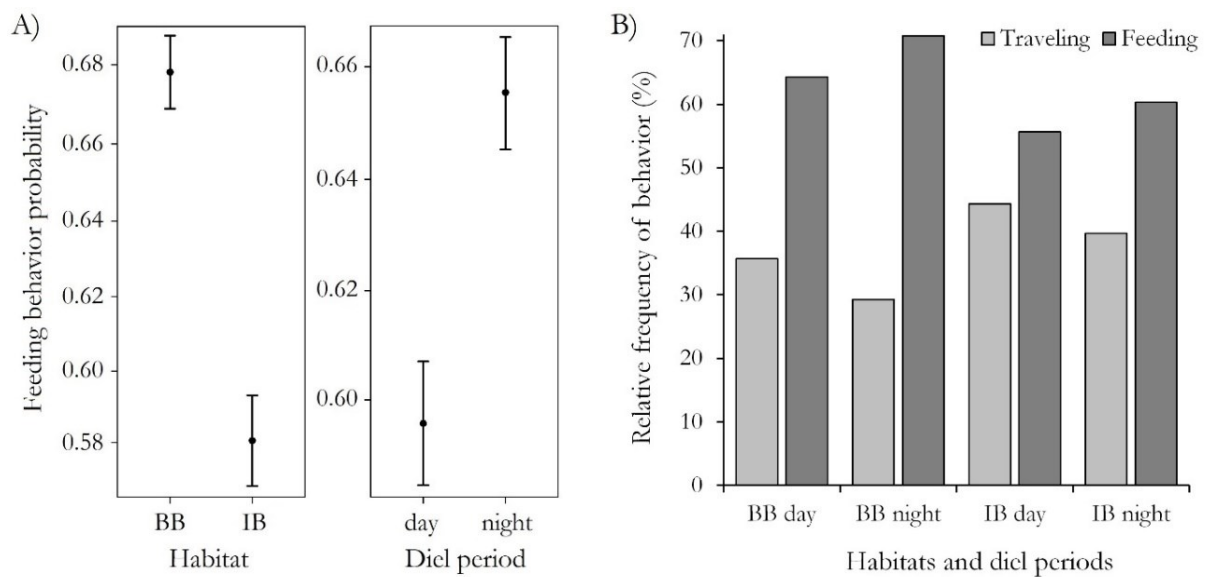


Figure 8: A) Probability of franciscanas feeding behavior in the sampled habitats (BB = Babitonga Bay, IB = Itapirubá Beach) and diel periods with both locations combined. Plots show the mean (dots) and the 95% confidence interval (whiskers), using predictions from the top ranked model. B) Relative frequency of behaviors, based on feeding buzzes and traveling click trains, in relation to habitats and diel periods.

## Discussion

### *Passive acoustic monitoring with C-POD*

This study reports the first use of passive acoustic monitoring (PAM) devices to long-term record the echolocation behavior of wild franciscana dolphins. The number of monitored days obtained was considered sufficient to answer the proposed questions, and a substantial data set was obtained from both chosen locations. The processing of such a large volume of data is only possible through an automated species classification and analysis method such as that of the C-POD system, which saves time and reduces the researcher's possible subjectivity bias (Rayment et al., 2009). We deployed our C-PODs in custom-made protective structures ("cages") that proved to be efficient in keeping the C-PODs safe and in an ideal vertical orientation for their operation. The recovery method also proved to be efficient, allowing for safe and easy localization and retrieval of the cages, showing promise for its application on a larger scale.

Limitations of PAM include potential uncertainty in species identification (Wang et al., 2005; Tougaard et al., 2006). Using T-PODs, the predecessor of the C-POD, NBHF click trains were consistently recorded and correctly classified when Hector's

dolphins were present in Flea Bay, New Zealand, while no detections were made when these dolphins were absent (Rayment et al., 2009). The C-POD system has more sophisticated detection algorithms to reduce false positive detections and is more versatile in terms of species classification than the T-POD (Roberts and Read, 2014). In Babitonga Bay it was occasionally possible to make visual records of franciscanas in the vicinity of the C-POD, and NBHF detections were consistent with these sightings (R.L. Paitach, personal observation). Babitonga Bay also houses a resident population of Guiana dolphins (*Sotalia guianensis*), with an estimated abundance of about 180 individuals (Cremer et al., 2011). This species produces broadband clicks (Leão et al., 2016), which makes it easy to distinguish from the franciscana dolphins in the C-POD data. When the Guiana dolphins were spotted visually in the vicinity of the C-POD, no false-positive NBHF detections were found (R.L. Paitach, personal observation). Furthermore, the two species tend not to use the same areas simultaneously and there is no record of mixed groups of franciscanas and Guiana dolphins (Cremer et al., 2018).

Different sources of ambient noise, such as sea surface waves and sediment transport, may also affect the detection of the NBHF click trains and possibly bias the results. In the present study, there was no substantial noise in the recorded data that could have compromised the acquisition or classification of franciscana detections in any of the locations. Rayment et al (2009) showed that detections with T-PODs of Hector's dolphins in the 'high' and 'moderate' quality categories—the same as those adopted in the present study—reliably represented the species' echolocation trains, while the 'low' and 'doubtful' quality categories occasionally contained detections from boat sonar. Robbins et al (2015), however, pointed out that the accuracy of the C-POD classifier by quality classes may be site-specific and highlighted the importance of exploring the data manually to make the most appropriate software settings based on the objectives of each study.

#### *Acoustic differences between habitats*

The main acoustic difference in the click trains observed between the two sites was related to the click frequency spectrum. In general, franciscanas in BB emitted click trains with slightly lower modal frequencies, but with higher maximum and lower

minimum frequencies, than those in IB, and with a frequency range almost twice that in IB. Melcón et al. (2012) recorded a click frequency bandwidth of 19 kHz for franciscanas in the Rio Negro estuary, in Argentina, a value very close to what we found in BB for train frequency range. The predominant frequency in the click power spectrum was much higher, reaching 139kHz (Melcón et al., 2012), which is 10kHz above that observed in our study. In an open sea environment, Barcellos and Santos (2021) recorded minimum frequencies of on average 104 kHz with a PAM device, lower than those recorded in the present study for both environments, but as they did not record maximum frequencies due to sampling limitations, it was not possible to analyze the bandwidth. However, since the data acquisition and analysis methods used in the present work differs substantially from those used by Melcón et al. (2012) and by Barcellos and Santos (2021), comparisons should be made with caution.

Differences in the frequency spectrum of clicks between populations of an NBHF species have been attributed to the sympatry with another NBHF species. In western Canada, where harbour and Dall's porpoises co-occur, harbour porpoises produce clicks with a higher centroid frequency and lower frequency range than its conspecifics living in Denmark, where there are no sympatric NBHF species (Kyhn et al., 2013). These authors suggest that these differences may be a biological mechanism to avoid hybridization (Kyhn et al., 2013). Unlike Uruguay and Argentina, where two other NBHF species, the Burmeister's porpoise, *Phocoena spinipinnis* (Reyes Reyes et al., 2018), and the Peale's dolphin, *Lagenorhynchus australis* (Kyhn et al., 2010) (only Argentina), occur in potential sympatry with the franciscana, in Brazil the franciscana is the only species of frequent occurrence that produces NBHF clicks and, therefore, the differences observed in this study are probably not due to a partition of the acoustic niche.

Click frequency differences observed may have been influenced by the presence of calves, since the PAM in BB was carried out the spring months, while in IB it was done in the fall. The spring is the main reproductive season of the species (Rosas and Monteiro-Filho, 2002; Danilewicz, 2003; Cremer et al. 2013), and thus, the lower minimum click frequency in the BB may have been caused by a greater proportion of calves there. Melcón et al., (2016) observed that a newborn franciscana calf emitted echolocation signals with minimum click frequencies much lower (<100 kHz) than that of adults, and with bandwidths that greatly exceeded 20kHz, which may

be associated with the sub-development of structures related to sound production (Frainer et al., 2015; Melcón et al., 2016). If this hypothesis is proven correct, it would have important implications for franciscana research and conservation, as click trains produced by calves then can be identified and differentiated in C-POD data—and even better with the F-POD, the next generation in the Chelonia system, which includes full sampled clicks in the logged click trains—based on the frequency range and minimum click frequency criteria. This would make it possible, with prior knowledge of how long post-partum old a calf generates these broadband clicks, to acoustically estimate relative density of calves and, consequently, the birth rate.

Another possible hypothesis for differences in the click frequencies of franciscanas in BB and IP is associated with morphological differences in these populations. It is unclear for how long franciscanas have been resident in BB, but there is strong genetic evidence of a high degree of isolation in this population, corroborated by field observations, satellite telemetry data and photoidentification (Cremer and Simões-Lopes, 2008; Cremer et al. 2018; Dias et al., 2013 Sartori et al., 2017). Alves (2013) compared the cranial morphometry of franciscanas inside and outside BB and observed that the skull of franciscanas from inside the bay is smaller, but with proportionally larger orbital cavities and frontal (nasal crest) bones. According to Berta et al. (2014), evolutionary modifications of the facial and nasal region of odontocetes may be related to the biosonar sound production.

No difference was found in the train duration between BB and IB, which indicates that the animals in both populations have the same scanning behavior, but the average click rate was almost 20% higher in BB. A very similar result was observed in a population of Guiana dolphins in northeastern Brazil, which generated higher click repetition rates in an estuarine environment compared to the open sea, but without significant differences in the click train duration between habitats (Leão et al., 2016). A higher click repetition rate may be associated with the dolphins locking on targets at closer ranges, which may be necessary in a more complex environment like the estuary (Monteiro-Filho and Monteiro, 2001). Also, the visibility is much lower in an estuarine environment like BB, than in the open sea, due to the presence of murky waters (Oliveira et al., 2006). Although no specific water transparency measures were taken in our study, this result is an indication that the physical characteristics of the environments may influence the variability of the acoustic behavior of the franciscanas.

However, it is important to emphasize that in BB there was a higher proportion of feeding buzzes than in IB, and this will affect the overall average click rate, thus expected to be higher in BB. Our study aimed to analyze the general variability of the acoustic parameters between habitats, but in future studies it would be important to analyze these parameters separated for each behavioral class of click trains, allowing for a deeper knowledge.

It is possible that the differences observed in the echolocation parameters are locality specific. Based on genetic and bioecological characteristics of populations, the franciscana distribution range has been divided into four zones, known as 'Franciscana Management Areas' (FMAs) in order to guide conservation and management actions at a regional basis: two in southeastern and southern Brazil (FMA I and II), one in southern Brazil and Uruguay (FMA III) and one in Argentina (FMA IV) (Secchi et al., 2003). Perhaps the franciscana's acoustic repertoire has variations associated with the conditions in these FMA's. Babitonga Bay and Anchieta Island—the study area of Barcellos and Santos (2021)—are part of FMA II, while Itapirubá Beach belongs to FMA III and the Rio Negro Estuary—the study area of Melcón et al., (2012)—to FMA IV. However, the limited bioacoustics information for most of the franciscana distribution prevents further elaboration of this hypothesis.

#### *Diel patterns of echolocation behavior*

The echolocation trains detected in both BB and IB have a higher proportion of trains with minimum ICI <10ms (68% and 58%, respectively), than reported in studies with the same ICI criterion applied to *P. phocoena* (27%) and *Tursiops truncatus* (4%) (Nuuttila et al., 2013). This is an indicator that the feeding rate of franciscanas is extremely high, suggesting that they have a high metabolic demand, which make them vulnerable to anthropic disturbances that reduce the availability of their preys, such as overfishing (Wisniewska et al., 2016). This difference in proportion between feeding and traveling click trains can be even greater if it is considered that feeding buzzes have lower source levels, as observed in both the current study and the study of Wisniewska et al. (2016), and therefore have a shorter potential propagation range and consequently a lower chance of being detected.

The C-PODs in our study were positioned close to the seabed, in order to avoid entanglement in driftnets, commonly used in the same areas of franciscana



distribution. In BB, the most important prey species of the franciscanas — reaching almost 70% of relative importance in their diet — is the rake stardrum (*Stellifer rastrifer*), a benthopelagic fish that forms small shoals (Cremer et al., 2012; Paitach, 2015). In other areas, in the open sea, although this species is also important in the diet here, other benthopelagic fish, such as *Micropogonias furnieri* and *Isopisthus parvipinnis* also play an important role (Di Benedetto et al. 2009; Paitach, 2015; Bassoi et al., 2020). This indicates that the franciscana forages close to the seabed, therefore, the way the equipment was deployed were ideal for monitoring the feeding activity of this species.

The results obtained point at a clear diel pattern in the feeding behavior of the franciscanas, with the greatest intensity at night for both studied environments. Barcellos and Santos (2021) also observed a higher proportion of high repetition franciscana click trains during the night than during the day, but without carrying out a systematic analysis in this regard. There are no more published data on diel echolocation patterns in the franciscana and, therefore, most of the following comparisons are made based on studies of other odontocetes species. In the North Sea, Todd et al. (2009) used T-PODs to monitor the echolocation behavior of the harbour porpoises around an offshore gas installation and observed results similar to ours, with higher feeding buzz proportion at night. Carlström (2005) also using T-PODs, observed the minimum ICI peaks and the highest proportion of feeding buzz at night, with minimum during the day.

It has been suggested that dolphins may increase their click rate for feeding during night to compensate for the loss of visual information (Carlström, 2005), but it is not expected to be a significant difference in visibility between day and night in the Babitonga. A more likely explanation is an increased availability of prey. It was observed that Dall's porpoises (*Phocoenoides dalli*), for example, have specific feeding times in each region which was related to the daily activity of the dominant prey (Amano et al., 1998). The diel pattern of habitat use of the Heaviside dolphin (*Cephalorhynchus heavisidii*) at Pelican Point is entirely opposite to that seen in the southern part of the species distribution in South African waters, and the clear pattern of daytime onshore-offshore migration observed in South Africa is probably associated with nocturnal feeding of demersal prey that migrate vertically (Elwen et al., 2006; Leeney et al 2011).

We observed a higher intensity of feeding in BB than in IB, which may be associated with a higher availability of prey in the estuarine environment. However, it is important to note that our study was based on a single location in each environment. According to Pirodda et al. (2014b), acoustic recordings in a feeding area are expected to contain a high proportion of feeding buzzes compared to areas used only for traveling. Schaffeld et al. (2016) observed changes in feeding click trains between locations, seasons, and time of day, leading them to the assumption that the long-term patterns of echolocation of harbour porpoises depend strongly on temporal changes in the availability and composition of preys in each habitat. In BB, the franciscana distribution is restricted to the innermost regions and the chosen PAM location is previously known as the core area of the population, reflecting a high prey availability in this area, as already demonstrated by ichthyological sampling (Paitach, 2015; Paitach et al., 2017; Cremer et al., 2018). There is yet no information available on habitat use, density, and distribution of franciscanas in IB. Therefore, analyzes of diel patterns need to be conducted preferable throughout all seasons and on large geographical scales to allow for a more generalized interpretation.

## **Conclusion**

This study documents the first use of this well-established PAM device to assess echolocating behavior of franciscanas in two different habitats in which the species occurs. The main acoustic difference between habitats was related to the frequency spectrum, with higher maximum and lower minimum values in BB, resulting in a frequency range of almost double that of IB. Some hypotheses were discussed for the differences identified and one specific deserves special attention: our results indicate a possibility of acoustic recognition of calves through a higher frequency range and lower minimum frequency of clicks in the C-POD data and if proven right it may have important implications for future research and conservation of the species. No difference in train duration was observed, but the click rate was almost 20% higher in the estuary. It was observed that the franciscana feeds more at night in both habitats, but in the estuarine environment the feeding rates were higher. The C-POD has a great potential as a tool to monitor occurrence, echolocation behavior, distribution and habitat use of franciscana dolphins. The main advantage is its continuous operation, allowing to monitor for 24 hours a day for long periods of time, and the automated data

processing system, which reduces the time and subjectivity of the analysis. Our work was carried out with a single PAM station in each area studied, and in just a few months. Expanding the monitoring to a full year or even more, and possibly to a wider spatial grid, will provide further insight into longer-term temporal and spatial patterns of echolocation behavior and habitat use by the franciscana.

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## **CAPÍTULO 2 – Fine-scale assessment of habitat use and distribution of the critically endangered franciscana dolphin population in Babitonga Bay, Brazil**

### **Abstract**

The resident population of franciscana dolphins in Babitonga Bay is threatened by several human activities. Understanding their habitat use and distribution in different spatio-temporal scales is essential for adequate management and mitigation of impacts. Using data from sixty passive acoustic monitoring stations (i.e., C-PODs), implemented in the bay between June and December 2018, the relationship between the occurrence of dolphins and several environmental variables was investigated with generalized additive models. The final model presented 51% of explained deviance and included “time of day”, “presence of Guiana dolphins”, “maximum slope”, and “bottom sediment”, among other less important variables. A daily distribution pattern was identified, with franciscanas remaining in the areas of greatest occurrence especially in the morning. Areas intensively used by Guyana dolphin were avoided. Franciscanas also seem to avoid steeper areas and prefer areas with sandy bottoms. For mapping their distribution, Empirical Bayesian Kriging was employed using “Hours of detection per day” and “Feeding Buzz Ratio” separately to, respectively, identify the main areas of occurrence and to identify important feeding areas. Franciscana dolphins are consistently predominant in the innermost region of the estuary, without expressive use of the entrance channel, with a wider area used in the winter than in spring. The entire central region of the islands, between the north and south banks, represents an important area for foraging, which occurs most often during the dawn and night. This study provides important insights into habitat use and distribution of this critically endangered population. Habitat modeling allowed the identification of their critical habitats and thereby is a strong tool to guide the main management requirements necessary for their conservation.

Keywords: critical habitat; passive acoustic monitoring; *Pontoporia blainvillei*.

### **Introduction**

Information about the habitat use and distribution of the species is necessary for guiding management, allowing the identification of opportunities for conciliating the ecological needs of the species and the human use of the territory (Hastie et al., 2003; Cañadas et al., 2005). For highly mobile species such as marine mammals, it is unfeasible to designate their entire distribution as protected areas. Therefore, it is essential to identify priority areas for the survival of the populations, such as those used for feeding and breeding (Hoyt, 2012). However, understanding the ecological requirements of small cryptic cetaceans is a major challenge. The franciscana dolphin (*Pontoporia blainvillei* – Gervais & D’Orbigny, 1844) is one of the smallest dolphins in the world, form small family groups, rarely perform aerial behaviors, and expose a very small part of the body when surfacing to breath (Wells et al., 2013; Cremer et al., 2018),

making it very difficult to observe visually. Also, visual observations, whether from vessels or aircrafts, are restricted to daylight periods and require very good weather conditions (Beaufort wind scale  $\leq 2$ ).

The franciscana is endemic to the Southwestern Atlantic Ocean, occurring from the state of Espírito Santo, Brazil (18°25' S), to Patagonia, Argentina (42°35' S) (Crespo, 2009), with two gaps in the distribution (for details see: Amaral et al., 2018). The species presents high risk of extinction mainly due to the high accidental mortality in fishing nets. The species is listed as “Vulnerable” globally by the IUCN (Zerbini et al., 2017), while in Brazil it is “critically endangered” (MMA, 2014). The habitat use of the franciscana is still poorly known, with information limited to depths and distance from the shore, with low spatial accuracy and without considering temporal dynamics (e.g., Danilewicz et al., 2009; Amaral et al., 2018; Sucunza et al., 2019). The species occurs mainly in coastal habitats on the continental shelf, between the surf zone and the 50m isobath, predominantly up to 30m deep (Danilewicz et al., 2009), but individuals are occasionally seen visiting bays and deltas throughout their distribution (Bordino et al., 1999; Di Benedetto et al., 2001; Azevedo et al., 2002; Failla et al., 2004; Santos et al., 2009; Zappes et al., 2018).

The only known distinct franciscana population residing exclusively in an estuarine habitat is the one inhabiting Babitonga Bay, southern Brazil (Cremer & Simões-Lopes, 2008; Cremer et al., 2018). This population only counts about 50 individuals, and there is evidence of a high degree of isolation, corroborated by satellite telemetry data, photoidentification and genetic analyses (Dias et al., 2013; Sartori et al. 2017; Cremer et al. 2018; Wells et al., in press). For conservation purposes, this population must be considered as a demographically independent management unit (sensu Moritz, 1994). In this sense, the survival of each individual is essential to the sustainability of the population, and accidental catches in gillnets, as reported by Pinheiro & Cremer (2003), constitute a serious threat. In addition, habitat degradation by chemical pollution (Alonso et al., 2012), and the construction and expansion of ports, which includes underwater blasting work and dredging, compromise the health of the Babitonga ecosystem and the survival of this franciscana population (Cremer et al. 2018; Paitach et al., 2019).

Surveys based on visual observations have reported a heterogeneous distribution of franciscanas in Babitonga Bay, restricted to the innermost regions of the

estuary and with focal areas close to the islands in the central part of the bay (Cremer & Simões-Lopes, 2008; Paitach et al., 2017; Cremer et al., 2018). There are also evidences of an effect of tidal cycles on the habitat use patterns of the species, in addition to seasonal variations in the size of its home range, probably reflecting the availability of prey fish (Cremer, 2007; Paitach, 2015; Paitach et al., 2017; Cremer et al., 2018). Another aspect that influences the distribution and habitat use of franciscanas in Babitonga Bay is the direct sympatry (sensu Bearzi, 2005) with a resident population of Guiana dolphins (*Sotalia guianensis*), estimated to be 180 individuals (Cremer et al., 2011). Previous studies have recognized spatial and trophic overlap between the two species in Babitonga Bay (Cremer, 2007; Cremer & Simões-Lopes, 2008; Cremer et al., 2011; Paitach, 2015; Cremer et al., 2018). Ecologically similar species sharing limited resources deserves special attention for conservation, since the species affect each other (Bearzi, 2005), and its consequences are often underestimated when analyzing the populations trends. This knowledge lacks complementary approaches at different spatio-temporal scales for a deeper interpretation.

Passive acoustic monitoring (PAM) allows the autonomous logging of the underwater sounds generated by cetaceans and is an efficient alternative to visual surveys, since the sound travels far in water. Cetaceans produce a wide variety of acoustic signals and odontocetes depend on sound for navigation, prey localization and communication (Tyack & Clark, 2000). Therefore, the use of passive acoustics is a highly efficient strategy to investigate various ecological and behavioral aspects of cetaceans (Batista & Gaunt, 1997). The possibility of long-term continuous logging, even in bad weather and at night, with low associated costs, is the main advantage of PAM (Mellinger et al., 2007; Van Parijs et al., 2009). The characteristics of the logged echolocation click trains allow to identify and quantify the foraging behavior of dolphins, making PAM also a tool for identifying potential foraging/feeding areas and periods (e.g., Pirodda et al., 2014; Tubbs et al. 2020). PAM has been widely used worldwide for studies on cetacean distribution, seasonal migrations, behavior, habitat use, and identification of impacts and threats (e.g., Verfuß et al., 2007; Mellinger et al., 2007; Castellote et al., 2009; Jaramillo-Legorreta et al., 2016; Carlén et al., 2018). For franciscanas, however, only two studies were carried out to analyze the acoustic repertoire (Tellechea et al., 2017; Barcellos & Santos, 2021), in addition to initiatives

to improve methods for species detection and identification by towed PAM arrays (Andriolo et al., 2018; Teixeira, 2021).

In this study, we used an array of PAM devices deployed in a grid for spatial-temporal analysis of the distribution and habitat use patterns of the franciscanas during winter and spring in Babitonga Bay. The objectives were to 1) identify the main environmental and ecological variables that influence the habitat use of the franciscana population; 2) identify temporal cycles of the distribution, such as diel and tidal cycles; 3) verify the influence of the Guiana dolphins on the franciscanas' spatial dynamics; and 4) design maps of franciscanas' distribution and feeding areas throughout the day in Babitonga Bay. The main hypothesis of the study was that franciscanas occupy predominant and time-dependent focal areas in Babitonga Bay, that are associated with environmental features and partitioning of spatial niche with the Guiana dolphins. Understanding such dynamics will be an important subsidy for their conservation.

## **Methods**

### *Study area and sampling design*

A systematic grid was constructed with sixty PAM stations in Babitonga Bay (26°02'-26°28' S - 48°28'-48°50' W), in state of Santa Catarina, southern Brazil (Fig. 1). The study area comprises a water surface of approximately 160 km<sup>2</sup>, with an average depth of 6 meters and wide extremely shallow areas, which are exposed at low tide (Vieira et al., 2008). The waters in the bay are supplied from several rivers, but still is considered a homogeneous estuary due to its physical-chemical conditions (IBAMA, 1998). It has a semi-diurnal regime of micro tides, that is, two well-defined daily cycles of floods and ebbs during spring tides, reaching a maximum amplitude of less than 2 m (Vieira et al., 2008). There is a channel in the northeastern portion, with a depth of up to 28 m, which is the only connection to the open sea since the grounding of the narrow channel south of the São Francisco do Sul Island in 1937, for the construction of the access road to the island (thick black segment in Fig. 1).

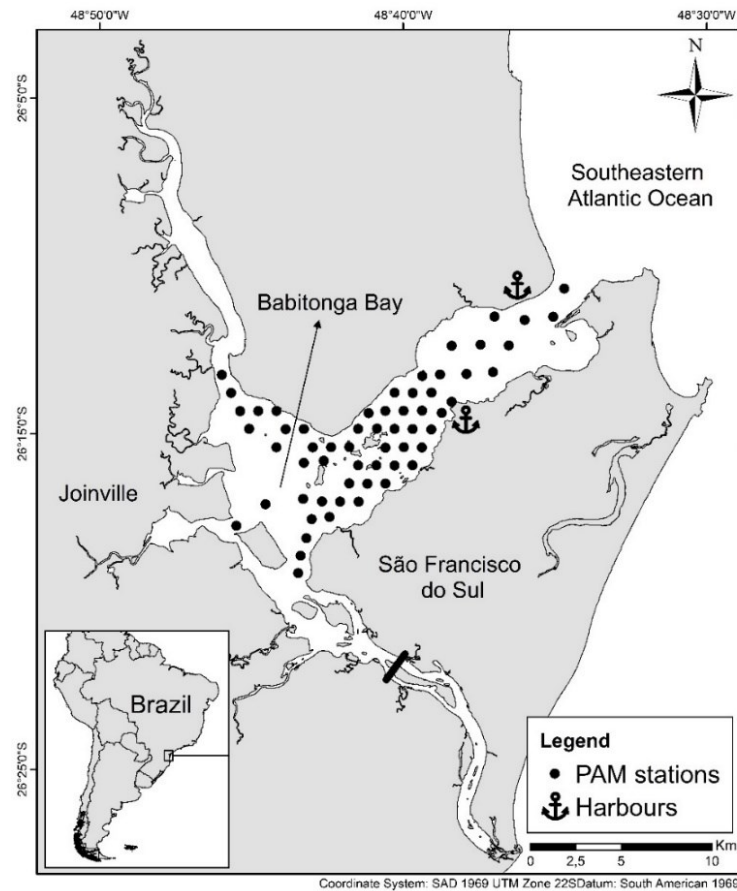


Figure 1: Location of the sixty passive acoustic monitoring (PAM) stations deployed in Babitonga Bay, southern Brazil, between June 26 and December 24, 2018.

### *Sampling methods*

Acoustic monitoring was performed using C-PODs (Chelonia Limited ©, UK), that are autonomous acoustic loggers designed to log trains of tone-like pulses between 20 and 160 kHz such as the narrow-band high frequency (NBHF) sonar click trains of the franciscanas (Melcón et al., 2012), but also the broadband clicks of the Guiana dolphins. Since the sonar clicks of the two species are so different, and no other dolphin species usually enter the bay, the risk of false species identification is virtually zero and hence these loggings can be used with a high degree of certainty and effectiveness (Paitach et al., 2016). The C-POD has an omni-directional hydrophone and an automated detection process and an approximate detection range of 400m. It can operate continuously for more than four months powered by ten D-cell alkaline batteries, and stores data on an SD card. The C-PODs were mounted inside custom-made “cages”, designed to protect them from being entangled in gillnets. These cages had a steel foundation and two PVC tube arches over the logger, causing

the least possible interference in the acoustic recording. The positions of stations were determined randomly within the survey area, adopting the criteria of minimum average depth of 4 meters; 800m spacing in inside bay areas; and 1,600m spacing in the access channel (Fig. 1). This difference in spacing was adopted considering the expectation in the intensity of use of the areas, according to prior knowledge (although limited) of the population distribution (c.f. Cremer et al., 2018).

Acoustic sampling was conducted from June 26 to December 24, 2018, with a varying number of days monitored at each station. Every 30 days approximately a subset of the cages was hauled and moved to new positions, each provided with another C-POD with fresh batteries and an empty SD card. Given that the detection threshold of C-PODs at 130kHz is well standardized by the manufacturer (Dähne et al., 2013), no significant variation in detection potential was expected between C-PODs, but to ensure that possible differences would not cause a systematic bias in the results, the devices were moved with each deployment, as recommended by Carlén et al. (2018). The relocations of the C-PODs were done with the aim to sample each position on average 30 days in the winter and 30 days in the spring. A total of 35 C-PODs were used in this randomized rotation, with a maximum of 20 C-PODs operating simultaneously. Ten subsets were defined with three station positions each, considering the closest possible positions for each group, and each of these positions was sampled at each exchange, ensuring that the distribution of the monitored points remained homogeneous in the area over the study period. After each period of data collection, the retrieved C-PODs were taken to the laboratory to upload data, change batteries and preparing them for the next exchange.

### *Data analysis*

The data on the SD cards were uploaded to a computer using the C-POD.exe software (Chelonia Inc., version 2.044). Using KERNO click train classifier, which is an automated classification algorithm in the analysis software, franciscana sonar click trains were identified. KERNO allows the identification of NBHF-type sounds with high robustness and lower levels of false positives than classifiers based on individual clicks (Dähne et al., 2013; Roberts & Read 2014.) Only click trains classified by KERNO as having a 'high' or 'moderate' probability of being generated by franciscanas were

included in the further analysis. After classification, an export function was used to extract the number of 'Detection Positive Minutes' (DPM; a minute with at least one franciscana click train) per hour; this measure was used as a proxy for franciscana presence. The data from the days of deployment and retrieval of the C-PODs were disregarded in the analyzes to avoid partial sampling on those days.

In some cases, acoustic sampling was totally or partially compromised by ambient noise, such as the sound of rain, moving bottom sand, or produced by living organisms such as shrimp and fish, all of which may generate pulsed sounds that can be logged by the C-PODs. To avoid data overload and, consequently, saturation of the memory card and battery consumption, the C-POD has a limited of 4,095 logged pulses per minute. After that limit, the logging is interrupted and only resumed in the following minute. In those cases, the data need to be carefully evaluated and, in some cases, disregarded. This assessment was made with the '*Detections and Environment*' tool in CPOD.exe and monitoring hours that reached the pulse-limited capacity and had some impairment in the sampling time were disregarded to ensure sampling homogeneity.

### *Habitat use*

For modelling of the franciscanas' habitat use on a fine scale, the intensity of their presence, expressed as DPM/h, as opposed to just presences and absences, was chosen to be modelled as a function of variables. This choice was made because DPM/h has more information on the heterogeneity of presences in different areas and times. The sampling unit adopted therefore were each hour of monitoring and Generalized Additive Models – GAM (Hastie & Tibishirani, 1990) were applied using the R software v.4.0.3 (R Core Team, 2020). GAMs are probably the most flexible and robust method currently available to model the complex relationships between marine mammal occurrence and habitat variables, which are not naturally expected to be linear (Wood, 2017). Because the data set to be modelled was large ( $n = 64,745$ ), models were fitted using function "bam" (mgcv R package; Wood, 2017) which allows relatively fast model fitting. Data inspection was performed to ensure that the data collected had the potential to present information to allow inference on habitat use. Using maps and graphics it was verified that the data was balanced in space and time. The negative binomial distribution showed the best fit and was adopted for modelling.



Several variables were obtained for each PAM station using ArcGIS Pro 2.3 (<https://www.esri.com>), with input data from morphosedimentary and topographic databases (provided by Vieira et al., 2008). We identified tidal conditions for each monitoring hour using the tide tables published by the Directorate of Hydrography and Navigation of the Brazilian Navy for the port of São Francisco do Sul. The DPM/h of the Guiana dolphin was also included as an ecological variable. The classification procedure for this species was similar that the adopted for the franciscana, however, using the “OD - *Other Dolphins*” classification, which allows the recognition of the Guiana dolphins broadband click trains (Paitach et al., 2016). All environmental and ecological variables explored in this study and their respective descriptions and categories may be seen in Table 1. All measures of depth were linearly correlated to each other, to slope measures and to geographic location, UTMX and UTM Y. Aspect and TCI were linearly correlated to each other. Correlated variables were not included in the same model. Concurvity, a measure of non-linear relation between smooth terms within a GAM, was also verified for a model including all variables available.

Table 1: Environmental and ecological variables used for modelling habitat use of franciscana dolphins in Babitonga Bay.

Variables	Range of values	Explanation and Categories
UTMX	723237 – 741747	Longitude in UTM.
UTMY	7086720 – 7101381	Latitude in UTM.
Hour.of.day	cyclic	24-hour circadian cycle.
Month	6 – 12	Months of the year, from June (6) to December (12).
Tide.state	categorical	Tidal cycles: flood, high, ebb and low.
Tide.type	categorical	Type of tidal amplitude as a function of the Sun-Moon gravitational conjunction: syzygy = full and new moons; quadrature = first quarter and third quarter moons.
Sg.DPM	0 – 60	Detection Positive Minutes of <i>Sotalia guianensis</i> per hour.
Season	categorical	Austral seasons: winter = from June 20 to September 21; spring = from September 22 to December 20.
Carbonate	categorical	Percentage of inorganic salts in the sediment within a radius of 400m: 0-10%; 10-20%; 20-30%; 30-40%.

Organic_matter	categorical	Percentage of organic matter in the sediment within a radius of 400m: 0-2%; 2-4%; 4-6%; 6-8%; 8-10%.
Sediment	categorical	Predominant texture of the bottom sediment within a radius of 400m: sand; sand with mud; mud with sand; mud.
Deep_max	2 – 22.3	Maximum depth in meters within a radius of 400m.
Deep_min	0.1 – 6.9	Minimum depth in meters within a radius of 400m.
Deep_mean	1.8 – 10.7	Average depth in meters within a radius of 400m.
Deep_range	1.5 – 18.1	Range between minimum and maximum depth within a radius of 400m.
Slop_mean	0.179 – 3.364	Average slope in degrees within a radius of 400m.
Slope_max	1.519 – 51.388	Maximum slope in degrees within a radius of 400m.
Aspect	59.096 – 258.092	Average direction of the slope in degrees from north within a radius of 400m.
TCI	0.0001 – 0.6613	Topographic complexity index calculated by multiplying scaled values for slope and aspect (Bouchet et al., 2015) averaged within a radius of 400m.
Margin_distance	146.5 – 1952.5	Distance in meters from the nearest margin: continent or island.
Nearest_margin	categorical	Geographic feature of the nearest margin: continent or island.

Preliminary models indicated that residual autocorrelation could be a problem. Correlation structures presented a cyclic pattern apparently with a peak every 24 units apart. To account for that, a 2-D smoother (Wood, 2017) for easting (i.e., “UTMX”) and northing (i.e., “UTMY”) combined, with a different tensor for each hour of the day, was added to all models. The two variables in conjunction represent the geographic location of the points sample, and that approach allowed the spatial heterogeneity in the data to be explicitly modelled as a function of time and space. Also, an AR1 (autoregressive function of order 1) error structure was added in the models. AR1 requires the specification of parameter  $\rho$  (the AR1 correlation parameter). For each model, the corresponding  $\rho$  was calculated by fitting models without correlation structure and measuring the first lag in the autocorrelation function (“acf”, R function). In the present modelling framework, the AR correlation structure corresponded to a GEE (Generalized Estimating Equations) approximation which, in practice, increased the uncertainty in the estimated smoothers; p-values for smooth terms became larger when compared to corresponding models without AR1 structure. Since the data set

was formed by time series, with observations representing repeated measurements for each location, a smooth term for each sampled PAM station as a random variable was used in all models.

Smooth functions were used to model the relationship between continuous variables and the response value. Except for the 2-D smoother for easting and northing combined with a tensor for each hour of the day and a cyclic spline for “Hour.day”, thin plate regression splines were used (R package “mgcv”; Wood, 2017). The dimension basis (i.e., parameter  $k$  on smooth functions, mgcv R package) was set to a maximum of seven for all tested smoother of variables, to both avoid overfitting and prevent smooth functions impossible to interpret. For variables “Aspect” and “Maximum Slope”, that parameter was further decreased to five, because preliminary modelling showed fitted smoothers of hard biological interpretation, i.e., with several peaks.

Model variables were selected in a forward step approach, based on minimum Akaike Information Criterion – AIC (Akaike, 1974): the initial model presented a 2-D smooth function for UTMX and UTM Y with a different tensor for each hour of the day, a smooth function for “Point” as a random variable, and a cyclic smooth term for “Hour of day”. In the first round of variable selection, models with only one additional variable were fitted, and the one presenting the smallest AIC score was considered as the initial model in the following step. In each step, only one additional variable was separately added to the model selected in the previous step. Those steps were repeated until the AIC could not be improved by the addition variables, and so the resulting model was retained as the most efficient to describe the variation in the presence of franciscanas.

### *Distribution*

The distribution analysis was performed through the interpolation of spatial data (“Kriging”), using the Geostatistical Analyst extension, option Geostatistical Wizard in ArcGIS Pro 2.3 (<https://www.esri.com>). Kriging is a geostatistical interpolation method that assumes that the distance or direction between the points in the sample reflects a spatial correlation that can be used to explain the variation in the surface (Oliver & Webster, 1990). Without imposing a priori environmental variables, the spatial autocorrelation of a specified number of points is modeled in semi-variograms which are used to estimate the output value for each location (Oliver & Webster, 1990).

In this study, Empirical Bayesian Kriging (EBK) was used, which automates the most difficult aspects of building a valid kriging model. Other kriging methods require that several projection parameters be adjusted manually, but EBK automatically calculates these parameters for each predicted location using a subset process and simulations of the data itself. EBK also differs from other kriging methods in that it takes the standard error introduced by the estimate of the underlying semi-variogram into account, considering the uncertainty when making predictions in unknown locations (Oliver & Webster, 1990; Krivoruchko, 2012). Semi-variogram parameters are estimated using restricted maximum likelihood (REML). This makes EBK more accurate with small data sets, valuing areas with higher values and reducing the value quickly with distance, which avoids overestimating restricted areas (Krivoruchko, 2012), as analyzed in the present study.

This different method was used to estimate the densities and project the distribution of franciscanas, instead of following the predictions of the top ranked habitat use model, because the objective was to identify general patterns of distribution associated with specific intervals of interest (seasons and periods of the day). Since the analysis of habitat use has a descriptive (and not predictive) purpose, including interactions between variables in the smallest space-time scale possible, the number of combinations between the factors included in the final model made it difficult to represent them on a few maps that allow relevant biological interpretation.

Two variables were separately used to run the kriging models and generate the distribution maps, with two distinct questions associated: 1) Detection Positive Hours (DPH) were used to identify the main areas of occurrence; and 2) adjusted Feeding Buzz Ratio (FBR) were used to identify important foraging areas. The DPH was obtained using the KERNO classifier and the same selection criteria as the DPM used in the analysis of habitat use, however with hours as period of interest (lower temporal resolution). The FBR is an index widely adopted to infer the frequency of the feeding behavior of echolocating odontocetes, where high repetition click trains (so called buzzes) are used as a proxy for the foraging/feeding behavior (e.g., Carlström, 2005; Madsen et al., 2005; Verfuß et al., 2009; Leeney et al., 2011). All click trains recorded throughout the study were exported using the '*full train details*' tool of the C-POD.exe program and were then classified as "buzzes", based on the criterion of Inter-Click Interval (ICI) <10ms (Carlström, 2005). Then, the FBR values were calculated as the

ratio between number of buzzes and number of non-buzz click trains (with ICI>10ms). After that, the FBR values were adjusted according to the intensity of the franciscanas occurrence in each area (i.e., multiplying the FBR by the DPH), generating a weighted metric of the importance of the feeding areas.

Two temporal scales were mapped: seasonal (winter and spring) and diel (dawn = 00:00-05:59, morning = 06:00-11:59, afternoon = 12:00-17:59, and night = 18:00-23:59). Although there is no clear biological reason for considering midday and midnight points of division, we understand that such a classification can allow a more complete understanding within the light and dark periods, and they can be more easily used for illustrating management strategies related to the time of the day. The average values of DPH and adjusted FBR were calculated separately for each day (for season maps), and for each period of the day (for diel period maps), and then averages for all sampled days were calculated for each PAM station. Days with less than 24 hours of data collected or periods of the day with less than 6 hours collected were disregarded to maintain sample homogeneity. Since the FBR values are adjusted, it is not possible a direct biological interpretation of the resulting values, so for representation in the maps the FBR values were grouped into classes of importance (moderate, high, and very high). For this, the resulting scale of values (without outliers) was divided into four equal classes, the lower part of the FBR values was disregarded (low importance), and the other parts were classified as 'moderate' = 3 to 6, 'high' = 6 to 9, and 'very high' > 9, for seasonal maps; and 'moderate' = 1 to 2, 'high' = 2 to 3, and 'very high' > 3, for diel period maps.

## **Results**

Out of the 60 monitoring stations planned in the study, 6 were not sampled in winter and 11 in spring, due to loss of equipment. No C-POD malfunctioned throughout the study. PAM stations were monitored for an average of 28 days (minimum 3; maximum 57 days) in winter and 24 days (minimum 2; maximum 91) in spring. A total of 66,350 hours of acoustic recordings were collected in 182 days, both seasons considered. After data filtering (i.e., screening and removing data with excess noise) 64,745 hours were analyzed, with franciscana dolphins recorded in 7,432 (11.5%) of that.

### *Habitat use*

The final habitat use model explained 51% of the deviance and fitted the data well, except for high values of the response variable. Despite the assumption of residual constant variance not being fully met, the negative binomial distribution ( $\theta = 0.092$ ) showed the best fit to the residuals. Residual autocorrelation was greatly reduced by the inclusion of an autoregressive function in the model, yet still mildly present (Appendix A). For that reason, the inclusion of variables in the final model must be interpreted carefully, especially for variables with lower significance (i.e., large p-values). Coefficients for factor variables and smooth functions included in the final model are presented in Appendix A.

The forward step variable selection resulted in the inclusion of smooth functions for intensity of presence of the Guiana dolphins ("SG.DPM") and maximum slope ("Slope.max"), in addition to the compulsory smother in the initial model (i.e., "Point" as a random variable; a 2D smoother for "UTMX" and "UTMY", with a tensor for each hour of the day; a cyclic smoother for "Hour.day") (Fig. 2). There was a clear cyclic pattern in the occurrence of franciscanas across the study area, indicating that in the areas where their occurrence was more intense, they were more likely to occur during the early hours of the day. Areas with high values of intensity of presence of Guiana dolphins were avoided by the franciscanas, but to a lesser extent they were tolerated. Franciscana seem to avoid steeper areas within the range of slopes in Babitonga Bay.

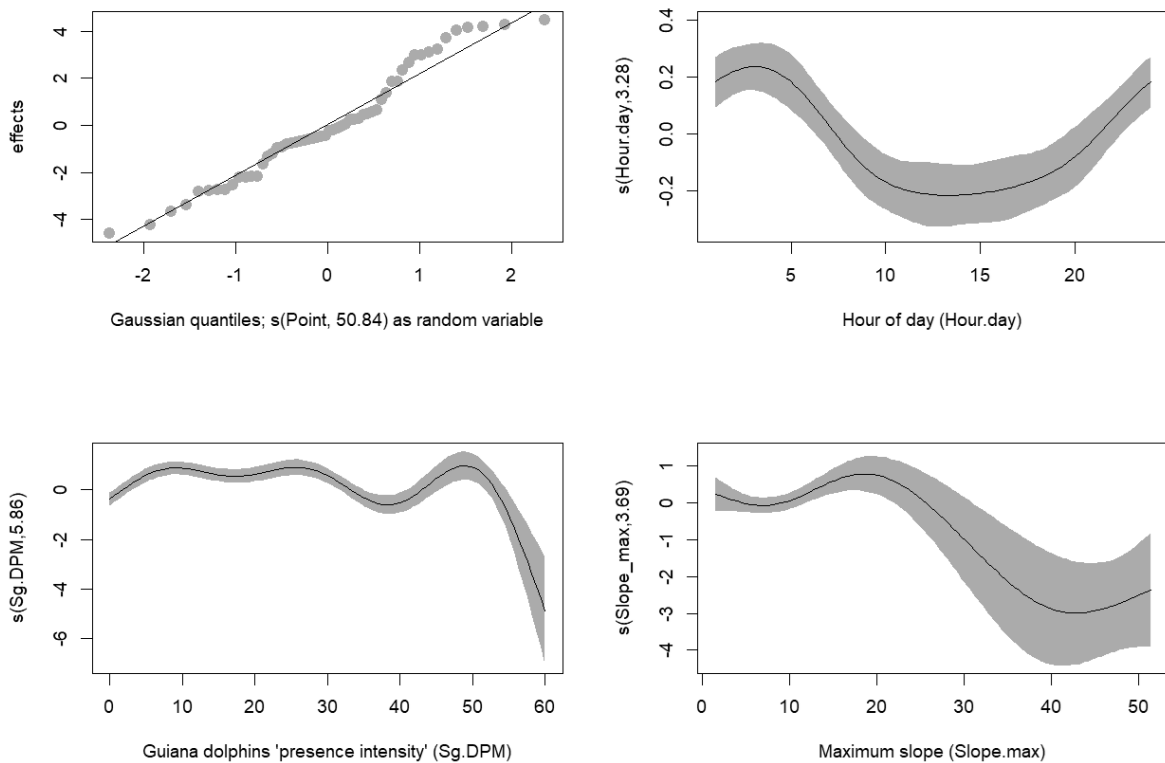


Figure 2: Smooth functions for variables included in the final model for habitat use of franciscana dolphins in Babitonga Bay. Degrees of freedom are shown inside parentheses.

The final model also included factor variables “Month”, “Sediment”, “Tide.type” and “Tide.state”. Because of multiple factor variables, partial effects for each combination of factor levels would require several plots. To make the results more interpretable, boxplots of values adjusted for the intensity of the presence of franciscana (Pb.DPM) for each selected factor variable are shown individually (Fig. 3). The presence of franciscanas seems to vary slightly over the months of study, but a clear seasonal pattern was not observed. The presence of franciscanas in Babitonga was associated with the granulometry of the bottom sediments, with a greater presence over sandy bottoms and less presence over mud bottoms. Despite contributing to improving the model AIC, it is not clear how tide variables were related to the variations of presence of franciscanas, since the levels were not precisely estimated, as indicated by large p-values (Appendix A).

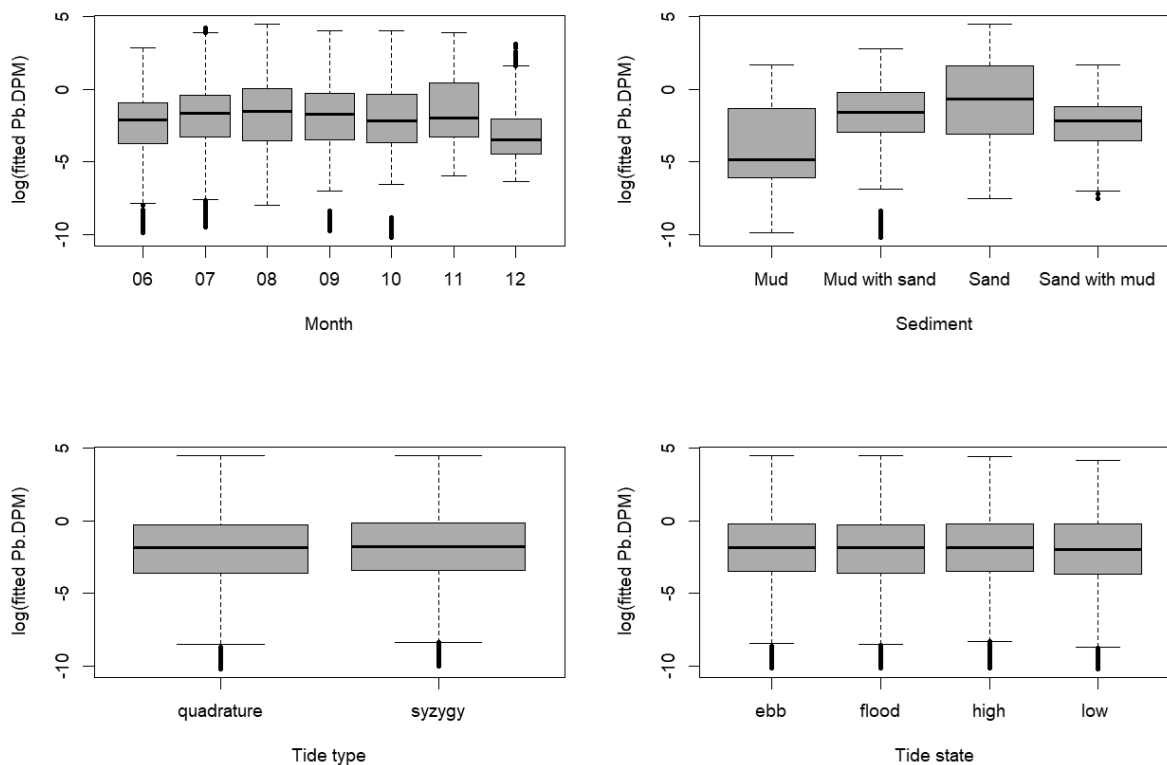


Figure 3: Boxplots for fitted values in the final model for different levels of the factor variables included in the final model for habitat use of franciscana dolphins in Babitonga Bay.

### *Distribution*

Predictive maps of occurrence and feeding areas were generated for each season (Fig. 4). Throughout the study, the distribution of franciscanas was predominant in the innermost region of the estuary, without a marked use of the open sea access channel. In the winter period the distribution was expanded, extending to the mouth of the Palmital River (northwest axis), the entrance to Saguacú Lagoon (west margin), and the Linguado channel (south axis), and further along the northeast margin of the bay. In the spring the distribution was predominantly in the central region of the bay, between the north and south margins. The area with the highest density in winter was located slightly towards the west than in spring, which remained closer to the north-central margin. The area between the north margin and the islands represents important franciscana feeding areas, both in winter and spring, but in winter the area between the islands and the south margin were also important for feeding. In winter, the northeastern margin, and the area close to the mouth of the Palmital River



(northwest axis) also appear to be areas used for feeding, which were not seen in the spring.

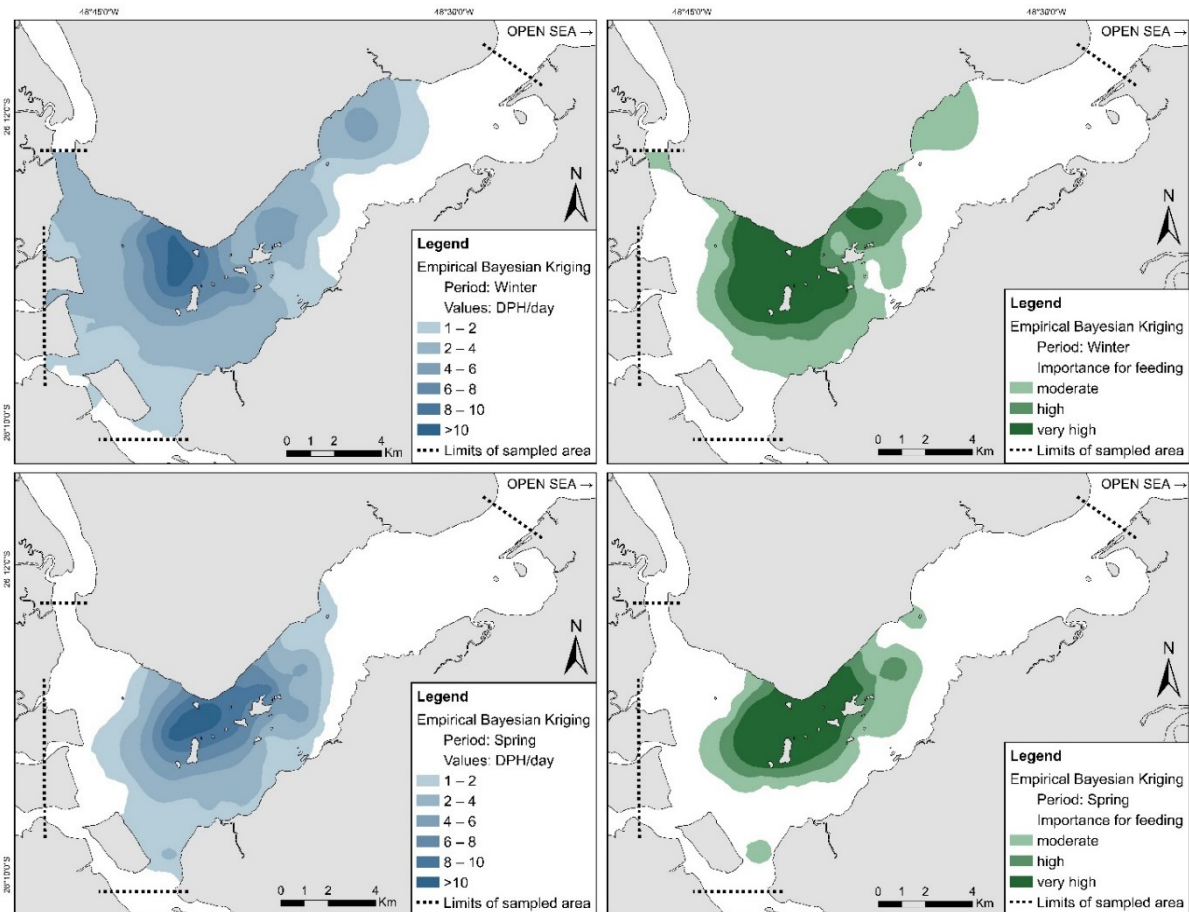


Figure 4: Occurrence (left) and feeding (right) areas of franciscanas in Babitonga Bay, in winter (top) and spring (bottom). (DPH/day = detection positive hours per day).

The areas of occurrence and of feeding for franciscanas varied throughout the diel periods in both seasons (winter: Fig. 5; spring: Fig. 6). The central area of the bay, between the islands and the north margin, remains the core area of franciscanas throughout the day, for both seasons, while the areas with less intensity of use vary throughout the day differently in each season.

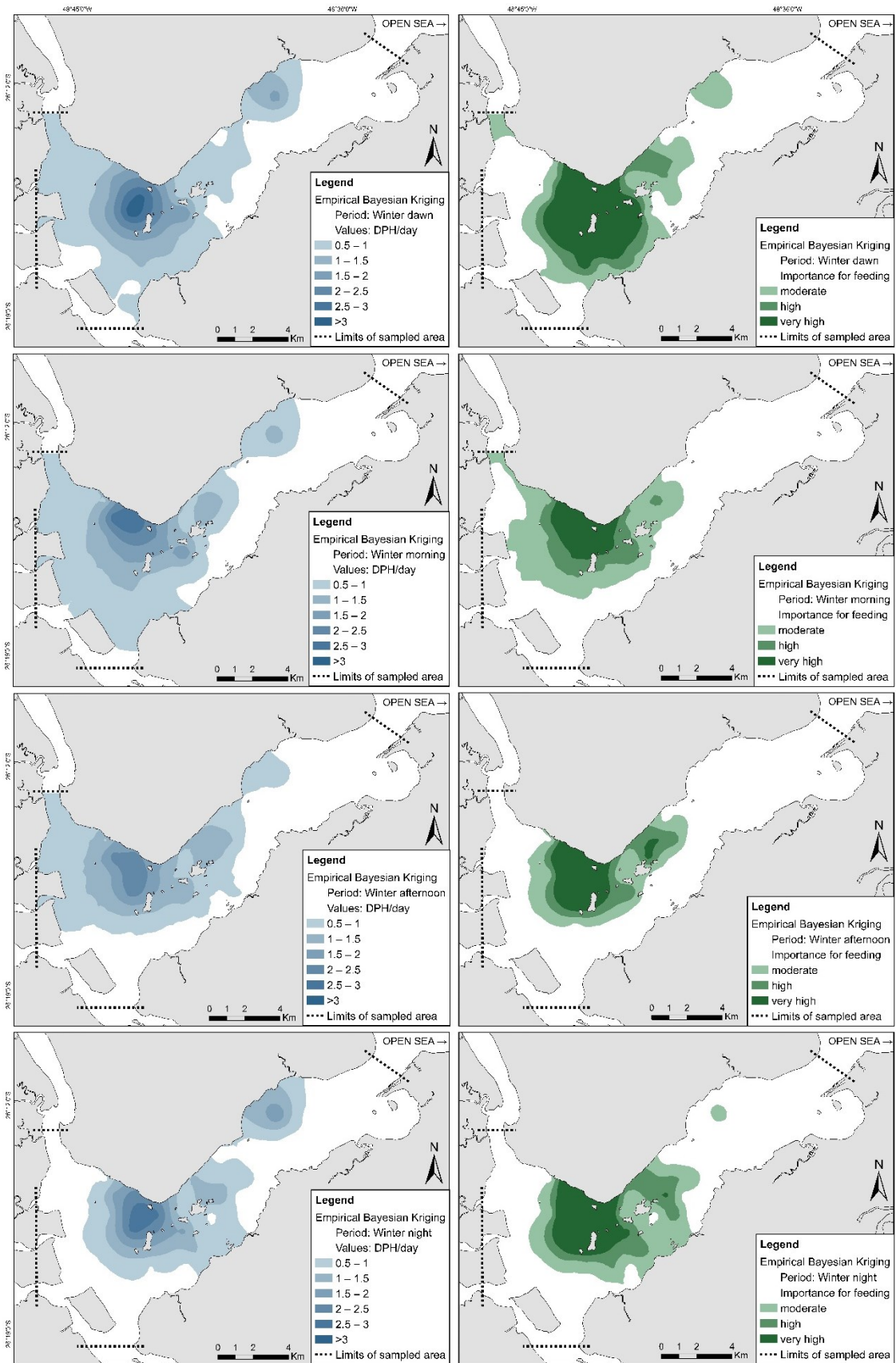


Figure 5: Winter diel occurrence (left) and feeding (right) areas of franciscanas in Babitonga Bay (from top to bottom: dawn, morning, afternoon, and night). (DPH/day = detection positive hours per day).

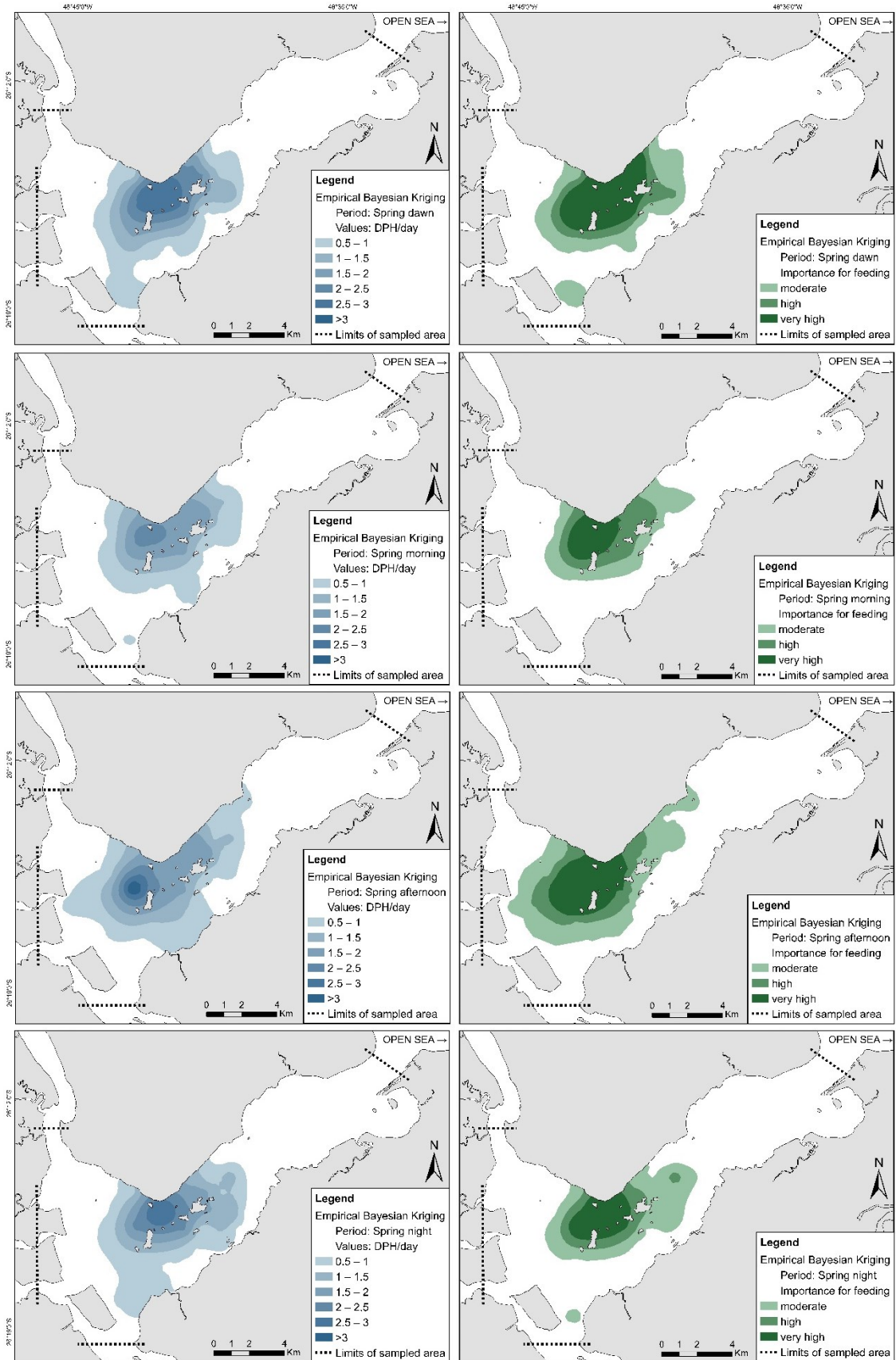


Figure 6: Spring diel occurrence (left) and feeding (right) areas of franciscanas in Babitonga Bay (from top to bottom: dawn, morning, afternoon, and night). (DPH/day = detection positive hours per day).

The areas used for feeding fluctuate throughout the diel periods. In winter, the feeding behavior is more concentrated near the core area during the morning and afternoon, and at night there is an expanse toward the south, a region known as Laranjeiras channel, which intensifies a lot at dawn (Fig. 5). In the spring the foraging areas are more restricted, with some oscillation in the east-west direction (Fig. 6). During the night there is an expansion towards the east, occupying the entire surroundings of the islands, and during the afternoon there is a movement in the opposite direction, with foraging in the innermost portion of the bay, up to its west margin, in an extensive area of shallow water and muddy banks (Fig. 6). In both seasons, the dawn period showed the biggest patches of 'very high' importance for feeding, indicating that the feeding behavior is more intense in this period, followed by the night in winter and the afternoon in spring (Fig. 5 and 6).

## **Discussion**

### *Passive acoustic monitoring: potential and limitations*

The PAM approach showed promising signs of a very valuable tool for investigating spatio-temporal patterns of habitat use and distribution of franciscanas in Babitonga Bay. Long-term passive acoustics studies have provided unique opportunities to explore heterogeneity in cetacean occurrence over seasonal and diel cycles that would have been impossible using visual methods (Verfuß et al., 2007; Van Parijs et al., 2009). PAM has been extensively used to study the distribution and habitat use of cetaceans (e.g., Verfuß et al., 2007; Pirotta et al., 2014; Carlén et al., 2018), however, for franciscanas this is the first systematic effort of this nature, and the C-PODs used proved to be extremely effective for the study of this species. The processing of the large data volume obtained (more than 66,000 hours) was only feasible through an automated procedure such as that of C-POD system, which, besides saving time also reduce the potential subjectivity bias of the researcher (Rayment et al., 2009).

In the present study, a key assumption is that the heterogeneity observed in the franciscana acoustic detections would reflect the density of these animals in the bay. That is an acceptable assumption according to comparative distribution studies using visual and acoustic detections (Verfuß et al., 2007). Failure to meet that could rise from when animals are present but not detected. However, similar to harbour porpoises

(*Phocoena phocoena*) in the wild, that click almost continuously and with maximum silent intervals of less than 15 seconds (Akamatsu et al., 2005), it is very likely that franciscanas continuously echolocate in the area. The habitat of the studied population is formed by estuarine waters of complex topography and very high turbidity with almost no visibility (Oliveira et al., 2006; Vieira et al., 2008). Furthermore, because this is a closed population (Dias et al., 2013; Cremer et al. 2018), numbers of acoustic detections in the study area are not expected to be influenced by emigration/immigration of individuals. A weakness in this study is that areas with an average depth of less than 4m (which can be even shallower at low tide) were under-sampled, because of either limited access or to avoid the risk of vessels collision. It is possible that in periods when lower detection numbers were recorded within the sampled area (i.e., where the water was continuously deeper than 4m), animals might be in those shallower areas.

In our analyzes we assume a homogeneous probability of detection of franciscanas by C-PDOs over space and time. It is known, however, that sound propagation may be influenced by spatial and temporal variations in the behavior of the dolphins (Verfuß et al., 2009; Leeney et al., 2011), and also by environmental conditions, such as water temperature and salinity (Richardson et al., 1995). There is a trade-off between the range and directionality of the sounds produced by dolphins during traveling and feeding behaviors (Tyack & Clark, 2000). Understanding how different behaviors can affect detection probability of franciscanas by PAM can assist the accuracy of future studies. Temperature and salinity affect the speed and absorption of sound in water (Richardson et al., 1995; Ainslie & McColm, 1998), but considering a low variation of these parameters in the study area we claim that this bias is negligible.

Another limiting aspect in the present study is the fact that C-PODs were deployed close to the sea floor. Areas in the bay with more irregular topography or the presence of rocks and slabs would increase the chance of acoustically shadowing the C-PODs. Acknowledging this bias, it was still decided to carry out the study in this way to avoid the entanglement of the equipment in drift fishing nets, which are commonly used in Babitonga Bay. In spite of the protective cages, entanglement in nets became a problem throughout the study, causing the loss of some units which compromised the sampling in some positions, a problem that was intensified during the spring and

forced us to finally terminate the study after six months. In future studies with this methodology, we recommend an extensive on communication effort towards and involvement of the fishing communities in the study area so that such incidents can be avoided or at least minimized, and if they still occur, that the PAM devices can be returned.

The two seasons sampled in the present study (i.e., winter and spring) were representative and strategic for the identification of priority habitats for the franciscanas. Studying their distribution in winter, the season of least availability of food (Cremer, 2007), allows the identification of the most critical places for feeding during a period of food scarcity; while spring represents the main birthing period for the population (Cremer et al., 2013). The protection of important breeding areas is essential for the conservation of small cetaceans, since the stages of young life are particularly vulnerable to species threats (Ross et al., 2011). Similarly, the protection of feeding areas is essential for small cetaceans, which are particularly vulnerable to environmental impacts that can reduce prey availability, due to their high food requirements and apex position in the marine food webs (Ross et al., 2011; Wisniewska et al., 2016).

### *Habitat use*

Acoustic detections of franciscanas allowed for modelling the habitat use in a fine spatio-temporal scale. Studies on the habitat use of franciscanas throughout its distribution are rare, partly explained by the difficulty of studying this species in the wild. Based on bycatch data, Danilewicz et al. (2009) observed that the distribution of franciscanas in Rio Grande do Sul reaches predominantly up to 30 meters in depth. That study, however, did not investigate whether water depth is an important factor related to the distribution of the species. More recently, Amaral et al. (2018) analyzed the influence of environmental variables to predict the spatial niche of franciscanas on a wide scale, verifying that depth and salinity can be limiting. Using aerial surveys of distribution over a wide area in southeastern and southern Brazil, Sucunza et al. (2019) observed 54 groups of franciscanas in waters with an average depth of 7.15 m. Although focused on a typical estuarine population, the novel fine-scale habitat use investigation presented here allow insights into important environmental features to the species in general.

There was a clear diel cyclic pattern in the occurrence of franciscanas across the study area. In the areas where their occurrence was more intense, they were more likely to occur during the early hours of the day (Fig. 3). That is possibly a reaction to environmental cycles, which modify the abiotic conditions of ecosystems, with biological organisms corresponding (Aschoff, 2013). Behavior patterns in response to diel cycles can be diurnal, nocturnal or twilight (Fernandez-Betelu et al., 2019). In coastal environments, tidal cycles can also cause environmental changes that can result in periodic movements of many species, including cetaceans (Gibson, 2003). Similarly to what happens in Anegada Bay, Argentina (Bordino et al., 1999), the franciscanas in Babitonga Bay were found to present movement patterns related to the tides, moving towards the mouth of the bay during ebb and in the opposite direction during the flood, following the current flow (Paitach et al., 2017). In the present study, although the tide was selected as an important factor for the habitat use, it was not possible to clearly identify a pattern. In fact, the tidal cycles effects on dolphin habitat use patterns can vary seasonally, and cetaceans appear to be less influenced by tides in open areas than in narrow channels (Pierpoint, 2008; Fernandez-Betelu et al., 2019).

The influence of environmental cycles on cetaceans is mainly a consequence of variations in the availability of their prey (Hastie et al., 2004). Predators must be able to take advantage of these temporal changes in the aquatic environment to optimize feeding success (Lin et al., 2013). However, the distribution dynamics between predators and prey are bidirectional—both sides in this relationship affect each other—so predators seek to optimize prey capture and prey correspondingly to reduce risk of predation (Trites, 2009; Becker & Suthers, 2014). Thus, the trade-off between foraging success and predator avoidance is decisive in the habitat use of a species (Trites, 2009). The Franciscanas have no frequent predators in Babitonga Bay, such as large sharks and orcas (Cremer, 2015; Gerhardinger et al., 2020). Therefore, the availability of prey is the main factor affecting its distribution. Franciscana is considered a species of generalist and opportunistic, preying on the most abundant small fish species in the environment (Cremer et al., 2012; Paitach, 2015). However, considering the bidirectionality of the predators-prey relationship mentioned above, it is expected that competing predators will affect each other, a subject that will be discussed below in the specific session on the sympatry between the franciscana and the Guiana dolphin.



Franciscanas seem to avoid steeper areas within the range of bottom slopes in Babitonga Bay. This may be linked to bathymetry also, since depth variables were not included because of their correlation with geographic location (i.e., UTMX, UTM Y). Holz (2014) observed the influence of the average depth on the distribution of this same population of franciscanas. Amaral et al. (2018) also identified depth as limiting the distribution of the species, without detecting slope effects. However, this study used wide spatial scales to assess the topographic slope of studied environments, which may have weakened the power of analysis of this variable. In two gulfs in southern Australia, Bilgmann et al. (2019) carried out modeling of habitat use of the bottlenose dolphin (*Tursiops truncatus*) and also observed an association between the presence of dolphins and a flat bottom topography.

The heterogeneous presence of franciscanas within Babitonga Bay was found to be associated with sand in the bottom sediment. The species occurs mainly in coastal regions, outside bays and estuaries, where sandy bottoms predominate, and although the Babitonga' population is exclusively resident in an estuarine environment (Cremer & Simões-Lopes, 2008), it may still maintain preferences related to the normal distribution of the species. The preference of sandy bottom areas by franciscanas has already been noted, especially in the spring, with an increase in the use of muddy areas in winter (Paitach et al. 2017). These findings were based on visual sightings, but they are now corroborated by the present study. However, when we look at the feeding areas at dawn and night, there was an increase in the use of muddy bottom areas, demonstrating that these areas are also important for the population in the spring. A very similar result was observed for the harbour porpoise in the Moray Firth, Scotland, where only sandy banks were identified as important feeding areas, without including time variables (Brookes et al., 2013). When the diel cycles were included in that investigation, then adjacent muddy areas were also found to be important habitats for them at night (Williamson et al., 2017).

Despite contributing to improving the model's AIC, it is not clear how many of the factor variables are related to the presence of franciscanas. Many levels were not precisely estimated, as indicated by large p-values. The modelling approach adopted here was adequate to provide insights into the environmental variables related to the occurrence of franciscanas within Babitonga Bay. However, model fit was not perfect, although optimal with the selected variables, and therefore, this ecological



investigation could greatly benefit from further modelling exploration, such as: inclusion of additional variables (e.g., prey availability), exploring more complex interactions between variables, modelling habitat use for specific periods (e.g., additional seasons), exploring models that accommodate more complex autoregressive structures, etc.

### *Sympatry with the Guiana dolphin*

The intensity of presence of Guiana dolphins was identified in the models as the main available variable related to habitat use of franciscanas in Babitonga Bay. Franciscanas seem to tolerate their presence to a certain degree, but avoid areas at times when the presence of dolphins is relatively intense. Cremer (2007) observed a high overlap in the spatial niche of these populations, but with no competition for interference between them (*sensu* Bearzi, 2005), which has been reaffirmed over the years (Cremer et al., 2018). Analysis of stomach content point to a high degree of sharing the prey species between franciscanas and Guiana dolphins in Babitonga Bay (Cremer et al., 2012, Paitach, 2015). It is interesting to note, however, that although both species have wider amplitudes of the trophic niche in the cold months, when the prey availability is lower (Cremer, 2007), there is a decrease in the trophic overlap between them, attenuating the effects of competition (Paitach, 2015). Different ecological processes may be involved in the niche partition between ecologically similar species living in direct sympatry, such as differences in behavior patterns and diet, differences in habitat use and temporal segregation in the use of resources (Bearzi, 2005).

Examples of sympatric dolphins are not rare, Méndez-Fernandez et al. (2013) analyzed the niche overlap in five small cetacean species in the Iberian Peninsula, concluding that a process of spatial-temporal partition of the niches is what enables the sympatry, because the species segregated their areas of distribution during the seasons with less resources available and overlapped again during periods of upwelling. From a temporal point of view in the use of resources, the harbor porpoise (*Phocoena phocoena*) and Dall's porpoise (*Phocoenoides dalli*), in the Salish Sea, near Seattle, Canada, share feeding areas and have an extremely high overlap in diet composition (almost 90%), but the harbour porpoise feed mainly during the day, while Dall's porpoise mainly feed at night (Nichol et al., 2013). In Bay of Biscay, France, Spitz

et al. (2006) suggested that the high spatio-temporal overlap of feeding behavior between the bottlenose dolphin (*T. truncatus*) and the harbor porpoise is the main explanation for the agonistic interactions frequently observed between them. In Cleveland Bay, the Indo-Pacific Humpback dolphin (*Sousa chinensis*) and the Australian Snubfin dolphin (*Orcaella heinsohni*) have a high degree of spatial overlap and similarity in their behavioral activities in space and time, leading Parra et al. (2006) to believe that the selection of fine-scale habitats between these species is the main mechanisms that promote their coexistence, even though agonistic interactions are occasionally observed. Considering the high overlap of the trophic and spatial niches, and the absence of agonistic interactions between franciscanas and Guiana dolphins in Babitonga Bay (Cremer et al., 2018), we suggest that the main factors that make possible the coexistence of these two species are fine-scale differences in the habitat use with temporal segregation in the foraging/feeding behavior. A fine-scale study of Guiana dolphin's habitat use and other analytical approaches that integrate different spheres of the realized niche of both species, would assist in elucidating that question.

#### *Spatio-temporal patterns of occurrence and feeding*

The distribution of the franciscanas was predominant in the central region of the bay, with greater dispersal in winter than in spring, with virtually no detections in the connection channel with the open sea in either season. This corroborates conclusions from previous studies on the distribution of this population, derived from visual observations (Cremer & Simões-Lopes, 2008; Cremer et al., 2018). The Guiana dolphins also have larger areas of distribution in seasons with less prey availability elsewhere (Wedekin et al., 2010) and in Babitonga Bay (Cremer et al., 2011). However, we observed a much more acute use of the center-south portion of the bay in relation to what was observed in previous studies. In fact, franciscana preys are known to concentrate in the region of the bay (Cremer, 2007; Paitach, 2015). In the present study, the central-southern portion of the distribution area was most frequented at night and at dawn, and mainly for feeding purposes. The innermost muddy banks in the western part of the estuary are also used for feeding, especially on spring afternoons. Since foraging is expected to intensify when/where individuals can maximize their food intake (Pirodda et al., 2014), cyclic of use of such areas can be related with the distribution of the Guiana dolphin. Not surprisingly, the central-southern portion of the

bay is considered the core area of Guiana dolphin distribution (Cremer et al., 2011; Cremer et al., 2018).

The present study is the first to analyze the distribution of franciscanas throughout the day and to preliminarily identify the main feeding areas in Babitonga Bay, on seasonal and diel scales. Multiscale approaches have been shown to be very useful in studies of distribution of highly mobile species that explore dynamic habitats (González-García et al., 2018), such as the characteristics of the environment and species dealt with here. In particular, the association of foraging with specific environmental characteristics must be considered in the management of anthropic disorders (New et al. 2013; Pirotta et al., 2014). In the present work, the distribution analyzes were descriptive and did not aim to relate the foraging behavior with environmental characteristics, however such an approach would be desirable in future studies.

#### *Implications for management and conservation*

Some anthropogenic activities in Babitonga Bay constitute direct or indirect threats to the survival of this population of franciscanas, such as the overfishing, water pollution, intense vessel traffic and port building and maintenance activities (Cremer, 2007; Paitach et al., 2019). Above all, the cumulative effects of the different anthropogenic impacts on coastal environments put aquatic mammal populations under strong pressure and are often neglected by environmental authorities (Cremer, 2007; Azevedo et al., 2017; Herbst et al., 2020). In the study by Tardin et al. (2020) on Guiana dolphins, the distances from seafood farms and fishing grounds were modeled explicitly, and the results indicated that these activities played a key role in determining the habitat use of these dolphins.

The establishment and operation of big ports represent a major threat to marine biodiversity, causing acute disturbances and a chronic decrease in environmental quality (Domit et al., 2009). Underwater blasting work, periodic dredging of the seabed and intensification of sea traffic result in suspension of sediments and thereby increase the bioavailability of contaminants, oil blades on the surface, increased underwater noise and the risk of collision between cetaceans and vessels, among other impacts that disrupt the natural communities, reduce the availability of prey and compromise

the entire health of the ecosystem (Domit et al., 2009; Jefferson et al., 2009; Herbst et al., 2020). It is known that franciscanas avoid areas with known higher levels of underwater noise in Babitonga, which are close to the existing ports (Holz, 2014). It was observed that after activities requiring the use of dredges, pile drivers and other heavy machinery, the Guiana dolphins abandoned the São Francisco do Sul port inlet for years (Cremer et al., 2018). Several new ports are planned in Babitonga Bay, of which at least three in the areas identified as critical habitats for the franciscanas. In light of the results presented here, some key aspects must be considered in environmental impact studies, such as: 1) the importance of franciscana feeding areas as critical habitats for their survival; 2) the impacts caused to the population of Guiana dolphins can also result in fundamental consequences for the franciscanas, considering the competitor-predator-prey relationship; 3) the exclusion of artisanal fishing areas, due to the delimitation of the vessels' maneuvering areas in ports, will cause an intensification of fishing in the center-north portion of the bay, increasing the bycatch risk of franciscanas; and 4) the cumulative and potentially synergistic impacts caused by the new ports added to the ports already operating in the territory.

In Babitonga, dredging for the extraction sand from the bottom is constant throughout the year (Herbst et al., 2020), and the uncontrolled removal of this substrate can also be an indirect threat to the franciscanas, as indicated by the association between the species' habitat use and this type of substrate found in our study. The operation of dredgers also generates substantial noise, which can be impactful for franciscanas (Holz, 2014). The licensing of new sand extraction areas needs to take this potential negative impact into account and adopt the necessary mitigation measures, such as avoiding critical franciscana habitats.

The franciscana bycatch in the artisanal fisheries, although not so frequent in Babitonga Bay, still represents a severe threat considering that the removal of any individual from this small population can be critical to its sustainability (Pineiro & Cremer, 2003; Cremer et al., 2018). Distribution and foraging maps presented here can guide a participatory construction and implementation of exclusion zones in periods of most intense use. Unfortunately, there is no efficient mechanism for fisheries management in the territory, making it difficult to implement strategies to prevent accidental captures, such as the implementation of fisheries exclusion areas or the use of acoustic deterrent devices on nets (FAO, 2021).

In recent years, many Marine Protected Areas (MPA) have been designated with the aim of managing human activities for the protection of marine mammals (Hoyt, 2012). Many of these MPA's, however, have static delimitations, and prove to be inefficient in covering the entire areas of distribution of cetaceans and hence guaranteeing their protection (e.g., Wedekin et al., 2002; Castro et al., 2014; Santos et al., 2017; Tardin et al., 2020). More dynamic approaches with flexible spatial and temporal limits of protection areas have been recommended for mobile species such as dolphins (Hoyt, 2012). Dynamic ocean management guidelines (sensu Hazen et al., 2018), which determine seasonal adjustments in the types, intensities and distribution of human activities permitted in the MPAs, may be a more effective alternative for the conservation of cetacean ecosystems. However, there are many difficulties for the creation or effective implementation and maintenance of MPA's in Brazil, such as lack of staff and funding, deficient or absent interinstitutional governance, excessive bureaucracy, and lack of political incentives for any significant change (Gerhardinger et al., 2011). The proposal to create an MPA in Babitonga Bay has been underway in the responsible agency (i.e., Chico Mendes Institute for Biodiversity Conservation – ICMBio, the Brazilian Ministry of the Environment's administrative arm) for more than ten years without any major advances (Paitach et al., 2019; Herbst et al., 2020).

Finally, the use of C-PODs has provided to be an essential strategy to get information for managing species and populations of low density of cetaceans worldwide, such as the vaquita (*Phocoena sinus*) (Jaramillo-Legorreta et al. 2016), the Maui dolphin (*Cephalorhynchus hectori maui*) (Rayment et al. 2011), and the Baltic harbour porpoise (Carlén et al., 2018). The present study provides novel insights on the habitat use and the distribution of the critically endangered franciscana population in Babitonga Bay. Habitat modeling made it possible to identify critical habitats and thereby indicate the main management requirements necessary for the conservation (sensu Cañadas et al., 2005). The challenge ahead is to identify effective ways to integrate this information into relevant public policies for the fisheries and coastal zone management, reconciling the ecological needs of the franciscana with the interests of the various social actors.

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### **CAPÍTULO 3 – Assessing effectiveness and side effects of “seal safe” pinger sounds to ward off endangered franciscana dolphins (*Pontoporia blainvillei*)**

#### **Abstract**

The franciscana (*Pontoporia blainvillei*) is the most endangered dolphin in the western South Atlantic Ocean due to bycatch in gillnets. Our goal was to test the efficiency of a "seal safe" (i.e., 50 to 120 kHz frequency spectrum) acoustic deterrent device (Banana Pinger, Fishtek Marine Ltd) to ward off franciscanas, as well as possible side effects of habituation and habitat exclusion. We deployed the pinger within a grid of click detectors (C-POD, Chelonia Limited) in Babitonga Bay, Southern Brazil, and acoustic detections were used as a proxy for presence and response to the pinger. The presence of franciscanas next to the pinger and at 100 m away decreased 19.4% and 15.4%, respectively, when the pinger was switched on, indicating that the franciscanas moved away from the pinger. This avoidance response could not be seen at 400 m away. No habituation effect was noted at any distance. There was a slight gradual decrease in detections over the days at all distances, which is probably related to seasonal variations in the population's habitat use rather than habitat exclusion, but this requires attention in future studies. The “seal safe” pinger sounds effectively ward off franciscana and thus has the potential to reduce bycatch.

Keywords: bycatch mitigation; acoustic deterrent devices – ADDs; Banana pinger.

#### **Introduction**

The restricted distribution and the high accidental mortality rates in gillnets (bycatch) make the franciscana, *Pontoporia blainvillei* (Gervais & D'Orbigny, 1844), the most endangered small cetacean in the western South Atlantic Ocean (Secchi, 2010). Between September/2015 and March/2020 a daily beach stranding monitoring program covering approximately 700km was conducted along the south-eastern and southern Brazil (referred as FMA II, sensu Secchi et al., 2003), and 2,428 dead franciscana dolphins were recorded (Barreto et al., 2020). Based on skin marks, almost all of them seem to have been caught in fishing nets and dumped by the fishermen (Barreto et al., 2020). The total abundance of franciscana in this area was estimated to be 6,827 (CV = 0.26) individuals (Sucunza et al., 2019). The observed mortality is alarming and unsustainable, especially considering that only a small fraction of the animals that die in the nets is believed to end up stranded on the beaches (Prado et al., 2013). In the extreme south of Brazil (Rio Grande do Sul, FMA III), for example, it was estimated that only 10% of the bycaught franciscanas end up stranded on the beaches (Prado et al., 2013). This scenario has prompted the Brazilian government to move the franciscana from the category "vulnerable" to "critically endangered" in the

national list of endangered species in just ten years (MMA, 2014). On a global scale, the species is still listed as “vulnerable” in the IUCN red list of threatened species, due to the lack of abundance information in time series that make it impossible to consistently infer population trends in most of the species’ range (Zerbini et al., 2017).

Available data indicate that the main fishing gear responsible for the franciscana bycatch is the bottom fixed gillnets, although it also occurs in surface fixed gillnets and eventually in drift gillnets (Bertozzi & Zerbini, 2002; Frizzera et al., 2012; Pinheiro & Cremer, 2003; Secchi et al., 2003). There are some regulations for gillnet fisheries in Brazil that can assist in preventing bycatch, including limitations on the length and height of the nets, restrictions on areas and periods for fishing and mechanisms for monitoring the fishing fleet. However, the regulations are most likely inefficient in reducing bycatch due to the low compliance followed by a lack of enforcement by authorities (Di Tulio et al., 2020). The artisanal fishing activities along the coast where the franciscana occurs have several local specificities regarding the characteristics of fishing gears, vessels, periods of activity and target species (Bertozzi & Zerbini, 2002; Secchi et al., 2003). There is also a fierce conflict between the artisanal and industrial fishing sectors, with bycatch of franciscana by both (Secchi et al., 2003). Strategies adaptable to the different conditions and realities of fishing communities should be considered for mitigating bycatch.

Among bycatch reduction strategies, acoustic deterrent devices, or “pingers”, should certainly be considered as an important option for some regions, especially because, if they can be proven effective in mitigating bycatch of the target species and implemented properly, pingers can have an immediate effect in reducing mortality (FAO, 2021). They are small battery-powered devices, designed to be attached to fishing nets, which transmit deterrent sounds that will ward off small cetaceans from the vicinity of the nets, thereby reducing the risk of entanglement (Dawson et al., 2013). This is one of the most effective and worldwide-adopted strategy for reducing bycatch in gillnets (e.g., Carretta & Barlow 2011; Palka et al. 2008). The frequency range of the sounds emitted by traditional pingers differs. Several of them generate multi-harmonic sounds extending from 20 kHz to above 100 kHz, but with the main energy in the 40-80 kHz range (Dawson et al., 2013). Pingers are relatively inexpensive—with caveats that will be better discussed—and easy to implement, but conclusive evidence that

they work for a particular species without significant side effects must first be produced (FAO, 2021).

Two potential side effects of acoustic deterrents are habitat exclusion and habituation (Dawson et al., 2013). Habitat exclusion is when the target animals permanently, or for a long-term period, abandon the area where pingers are used, which may represent a significant negative impact on some populations, particularly those with coastal and restricted distribution (Dawson et al., 2013; Kyhn et al., 2015), such as franciscanas. Habituation is the progressive increase in the tolerance of the target species to the pinger sounds until reaching a point where the deterrent effect is no longer detectable, and thus potentially—but not necessarily—losing its efficiency in reducing bycatch mortality (Dawson et al., 2013; Kindt-Larsen et al. 2018; Kyhn et al. 2015).

The efficiency of pingers for franciscana bycatch reduction was tested for the first time in Argentina and demonstrated a highly significant effect (Bordino et al., 2002). However, this study tested a low frequency pinger (i.e., 10kHz sounds with regular 4s intervals – Dukane Netmark 1000), and it was rejected by the local fishermen since these pinger sounds also attracted pinnipeds, especially the South American sea lion (*Otaria flavescens*) due to the so called “dinner-bell” effect (Bordino et al., 2002; Carretta & Barlow, 2011). The pinnipeds associated the sounds with easily accessible fish entangled in the nets and, besides removing the fish, they destroyed the nets in the process, and often causing damage to the remaining fish, decreasing their commercial value; they also become more likely to be themselves bycaught (Bordino et al., 2002; Königson & Hagberg, 2007). The South American sea lion is the pinniped most involved in depredation conflicts with fishing along the distribution of franciscanas, especially in Argentina, Uruguay, and southern Brazil, but eventually these conflicts have also been reported with the fur seal (*Arctocephalus australis*) (Pont et al., 2016). Therefore, Bordino et al. (2002) stressed the importance to avoid the pinnipeds depredation by using alarms with higher frequencies, above the hearing range of the sea lions, so-called “seal safe” pingers.

The experimental Banana Pinger (Fishtek Marine Ltd, UK) tested in our study was designed to be inaudible to grey seals (*Halichoerus grypus*) and harbour seals (*Phoca vitulina*), species often involved in fishing nets depredation, with the low frequency cut-off raised in order to make it “seal safe”. In grey and harbour seals the



hearing extends beyond 20kHz but is poor above 60kHz (Cunningham et al., 2014; Cunningham & Reichmuth, 2016). For California sea lion (*Zalophus californianus*) and the northern fur seal (*Callorhinus ursinus*), which are two of the few otariids for which audiograms have been obtained, the best underwater hearing sensitivity extends to 20kHz and 40kHz, respectively, and above this the sensitivity drops sharply (Cunningham & Reichmuth, 2016; Nedwell et al., 2004; Reichmuth et al., 2013). Assuming that *O. flavescens* and other pinniped species involved in depredation—and whose distributions overlap with that of the franciscanas—have similar hearing range as the species mentioned above, the lowest frequency components (ca. 58 kHz) of the experimental Banana pinger should be audible to these species only at very short distances ( $\leq 25\text{m}$ ) (c.f. Königson et al., unpublished data), and thus would not provide useful acoustic cues allowing the pinger to act as a “dinner bell”. But it is still necessary to keep attention on this issue and test this assumption in due time.

The aim of our study was to test the deterrent range and possible habituation and habitat exclusion side effects of the “seal safe” Banana pinger for franciscanas, using passive acoustic monitoring (PAM) devices. These devices log the franciscanas’ echolocation sounds, which are used as a proxy of their presence and as an indirect measure of their behavioral response to the pinger sounds (e.g., Kindt-Larsen et al., 2018; Kyhn et al., 2015; Omeyer et al., 2020). This approach allows for testing the effects of a pinger without any risk of dolphin mortality, since no fishing nets are used in the experiment, and is therefore suitable for initial tests before testing and implementing pingers in commercial fishery.

## Methods

We conducted a controlled exposure experiment between April 11 and June 14, 2018, totaling 65 days of experiment. The study was conducted in Babitonga Bay ( $26^{\circ}02'-26^{\circ}28'S$  and  $48^{\circ}28'-48^{\circ}50'W$ ), in southern Brazil (Fig. 1). The bay is a shallow estuary, with an average depth of 6 m, but in the only channel connecting the bay with the Atlantic Ocean, it can reach a depth of 28 m. Although it receives the input of several rivers, the estuary is considered physically and chemically homogeneous (IBAMA, 1998). The water depth at the test site (see Fig. 1) was an average of 6.5 m.

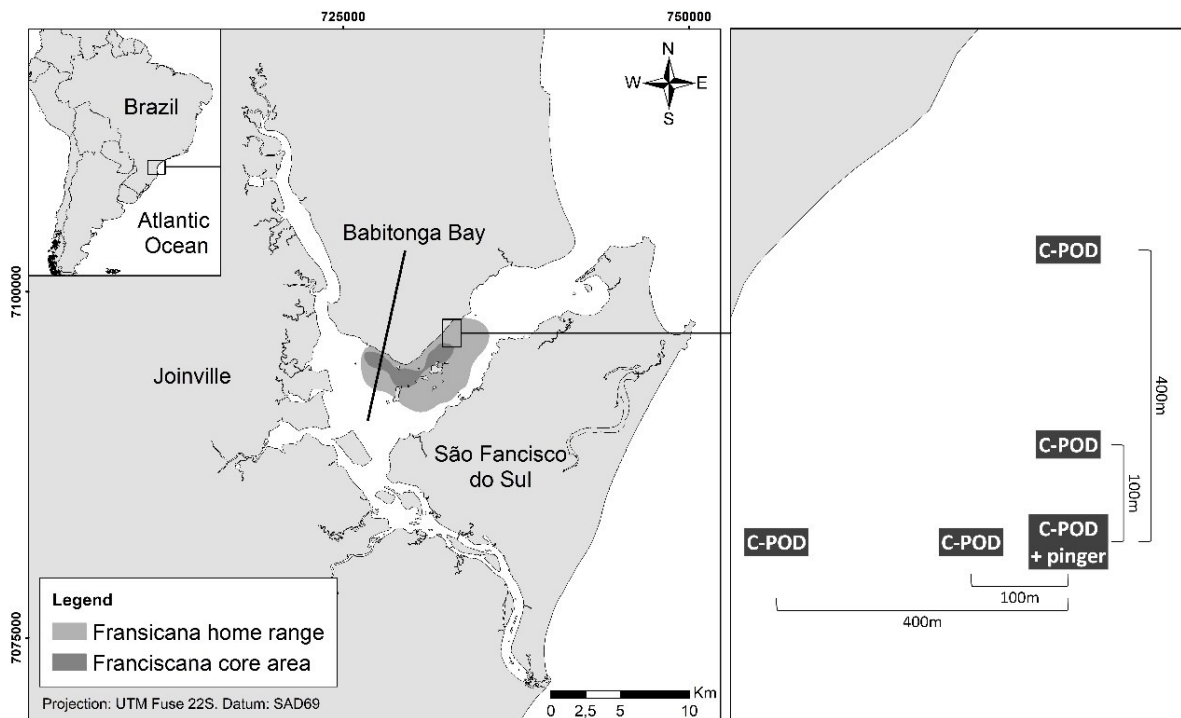


Figure 1: Map of Babitonga Bay, in southern Brazil, with the home range and core area of resident franciscana dolphins (*Pontoporia blainvillei*) (c.f. Cremer et al., 2018), and schematic drawing of the positions of the static acoustic monitoring devices (C-POD, Chelonia Limited ©) in the experiment carried out to test the deterrent effect of an experimental Banana Pinger (Fishtek Marine ©).

Babitonga Bay is home of the only known franciscana population that resides exclusively in an estuarine environment, with an estimated abundance of 50 individuals (CV = 0.29) and average group size of 5 ( $\pm 3.62$ ) individuals (Cremer & Simões-Lopes, 2008). The place chosen to perform the pinger experiment was in the eastern margin of the franciscana home range (Figure 1), to alleviate possible negative effects of the pinger on the core distribution of this population.

The Banana Pinger (Fishtek Marine ©, UK) used in this study is an experimental version that transmitted deterrent sounds in 22-hour on/off cycles, different from the commercial version that stays on constantly when it is under water. Except for this pattern of turning on and off in cycles when submerged, all other features of the experimental version are the same as the commercial version. The sounds lasted 300 ms and were multi-harmonic and frequency modulated with semi-randomized 4-12 s intervals, with a frequency spectrum ranging from 50 to 120 kHz, and with a source level of 145 dB  $\pm$  3 dB at 1 m. The pinger was deployed vertically (to be horizontally omnidirectional) in the center of an L-shaped grid with five dolphin echolocation logging

devices, called C-PODs (Chelonia Limited®, UK; Fig. 1). The C-POD is designed to log trains of tone-like pulses such as the narrow-band high frequency – NBHF sonar click trains of the franciscana (Melcón et al., 2012). As the franciscana is the only species in the study area with this stereotyped NBHF biosonar, the risk of false species identification is virtually zero and hence these loggings can be used with a high degree of certainty. These loggings were used as a proxy for the presence of franciscanas and, consequently, their response to the pinger; if no click trains were logged, it was assumed that the animals had moved away. The detections are also determined by how the beam is pointed considering that the echolocation sonar is highly directional (Tyack & Clark, 2000), but considering the time window used for each sample unit (1 h), it is very unlikely that a franciscana present in the area will remain for all this time without echolocating towards the C-POD at least once. One C-POD was deployed together with the pinger in the center of the L-shaped grid. Along each direction of the grid legs, one C-POD was deployed at 100 m—which represents half the distance between pingers for fishing nets recommended by the Banana Pinger manufacturer and as stated in the EU Regulation No. 812/2004—and one at 400 m from the center of the grid. All C-PODs were periodically substituted (approximately every 20 days) to upload data and change batteries.

We detected the franciscana presence following a procedure similar to that applied for *Phocoena phocoena* by Omeyer et al. (2020), using the analysis software CPOD.exe (Chelonia Inc., UK, version 2.044). All sonar click trains that had characteristics similar to those of the franciscanas were identified using the modal frequency range setting of 120–145 kHz and a click rate in the range of 15–100 per second. We used this manual classification criterion because the automatized KERNO classifier of CPOD.exe may fail to recognize NBHF click trains in the presence of pinger sounds (false negatives) and therefore would give a false picture of the franciscanas' response to the pinger sounds. It was expected that this weaker classifier resulted in a substantive rate of false positives (caused mainly by surface and sediment transport noise), but since this would be independent of the pinger status, it would not reduce the validity of any positive pinger effects found (Omeyer et al., 2020). When this classification process was done, an export function was used to extract the absence/presence (0-1) of franciscanas, where franciscanas were categorized as either absent (0) if no click trains were recorded or present (1) if one or more click trains

were recorded in each hour of monitoring for each C-POD. To find the pinger sounds, the automatized KERNO classifier was set to accept sonar sound sources and extracting detection positive minutes per hour (DPM/h) from the C-PODs at the zero-meter position, it was possible to identify the exact minute when the pinger turned on and off. The pinger on cycles always had 60 or close to 60 DPM/h, whereas the pinger off cycles had very few or none. The timing of the pinger on/off cycles was then applied to the data of the other positions. Intermediate hours between the on and off cycles, in which only part of the pinger signal was observed, were removed from the analyzes to maintain uniform sampling intervals.

To statistically analyze the effects of the pinger sounds on the behavior of the franciscanas, we used a Binomial Generalized Linear Model with a logit link function (Zuur et al., 2009), in the MASS package (Venables & Ripley, 2002), using the R software v.4.0.3 (R Core Team, 2020). The pinger was systematically switched on and off in 22-hour cycles during the entire experiment and therefore we used the “*pinger*” status as a categorical variable. To investigate how far away from the pinger the presence of franciscanas was affected, we included in the analyses the variable “*distance*”, categorically grouped in the classes 0, 100 and 400 m, and tested its interaction with the “*pinger*”. Although for each pingers distance we have samples in two directions (north and west), the directions were treated as replicates and not as a variable of interest in the study, since the objective here was to analyze the effect range and not related differences to habitat use. We also investigated how the presence of franciscanas was associated with “*monitoring days*”, which was used as a continuous variable from the beginning of the experiment (day 1) until the end of the experiment (day 65). We considered the interaction between “*monitoring days*” and “*pinger*” to test for possible habituation and habitat exclusion effects: a significant increase of detections over consecutive days correlated with the periods with the pinger on would indicate habituation, while a gradual decrease correlated with periods with the pinger off may be indicative of a lasting pinger effect and potential habitat exclusion. We also considered the variables average daily “wind speed”, which can be a source of noise and influence detections, and “periods of day” (categorical: dawn = 00:00–05:59, morning = 06:00–11:59, afternoon = 12:00–17:59, night = 18:00–23:59), since diel patterns of distribution of franciscanas in the study area have already been identified (Paitach et al., unpublished data). All combinations of terms were examined and

ranked by lowest AIC value (Akaike Information Criterion) (Burnham & Anderson, 2002), and the 'DHARMA' package in R was used to evaluate the fit of the selected model.

## Results

A total of 1,594 hours of acoustic monitoring were recorded, of which eleven hours (<1%) were removed because they were incomplete. Franciscanas were detected in 63% (1,009h) of the sampled time by the central C-POD close to the pinger, including both pinger on and off periods. In the C-PODs at 100m from the pinger, the data collected in the first 14 days of the experiment had to be excluded from the analysis due to an operational error. Therefore, a total of 1,203 hours was collected at this distance, 66% of which (794h) contained franciscana detection. In the C-PODs at 400m from the pinger franciscanas were detected in 75% (1,262h) of the total sampled period.

Seventy-two models were tested, and the top ranked model selected showed a significant effect of the '*pinger*' on the presence of franciscanas, and this effect was conditioned by the distance to the pinger (Table 1). Franciscanas were 19,4% less likely to be detected by the C-POD with the pinger when it was activated, while at 100m from the pinger the reduction in the detection probability was 15,4% (Fig. 2). At 400m this effect was significantly different from that observed for the C-POD at zero meters from the pinger, which means that at this distance the effect of the pinger is no longer observed, and the presence of franciscanas was similar for both pinger on and off status (Fig. 2). There was a variation in the detection of franciscanas among the diel periods, however the differences related to the pinger effect remained constant (Appendix B).

Table 1: Coefficients of the top ranked model describing the influence of the experimental Banana Pinger sounds on the detections of franciscana dolphins ( $df = 12$ ,  $\log\text{Lik} = -3864.764$ ,  $\text{weight} = 0.415$ ).

Model terms	Estimate	SE	Z value	$p$ value
(Intercept)	1.228	0.141	8.723	< <b>0.001</b>
Pinger (on)	-0.646	0.111	-5.839	< <b>0.001</b>
Distance (100m)	1.141	0.231	4.949	< <b>0.001</b>
Distance (400m)	0.441	0.169	2.603	<b>0.009</b>
Monitoring days	-0.011	0.003	-3.603	< <b>0.001</b>
Day period (morning)	0.276	0.078	3.543	< <b>0.001</b>
Day period (afternoon)	0.400	0.079	5.052	< <b>0.001</b>
Day period (night)	-0.137	0.075	-1.816	0.069
Pinger (on) x Distance (100m)	0.115	0.148	0.774	0.439
Pinger (on) x Distance (400m)	0.586	0.139	4.199	< <b>0.001</b>
Distance (100m) x Monitoring days	-0.023	0.005	-4.758	< <b>0.001</b>
Distance (400m) x Monitoring days	-0.008	0.004	-2.075	<b>0.037</b>

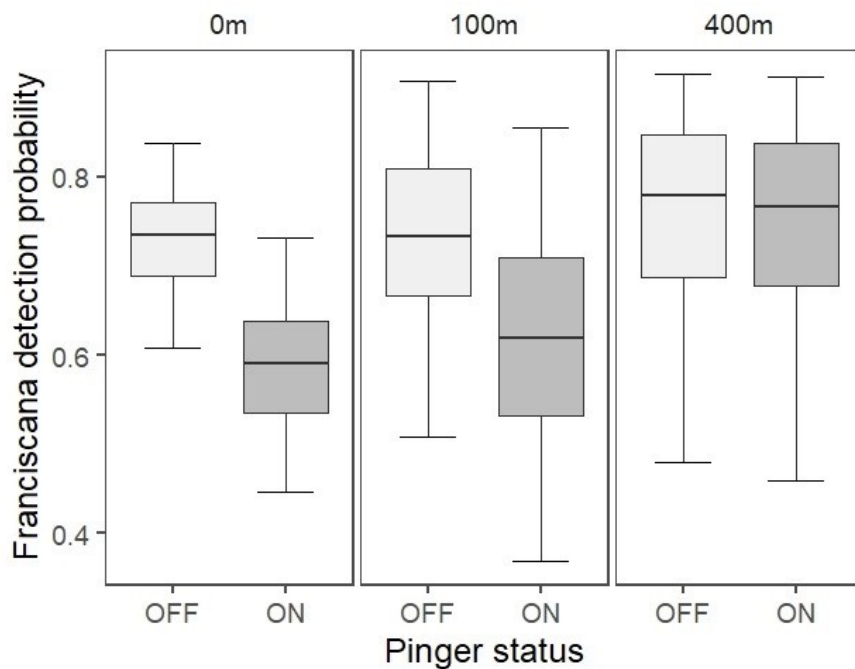


Figure 2: Detection probability of franciscana dolphins relative to '*pinger*' status at differences distances from the pinger. Boxplots represent the median (bars), interquartile interval (box) and range (whiskers), using predictions from the top ranked model presented in Table 1.

The consecutive '*monitoring days*' affected the presence of franciscanas in general, indicated by a small gradual decrease in the detections throughout the study, even at 400 meters where there was no pinger effect (Table 1, Fig. 3). The interaction between the '*pinger*' and '*monitoring days*' was not selected as a relevant variable in

the model, indicating that the variation in the probability of franciscana detection over the days was not related to the sound of the pinger. There was a significant interaction between '*monitoring days*' and '*distance*', showing that this decrease in the use of the area occurred at different intensities at different distances from the pinger (Table 1, Fig. 3). At zero and 400m the decrease was <1% per day, while at 100m the daily decrease was almost 3%.

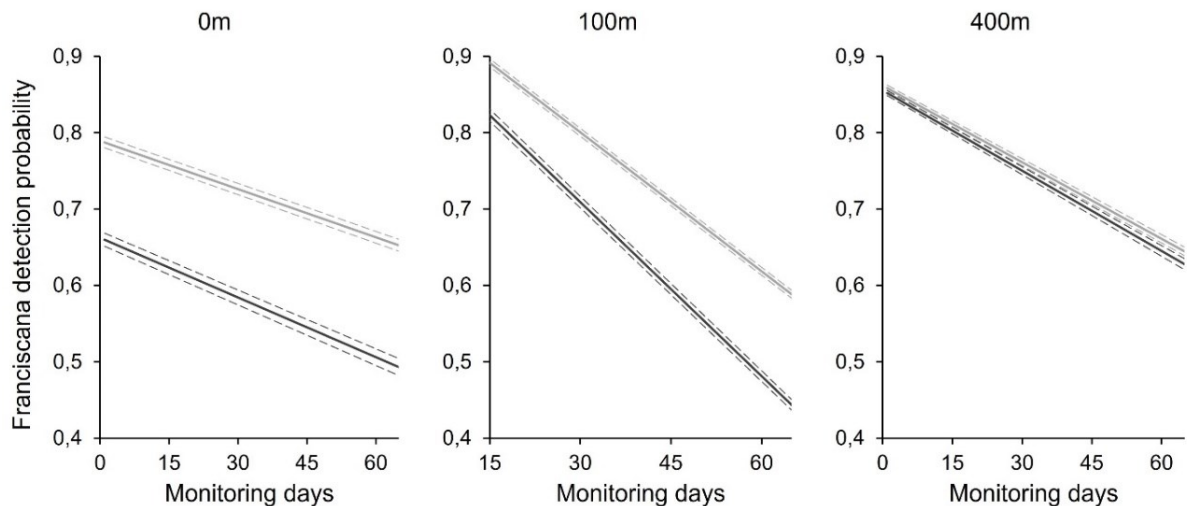


Figure 3: Temporal variation of the detection probability of franciscana dolphins as a function of pinger status (light gray line: pinger off; dark gray line: pinger on) at different distances from the pinger. Solid lines denote predictions from top ranked models presented in Table 1 and dashed lines are standard errors.

## Discussion

### *Effectiveness and range*

This study reports the first test of the effect of a high frequency "seal safe" pinger on franciscanas, and documents important findings about possible side effects. When the pinger sounds were turned on, the franciscana detections at 0 m and 100 m from the pinger were significantly reduced, indicating that the dolphins moved away from the pinger. This effect was absent at 400 m. Similarly, studies on different dolphin, porpoise and beaked whale species have reported optimistic results of bycatch reduction by pingers (Carretta et al., 2008; Gearin et al., 2000; Mangel et al., 2013; Palka et al., 2008). However, for the bottlenose dolphin, a species with a wide

behavioral diversity, the success of the pingers as deterrents is controversial (Buscaino et al., 2009; Cox et al., 2003).

Promising results of deterrence by the same pinger model as tested here were also reported for the harbour porpoise, *Phocoena phocoena* (Königson et al., unpublished data; Omeyer et al., 2020). In our study, however, the reduction in the click train detection probability of franciscanas in the immediate vicinity of the active pinger was almost half of that observed in harbor porpoises in the study by Omeyer et al. (2020), 19.4% and 37%, respectively, but it was higher at 100m from the pinger (15.4% and 8%, respectively), demonstrating that the same pinger can influence species differently. Such differences may also be associated with the environment, since our study was conducted in a subtropical estuarine environment with high temperatures, much sediments suspended in the water, and strong tidal currents (Oliveira et al., 2006), while the experiment done by Omeyer et al. (2020) was conducted in the cold, clear and deeper waters of the Celtic Sea. Hence, results on pinger effectiveness may vary, depending on species and location (Berrow et al., 2008; Culik et al., 2001; Dawson et al., 2013).

It has been suggested that the reduced click train detections in the vicinity of an active pinger were caused by a reduction in vocalizations rather than the dolphins leaving the area (Cox et al., 2003; Kyhn et al., 2015; Leeney et al., 2007). On the other hand, the sound of a pinger may stimulate a dolphin to start echolocation or echolocate at a higher rate (Koschinski et al., 2006). For the franciscana, there is evidence to support the explanation that it is a true withdrawal of the animals in the presence of an active pinger. In experiments with a 70 kHz pure tone pinger (Future Oceans, UK), in which the responses of the franciscanas to the pinger sounds were measured by visually logging the surfacing of the animals, a clear withdrawal from the pinger was seen, which would have reduced the logged echolocation activity in the vicinity of the pinger (Bordino, 2018). This is consistent with what is known for this species, which is reported to move away from any source of intense noise, such as vessels or port areas (Bordino et al., 1999; Cremer and Simões-Lopes, 2008; Holz, 2014). Kastelein et al. (2000) and Teilmann et al. (2006) also demonstrated that the harbor porpoises swam away from a source of pinger sound.

Our study demonstrates that the deterrent effect of the banana pinger sounds on franciscanas is significant up to 100 m but is lost somewhere between this distance



and 400 m. Our experimental design does not allow us to infer what the maximum effective range of the deterrent effect would be, and if it ceases abruptly or gradually. Assuming that the franciscana dolphin's hearing threshold at these frequencies is similar to another NBHF species, the harbor porpoise (c.f. Kastelein, et al., 2002), a pinger source level at 145 dB re  $\mu\text{Pa}$  at 1 m and based on the transmission of the main pinger frequency component 70 kHz, the pinger should theoretically be audible by the franciscanas at 400 m. Obviously, received levels considerably higher than threshold is required to cause displacement.

In this study, the experiment was focused on the response to a single pinger, and the behavioral response of franciscanas to a fishing net with an array of pingers remains an open issue that needs to be addressed. In the Danish North Sea, Larsen et al. (2013) recorded a 0% bycatch rate of harbor porpoise with AQUAmark100 pingers spaced up to 455 m apart, with bycatch rates increasing with larger spacing. For the implementation of this Banana Pinger in the coastal fisheries, we suggest adopting a maximum spacing between pingers of 200 m (as recommended by the supplier); further studies should be carried out to verify if it is possible with a larger spacing, which then would have implications on the costs to provide fishermen with pingers.

### *Habituation*

No sign of habituation to the pinger sounds was detected in our study. Considering the duration of the experiment (65 days), we consider this result very promising. Habituation was neither observed for *P. phocoena* during eight months of experiments with the same pinger (Omeyer et al., 2020). In contrast, Cox et al. (2003) using a theodolite to record bottlenose dolphin surfacing in the vicinity of a Netmark 1000 pinger (Dukane Corporation's Seacom Division, Illinois, USA), observed no significant deterrent effect after only 11 days of study, strongly suggesting that habituation occurred. Bottlenose dolphins, however, are known to be much bolder than franciscanas and are even involved in depredation (e.g., Buscaino et al., 2009). The Netmark 1000 pinger used in the experiment by Cox et al. (2003) transmitted 10 kHz pings with fixed 4 s intervals, whereas the experimental Banana Pinger in our study produced several slightly varying multi-harmonics, frequency modulated sounds with

semi-randomized 4-12 s intervals (Omeyer et al., 2020), a strategy believed to reduce possible habituation effects. On the other hand, Amano et al. (2017) observed possible habituation in finless porpoises (*Neophocoena asiaorientalis*) to an AQUAmark100 pinger (Aquatec Subsea Ltd, UK), that also transmits different multi-harmonic, frequency modulated sounds with 5-30 s semi-random intervals, after 4-5 months from the start of the experiment. However, despite the apparent habituation over time, no bycatch occurred over the entire 2 years of study (Amano et al., 2017). According to Kindt-Larsen et al. (2018), as long as the reduction of bycatch is maintained, habituation to a certain extent should be considered positive, since it would reduce a possible effect of habitat exclusion.

### *Habitat exclusion*

A gradual decrease in overall franciscana detections was observed over the consecutive days of our study, but we do not believe that this may be an indication of habitat exclusion. Habitat exclusion has never been verified empirically and remains a theoretical side effect (e.g., Carlström et al., 2009; Culik et al., 2001, Kyhn et al., 2015; Van Beest et al., 2017). In our study there was no significant interaction between the decrease in the presence of franciscanas with the sound of the pinger, in addition to the observed decrease having been generalized, even at 400 m where the pinger effect is no longer detected. We believe that the decreased presence is due natural oscillation in the distribution and habitat use of the population throughout the seasons, as has been shown by previous systematic studies using visual observation methodologies (Paitach et al., 2017). The present study was carried out in the fall, and in the two subsequent winter and spring seasons passive acoustic monitoring of the entire study area was carried out. It was found that the presence of franciscanas in this area was low in the winter and returned to be more frequent in the spring (Paitach et al., unpublished data).

Even so, we must consider that the present study analyzed the effect of a single pinger at a fixed location. If multiple fishing nets with pingers are used concomitantly or sequentially in preferred or crucial franciscana habitats, this can pose a threat to the populations and therefore needs to be monitored carefully during a future implementation of pingers in fisheries. With the harbour porpoise in the Danish part of the North Sea, Larsen and Hansen (2000), reported that if the entire Danish gillnet

fishing fleet was equipped with pingers, this would account for only <1% of the harbour porpoises' habitat, and therefore would not be a problem for the population. This is probably not the case for the franciscana, where the strictly coastal distribution of the species strongly overlaps with the distribution of the gillnet fishing effort (Danilewicz et al., 2009).

### *Implications for fisheries management*

Experiments with pingers on fishing nets and measuring the actual bycatch rate provide the most accurate test of their effectiveness as a mitigation strategy (e.g., Bordino et al., 2013; Carlström et al., 2002; Larsen & Eigaard, 2014). Despite the difficulties and challenges, the next step is to test the Banana Pinger in the commercial fishery, with careful bycatch monitoring and preferably with the parallel use of PAM devices to monitor the effect on the franciscanas' habitat use. This is the only way to understand the full scope of the matter, which includes other issues besides the effectiveness of the pinger, such as its correct use, acceptance and compliance by the fishermen, and trustworthy bycatch monitoring.

Another strategy that has been suggested to reduce bycatch is to use acoustically enhanced and physically stiffened gillnets (by BaSO<sub>4</sub> or Fe<sub>2</sub>O<sub>3</sub> treatment (Larsen et al., 2007; Mooney et al., 2004; Mooney et al., 2007). Bordino et al. (2013) tested BaSO<sub>4</sub> enhanced gillnets, but they proved not to reduce franciscana dolphin's bycatch. Replacing gillnets with other types of fishing gear may also be a possibility for reducing bycatch. Recently, Berninsone et al. (2020) demonstrated that the replacement of gillnets with longlines appears to be a practical approach that might result in significant mitigation of bycatch of franciscana dolphins in Argentina. Although expressive bycatch of other species was not recorded by Berninsone et al. (2020), longlines also have a potential for bycatch of other small cetaceans, birds and even pinnipeds, which could be aggravated by the intensification in the use of this fishing gear (Königson & Hagberg, 2007; FAO, 2021). Furthermore, acceptance and compliance for changes in fishing gears is a major challenge and may demand a long time (Berninsone et al., 2020), as they often affect cultural aspects of fishing activity and therefore face greater resistance.

The community involvement is fundamental for the definition and implementation of any bycatch mitigation strategy, and in many cases, this may depend on well-structured incentives and surveillance programs (Komoroske & Lewison, 2015). The Banana Pinger is the cheapest "seal safe" acoustic deterrent currently available on the market (i.e., unit price of £45 on September 3, 2020, prices may vary by the quantity ordered), with an expected lifespan of >5 years. Each pinger operates for up to one year (50% of use time) with a C-cell alkaline battery, which costs on average £2. That is, considering the proposed 200 m spacing between pingers, for every 1,000 m of gillnet the acquisition of banana pingers would cost £225, and £10 more for batteries for each year of use. Artisanal gillnets along the coast can range from a few hundred to more than 10,000 m (Secchi et al., 2003). These costs may not be acceptable for some of the low-income fishing communities in Brazil and management program aimed at ensuring the proper use of pingers must necessarily include financial subsidies for these communities.

Franciscanas urgently need effective short-term measures to reduce bycatch. The bycatch problem is complex and possibly requires the implementation of a set of strategies adaptable to the different conditions and realities of fishing communities, such as the use of acoustic deterrent devices, spatial closures, modifications to fishing gear and operations, in addition to promoting an increase in the market price of "bycatch free" fishes and other economic strategies (Kraus, 1999; FAO, 2021). Species conservation is a concern and responsibility of all involved stakeholders, such as fishermen, managers, and conservationists and, therefore, solutions must be built and implemented collaboratively (Komoroske & Lewison, 2015; FAO, 2021).

## **Conclusions**

Our study shows that "seal safe" sound of the Banana Pinger can be an effective acoustic deterrent to franciscanas, with the potential to reducing bycatch, with no lasting avoidance and a deterrent effect only at a short distance from the pinger. No habituation effect was noted at any distance from the pinger. There was a general and gradual decrease in the detections over the consecutive experimental days, which is probably related to seasonal variations in the habitat use of this population, but this requires attention in future studies. Effective long-term measures for the conservation

of this species are complex and fishermen and other stakeholders should be involved when strategies are developed and implemented.

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## CONCLUSÃO GERAL

No primeiro capítulo foram realizadas comparações entre os parâmetros acústicos dos sons de ecolocalização, e analisada a frequência do comportamento de forrageio da toninha ao longo do dia, entre dois diferentes habitats de ocorrência da espécie: estuarino (Baía Babitonga, norte de Santa Catarina) e mar aberto (Praia de Itapirubá, sul de Santa Catarina). A principal diferença acústica encontrada entre os habitats foi relacionada ao espectro de frequências, com maiores valores máximos e menores valores mínimos no ambiente estuarino, ocasionando uma largura de banda de 17kHz, enquanto no ambiente de mar aberto foi de 10kHz. Nenhuma diferença foi observada na duração das cadeias, mas a taxa de emissão de cliques foi quase 20% maior no estuário. Ambos os habitats estudados apresentaram elevada proporção de cadeias de clicks de alimentação (Baía Babitonga = 68%; Praia de Itapirubá = 58%), mas com maior probabilidade de ocorrência na Baía Babitonga ( $p < 0,001$ ) e no período noturno ( $p < 0,001$ ), para ambos os habitats. Os C-PODs apresentaram grande potencial para monitorar os parâmetros bioacústicos e comportamento de ecolocalização de toninhas. O monitoramento temporal e espacial de longo prazo é necessário para elucidar várias questões levantadas neste estudo.

No segundo capítulo, sessenta estações de MAP com C-PODs foram implementadas entre junho e dezembro de 2018 na Baía Babitonga para analisar o uso de habitat e distribuição de toninhas em diferentes escalas espaço-temporais. Modelos Aditivos Generalizados foram usados para analisar as relações complexas entre a presença de toninhas e as covariáveis ambientais. O modelo final incorporou 51% da variação dos dados e as principais variáveis selecionadas foram: hora do dia, presença de botos-cinza, declividade máxima e sedimento de fundo. Foi observado um padrão diário, com as toninhas permanecendo nas áreas de maior ocorrência, principalmente nas primeiras horas do dia. As áreas intensamente utilizadas pelos botos-cinzas são evitadas pelas toninhas, mas em menor intensidade são toleradas. As toninhas parecem evitar áreas mais íngremes e preferem áreas com fundos arenosos. A distribuição foi analisada por meio da Krigagem Bayesiana Empírica, e foi observada uma ocorrência predominante de toninhas na região mais interna do estuário, sem uso expressivo do canal de entrada da baía. No inverno, a distribuição foi mais ampla do que na primavera. Toda a região central das ilhas, entre as margens

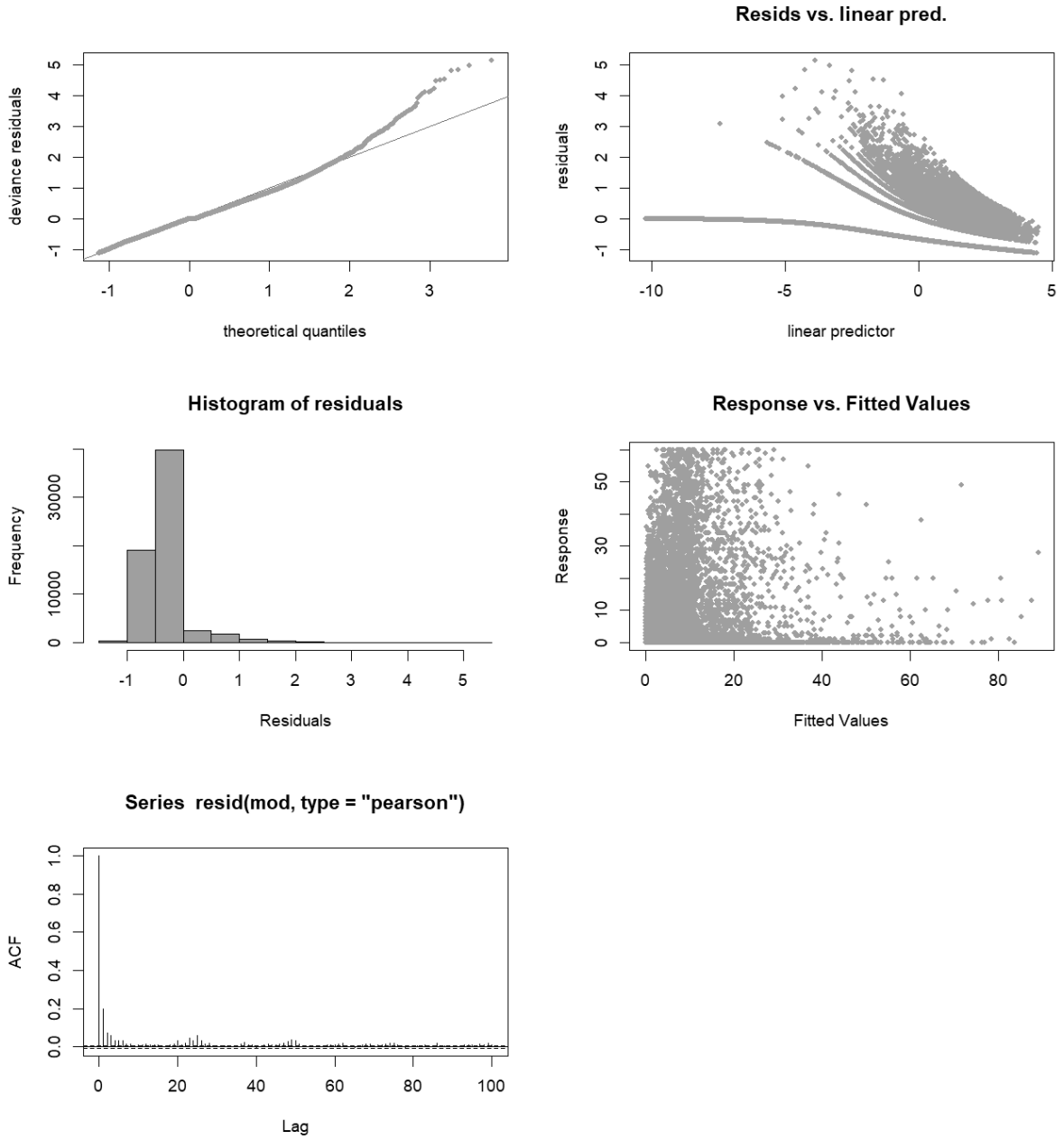
norte e sul, representam importantes áreas de alimentação, comportamento que ocorre com maior frequência durante a madrugada e a noite. Este estudo fornece um novo olhar sobre o uso de habitat e distribuição dessa população criticamente ameaçada de extinção. As duas estações amostradas (inverno e primavera) são expressivas e estratégicas para a identificação de habitats críticos para as toninhas. O desafio agora é identificar a melhor forma de integrar estas informações em instrumentos eficientes de gestão marinha, conciliando a conservação da toninha com as atividades humanas no território.

No terceiro capítulo, foi demonstrado que o Banana Pinger (Fishtek Marine, UK), um repelente acústico de alta frequência que presumidamente descarta o efeito atraente sobre pinípedes (efeito “*dinner bell*”), pode ser um dissuasor acústico eficaz para as toninhas, com potencial para reduzir a mortalidade incidental da espécie em redes de pesca. O pinger causou o afastamento apenas uma curta distância (até 100m). Nenhum efeito de habituação foi observado a qualquer distância. Houve uma diminuição geral e gradual nas detecções ao longo dos dias de experimento, mesmo em distâncias em que o efeito do pinger sobre as toninhas não é mais detectado, o que provavelmente está relacionado a variações sazonais no uso do habitat pela população, mas isso requer atenção em estudos futuros. O uso de tecnologias como pingers podem ser importantes para reduzir a captura acidental. Medidas eficazes de longo prazo para a conservação das espécies são complexas e devem ser adaptativas a cada realidade local. O envolvimento de pescadores no

O monitoramento acústico passivo com C-PODs demonstrou um grande potencial para o estudo de toninhas. Este trabalho apresenta bases metodológicas para a utilização deste dispositivo para a espécie, com diversas abordagens possíveis, permeando aspectos de sua etologia, ecologia e conservação.

## APÊNDICE A – (Cap. 2) Diagnostic plots and coefficients for the final model

Appendix A.1. Diagnostic plots for the final model of habitat use of franciscana in Babitonga Bay:



Appendix A.2. Coefficients for factor variables included in the final model of habitat use of franciscana dolphins in Babitonga Bay:

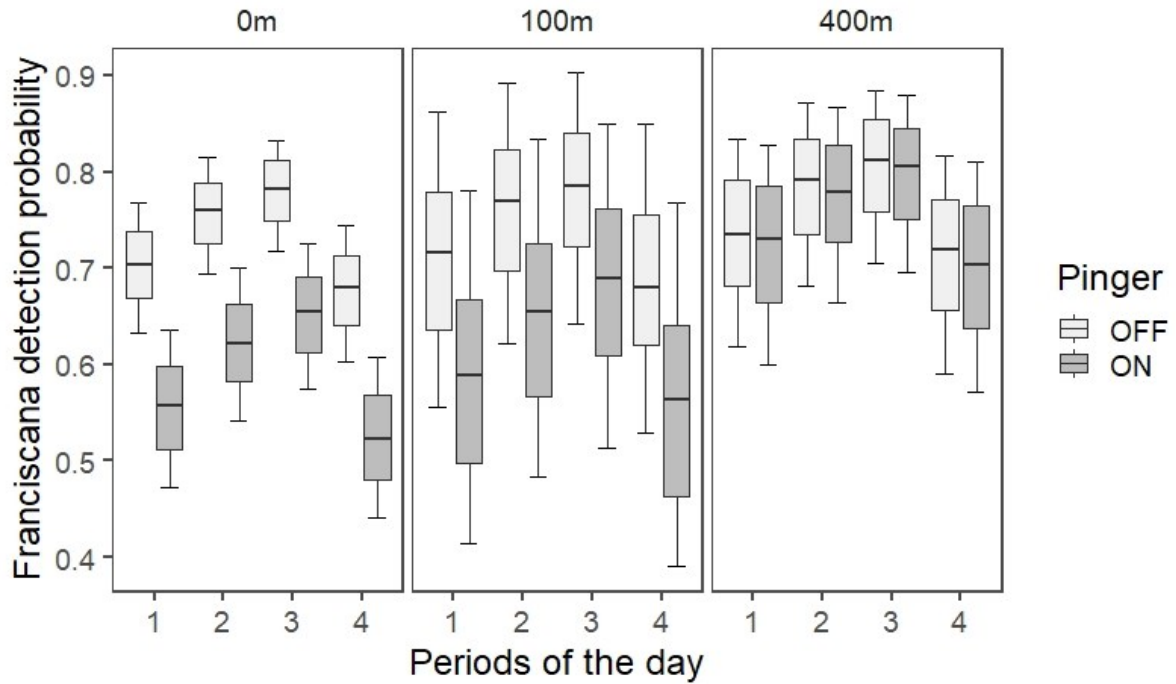
<b>Parametric coefficients</b>	<b>Estimate</b>	<b>p-value (t-distribution)</b>
(Intercept)	-3.253	< 0.001
Month07	0.428	0.012
Month08	0.685	< 0.001
Month09	0.591	0.002
Month10	0.119	0.516
Month11	-0.006	0.974
Month12	-0.404	0.123
Sed. – mud + sand	1.830	< 0.001
Sed. – sand	0.679	0.124
Sed. – sand + mud	1.776	< 0.001
Tide.type.syzygy	0.103	0.060
Tide.state.flood	-0.007	0.880
Tide.state.high	0.021	0.673
Tide.state.low	-0.073	0.147

Appendix A.3. Results for smooth functions included in the final model of habitat use of franciscana dolphins in Babitonga Bay. (edf = effective degrees of freedom):

<b>Smooth terms</b>	<b>edf</b>	<b>p-value (F-statistic)</b>
s(Point)	50.843	< 0.001
s(UTMY,UTMX) - Hour.day 1	15.399	0.002
s(UTMY,UTMX) - Hour.day 2	14.826	0.015
s(UTMY,UTMX) - Hour.day 3	9.548	0.035
s(UTMY,UTMX) - Hour.day 4	18.351	0.002
s(UTMY,UTMX) - Hour.day 5	8.325	0.053
s(UTMY,UTMX) - Hour.day 6	14.545	< 0.001
s(UTMY,UTMX) - Hour.day 7	13.102	0.008
s(UTMY,UTMX) - Hour.day 8	2.000	0.060
s(UTMY,UTMX) - Hour.day 9	2.001	0.085
s(UTMY,UTMX) - Hour.day 10	2.001	0.011
s(UTMY,UTMX) - Hour.day 11	17.015	< 0.001
s(UTMY,UTMX) - Hour.day 12	2.000	0.010
s(UTMY,UTMX) - Hour.day 13	2.000	0.065
s(UTMY,UTMX) - Hour.day 14	16.314	0.003
s(UTMY,UTMX) - Hour.day 15	2.002	0.068
s(UTMY,UTMX) - Hour.day 16	17.340	< 0.001
s(UTMY,UTMX) - Hour.day 17	2.002	0.050
s(UTMY,UTMX) - Hour.day 18	2.001	0.107
s(UTMY,UTMX) - Hour.day 19	16.523	0.002
s(UTMY,UTMX) - Hour.day 20	12.259	0.006
s(UTMY,UTMX) - Hour.day 21	10.998	0.003
s(UTMY,UTMX) - Hour.day 22	9.488	0.073
s(UTMY,UTMX) - Hour.day 23	11.014	0.003
s(UTMY,UTMX) - Hour.day 24	11.824	< 0.001
s(Hour.day)	3.281	< 0.001
s(Sg.DPM)	5.861	< 0.001
s(Slope.max)	3.695	< 0.001

### APÊNDICE B – (Cap.3) Supplementary data

Appendix B.1. Boxplots of the detection probability of franciscana dolphins relative to period of day (1 = dawns, 2 = morning, 3 = afternoon, 4 = night):



Appendix B.2. Top-ranked model fit assessments:

#### DHARMA residual diagnostics

