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Bianca Romeu

Variações espaciais e temporais dos botos-da-tainha via monitoramento contínuo do comportamento acústico

Florianópolis
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Bianca Romeu

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com pouco recurso e muita criatividade.

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RESUMO

Os cetáceos têm sua distribuição relacionada principalmente à disponibilidade de recursos alimentares e, como outros predadores, apresentam seus ciclos circadianos associados aos de suas presas. Diferentemente de outros mamíferos, os cetáceos não podem ser classificados como diurnos ou noturnos, por se manterem ativos independente do período do dia, de modo que é necessário observá-los ao longo das 24 horas do dia para entender, em um contexto mais abrangente, como se distribuem e usam suas áreas de vida. Estudar os cetáceos através do comportamento acústico permite realizar este monitoramento contínuo, pois eles são animais que usam os sons como um elemento importante em suas vidas, seja na percepção do ambiente ou nas interações sociais. Neste sentido, implementei um monitoramento acústico passivo (MAP) para investigar a população residente de golfinhos *Tursiops truncatus gephyreus* em Laguna, Santa Catarina, respondendo a questões a respeito da distribuição temporal e espacial dos indivíduos. Conhecidos localmente como botos-da-tainha, eles desenvolveram um comportamento único de interagirem positivamente com pescadores artesanais na chamada pesca cooperativa. Sabemos que tal tática de forrageio influencia aspectos ecológicos e biológicos da população, mas algumas questões permanecem em aberto, como a possível influência da tática de forrageio na definição da área de vida dos botos e a distribuição deles à noite nesta área. Assim, o MAP foi implementado ao longo de 2020, monitorando a população por 2-3 dias consecutivos por estação do ano, para avaliar possíveis variações na distribuição destes animais relacionada ao período do dia, com possível influência das marés e ventos. Antes de iniciar o monitoramento, foi necessário confirmar a efetividade da taxa de amostragem a ser utilizada para gravar a ecolocalização, som de alta frequência muito usado pelos botos. A partir de gravações feitas de grupos de *Tursiops truncatus*, em Laguna e outras localidades em águas abertas, com taxa de amostragem de 192 kHz, testou-se se taxas de amostragem menores, de 96 e 48 kHz, também registravam a ecolocalização. Confirmou-se que tais frequências podem ser utilizadas, com perdas na gravação de partes da ecolocalização, mas ainda registrando a presença/ausência dos animais. Com isso, o MAP foi implementado utilizando-se 4-6 gravadores na área de concentração dos botos. Ecolocalização e assobios foram os indicadores da presença dos botos nos locais monitorados. Os resultados confirmaram a presença dos botos na área todos os dias, inclusive à noite e com maior probabilidade de ocupação neste período, comparado ao dia. A maré e o vento influenciam na probabilidade de ocupação dos locais monitorados, provavelmente devido à distribuição das presas e estratégias de forrageio. Para entender melhor o uso heterogêneo da área, focou-se nos indivíduos, através dos assobios assinatura. Concluiu-se que a área mais utilizada, independente do período do dia, é a porção central da área de concentração dos botos, próxima a alguns pontos de pesca cooperativa, mas não sendo centrada em nenhum deles. Assim, aparentemente a interação com os pescadores não é o fator determinante da área de vida dos botos, e as ações de conservação da população podem ser focadas na área de concentração dela.

Palavras-chave: *Tursiops truncatus gephyreus*; monitoramento acústico passivo; pesca cooperativa; ecolocalização; assobios; assobios assinatura; taxa de amostragem.

ABSTRACT

Cetaceans are distributed mainly according to the food resource availability and, like other predators, show circadian cycles related to their prey. Different from other mammals, cetaceans cannot be classified as diurnal or nocturnal because they keep active independently of the period of the day. In this way, it is necessary to observe them through the diel cycles to understand, in a global context, how they are distributed and use their home range. Studying cetaceans through acoustic behavior allows that continuous monitoring because they are animals that use sounds as a fundamental element in their lives, whether perceiving the environment or interacting socially. In this way, I have implemented passive acoustic monitoring (PAM) to investigate the *Tursiops truncatus gephyreus* resident dolphin population in Laguna, Santa Catarina, answering questions about the spatial and temporal distribution of these individuals. Locally known as “botos-da-tanha”, they have developed a singular behavior, interacting with artisanal fishers positively in the called cooperative fishing. We know that such foraging tactic influences biological and ecological aspects of this population. But some questions remain open, like the possible influence of the cooperative fishing in the home range definition of the population and the dolphins distribution at night in that area. The PAM was implemented in 2020, monitoring the population for 2-3 consecutive days for the season to evaluate possible variations in the distribution of these animals related to the period of the day, with the tide and wind possible influence. Before starting the monitoring, it was necessary to confirm the effectivity of the sampling rate to be used to record the echolocation, high-frequency sound frequently used by the dolphins. Using recordings made from groups of *Tursiops truncatus*, from Laguna and other localities in open water, with a sampling rate of 192 kHz, it was tested if lower sampling rates, of 96 and 48 kHz, also recorded the echolocation. It was confirmed that such sampling rates can be used, with some loss of parts of the echolocation but registering the dolphins’ presence/absence yet. Then, the PAM was implemented using 4-6 recorders in the dolphins’ core area. Echolocation and whistles were the indicators of the dolphin’s presence in the monitored sites. Results confirm the dolphins’ presence every day, including at night when the occupancy probability is higher than during the day. Tide and wind influence the occupancy probability on sites, perhaps due to prey distribution and foraging tactics. To better understand the heterogeneity in the use of the area, the focus was on the individuals through the signature whistles. The conclusion was that the most used area is the central part of the core area, independent of the period of the day, which is close to some cooperative fishing sites but is centered on none of them. Thus, apparently, the interaction with fishers is not a determinant factor in the dolphins’ home range, and conservation actions can focus on the core area of the population.

Keywords: *Tursiops truncatus gephyreus*; passive acoustic monitoring; cooperative fishing, echolocation, whistles, signature whistles, sampling rate.

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1 INTRODUÇÃO

A distribuição espacial e temporal dos vertebrados é dinâmica, heterogênea e dependente da disponibilidade e abundância dos recursos, principalmente recursos alimentares (MITCHELL; POWELL, 2007; PRANGE; GEHRT; WIGGERS, 2004; SCHOFIELD et al., 2010). A disponibilidade de presas costuma ter variações sazonais, motivando deslocamentos regionais ou movimentos migratórios dos predadores (ALERSTAM; HEDENSTRÖM; ÅKESSON, 2003; e.g., WILMSHURST et al., 1999), enquanto a variação na abundância de presas pode definir o tamanho da área de vida ou território de um predador (PRANGE; GEHRT; WIGGERS, 2004; SCHOFIELD et al., 2010). Há ainda outro elemento temporal, além da sazonalidade, que deve ser inserido nesta equação. Não basta estar no lugar certo na época certa, também é preciso estar presente na hora certa para acessar o recurso. Esta “hora certa” é ajustada pelo ritmo circadiano que, entre outras coisas, define os períodos de atividade e descanso dos animais. Mamíferos, por exemplo, podem apresentar períodos específicos de atividade e descanso associados a alternância entre dia e noite. Isto leva a classificação destes animais como diurnos, noturnos ou crepusculares, de acordo com o período do dia em que estão ativos (ASHBY, 1972; HALLE; STENSETH, 2000). Ou seja, para entender a dinâmica da distribuição espacial e temporal de um animal deve-se considerar a dinâmica ambiental, principalmente dos recursos, e o ritmo circadiano do próprio animal, considerando em que período ele estará efetivamente ativo.

Embora a variação entre dia e noite ajude a regular os ritmos circadianos, também existe um componente adaptativo às implicações ecológicas do ambiente onde o animal está inserido e seu modo de vida (BLOCH et al., 2013; HALLE; STENSETH, 2000; YERUSHALMI; GREEN, 2009). O período de atividade de um animal nem sempre é pré-definido, podendo variar na mesma espécie entre diferentes ambientes, épocas do ano, demandas fisiológicas (reprodução, amamentação, migração), entre outros (BLOCH et al., 2013), sendo o forrageio um importante fator na adaptação do ritmo circadiano, em nível fisiológico (HOUSER et al., 2021; VERWEY; AMIR, 2009). Por isso, predadores costumam ter seus ritmos circadianos relacionados aos de suas presas, também de modo que consigam acessá-las mais facilmente e com menor gasto energético no forrageio (HALLE; STENSETH, 2000; MONTERROSO; ALVES; FERRERAS, 2013). Um exemplo de grupo animal que apresenta não somente seu ritmo circadiano associados ao padrão de atividades de suas presas, mas também sua distribuição espacial e temporal relacionadas a disponibilidade e abundância de suas presas, são os cetáceos.

Os cetáceos compreendem as baleias, golfinhos e botos. São uma infraordem da ordem Cetarctiodaclyla, formada por duas superfamílias: Mysticeti, que são as baleias de barbatana, e Odontoceti, formada pelos botos, golfinhos e baleias com dentes (FORDYCE; MUIZON, 2001; PRICE; BININDA-EMONDS; GITTLEMAN, 2005). A superfamília mais diversa é a dos Odontocetos, com 77 espécies, enquanto os Misticetos contam com 14 espécies (FORDYCE, 2018). Estes animais ocorrem em todo o planeta, habitando principalmente os oceanos, mas também regiões costeiras, estuários e rios (CORREIA et al., 2020; SHIRIHAI; JARRETT, 2006). Quanto a alimentação, todos os cetáceos são considerados carnívoros, com suas presas variando desde pequenos crustáceos e peixes até lulas gigantes, aves e mesmo outros cetáceos (SHIRIHAI; JARRETT, 2006; WERTH, 2000). A forma como se alimentam também varia, podendo ser por filtração, sucção ou raptorial (predação) (JOHNSTON; BERTA, 2011; WERTH, 2000). Diferente de outros mamíferos, os cetáceos não podem ser classificados como diurnos, noturnos ou crepusculares, porque eles se mantêm ativos quase continuamente. Os golfinhos, por exemplo, raramente descansam (GOWANS; WÜRSIG; KARCZMARSKI, 2007), sendo que nos primeiros meses de vida podem apresentar de poucos a nenhum período de descanso (LYAMIN et al., 2005).

Assim, somado ao fato de se alimentarem de presas (móveis) e não apresentarem um período pré-definido de atividade, algumas espécies de cetáceos respondem aos ritmos circadianos de suas presas, realizando deslocamentos ao longo das 24-horas acompanhando os ciclos delas. Golfinhos-rotadores (*Stenella longirostris*) do Havaí, por exemplo, seguem os ciclos de migrações verticais e horizontais de suas presas, forrageando mais perto da costa à noite e a diferentes profundidades dependendo da hora do dia (BENOIT-BIRD; AU, 2003). Ao sul do Havaí, no Atol Palmyra, golfinhos-cabeça-de-melão (*Peponocephala electra*) usam águas mais rasas durante o dia, para descansar e socializar, movendo-se para águas mais profundas à noite, onde forrageiam (BAUMANN-PICKERING et al., 2015). Também outras espécies pelágicas de cetáceos apresentam padrões de mergulho que acompanham a migração vertical das presas na coluna d’água ao longo do dia (BAIRD et al., 2001; FRIEDLAENDER et al., 2013; SOLDEVILLA; WIGGINS; HILDEBRAND, 2010), inclusive com períodos de menor atividade (descanso) em turnos opostos aos de forrageio, supostamente quando há menor disponibilidade de presas (FRIEDLAENDER et al., 2013; IZADI et al., 2018).

Considerando que estes animais vivem a maior parte de suas vidas submersos, tais informações a respeito dos períodos de atividade e forrageio só puderam ser geradas a partir de inovações nas técnicas de amostragem (NOWACEK et al., 2016), já que a simples dependência de dados visuais acaba limitando a amostra aos períodos em que os animais estão na superfície, ou períodos de condições ambientais favoráveis, o que resulta em dados fragmentados e potencialmente enviesados (IZADI et al., 2018; NOWACEK et al., 2016). Uma das abordagens mais aplicadas para o estudo de cetáceos nas últimas décadas é a acústica. Sabe-se que o som se propaga mais rápido na água do que no ar e pode percorrer grandes distâncias. Assim, os cetáceos ao longo da evolução desenvolveram a acústica como sentido usado nos diversos aspectos de suas vidas (JANIK, 2009; MOONEY; YAMATO; BRANSTETTER, 2012). O uso mais comum dos sons, que primeiro vem às nossas mentes, é a comunicação. Os misticetos usam os sons principalmente com esta função. Seus sons de baixa frequência (p. ex., 18-35 Hz para baleia Fin – *Balaenoptera physalus*, 90-180 Hz para baleia de Bryde – *Balaenoptera edeni*, 100-3000 Hz para baleia cinzenta – *Eschrichtius robustus*; ver EDDS-WALTON, 1997) são muito úteis para se comunicarem a quilômetros de distância, pois as ondas sonoras de baixa frequência e, consequentemente, grande comprimento de onda, se propagam a longas distâncias (EDDS-WALTON, 1997; SAYIGH, 2014; ŠIROVIĆ; HILDEBRAND; WIGGINS, 2007; TYACK; CLARK, 2000). Algumas teorias defendem que, para além da comunicação, as emissões sonoras das baleias seriam usadas também para a navegação. O comprimento de onda destes sons permitiria a detecção, por meio do retorno do som (eco), de características batimétricas do ambiente (TYACK, 1997). Já os odontocetos desenvolveram um tipo sonoro especializado para navegação e localização de presas, a ecolocalização. Com características opostas aos sons das baleias, a ecolocalização é um som de alta frequência (p. ex., picos de frequência entre 40-160 kHz, dependendo da espécie; ver AU, 2000) e comprimento de onda curto, que tem sua propagação limitada a distâncias mais curtas (TYACK; CLARK, 2000). Composta por sons pulsados, chamados de cliques, as características sonoras da ecolocalização são ideais para a identificação de obstáculos e presas, mesmo as de pequeno tamanho, que podem ser percebidos em detalhes a partir do eco destes sons (AU, 2000; TYACK, 1997; TYACK; CLARK, 2000). Os cliques, além da ecolocalização, também podem ser usados para compor sons de comunicação de algumas espécies de odontocetos, como as toninhas ou botos (em tradução livre) da família Phocoenidae, os cachalotes (*Physeter macrocephalus*) e alguns golfinhos da família Delphinidae (JANIK, 2009; MADSEN; WAHLBERG; MOHL, 2002; SAYIGH, 2014; TYACK, 1997). Esta última família também apresenta outro tipo de som específico para a comunicação, os assobios (HERMAN; TAVOLGA, 1980). De aparência modulada e frequências mais baixas em comparação aos cliques de ecolocalização, os assobios são reportados para muitas espécies de delfinídeos, mas também para espécies de outras famílias de odontocetos, como os botos-rosa (*Inia* spp.) e as toninhas (*Pontoporia balinvillei*) (CREMER et al., 2017; MAY-COLLADO; WARTZOK, 2007; MELO-SANTOS et al., 2019).

Esta gama de produções sonoras permitiu o desenvolvimento de técnicas que buscam entender aspectos da vida destes animais que passam pouco tempo de suas vidas na superfície (GORDON; TYACK, 2002). Nas últimas décadas têm se estabelecido o monitoramento acústico passivo (MAP) como método não só para estudos científicos, mas também para a mensuração e monitoramento de impactos antropogênicos sobre os cetáceos (ZIMMER, 2011). O monitoramento acústico é passivo quando apenas o som que ocorre no ambiente é registrado, diferente do ativo, onde um som é emitido e seu eco é analisado (MELLINGER et al., 2007). Algumas das formas de realizar um MAP é utilizando o modo estático ou de arrasto. O tipo estático é realizado com hidrofones cabeados, mais utilizado para fins militares devido aos custos de instalação, ou gravadores autônomos (MELLINGER et al., 2007). Os gravadores autônomos consistem em hidrofones conectados a gravadores de som ou “gravadores” de dados (*data loggers*), alimentados por baterias, que podem operar por meses (SOUSA-LIMA et al., 2013). Estes equipamentos costumam ser colocados em arranjos de mais de um dispositivo, para cobrir uma grande área ou mesmo localizar o indivíduo que emitiu determinado som através da triangulação de dois ou mais dispositivos. São colocados submersos ancorados no fundo ou presos a cabos com flutuadores, mantidos na coluna d’água (MELLINGER et al., 2007). O MAP de arrasto consiste em um arranjo de hidrofones que é rebocado por um navio, conectado a um computador onde a gravação dos sons é feita, algumas vezes com acompanhamento deste monitoramento acústico em tempo real. Pelo arranjo dos hidrofones, também é possível identificar a localização aproximada do indivíduo emissor do som (e.g., VON BENDA-BECKMANN; BEERENS; VAN IJSSELMUIDE, 2013; YACK et al., 2013). Existem ainda as tags, que são equipamentos temporariamente fixados nos animais e que podem registrar diversas informações, incluindo seus sons e, recentemente, os veículos autônomos subaquáticos: gravadores autônomos que se deslocam controlados remotamente (KLINCK et al., 2016; MELLINGER et al., 2007).

O MAP vêm sendo usado em diversos estudos de impactos e mitigação de atividades antropogênicas. O MAP estático, por exemplo, permitiu observar o impacto que a produção de energia maremotriz pode causar nas toninha-do-porto (*Phocoena phocoena*), reduzindo sua presença em áreas a distâncias de 10 a 150 metros das turbinas, quando em funcionamento (PALMER et al., 2021), e também os impactos negativos da energia eólica, principalmente durante a instalação da porção subaquática (MADSEN et al., 2006). Já nas atividades de prospecção de petróleo através da sísmica, o MAP no modo arrasto tem sido usado como ferramenta de mitigação. Durante as operações dos canhões de ar, empregados na prospecção sísmica, o MAP complementa a observação visual na detecção de cetáceos antes e durante o funcionamento dos canhões, de modo que suas atividades sejam suspensas quando constatada a presença de animais nas proximidades (BARLOW; GISINER, 2006; COMPTON et al., 2008; IBAMA, 2005). Em estudos científicos, o MAP estático tem sido usado em áreas que vão desde lagoas e canais até águas oceânicas costeiras ou próximas às ilhas, e permitem investigar questões populacionais diversas como distribuição, uso de habitat e abundância (DAVIS et al., 2017; MARQUES et al., 2012; PALMER et al., 2019; SIMON et al., 2010).

Quando a espécie-alvo do estudo é um odontoceto, a emissão sonora mais comum e mais importante a ser registrada é a ecolocalização (AKAMATSU et al., 2005, 2007). Mas os assobios também são de interesse para o estudo das populações. Em particular um tipo específico de assobio: o assobio assinatura. Descrito pela primeira vez em 1965 por Caldwell e Caldwell (1965), para golfinho-nariz-de-garrafa (*Tursiops truncatus*) de cativeiro, este som se caracteriza por ser único de cada indivíduo e estável ao longo da vida (LUÍS; COUCHINHO; SANTOS, 2016; SAYIGH et al., 1990). É utilizado para o reconhecimento do golfinho, principalmente em situações de isolamento forçado, separação do grupo, contato entre mãe e filhote, reencontros e manutenção de relações sociais (e.g., CHERESKIN et al., 2022; JANIK, 2000; JANIK; SLATER, 1998; NAKAHARA; MIYAZAKI, 2011; SAYIGH et al., 1990). Por ser exclusivo, o assobio assinatura tem potencial de ser um marcador individual em MAP (e.g., BAILEY et al., 2021; FEAREY et al., 2021; LONGDEN et al., 2020), principalmente de populações residentes que sejam estudadas em longo prazo e, portanto, com maiores chances de terem seus assobios assinatura identificados. Conhecendo os assobios assinatura de uma população, pode-se usá-los de modo semelhante à fotoidentificação da nadadeira dorsal dos golfinhos e responder a perguntas ecológicas diversas que exigem o reconhecimento individual.

Assim, a aplicação do MAP para os estudos de cetáceos é eficiente, inclusive como complemento aos métodos visuais tradicionalmente aplicados (DALPAZ et al., 2021). Entre as vantagens do MAP, comparado aos métodos visuais, está a possibilidade de monitorar os animais mesmo em más condições climáticas e por longos períodos, de dias a meses (ZIMMER, 2011). Esta característica permite estudar animais que não apresentam ciclos circadianos com períodos específicos de descanso, pois o monitoramento é mantido continuamente ao longo das 24 horas do dia. Assim, é possível entender questões de distribuição e uso de habitat incluindo períodos em que métodos visuais não podem ser usados. Neste sentido, o MAP permite complementar os dados de fotoidentificação, devido às características citadas anteriormente quanto ao tempo de monitoramento contínuo e condições climáticas em que pode operar, além da possibilidade de monitorar mais de um local simultaneamente, possibilitando assim confirmar se os métodos acústicos e visuais convergem para resultados semelhantes quando aplicados a mesma população e para as mesmas perguntas ecológicas. Por todos estes fatores, na presente tese buscou-se utilizar o MAP para complementar as informações procedentes via métodos visuais para a população de botos-da-tainha residente no complexo estuarino situado em Laguna, Santa Catarina.

A população de golfinhos-nariz-de-garrafa de Laguna, conhecidos localmente como botos-da-tainha, pertence a *Tursiops truncatus*, a espécie mais conhecida entre os cetáceos. Esta espécie é cosmopolita, encontrada em águas tropicais e temperadas, com sua distribuição limitada pela temperatura da água seja direta ou indiretamente, devido à distribuição de suas presas (WELLS; SCOTT, 1999, 2009). Está entre os maiores golfinhos, podendo atingir até 4m de comprimento, porém apresentando fenótipos que variam entre populações costeiras e oceânicas (SHIRIHAI; JARRETT, 2006; SIMÕES-LOPES et al., 2019). Apresenta uma plasticidade comportamental quanto às estratégias de forrageio que são tão diversas quanto sua gama de presas (SHANE; WELLS; WÜRSIG, 1986). A população que reside em Laguna representa bem as características da espécie no que se refere a distinção fenotípica e plasticidade comportamental. Estudados deste o final da década de 1980 (SIMÕES-LOPES, 1991; SIMÕES-LOPES; FÁBIAN; MENEGHETI, 1998), o boto-da-tainha foi recentemente recategorizado como uma subespécie endêmica das áreas costeiras do Atlântico Sul Ocidental, *Tursiops truncatus gephyreus* (COSTA et al., 2019; VERMEULEN et al., 2019), porém com certo grau de isolamento genético das outras populações (COSTA et al., 2015; FRUET et al., 2014). Isto se deve, em parte, ao alto grau de residência e fidelidade à área que estes botos apresentam, formando uma população muito pequena, de cerca de 54-60 indivíduos (BEZAMAT et al., 2019; DAURA-JORGE; INGRAM; SIMÕES-LOPES, 2013; SIMÕES-LOPES; FABIAN, 1999). Apresentam características morfológicas na forma da nadadeira dorsal e padrão de coloração que permite diferenciá-los dos indivíduos da subespécie que vive em habitat oceânico, *Tursiops truncatus truncatus* (SIMÕES-LOPES et al., 2019). Mas a característica que mais chama a atenção nesta população é uma tática de forrageio que desenvolveram, interagindo positivamente com os pescadores artesanais que usam a tarrafa como artefato de pesca (SIMÕES-LOPES, 1991; SIMÕES-LOPES; FÁBIAN; MENEGHETI, 1998). Tal tática envolve conduzir o cardume até às margens do estuário, onde os pescadores aguardam dentro da água ou em canoas, lado a lado e com suas tarrafas em mãos. No momento certo, os botos sinalizam para os pescadores, com movimentos estereotipados na superfície, que é a hora de lançarem as tarrafas. Desta forma, os pescadores funcionariam como uma barreira ativa, pois ao lançar as tarrafas e estas caírem na água, promoveriam a dispersão do cardume, facilitando a captura dos peixes, desorganizados e desorientados, pelos botos (SIMÕES-LOPES, 1991; SIMÕES-LOPES; FÁBIAN; MENEGHETI, 1998).

Nem todos os indivíduos da população interagem com os pescadores com a mesma frequência. Aqueles que interagem mais frequentemente são conhecidos como botos cooperativos, enquanto os botos que não interagem com frequência são conhecidos como não cooperativos. Esta diferença comportamental se reflete na área de vida, probabilidade de sobrevivência, relações sociais e comunicação acústica. Por exemplo, os botos cooperativo têm uma área de vida menor do que os não cooperativo (CANTOR; SIMÕES-LOPES; DAURA-JORGE, 2018). Esta área de vida está sobreposta aos principais pontos de pesca com interação com os pescadores, chamada de pesca cooperativa, e pode ser explicada pela disponibilidade e/ou facilidade na captura das presas devido ao “auxílio” dos pescadores (CANTOR; SIMÕES-LOPES; DAURA-JORGE, 2018). A área de vida menor e a interação com os pescadores também são fatores que tornam a probabilidade de sobrevivência dos botos cooperativos ligeiramente maior, em comparação aos não cooperativos, provavelmente por reduzir a exposição a atividades de pesca potencialmente promotoras de emalhes acidentais (BEZAMAT et al., 2019). Nas relações sociais, os botos cooperativos preferem passar mais tempo entre si do que com botos não cooperativos, o que acontece não só durante o forrageio, mas principalmente em outras ocasiões, como socialização e deslocamento (DAURA-JORGE et al., 2012; MACHADO et al., 2019). Isto se reflete na comunicação acústica, com os parâmetros acústicos dos assobio dos botos cooperativos sendo mais semelhantes entre si do que com os dos botos não cooperativos, principalmente quanto não estão forrageando (ROMEU et al., 2017).

Além da importância e interesse ecológico destes botos, por serem predadores de topo na cadeia trófica do ambiente que habitam e possibilitarem a investigação de diversos mecanismos ecológicos e evolutivos devido à pesca cooperativa, estes animais têm grande importância social e econômica. Na pesca cooperativa, os pescadores capturam peixes maiores e em maior quantidade em comparação a pesca sem o auxílio dos botos (SIMÕES-LOPES; FÁBIAN; MENEGHETI, 1998). A importância econômica e cultural dos botos para a comunidade resultou no seu reconhecimento como Patrimônio Natural do Município (Lei Municipal N° 521/1997), na criação do Dia Estadual da Preservação do Boto Pescador (Lei Estadual Nº 17.084/2017) e no título de Capital Nacional dos Botos Pescadores dado à Laguna (Lei Federal Nº 13.318/2016). Atualmente busca-se um reconhecimento frente a UNESCO como Patrimônio Imaterial.

Mas nem todos estes reconhecimentos têm sido efetivos para a proteção da população, que sofre com diversos impactos antropogênicos. Os registros de doenças relacionadas a lesões de pele são de longa data e os casos têm se agravado, com o registro de um indivíduo da população com a doença conhecida como Lobomicose em 1993 e sete indivíduos reportados com lesões de pele em 2009 (DAURA-JORGE; SIMOES-LOPES, 2011; SIMÕES-LOPES et al., 1993). Também já foi comprovada a bioacumulação de poluentes orgânicos persistentes na população, em níveis suficientes para oferecer riscos à saúde (RIGHETTI et al., 2019). O tráfego de embarcações na área onde vivem, inclusive no local mais conhecido por ocorrer a pesca cooperativa, afeta o comportamento acústico dos botos, possivelmente alterando o desempenho deles durante o forrageio (PELLEGRINI et al., 2021), além dos riscos de colisão. Mas a ameaça mais crítica à sobrevivência da população são os emalhes acidentais (BEZAMAT et al., 2021). As redes de emalhe, especialmente as usadas à noite para a pesca de bagre e em uma área de uso frequente dos botos, oferecem um risco real à população (PETERSON; HANAZAKI; SIMOES-LOPES, 2008). Por causa disto, em 2018 foi sancionada a Lei Municipal Nº 1.998 definindo uma área de manejo de pesca onde está proibida a pesca com redes de emalhe. Esta área de manejo foi definida de acordo com a área mais usada pelos botos dentro do estuário (ver CANTOR; SIMÕES-LOPES; DAURA-JORGE, 2018). Nos últimos três anos, talvez em consequência da área de manejo, nenhum boto foi encontrado morto por emalhe acidental (comunicação pessoal Pedro Castilho, de acordo os animais resgatados mortos pelo Projeto de Monitoramento de Praias da Bacia de Santos – PMP/BS).

Considerando que a informação a respeito da área mais usada pelos botos é proveniente dos dados de fotoidentificação, ou seja, relacionados a distribuição e uso do habitat pelos botos durante o dia, e que esta área está relacionada com os locais onde acontece a pesca cooperativa, também no período diurno, fica o questionamento sobre o uso da área à noite. Aparentemente, pela redução das capturas acidentais após a sanção da área de manejo, os botos permanecem ali também à noite e, na ausência de pesca, o emalhe acidental foi reduzido. Porém, não há uma confirmação desta informação, ou se os botos mudam sua distribuição dentro dessa área. Assim, considerando tudo o que já se sabe sobre a população de botos-da-tainha de Laguna e o que ainda precisa ser respondido, a presente tese teve como objetivo geral desenvolver uma abordagem de MAP para avaliar se existem variações na distribuição e frequência de uso, pelos botos, na principal área de concentração da população, em escala temporal diária. Para responder a este objetivo, a tese está estruturada em três capítulos, cada um com objetivos específicos.

No capítulo 1, a partir da hipótese de que parte dos cliques de ecolocalização podem ser registrados em baixas e médias frequências, testamos a eficiência de taxas de amostragem de 96 e 48 kHz na gravação de cliques de ecolocalização de duas subespécies de *Tursiops truncatus*. Considerando que os cliques de ecolocalização são emitidos em altas frequências, o objetivo específico deste capítulo foi confirmar que parte destes cliques podem ser gravados efetivamente com frequências mais baixas. A partir de gravações feitas com uma taxa de amostragem de 192 kHz, em Laguna (*T. t. gephyreus*) e em águas abertas (*T. t. truncatus*), avaliamos a proporção de cliques também registrados em frequências menores. Com isto, pudemos validar a taxa de amostragem das gravações feitas no monitoramento acústico passivo estático, realizado no capítulo seguinte. Este capítulo encontra-se publicado na revista Royal Society Open Science (DOI: 10.1098/rsos.201598).

No capítulo 2 investigou-se a hipótese de que os botos utilizam sua área de vida de modo diferente à noite, comparado ao dia. O objetivo específico foi avaliar se a distribuição geral da população na área monitorada responde ao período do dia, bem como a influência dos fatores ambientais maré e vento nesta distribuição. Assim, consideramos todas as emissões sonoras dos botos para registrar a presença deles em cada ponto monitorado e, a partir desses dados, avaliar variações no uso que a população faz de sua área de vida, em especial da área de concentração. Desta forma, foi possível argumentar a respeito da importância desta área de concentração dos botos para a conservação da população, bem como a influência da pesca cooperativa na presença dos botos na área.

Por fim, no capítulo 3 refinamos o olhar sobre a distribuição da população na área focando nos indivíduos, através dos assobios assinatura. Averiguamos a hipótese de que, mesmo dentro da área de maior concentração da população, o uso da área não é homogêneo. Eram objetivos específicos deste capítulo estimar a probabilidade de encontro de indivíduos em cada ponto monitorado, avaliando o uso heterogêneo da área, e fazer uma estimativa preliminar da abundância da população a partir dos assobios assinatura e suas recapturas em cada ponto de monitoramento. Este capítulo foi recentemente submetido para a revista Marine Mammal Science.

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2 CHAPTER 1:
LOW FREQUENCY SAMPLING RATES ARE EFFECTIVE TO RECORD BOTTLENOSE DOLPHINS

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2.1 SUMMARY

Acoustic monitoring in cetacean studies is an effective but expensive approach. This is partly because of the high sampling rate required by acoustic devices when recording high-frequency echolocation clicks. However, the proportion of recording echolocation clicks at different frequencies is unknown for many species, including bottlenose dolphins. Here, we investigated the echolocation clicks for two subspecies of bottlenose dolphins in the western South Atlantic Ocean. The possibility of record echolocation clicks at 24 and 48 kHz was assessed by two approaches. First, we considered the clicks in the frequency range up to 96 kHz. We found a loss of 0.95-13.90% of echolocation clicks in the frequency range below 24 kHz, and 0.01-0.42% below 48 kHz, to each subspecies. Then, we evaluated these recordings downsampled at 48 and 96 kHz and confirmed that echolocation clicks are recorded at these lower frequencies, with some loss. Therefore, despite reaching high frequencies, the clicks can also be recorded at lower frequencies because echolocation clicks from bottlenose dolphins are broadband. We concluded that ecological studies based on presence-absence data are still effective for bottlenose dolphins when acoustic devices with a limited sampling rate are used.

Key words: acoustics, wildlife monitoring, conservation, cetaceans, echolocation, *Tursiops truncatus*

2.2 **INTRODUCTION**

Acoustic behavior is a crucial element of many marine species. This is particularly the case for cetaceans which use acoustics for practically all activities. Odontocetes use whistles and clicks. Whistles—narrow-band and frequency-modulated signals—are used to transmit information, for individual recognition, and group cohesion [1–3]. Click—pulsed sounds—are used during socialization [2,4], navigation, and foraging [5,6]. Cetaceans spend a small proportion of their time at the surface and travel kilometers in a couple of hours. Therefore, the use of acoustic methods to investigate and record acoustic emissions is an effective way to study their ecology [7].

Passive acoustic monitoring (PAM) has been successfully used in ecological studies [8–10]. It enables extensive geographical areas to be monitored, from hours to months [11], and reveals the occupancy patterns in space and time [12]. Such studies can improve conservation and management plans, determining the presence of dolphins in marine protected areas or areas important for fishery activities, investigate their habitat use, monitor their responses to anthropogenic activities, and estimate population parameters [8,13–17]. When using PAM, however, researchers need to make decisions about the most appropriate acoustic devices and their sampling protocol. These are based on the research aims and budget, and target species particularities, such as the amplitude of their acoustic emission frequencies [18,19].

For odontocetes, echolocation clicks are the key emissions recorded by PAM because they are used in their most frequent behaviors, such as navigation and foraging [20–23]. Echolocation clicks can be produced over a wide frequency range, and acoustic devices with high sampling rates, ranging up to 576 kHz, may be important in some situations [8,14,24]. These acoustic devices can be expensive [7], which constrains the use of PAM when the study budget is limited [25,26]. However, when the aim of the study is only to detect presence-absence patterns (i.e., distribution, occupancy and use of habitat), an acoustic device that, even partially, records clicks in the lower frequencies, can be a cost-effective alternative. To use these lower-frequency devices, it is crucial to know the possibility of recording clicks at different frequencies.

The minimum sampling rate required for echolocation acoustic records also depends on the target species. Some cetacean species, as *Kogia* spp and *Pontoporia blainvillei*, produce narrowband high frequency (NBHF) echolocation clicks [28,29], which often restrict the minimum sampling rate to higher frequencies. In contrast, if clicks have a wide frequency range, they can be recorded at lower frequencies. For instance, for some species of the Delphinidae family, such as the common dolphins (*Delphinus delphis*), the detection rate of burst pulse clicks was similar between sampling rates at 96, 192, and 300 kHz, and the burst pulse acoustic parameters were also similar between those frequencies [27]. This indicates that the use of more cost-effective devices, that do not record higher frequencies, may be effective for at least some species. Furthermore, the use of lower sampling rates would improve the storage and processing of the large volume of data collected during a PAM [27].

The use of lower frequencies also seems a possibility for researches on *Tursiops truncatus*, which has broadband echolocation clicks [30–32]. Their echolocations occur from audible frequencies (<20 kHz) to at least 150 kHz [33]. However, there are no studies that describe the proportion of echolocation clicks that occur in different frequencies through this frequency range, neither how efficient lower sampling rates are to record these clicks of free-living animals. Here, we evaluated whether the echolocation clicks produced by the bottlenose dolphins can be effectively recorded in frequencies up to 24 and 48 kHz. We aim to promote the use of PAM in ecological research on bottlenose dolphins, because it is a useful tool that can inform conservation and management plans, especially in countries where science budgets are limited.

2.3 METHODS

2.3.1 Data sampling

Echolocation clicks of two bottlenose dolphin subspecies that occur across different environments in the western South Atlantic Ocean (wSAO) were analyzed. These were *Tursiops truncatus truncatus*, which are found in open waters, and *T. t. gephyreus*, which are found in coastal areas. We collected *T. t. gephyreus* data from the lagoon system adjacent to Laguna (28º20'S, 48º50' W), southern Brazil (Fig. 1). This lagoon system has depths of between 0.4 and 13 m, with an average depth of 1.8 m. The data were collected from December 4th to 12th, 2017, using a 4.4 m inflatable research boat with a 30 hp outboard engine. The recordings were made with the engine off at sites with depths of 2.5 to 5.0 m. The hydrophone was positioned 1.5 m from the surface and 15 groups were sampled using recordings that lasted around 4 to 34 min. Each sampled group contained two to seven dolphins that were displaying travel or foraging behavior (Table S1).

The *T. t. truncatus* were opportunistically recorded in open waters by the Cetaceans Project Monitoring in the Santos Basin area, south and southeastern Brazil. The data were collected on February 14th and 24th, 2017, from three sites near the coast, at depths of 21, 28, and 35 m (Fig. 1; Table S1). Photographic records confirmed the subspecies *T. t. truncatus* [34]. The group sizes ranged from 12 to 30 individuals, and two groups showed travelling behavior, and one was travelling/foraging. The recordings lasted approximately 7 to16 min (Table S1). Two types of vessels were used: a 23.7 m mini supply vessel with two 325 hp engines and a 5 m inflatable boat with a 50 hp outboard engine. The hydrophone was positioned 5 m from the surface and the engines were off during the recordings.

All the recordings from both subspecies were made using a Reson TC 4032 hydrophone (0,005-120 kHz) connected to a Sony PCM-D100 recorder with a sampling rate of 192 kHz/24 bit (maximum frequency of 96 kHz – Nyquist frequency).

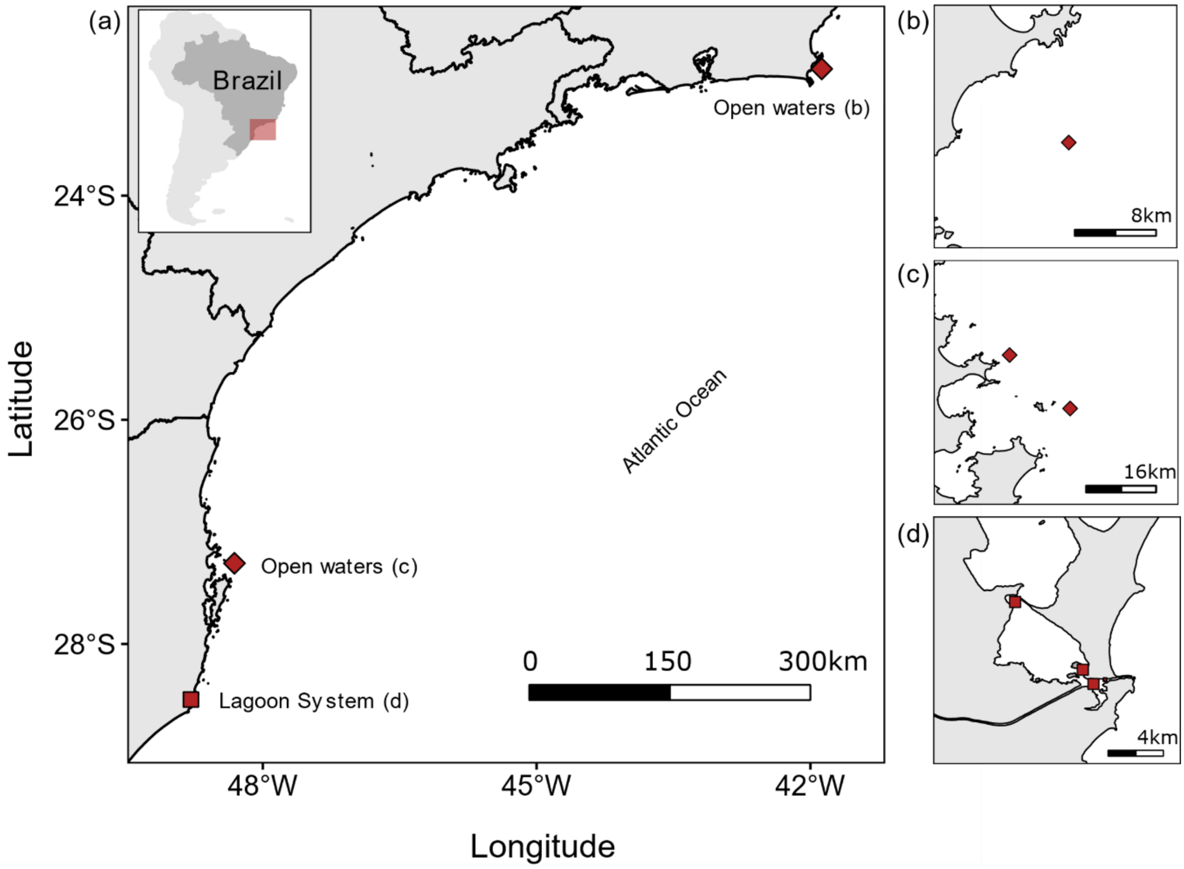

Figure 1: Data collection sites in the Brazilian coast of the western South Atlantic Ocean. Recording sites of *Tursiops truncatus truncatus* in open waters (b and c) and recording sites of *Tursiops truncatus gephyreus* in a lagoon system in southern Brazil (d). Coordinates were re-projected to WGS84 datum.

2.3.2 Sample processing

Two different approaches were used to analyze if echolocation clicks recorded in a frequency range up to 96 kHz can be recorded in frequency ranges below 24 and 48 kHz. First, the recordings were assessed visually through spectrograms to quantify the proportion of echolocation clicks occurring in each frequency range of interest. That is, each click observed in the spectrograms was verified if it occurred below and above frequency thresholds of 24 and 48 kHz. Second, the recordings were downsampled at 48 and 96 kHz (Nyquist frequency of 24 and 48 kHz, respectively) and processed by an automatic signal detector, to test if echolocation clicks are recorded when recordings are made at a lower sampling rate.

2.3.3 Proportion of echolocation clicks in each frequency range

The recordings from each dolphin group were fractionated into 1-minute samples to standardize the sample units. However, some recording durations were longer than multiples of 1 minute. Therefore, to use all records, we included samples of less than 1 minute in the analysis, that is those sections beyond the 1-minute limit of the last sample. We analyzed the samples in spectrograms using Raven Pro 1.6.1 software, with a sampling rate of 192 kHz/ 24 bit, Hann window, 512 points in size, and overlap of 50%. Raven uses Fourier transform to create spectrograms as a frequency domain representation of the signal.

The spectrograms were visually inspected to identify echolocation clicks. These clicks were defined and identified as those belonging to click trains with interclick intervals longer than 10 ms [9,35,36]. The total number of echolocation clicks recorded up to 96 kHz was counted manually. Each echolocation click was visually inspected to verify its occurrence below and/or above frequency thresholds of 24 kHz and 48 kHz given the full frequency range of the recordings. Then clicks were counted in each frequency threshold to estimate the proportion of clicks that appear in each threshold. The total number of echolocation clicks recorded up to 96 kHz was paired with the total number of echolocation clicks that occurred in 24 kHz and/or 48 kHz thresholds (Fig. 2). This is because the same click, when visualized below 24 kHz, was counted as “up to 24 kHz” and “up to 48 kHz” (Fig. 2, the solid line brown rectangles), while the clicks with frequencies above 24 kHz, but below 48 kHz, were only counted as “up to 48 kHz” (Fig. 2a, the dashed line brown rectangle).

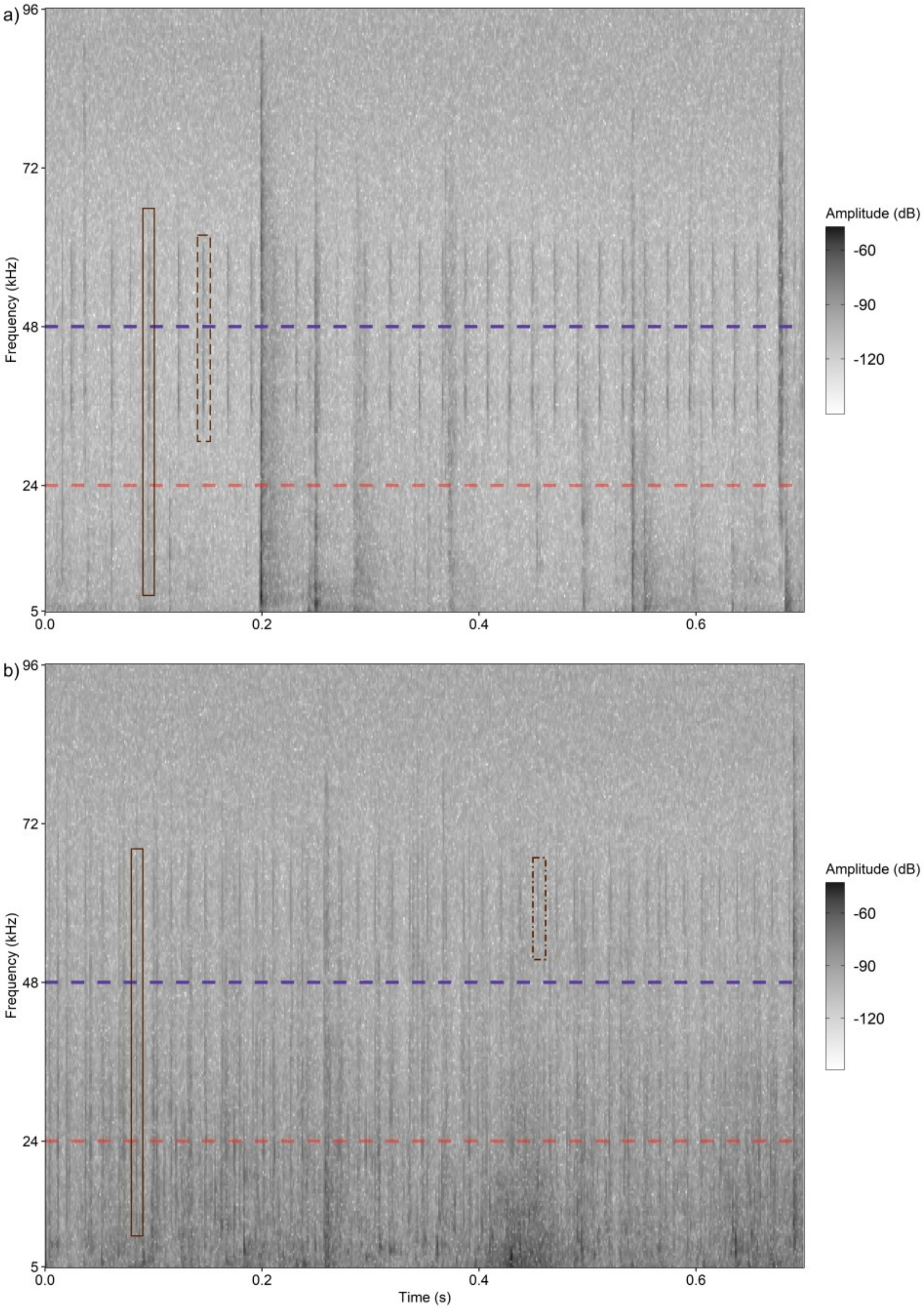

Figure 2. Spectrograms of a sample subset show the broadband frequency (kHz) of bottlenose dolphins echolocation clicks over time. Dashed lines are color coded to define the 24 and 48 kHz frequency thresholds. Brown rectangles indicate echolocation clicks detected below 24 and 48 kHz (solid line),

clicks detected below 48 kHz and above 24 kHz (dashed line in a), and clicks detected above 48 kHz (dot dash line in b).

2.3.4 Downsampling and automatic detections

A sampled high-frequency signal can change when it is sampled in different, lower sampling rates [30]. Because of this, in our second approach, the recordings were downsampled at 48 and 96 kHz to analyze if echolocation clicks are recorded at 24 and 48 kHz, using an automatic signal detector. The downsample and the following automatic clicks detection were made using R 3.6.0 [37]. First, a fourth-order Butterworth 15 kHz high-pass filter and an anti-aliasing Finite Impulse Response (FIR) low-pass filter to the 24 or 48 kHz were applied in the original recordings, for each corresponding downsample frequency. Then, the downsample was made using the “downsample” function of the “tuneR” R package [38]. Next, we used the “auto_detec” function of the “warbleR" R package [39] to detect the echolocation clicks automatically in recordings at 96, 48, and 24 kHz—in other words, the original and downsampled frequencies. The parameters to configure the “auto_detec” were defined through the “optimize_auto_detec” function from the “warbleR" R package [39].

The “optimize_auto_detec” function takes a selection table containing the times of each signal (echolocation clicks, in this case), and then run the automatic detection with multiple parameters to find the ones that maximizes sensitivity and specificity of signal detections compared to the selection table. Subsamples of 5-seconds from different recordings and different dolphins’ groups were used to select the echolocation clicks and validate automatic detections. The selection tables contained one subsample of each *T. t. truncatus* group (total of three groups), and one subsample of two different *T. t. gephyreus* groups. The signals were manually selected in the subsamples of each sampling rate, to define the best-adjusted parameters to detect clicks in each frequency (96, 48, and 24 kHz). The least number of subsamples from *T. t. gephyreus* used was due to these dolphins are from the same population and environment (lagoon system).

Even though we have selected the optimal parameters to configure the signal detector based on *a priori* manual detections, the sensibility and specificity of the detector were not the same to all recordings. Then, only the presence/absence of signal detections were considered, since we cannot guarantee that all detections are true positive. Furthermore, additional filters were applied to reduce the number of false-positive detections. First, all detections were filtered based on the interval of signals detected, similar to interclick intervals [see 40], excluding detections with an interval longer than 0.2 s, since echolocation clicks occur in click trains, not isolated. Second, the detection localization (in time) in the original recording was compared with detection localization in downsampled recordings, assuming the detector performance was better in recordings at 96 kHz. Since the echolocation clicks in the downsampled recordings tend to be longer than in the original record, a buffer was created around each detection of the original recordings by expanding the start and end time of detections by the length of each signal (i.e. click duration) to guarantee the match between the same detections at each frequency. Next, recordings were divided into bins of one second and matching bins from the division of the 1-minute samples from the first approach.

The bins from the original recordings (96 kHz) were binarized. Only 1-second bins with at least one signal detected present were kept and compared with the same respective bins in 24 and 48 kHz. Finally, the matches between bins with the presence of signals in downsampled recordings (24 and 48 kHz) and in original recordings (96 kHz) were quantified. Finally, this yields a proportion of seconds with signals detected in downsampled recordings given the total number of seconds with detections in the original files. These proportions in each 1-minute sample (or fractions) were used to calculate the probability to detect echolocation clicks at 24 or 48 kHz.

2.3.5 Sampling rate assessment

First, the hypothesis that bottlenose dolphins echolocation clicks occur equally in frequencies ranges of up to 24, 48 and 96 kHz, when recorded from free-living animals, was tested. A generalized linear mixed-effects models (GLMM) was constructed using a binomial error structure with a logit link function. The proportion of echolocation clicks that occurs at each frequency range out of the total number of echolocation clicks recorded up to 96 kHz was the response variable and the frequency range and environment (lagoon system or open water) were fixed effect terms. To account for sample pairing (up to 24 kHz and up to 48 kHz), pairs of samples were treated as random effects and were used nesting within recording identities to account for autocorrelation in group composition and behavioral context during sampling.

A candidate model was built to test the hypothesis and it was compared to a null model containing only the intercept. Models were compared using the Akaike information criterion corrected (AICc) for small samples and the Akaike weights [41]. The model with the lowest AICc value and the highest Akaike weight was considered to be the most parsimonious and the one that better supported data variation [41]. We simulated 10,000 datasets from the fitted model to validate the model assumption. Then, the Kolmogorov-Smirnov test was used to determine whether the deviations between the observed and expected residual distributions were significant [Fig. S1; for details about validation methods see 42]. The random effects were validated by visually comparing a QQ-plot of the random effects quantiles against the standard normal quantiles (Fig. S2 and Fig. S4). The assumptions were valid if most values fell along the line. Model fit was assessed using the theoretical marginal and conditional R^2_{GLMM} [43]. Marginal R^2_{GLMM} represents the proportion of the total variance explained by the predictors (fixed effects) and conditional R^2_{GLMM} represents the proportion of the variance explained by both the fixed and random effects.

Finally, the hypothesis that the echolocation clicks are recorded at frequencies up to 24 and 48 kHz, was tested. A second set of GLMM was constructed using a binomial error structure to test if echolocation clicks can be detected equally across the different sampling rates (the downsampled recordings). Considering only the bins with presence of at least one signal in the original frequency, the response variable was the proportion of bins with detections that occurs in the 1-minute samples at each downsampled frequency out of the total number of bins with detections in the equivalent sample in original frequency. The frequency and the environment (lagoon system or open water) were used as predictors, similar to the first model. The 1-minute samples were treated as random effects, nested within recording identities to account for autocorrelation in group composition and behavioral context during sampling. The next steps in this analysis, which involved candidate model build, models comparison, until the model fit assessment, were conducted as in the first model. All analyses were conducted using R 3.6.0 [37]. R Code used in the analyses is available in https://github.com/machadoams/botoclicks/.

2.4 RESULTS

A total of 3 h 16 min were recorded, 2 h 45 min from *T. t. gephyreus* and 31 min from *T. t. truncatus*, which resulted in 196 samples (158 lasting 1 min and 38 < 1 min). A total of 74,187 echolocation clicks were counted manually in the 96 kHz frequency range. Echolocation clicks occurred below the 24 and 48 kHz frequencies ranges in all samples analyzed visually (Table 1). A total of 8527 1-second bins with detection present from original recordings were compared with the same bins from 24 and 48 kHz downsampled recordings.

Table 1. Sample size per group and descriptive results of clicks counted manually. Samples where echolocation clicks occurred below 24 kHz and 48 kHz frequencies ("Samples with occurrence"), and the total echolocation clicks occurrence below each of these frequencies ("Total clicks observed") on each analyzed subspecies in their environment, lagoon system and open waters. The total variation of clicks counted in each frequency ("min-max clicks counted")

Subspecies/ Environment	Frequency threshold	Samples with occurrence (N observed/Total)	Total clicks observed (Mean ± SD)	min–max clicks counted
T. t. gephyreus/ Lagoon system	24kHz	159/159	44,546 (280 ± 293)	7–1,668
T. t. gephyreus/ Lagoon system	48kHz	159/159	49,627 (312 ± 336)	7–2,163
T. t. truncatus/ Open Waters	24kHz	37/37	19,932 (539 ± 528)	10–2,120
T. t. truncatus/ Open Waters	48kHz	37/37	24,028 (649 ± 597)	13–2,243

2.4.1.1 Probabilities of record echolocation clicks below 24 and 48 kHz

To our first approach, using spectrograms, the most parsimonious model explaining differences in the likelihood of occurrence at the full range of echolocation clicks included an interaction between environment and frequency range (Table 2). The 24, 48, and 96 kHz frequencies were not equally efficient. The likelihood of occurrence of echolocation clicks at the frequency range up to 24 kHz was lower than that up to 48 kHz in both the lagoon system (Log Odds ratio = -5.2, Std. Error = 0.104, df = 386, t = -50.430, P < 0.001) and open waters (Log Odds ratio = -3.655, Std. Error = 0.084, df = 386, t = -43.538, P < 0.001). Our model predicted a mean error in occurrence of only 0.95% in the frequency range up to 24 kHz (mean probability = 99.05% ± 0.003 SE; CI = 98.3-99,46%) and 0.01% in 48 kHz (mean probability = 99.99% ± 0.00001 SE; CI = 99.99-99.99%) in the lagoon system (Fig. 3). In open waters, we observed a mean error of 13.9% at 24 kHz (mean probability = 86.1% ± 0.061 SE; CI = 69.26-94.45%) and only 0.42% at 48kHz (mean probability = 99.58% ± 0.002 SE; CI = 98.85-99.85%) (Fig. 3; See Table S2 for more details on the comparisons). Such fixed effects accounted for 56.70% (marginal R^2_{GLMM}) of the differences in the number of echolocation clicks detected, and 99.94% (conditional R^2_{GLMM}) when both the fixed and random effects were considered.

Table 2: Comparison between null models and the candidate models for the proportion of clicks recorded in different frequency ranges and reduced sampling rates. Predictors included in binomial Generalized Linear Models are shown in the columns "Env" (Environment), "Freq" (Frequency Threshold) and "Env:Freq", which represents the interaction term between the two predictors. The response variables were the proportion of echolocation clicks recorded in each frequency range out of the total clicks recorded/detected up to 96 kHz (Proportion of echolocation clicks in each frequency range), and the proportion of seconds with signals detected in downsampled recordings given the total number of seconds with detections in the original files (Proportion of detection in each frequency). Models are ranked by AICc (Akaike Information Criteria corrected for small samples), and presented along with the degrees of freedom (df), log-likelihood (log-like), the change in AICc relative to the best model (ΔAIC), Akaike Weights

Model	Intercept	Env	Freq	Env: Freq	*df*	log-like	AICc	ΔAICc	Akaike Weight
Proportion of echolocation clicks in each frequency range									
M1	4.650	+	+	+	6	-1404	2820	0	1
Null Model	4,822	-	-	-	3	-8435	16876	14056	0
Proportion of detection in each frequency									
M1	0.8532	+	+	+	6	-1291.515	2595.2	0	1
Null Model	1.6240	-	-	-	3	-2454.155	4914.4	2319.17	0

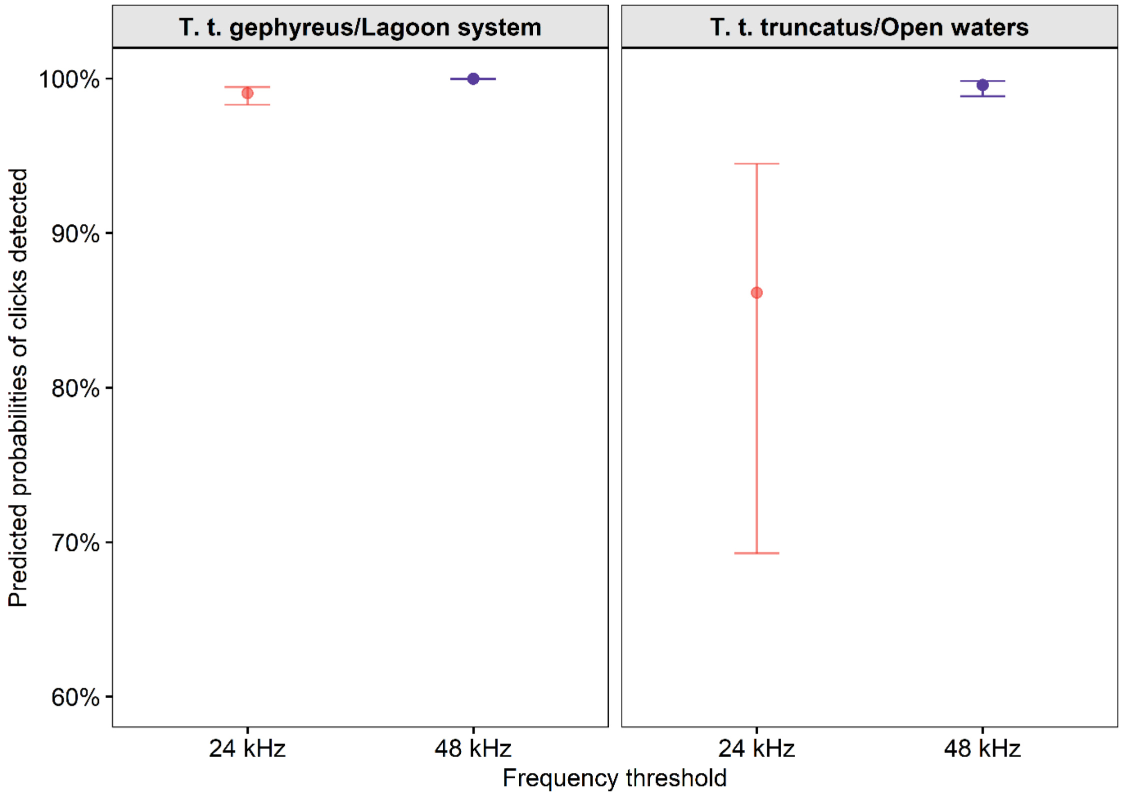

Figure 3: Predicted probabilities of echolocation clicks recorded below 24 and 48 kHz. Dots and whiskers indicate the estimated marginal means for each frequency range and the 95% confidence intervals, color coded by the frequency range. Estimated marginal means are back-transformed from the logit scale.

2.4.1.2 *Probability of detecting clicks in downsampled recordings*

To the approach using the automatic signal detector, the candidate model had better support than the null model (Table 2). The 24, 48, and 96 kHz frequencies were not equally efficient. The likelihood of detecting the signals from the original frequency (96 kHz) at the 24 kHz was lower than that at 48 kHz in both the lagoon system (Log Odds ratio = -2.089, Std. Error = 0.054, df = 558, t = -38.241, P < 0.001) and open waters (Log Odds ratio = -1.878, Std. Error = 0.137, df = 588, t = -13.620, P < 0.001). Our model predicted a mean error in detection of 29, 88% at 24 kHz (mean probability = 70,12% ± 0.02 SE; CI = 66.14-74.1%) and 5,01% in 48 kHz (mean probability = 94.99% ± 0.005 SE; CI = 93.99-95.99%) in the lagoon system

(Fig. 4). In open waters, we observed a mean error of 12.37% at 24 kHz (mean probability = 87.62% ± 0.023 SE; CI = 82.95-92.3%) and 2,11% at 48kHz (mean probability = 97.88% ± 0.005 SE; CI = 96,88-98,89%) (Fig. 4; See Table S3 for more details on the comparisons). Such fixed effects accounted for 55.7% (marginal R^2_{GLMM}) of the differences in the number of detections, and 95.9% (conditional R^2_{GLMM}) when both the fixed and random effects were considered. The scaled residuals slightly deviate from the expected distribution (Fig. S3).

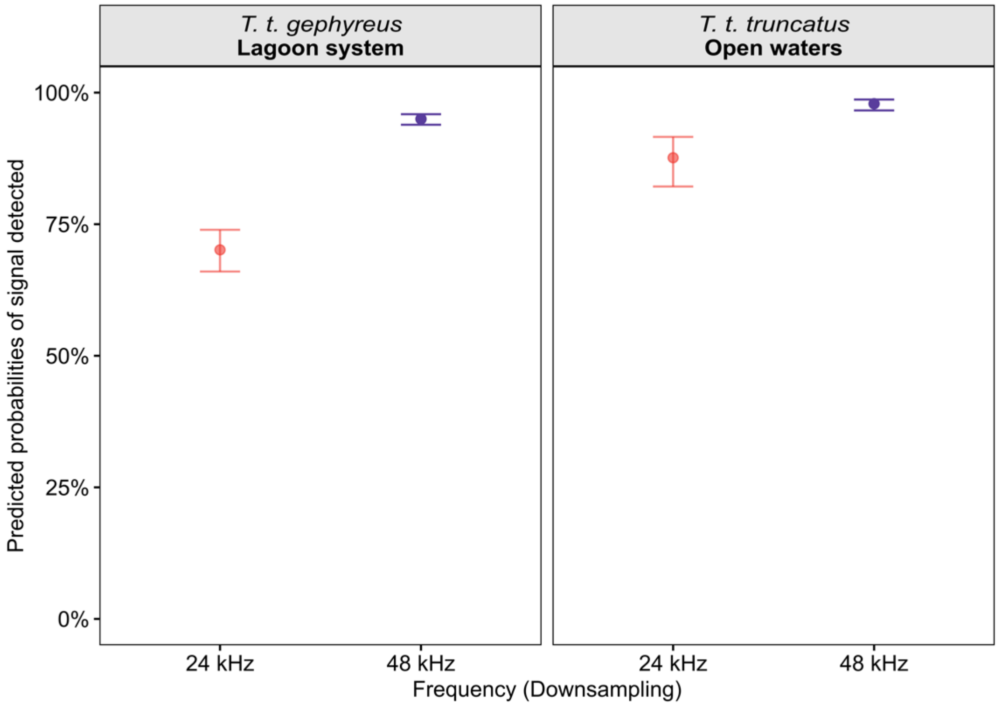

Figure 4: Predicted probabilities of detecting signals in downsampled recordings below 24 and 48 kHz. Dots and whiskers indicate the estimated marginal means for each frequency and the 95% confidence intervals, color coded by the frequency. Estimated marginal means are back-transformed from the logit scale.

2.5 DISCUSSION

We show for the first time that most of the echolocation clicks of free-living *Tursiops truncatus* recorded up to 96 kHz also occur in frequency ranges below 24 kHz and 48 kHz. In downsampled recordings, echolocation clicks are also detected below these frequencies. This showed that *T. truncatus* often produce echolocation clicks in a frequency range that can still be recorded with reduced sampling rates.

These findings showed that acoustic devices that only record maximum frequencies of 24 kHz and 48 kHz could be used to investigate ecological aspects of bottlenose dolphins, such as distribution and habitat use [44,45]. These reduced frequencies could improve PAM programs, reduce equipment costs, and facilitate data storage and management. Ultimately, this research will benefit bottlenose dolphin conservation in developing countries or where PAM programs to study this species are compromised by costly equipment.

Our estimate of the proportion of echolocation clicks recorded with frequency ranges below 24 and 48 kHz shows that these clicks can be recorded at lower frequencies. However, this proportion cannot be extrapolated to the echolocation clicks recorded at lower sampling rates. When a high-frequency signal is sampled with a low sampling rate, the sampled signal can be different from the real signal [30]. Then, we downsampled the recordings to simulate recordings made with lower sampling rates and confirm that echolocation clicks are still preserved in these frequencies. Therefore, unfortunately, we cannot present a definitive evaluation of the performance of lower sampling rates in recording echolocation clicks because of the effect of three main reasons discussed below: frequencies evaluated, soundscape, and detector performance.

Downsampling the original files at 48 and 96 kHz sampling rates increase the soundscape interference in the signal detection. Snapping shrimp snaps, for example, are commonly present in the soundscape, and their sound is similar to dolphin clicks [46–49]. In our study area, mainly in the lagoon system, snapping shrimp snaps are part of the soundscape. Then, when we used the automatic detector in the downsampled recordings, especially at 24 kHz, the detection performance was limited. It is not difficult to differentiate the echolocation clicks from the snapping shrimp snaps when visually inspecting spectrograms. The former has patterns in inter-clicks intervals [46]. However, the soundscape composition can limit the use of an automatic detector [50]. To avoid counting shrimp snaps, we could exclude as much as possible the false positive detections using some addition steps in our processing protocol. However, there are not a definitive solution to this problem [50], and the use of automatic detector at lower sampling rates has some limitations.

Despite these limitations considered, our main goal here was to test if lower frequencies can be used to record the presence of bottlenose dolphins through echolocation signals. Analyzing the downsampled recordings, we showed that echolocation clicks are recorded even in recordings at low sampling rates. Therefore, our results, from both frequency range and detection analysis, show that echolocation clicks emissions from *T. truncatus* can be recorded using at least 24 kHz (sample rate of 48 kHz) and a 1-minute sample size is sufficient to record the clicks. However, there were differences in the proportion of echolocation clicks that occur and the probability of detection below 24 kHz between the two subspecies.

Analyzing the frequency ranges, we found that the chance of occur echolocation clicks from *T. truncatus truncatus* below 24 kHz was smaller and more inaccurate, although clicks were visualized below this frequency in all samples. We decided to analyze two subspecies in two different environments, even with few records of *T. t. truncatus*, because the acoustic parameters of echolocation clicks can vary between different *Tursiops* species [51] and environmental characteristics can affect sound production and propagation [5,52,53]. However, we were unable to distinguish whether the reduction in the occurrence of echolocation clicks from *T. t. truncatus* below 24 kHz is due to environmental variations, differences in sound emissions between subspecies, or both, because each subspecies inhabits a different environment and can adapt their sound emissions according to environmental characteristics [54]. Furthermore, the random effects of our models show that other factors than the subspecies and the environment can also explain such variations in the frequency range of echolocation clicks. Many of these factors cannot be controlled when we record free-living animals, such as the distance and position of a moving dolphin to the hydrophone [55]. However, more samples from *T. t. truncatus* can help us to understand this pattern, as well as consider other variables such as behavior, group size and composition, environmental conditions, etc.

The results from the automatic detector showed that clicks are more likely to be detected in recordings at 24 kHz from *T. t. truncatus* than in recordings from *T. t. gephyreus* at same frequency. This result can be representing the effect of the soundscape. Since the soundscape in our samples from the open waters had fewer snapping shrimp snaps, the detection performance in this environment was quite better. Despite the limitation aforementioned, the general results from the automatic detections reinforces our findings using manual inspection of the frequency ranges: recordings at 48 kHz are better than 24 kHz to record or detect echolocation clicks, but the 24 kHz can still record echolocation clicks. In this respect, our results also indicated frequencies at which the acoustic repertoire of *T. truncatus* can be recorded.

By showing that echolocation clicks could still be recorded and detected below 48 kHz, our results reinforce the idea that most sounds made by *T. truncatus* can be recorded at low frequencies, even below 24 kHz [56]. Although some burst pulsed sounds and echolocation clicks are exclusively ultrasonic [56], this seems to be uncommon. Burst pulsed sounds that are formed by broadband pulses in a similar way to echolocation signals, generally present frequency components in the audible frequency range [57–59]. The components of echolocation clicks that have low frequencies appear when recordings are made outside of the transmitting beam of the dolphin. Echolocation clicks are emitted in a directional beam forward from the melon in the dolphin head. High frequency echolocation clicks are recorded mainly when recordings are made on the axis of the beam [5]. Outside the beam, the low-frequency portion of echolocation clicks suffer less attenuation and lower-frequency components are introduced in the click frequency spectrum [60–62]. Therefore, it is expected low-frequency elements become more common when recording free-living animals because these recordings are mainly off-axis of the dolphin transmitting beam. Finally, *T. truncatus* whistles usually occur at frequencies up to 30 kHz [59,63]. Specifically, in the *T. t. gephyreus* population sampled, less than 1% of whistles had part of fundamental frequency above 24 kHz [64]. Therefore, we can conclude that all sounds produced by *T. truncatus* can be recorded using a frequency of 48 kHz. It is also possible to use a frequency of 24 kHz if some information loss is acceptable.

Here, we showed that lower frequencies record bottlenose dolphins' echolocation clicks efficiently for a set of ecological studies. In other words, studies that investigate the occurrence or distribution of individuals in a population, when presence/absence data are sufficient, can use recordings at low frequencies. However, it is necessary to highlight, when the goal is to analyze acoustic parameters of clicks or identify different dolphins' species, it is recommended to record, as much as possible, all clicks frequency ranges [51,65]. Also, it should consider the soundscape of the study area, thinking about possible solutions to the acoustic data analysis.

Despite the limitations discussed here, the effectiveness of reduced sampling rates when recording echolocation clicks should stimulate the acoustic monitoring of bottlenose dolphins, maybe other cetaceans, in developing countries where the available methods for studying marine mammals remain limited due to budget restrictions [26]. Despite being an effective way to study cetaceans [19,66], PAM is still expensive [25]. Inexpensive alternatives with modular hardware and open-source software exist for PAM in terrestrial environments [67], but adaptations to record high frequencies are still required. Recently, a low-cost acoustic device has been developed with sampling rates up to 384 kHz [68]. Its new version permits connecting a hydrophone on it. It can be a solution to implement a PAM project with a limited budget, but the costs can be higher when considering import taxes and shipping costs. Although it is necessary to investigate other dolphins species, showing that *T. truncatus* echolocation clicks are effectively recorded at lower frequencies will encourage the use of alternative acoustic devices with lower sampling rates. This will help to alleviate the prohibitive cost faced by researchers in developing countries even though some compromises need to be accepted when using lower sampling rates [19].

2.6 CONCLUSION

We conclude that a frequency of 48 kHz is effective on recording the entire acoustic repertoire of *T. truncatus*, including echolocation clicks. However, it is also possible to use 24 kHz to record *T. truncatus* if some information loss is acceptable. Furthermore, 1-minute sample size is sufficient to record echolocation clicks with frequencies of 24 and 48 kHz, considering the limitations of these frequencies. Ultimately, our results can expand the use of PAM as an accessible tool to ecological studies that can help conserve bottlenose dolphins, especially *T. t. gephyreus*, an endemic subspecies that occurs from southern Brazil to central Argentina and has recently been categorized as vulnerable [69].

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2.9 AUTHOR CONTRIBUTIONS

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3 CHAPTER 2:

24 HOURS WITH BOTTLENOSE DOLPHINS: AN ACOUSTIC EVALUATION OF TEMPORAL AND SPATIAL VARIATIONS

3.1 SUMMARY

Cetaceans do not have a pre-defined time for activities and rest. However, they are influenced by prey distribution and availability, which means that their behavior is influenced indirectly by environmental variables to which the prey responds. Thus, to understand the behavioral patterns, distribution, and habitat use of cetaceans, it is necessary to observe them continuously through diel cycles or to understand the prey dynamic, which is challenging. We implemented passive acoustic monitoring (PAM) to monitor and evaluate the resident bottlenose dolphin population in Laguna, Santa Catarina state, on a spatial and temporal fine-scale. That population shows a rare foraging strategy, interacting positively with artisanal fishers, which might influence the dolphins' home range—previously mapped from photo-identification data. PAM allows for evaluation of the effects of environmental factors (wind, tide, and period of the day) in the dolphins’ distribution through the diel, besides determining the role of the interaction with fishers in the home range definition. Our results agree with the known spatial pattern, suggesting that the occupancy proportion of the area increases at night, and wind and tide influence space use. From a conservation point of view, such results confirm that the core area is adequate for management actions since this area is used all the time, even at night, when the dolphins are not interacting with the fishers.

3.2 INTRODUCTION

Mammals have circadian rhythms with time for activities and rest associated with day and night alternation, classified as nocturnal, diurnal, or crepuscular according to the period during which they are active (ASHBY, 1972; HALLE; STENSETH, 2000). However, circadian rhythm also shows an adaptative component related to the ecological implications of the environment, where each species live, and also according to the way of life (BLOCH *et al.*, 2013; HALLE; STENSETH, 2000; YERUSHALMI; GREEN, 2009). Food resource availability is one of the factors adapting the circadian rhythm at a physiological level (HOUSER *et al.*, 2021; VERWEY; AMIR, 2009). Predators tend to have activities periods associated with the activities period of their prey, ensuring access to that prey with a lower energetic cost in the foraging (HALLE; STENSETH, 2000; MONTERROSO; ALVES; FERRERAS, 2013). That is the case with the cetaceans. They are at the top of the trophic chain (BALLANCE, 2018), and do not restrict their time of activity according to the day and night alternation, but they show activities patterns modulated by prey distribution (FRIEDLAENDER *et al.*, 2009; HOUSER *et al.*, 2021; IZADI *et al.*, 2018; WANG *et al.*, 2014).

Some cetaceans species can show movement patterns that vary between day and night because of the prey's vertical or horizontal migration in the water column or between shallow and deep water, respectively (e.g., FRIEDLAENDER *et al.*, 2009; GANNIER, 1999). Prey also respond to environmental factors such as water temperature, salinity, depth, chlorophyll concentrations, etc., which means that such factors can indirectly define the cetaceans' behavioral context, defining movements and foraging activity cycles (STOCKIN *et al.*, 2008; TORRES; READ; HALPIN, 2008). Therefore, for a comprehensive understanding of cetacean behavioral aspects, like distribution and habitat use, it is necessary to understand the prey dynamic, which is logistically challenging (AU *et al.*, 2013), or observe the cetaceans during diel cycles.

The present study monitored a *Tursiops truncatus gephyreus* population that, besides being well-known and studied for a long time, has some questions to be answered about their ecology. One of these questions is about the distribution of these dolphins, which may be influenced by environmental factors and foraging strategies. This bottlenose dolphin population is small (~60 individuals) (BEZAMAT *et al.*, 2019) and inhabits the lagoon adjacent to Laguna city, in Southern Brazil. This population is highly resident and has been studied since begin 1990’s (DAURA-JORGE; INGRAM; SIMÕES-LOPES, 2013; SIMÕES-LOPES; FABIAN, 1999), mainly because these dolphins have developed a specialized foraging tactic, interacting cooperatively with artisanal net-casting fishers, in the cooperative fishing (ver SIMÕES-LOPES, 1991; SIMÕES-LOPES; FÁBIAN; MENEGHETI, 1998). Such foraging specialization, which is not equally practiced by all dolphins in terms of the frequency they use the tactic, defines multiple aspects of the ecology of these animals, such as social relationships, acoustic communication, home range, and survival probability (BEZAMAT *et al.*, 2019; CANTOR; SIMÕES-LOPES; DAURA-JORGE, 2018; DAURA-JORGE *et al.*, 2012; MACHADO *et al.*, 2019; ROMEU *et al.*, 2017). However, all these relations and patterns known until now are from data collected during the day, disregarding nocturnal behavior.

Understanding how this population uses their home range at night is relevant to define local management and conservation actions, besides helping understand the factor that modulates the distribution of these animals. The main threat to the long-term viability of this dolphin population is the bycatch in trammel nets (BEZAMAT *et al.*, 2021), used mainly at night to fish catfish (PETERSON; HANAZAKI; SIMÕES-LOPES, 2008). In response to dolphins mortality in that nets, in 2018 a municipal law was sanctioned (number 1,998) prohibiting fishing with trammel nets in the core area of dolphins (see BEZAMAT *et al.*, 2021). However, that core area was mapped by photo-identification data, exclusively collected during the day (CANTOR; SIMÕES-LOPES; DAURA-JORGE, 2018). To confirm the adequacy of this fishing exclusion area as a conservation strategy, it is necessary to know if the dolphins use the area with the same frequency at night. Then, passive acoustic monitoring (PAM) was implemented for continuous monitoring of the dolphins in diel cycles.

Passive acoustic monitoring has been an efficient tool for studying cetaceans, which use sounds in many aspects of their lives (ZIMMER, 2011). Clicks and whistles are among the acoustic signals emitted by dolphins (HERMAN; TAVOLGA, 1980). Clicks are pulsed sounds with their energy spread in a broad range of frequency used for echolocation (HERMAN; TAVOLGA, 1980; JONES *et al.*, 2020). Echolocation can be used for navigation and foraging, therefore, frequently used during most parts of dolphins' behavior (e.g., AKAMATSU *et al.*, 2005, 2007; EVANS; PRESCOTT, 1962). Another kind of acoustic signal is whistles. They apparently are frequency-modulated and used for communication (HERMAN; TAVOLGA, 1980).

From the recorded echolocation and whistles, it was possible monitoring the presence of the dolphins during diel cycles to test the hypothesis that their distribution, among specific sites in their home range, varies according to factors like period of the day, tide, and wind. Then, our main objective was to evaluate the diel variation in the distribution and space used by the dolphins in their core area. The specific objectives were: (a) to evaluate the existence of variation in the dolphins' detection between day and night; (b) to investigate the influence, if any, of tide height and direction; (c) and the influence of wind intensity and direction, if any, in the dolphins' distribution at each monitored site. Then, we expect to inform and contribute to the effectiveness of local conservation actions and discuss the role of the cooperative foraging tactic in modulating the spatial patterns modulation of this population, evaluating the distribution of the dolphins through the day—when the interaction happens—and at night—when it does not happen.

3.3 MATERIAL AND METHODS

3.3.1 Study area

The bottlenose dolphin population (*Tursiops truncatus gephyreus*) studied here inhabits the lagoon system, consisting of three interconnected lagoons: Santo Antônio, Imaruí, and Mirim, located in Laguna city, Southern Brazil (28°28’57” S; 48°46’51” W). The lagoon system has a total area of 200 Km², an average depth of 1.8 m (0.4-13 m) and is connected to the sea by a channel in the Santo Antônio lagoon. Among the rivers which flow to that lagoon is the Tubarão River (Fig. 1).

Santo Antônio lagoon is part of the dolphins’ home range, and there is a core area located close to where the Tubarão River flows in the lagoon and the channel that connects the lagoon system with the sea (Fig. 1a; CANTOR; SIMÕES-LOPES; DAURA-JORGE, 2018). That core area is the home range of the dolphins that interact with fishers frequently, including part of the home range of the dolphins that do not tend to interact (CANTOR; SIMÕES-LOPES; DAURA-JORGE, 2018). Passive acoustic monitoring was concentrated in that area (Fig. 1b).

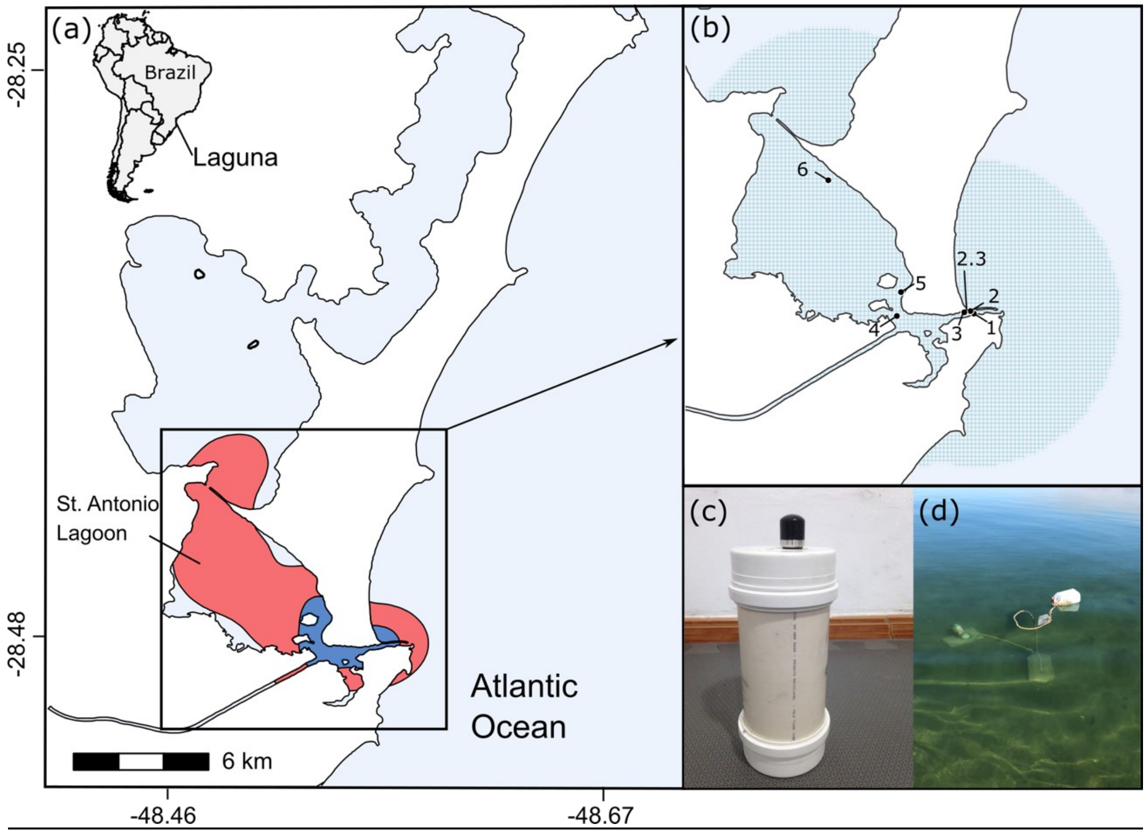

Figure 1: Lagoon system localization in Laguna, Southern Brazil (a), showing the home range of the dolphins that interact with fishers frequently in red and that of the dolphins that do not use to interact in blue. Study area detail (b), with numbers, lines, and dots indicating the sites where the recorders were deployed during the passive acoustic monitoring, according to the section "*Data collection*". Sites 2, 2.3, 3, and 5 are where happen the interaction between dolphins and fishers. The waterproof case for the recorders and the hydrophone outside (c). Mooring system for the recorder in site 6 (*Interior*; d).

3.3.2 Data collection

Static passive acoustic monitoring (PAM) was made using four to six recorders, moored across the study area (Fig. 1b-d). The data collection was carried out in 2020, once by season: 11th – 13th February (summer), 16th – 18th May (autumn), 23rd – 25th August (winter), and 14th – 16th October (spring). The recorders worked for two to three continuous days, depending on the battery time life, synchronized through the memory flash for a duty cycle of 5 minutes on and 5 minutes off.

In summer, four recorders operated: I) site 1, or *Boia*, the most external to the study area, located in the navigation channel that connects the lagoon system to the sea; a site where dolphins move through to enter or leave the lagoon system, sporadically foraging and rarely interacting with fishers in the cooperative fishing; II) site 2.3, located between the *Tesoura* and *Quarto* beaches, where the cooperative fishing happens during all the year, every day; III) site 4, or *Bambu*, close to the area where the Tubarão River flow to the lagoon, it is a site where dolphins move through and foraging; IV) site 5, or *IC*, in front of the Yacht Club, where the dolphins move through, foraging, and sporadically interacting with fishers (Fig. 1b).

In autumn and winter, six recorders were deployed. Besides sites 1, 4, and 5 deployed in the summer, another recorder was deployed in site 6 or *Interior*. That site is out of the dolphins' core area, more internal in the lagoon, and occasionally used by dolphins for different behavioral activities. Site 2.3 needed to be replaced by the recorder in sites 2, *Tesoura*, and 3, *Quarto*, due to a request from fishers who participate in cooperative fishing at those areas. In spring, the recorders were deployed in sites 1 to 5 but not in site 6 due to the tide condition that limited navigation.

When the recorders were operating, environmental variables were measured: tide height and direction, wind velocity and direction. Such data were collected per hour, for the locality Laguna (tide data) and Itapirubá (wind data, unavailable to Laguna) and provide by the *Centro de Informações de Recursos Ambientais e de Hidrometeorologia de Santa Catarina*, of the *Empresa de Pesquisa Agropecuária e Extensão Rural de Santa Catarina* (EPAGRI/CIRAM).

For the acoustic monitoring, we used SOLO audio recorders (WHYTOCK; CHRISTIE, 2017) connected to Aquarian H2c hydrophones (sensibility -180 dB re: 1V/µPa) (Fig. 2). We built SOLO recorders with Raspberry Pi A+ boards, Time Clock RTC DS3231, sound card Sound Blaster Play! 3 (to connect the hydrophones), Xiaomi Redmi 20.000 mAh power banks, and memory flashes. Due to the sound card limitation, the recordings were made with a sampling rate of 48 kHz/ 16 bits (Nyquist frequency: 24 kHz). Recorders were put into waterproof cases, made with PVC pipe and caps, keeping the hydrophone outside (Fig. 1c).

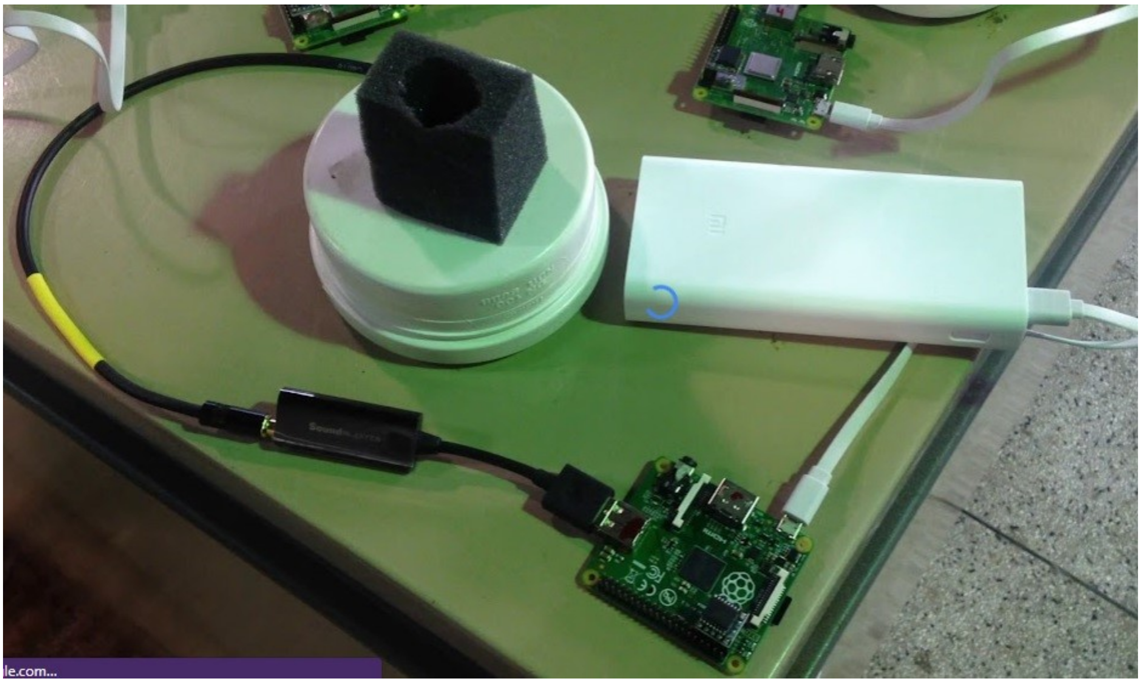

Figure 2: The SOLO audio recorder: a Raspberry Pi A+ board connected to a power bank and a hydrophone (attached to the PVC cap).

3.3.3 Data processing

For the analysis, we considered only recordings made when all recorders were operating. A dolphin detection was considered when clicks and/or whistles were recorded. The acoustic signal detection was made with Pamguard software, using the Click Detector module for clicks and Whistle and Moan Detector for whistles (GILLESPIE *et al.*, 2013). Whistles could be detected automatically. However, due to the background noise, composed mainly of snapping shrimps, to identify the recordings with echolocation clicks was necessary to analyze the recordings visually after the Click Detector results. Some filters were created to reduce the clicks from other sources, so all recordings needed to be manually screened to search for clicks trains with regular inter-click intervals which characterize echolocation signals and similar amplitude values.

3.3.4 Data analysis

For data analysis, we defined one hour as a sampling unit, which can be complete or fractional. As each recording lasts 5 minutes and is followed by a 5-minutes break without recording, in most cases a sampling unit (one hour) had 6 recordings. However, as the recordings at the end of the monitoring could be ended before completing one hour, for some samples the effort was less than 6 recordings. Thus, we defined as our response variable, the dolphin's occupancy probability of each monitoring site, as the proportion of 5-minutes recordings with positive detections in our sampling unit, which varied from 0 to 6 recordings in total.

For each sampling unit, we registered: date, hour, recording site, period (day or night), tide height, tide direction (ebb or flood), wind intensity (speed), and wind direction (south or north). We considered data from sites 1 (*Boia*), 4 (*Bambu*), and 5 (*IC*), and combined data from sites 2.3 and 3 (*Quarto*), for the analysis. Data from *Tesoura* and *Interior* were not considered, the first due to redundancy with *Quarto*, and the latter because was not sampled in all seasons.

After following the data exploration pre-defined protocols (see ZUUR; IENO; ELPHICK, 2010), a set of generalized linear mixed models (GLMM) was adjusted with different structure errors and link functions (BOLKER *et al.*, 2009; ZUUR *et al.*, 2009) to test if the dolphins' occupancy probability varied temporally, spatially and in response to the environmental variables. In all models, a first-order autocorrelation term was included nested to the season when the sample was collected to deal with autocorrelation. The sampling unit was included as random variable to deal with data overdispersion. Period (day or night), site, tide height and direction, wind intensity, and direction were included as explanatory variables. Interaction terms between site and tide height, site and tide direction, site and wind intensity, and site and wind direction were included to test specific hypotheses defined after data exploration. We first built addictive models, including all pre-defined explanatory variables, selecting those determinants by simplifying the model from stepwise backward elimination. Next, the interaction terms were included. We then used Akaike Information Criterion (AIC) and Akaike weight to rank and find the most parsimonious model (BURHAM; ANDERSON, 2002). Models were fitted in the R environment (R DEVELOPMENT CORE TEAM, 2019) with package 'glmmTMB' (MAGNUSSON *et al.*, 2017). The model selection protocol used the R package 'MuMIn' (BARTON, 2022). We considered plausible models when ΔAIC (model-minimum) < 2 (BURHAM; ANDERSON, 2002). Scaled residuals checking was executed with 'simulateResiduals' function of DHARMa package (HARTIG, 2020). Selected model predictions were plotted using the sjPlot package (LÜDECKE, 2022). The significance level in all statistical tests was 95% ($p < 0,05$).

3.4 RESULTS

Passive acoustic monitoring was carried out for 12 days, totalizing 195h40min of recordings per recorder, distributed in 46h30min in summer, 46h40min in autumn, 51h10min in winter, and 51h20min in spring. For all seasons, at least one 5-minutes recording had acoustic detection of dolphins at each hour (sampling unit) of the day in almost all monitored sites. The general average for all monitored sites was three 5-minutes recordings with acoustic detection per hour from the six possible recordings in one hour, defining an occupancy probability equal to 0.5. However, this occupancy probability varied among sites, with 0.3 recordings with detection per hour in Interior (site 6)—an occupancy probability equal to 0.05— 3.9 recordings with detection per hour in Bambu (site 4)—an occupancy probability equal to 0.65.

From 12 adjusted models, the most parsimonious suggests period and site as the most important factor affecting the dolphins' occupancy probability. For the site, such effect was conditioned to tide height and direction, and wind intensity and direction (Table 1 and Table 2). Occupancy probability was higher at night for all sampled sites (Odds: 2.19, CI: 1.55 – 3.11, $p < 0.001$; Table 2; Figure 3a, b). Besides the period of the day, the increase in wind intensity increased the occupancy probability in *Bambu*, *Quarto*, and Yacht Club (*IC*), decreasing the probability in *Boia* (Odds: 0.90, CI: 0.86 – 0.95, $p < 0.001$; Table 2; Figure 3a, c). In general, the occupancy probability was slightly higher during south winds in all sites but *IC*, where it was higher during north winds (Odds: 0.47, CI: 0.25 – 0.89, $p = 0.021$; Table 2; Figure 3a, d). When the tide was higher, occupancy probability increased in *Quarto* and *Boia* (respectively, Odds: 1.06, CI: 1.02 – 1.09, $p <0.001$; Odds: 1.04, CI: 1.01 – 1.06, $p < 0.015$; Table 1; Figure 3a, e), and decreased in *Bambu* and *IC*. The occupancy probability was also higher during ebb tide for all sites but *Quarto* (Odds: 2.97, CI: 1.53 – 5.76, $p = 0.001$; Table 2; Figure 3a, f).

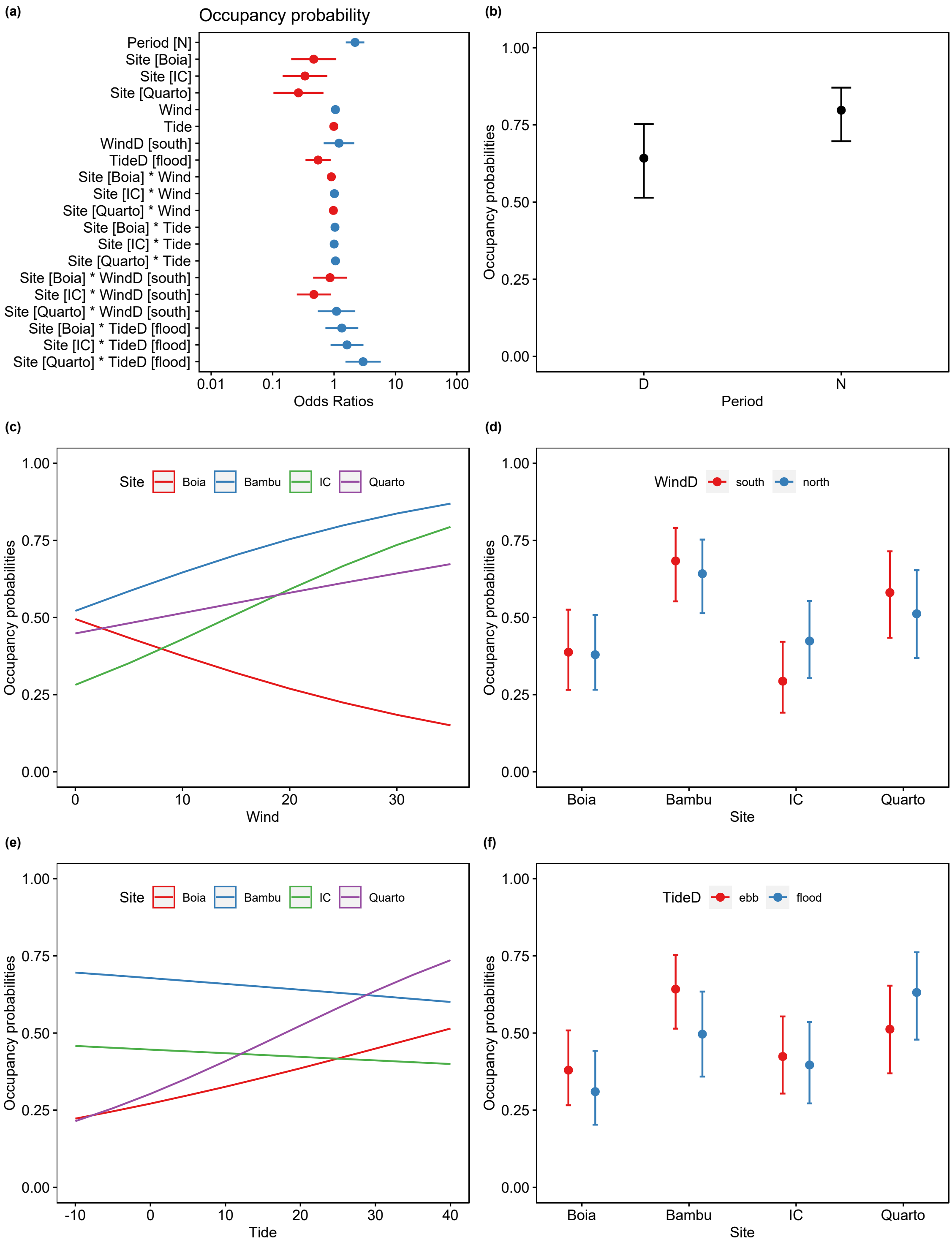

Figure 3: Odd ratios (a) and predicted values of fixed effects from the most parsimonious models (Table 1) describing the occupancy probabilities variation as a function of period (b) site and wind intensity (c) site and wind direction (d) site and tide height (e) and site and tide direction (f). Standard errors are represented.

Table 1: Generalized linear mixed models (GLMMs) for the response variable occupancy probability as a function of Period, Site, Tide, Tide direction (TideD), Wind and Wind direction (WindD), ranked by the lowest Akaike Information Criterion (AICc). Relative support for the models is given by the difference in delta AIC and AIC weights, while the model's goodness of fit is given by log-likelihood (logLik)**. df: degrees of freedom.**

GLMMs Models (fixed structure)	**df**	**logLik**	**AICc**	**delta**	**weight**
~Period + Site*Tide + Site*TideD + Site*Wind + Site*WindD	24	-1250,79	2551,36	0,00	0,8
~Period + Site*Tide + Site*Wind	16	-1260,70	2554,20	2,84	0,19
~Period + Site*Tide	12	-1272,04	2568,53	17,17	0,01
~Period + Site*Wind	12	-1273,83	2572,12	20,77	0
~Period + Site*TideD + Site*WindD	16	-1276,59	2585,98	34,62	0
~Period + Site*WindD	12	-1282,67	2589,80	38,44	0
~Period + Site*TideD	12	-1282,95	2590,35	38,99	0
~Period + Site	8	-1289,27	2594,75	43,39	0
~Period + Site + Tide + Wind	10	-1287,72	2595,77	44,41	0
~Period + Site + Tide + TideD + Wind	11	-1287,06	2596,50	45,14	0
~Period + Site + Tide	8	-1428,74	2873,70	322,34	0
~Period + Site + Tide + TideD + Wind + WindD	12	-1426,69	2877,84	326,48	0

Table 2: The most parsimonious generalized linear mixed model describing the occupancy probability (proportion of detections) as a function of period, site tide and wind. We present the odds ratios, 95% confidence interval and p values for each variable and variance for random effects. Significant effects are in bold.

Predictors	Selected model: Occupancy probability ~ Period + Site*Tide + Site*TideD + Site*Wind + Site*WindD + ar1(as.factor(day_time) + 0 | Season) + (1|Sample)		
	Odds Ratios	*CI*	*P value*
(Intercept)	1.08	0.48 – 2.44	0.850
Period [N]	2.16	1.53 – 3.05	**<0.001**
Site [Boia]	0.50	0.22 – 1.15	0.102
Site [IC]	0.36	0.16 – 0.81	**0.014**
Site [Quarto]	0.37	0.15 – 0.92	**0.032**
Wind	1.05	1.00 – 1.10	**0.043**
Tide	0.99	0.97 – 1.02	0.599
Site [Boia] * Wind	0.91	0.86 – 0.95	**<0.001**
Site [IC] * Wind	1.01	0.96 – 1.07	0.673
Site [Quarto] * Wind	0.99	0.93 – 1.04	0.639
Site [Boia] * Tide	1.03	1.01 – 1.06	**0.016**
Site [IC] * Tide	1.00	0.97 – 1.02	0.810
Site [Quarto] * Tide	1.06	1.03 – 1.10	**<0.001**
Random Effects			
σ^2	4.51		
$\tau_{00\ \text{Sample}}$	1.22		
$\tau_{11\ \text{Season.as.factor(day\_time)}}$	0.45-0.00		
ICC	0.00		
N_{Season}	4		
N_{Sample}	697		
Observations	697		
Marginal R^2 / Conditional R^2	0.117 / 0.117		

3.5 DISCUSSION

Our results confirm that the distribution of dolphins in their core area is not homogeneous and is influenced by environmental factors such as the period of the day, tide, and wind. For the first time, this dolphin population was acoustically monitored during the diel cycle, showing that dolphins also use their core area at night. The higher occupancy probability observed at night, in particular, reinforces the importance of monitoring efforts during this period. Additionally, the passive acoustic monitoring revealed sensitivity to detect the influence of the environmental variables, here tide, and wind, in the dolphins' distribution and can be used to predict how the population uses their habitat.

This dolphin population has been studied through photo-identification data. Now, for the first time, it is confirmed that they use the core area also at night. From a conservationist or management perspective, such information about the core area reinforces the adequacy of recent efforts to protect this population (see CANTOR; SIMÕES-LOPES; DAURA-JORGE, 2018), such as the exclusion fishing area implemented to avoid bycatch. Besides that, since the dolphins remain in the area of the cooperative fishing sites at night, this result suggests that the use of this area is not just to interact with fishers. Fishers' presence in that area at night is occasional and, when it happens, they are not involved in cooperative fishing. Therefore, other factors likely related to the habitat quality and structure can be determinants of their continuous permanence in that area. However, factors such as tide and wind can modulates this spatial pattern and were preliminarily explored here.

Despite being new information for this population, the increase in the activity rate and acoustic emissions at night—especially echolocation—seems to be a pattern for odontocetes. Many species in different habitats show an increase in echolocation emissions at night, generally associated with foraging activity (AU *et al.*, 2013; BAUMANN-PICKERING *et al.*, 2015; GANNIER, 1999; SOLDEVILLA; WIGGINS; HILDEBRAND, 2010; WANG *et al.*, 2015). For *Tursiops truncatus* it is reported an increase in the acoustic detections at dusk, in the Doubtful Sound population, in New Zealand. However, the authors did not find significant differences in detections between dusk and dawn (ELLIOTT; DAWSON; HENDERSON, 2011). Detections are more frequent at dawn in Enseada de La Paz, Mexico (GAUGER *et al.*, 2022). Also, *T. truncatus* that use protected marine areas in the Mediterranean Sea show higher detections at night (LA MANNA; MANGHI; SARA, 2014). Faced with this, some hypotheses to explain our result could be: (1) the most frequent use of the core area at night, (2) the species is indeed more active at night than in the day, (3) or the increase in the acoustic activity at night. Studies indicate a change in echolocation rates at night due to the lack of light to see the prey and to recognize the environment around them (CARLSTRÖM, 2005; CARUSO *et al.*, 2017). However, in our study area, the water is almost constantly turbid, and recognizing the environmental is a constant challenge. Besides that, considering that the habitat used by the dolphins usually is linked with foraging activities (HASTIE *et al.*, 2004; TORRES; READ, 2009), the answer for the increase in acoustic detection can also be related to prey availability (CARUSO *et al.*, 2017).

Prey behavior can vary through the diel cycle. Though we do not have information about the potential prey in the Laguna lagoon system, studies about some fishes species report a reduction in school fish aggregation in turbid water (CHAMBERLAIN; IOANNOU, 2019). Such an explanation by itself does not answer what could be affecting the prey behavior in our study area since the water is turbid most of the time. But, if the low visibility in turbid water is more accentuated at night when the lack of light is added to the turbidity, perhaps at night, the prey will be more dispersed too. Thus, the dolphins might use echolocation more often to localize smaller targets (individuals instead of school fish) during the night.

Except for the differences between day and night, the other environmental variables explaining the occupancy probability were associated with the monitored sites. For example, tide height influences the dolphins' distribution in the region close to the channel that links the lagoon system to the sea and the innermost part of the study area. The lower tide lightly increases the occupancy in sites *Bambu* and *IC*, respectively 4 and 5, which are more internal. Since the Santo Antônio lagoon's mean depth is only 1.8m, the more into the lagoon more common are de shallow water areas and sandbanks. In this way, *Bambu* and *IC* have many shallow water areas around them, so the dolphins can be using that low depth as a foraging strategy, reducing the escape space of their prey. Tactics like this is a well-reported for this dolphin species, such as the foraging tactics that include intentional stranding and barriers to trap the school fish. Stranding tactics, in which the dolphins pursue the fish, conducting it to a sand bank where the dolphin goes partially or totally out of the water to catch the fish, are reported to many populations, in the United States, Mexico, Ecuador, Portugal, and Australia (DOS SANTOS; LACERDA, 1987; DUFFY-ECHEVARRIA; CONNOR; ST. AUBIN, 2008; HOESE, 1971; JIMÉNEZ; ALAVA, 2015; TORRES; READ; HALPIN, 2008). Such behavior is usually found in mangroves and wetlands on days when the tide is much low, resulting in mud or sandbanks emerging (DUFFY-ECHEVARRIA; CONNOR; ST. AUBIN, 2008; JIMÉNEZ; ALAVA, 2015).

Even though the Laguna lagoon system offers many areas with low depth and sandbanks, there are no official reports about that kind of foraging tactics in the region. But, the use of barriers like sand banks and mangrove islets to trap the school fish (TORRES; READ, 2009) could be the reason for the frequent use of the internal part of the lagoon by the dolphins when the tide is lower. Following the same idea, during high tides, it could not be advantageous to use that area since it is not so shallow. In that case, it could be advantageous to use cooperative fishing sites, like *Quarto* (3), or depth areas, like *Boia* (1). The ocupancy probability of these sites increase around twice to three times when the tide is higher. That could be because other kinds of barriers are used in that area to trap the school fish: static (rocky shores) or active (throwing of the nets by fishers during cooperative fishing; SIMÕES-LOPES; FÁBIAN; MENEGHETI, 1998) barriers.

Many studies suggest tide direction as a relevant environmental variable to the dolphins because it influences their prey behavior (e.g., IRVINE *et al.*, 1981; LIN; AKAMATSU; CHOU, 2013; MENDES *et al.*, 2002; SCOTT; WELLS; IRVINE, 1990). Althrough, our results did not show a significant effect of the tide direction on the dolphins' distribution, we found a subtle increase in the acoustic detections during the ebb tide in sites where cooperative fishing does not happen: *Boia* and *Bambu*. That result agrees with what we previously studies about this population that indicate an increase in the use of areas most close to the channel, compared to that most into the lagoon, during the ebb (DAURA-JORGE, 2011). However, in *Quarto* the occupancy probability was higher during flood tide. Perhaps, during flood tides, schools of fish from the sea enter through the channel more often, being more advantageous for dolphins conduct them toward fishers, catching the during cooperative fishing.

Wind also influenced on the occupancy probability. When the wind speed is higher, in most internal sites' occupancy probability increases: *Quarto*, *Bambu*, and *IC*. The opposite happens for low-speed wind, when the occupancy increases in *Boia*, in the channel that connects to the sea. Such a pattern can indicate a reduction in the dolphins entering and leaving the lagoon system when the wind is more intense. It is because the decrease in the occupancy in the *Boia* is followed by an increase in the sites *Quarto*, *Bambu*, and *IC*, indicating that dolphins tend to stay in de lagoon system. This increase in detections in more internal locations when the winds are intense suggest the search for more sheltered locations, protected from the wind. More studies are required to understand this relationship better, considering a possible indirect interference of wind on prey availability. Wind direction has a similar effect among the monitored sites, with winds from the north quadrant slightly increasing the occupancy probability only in *IC*, the most internal site monitored in the lagoon system.

In conclusion, the dolphins' distribution in the core area is heterogenous, apparently influenced by the period of the day, tide height, and wind intensity, and subtly by tide and wind direction. The influence of all these variables in the dolphins' distribution can be explained by foraging tactics. Another important conclusion for this population is that the specialized foraging tactic involving artisanal fishers is not the only factor explaining the core area. The absence of fishers at night indicates that there should be other factors attracting and maintaining dolphins in that area. Perhaps, those factors are also key to the maintenance of the cooperative foraging tactic, and better understand them is key to explaining the required conditions to protect this rare foraging specialization.

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4 CHAPTER 3:

ASSESSING SPATIAL PATTERNS AND DENSITY OF DOLPHINS' POPULATION THROUGH SIGNATURE WHISTLES

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4.1 SUMMARY

Cetacean populations are studied by identifying individuals by their natural marks to access information like abundance and habitat use. However, identifying the individuals by their sounds increases the possibility of monitoring and answering biological and ecological questions about these animals. Some dolphin species produce the signature whistle, which allows for the identification of each dolphin individually in passive acoustic monitoring. In this way, we explored the potential of signature whistles to investigate some ecological aspects of a dolphin population. As preliminary data, eight signature whistles were identified in the well-known resident bottlenose dolphin population from southern Brazil. Using the spatial capture-recapture (SCR) method, the spatial patterns of this population and a density estimative were assessed. The data were collected once per season for a year, using 4-6 recorders in static passive acoustic monitoring. Compared with the known population size, the density was underestimated, which was expected because our study is exploratory. However, even with a few signature whistles identified, our results show the centre of the core area of these dolphins, described in the literature, as the area with the highest encounter probability. Besides that, our results bring new information. These dolphins keep the same spatial pattern at night compared to their daylight distribution. That is relevant information for conservation for that population, threatened by the trammel nets used at night. In conclusion, signature whistles associated with the SCR method can answer ecological questions about dolphins' populations, like density, spatial distribution, and even home range.

Keywords: bottlenose dolphin, spatial capture-recapture, passive acoustic monitoring

4.2 INTRODUCTION

Individual recognition is crucial in answering many important questions in evolutionary biology and ecology (Clutton-Brock and Sheldon, 2010). For cetaceans, when natural marks permit individual identification, longitudinal studies can describe life history and multiple demographic processes (e.g., Fruet, Daura-Jorge, Möller, Genoves, and Secchi, 2015; Hammond et al., 2021; Smith, Pollock, Waples, Bradley, and Bejder, 2013). For instance, dolphins are usually recognized individually by photo-identification of their dorsal fin. Such an identification process allows the use of mark-recapture methods to estimate population parameters and investigate other ecological and biological aspects of the individual and its population (Hammond et al., 2021; Würsig and Jefferson, 1990). Habitat use, for example, is a result of individual behaviour (e.g., Cantor, Simões-Lopes, and Daura-Jorge, 2018; de Gabriel Hernando et al., 2021; Ofstad et al., 2019), then knowing the individuals and monitoring them in time and space is additional information to understand such spatial pattern.

In the last decades, passive acoustic methods have been proposed to study cetaceans, considering that these animals spend most of their time underwater, use sound in many aspects of their lives, and the sound propagation allows for monitoring them at greater distances (Cato, Noad, and McCauley, 2005; Mellinger, Stafford, Moore, Dziak, and Matsumoto, 2007). Passive acoustic can be used to estimate abundance, density, and habitat use (e.g.; Clay, Mangel, Alfaro-Shigueto, Hodgson, and Godley, 2018; Marques et al., 2013; Palmer, Brookes, Davies, Edwards, and Rendell, 2019; Taylor et al., 2017). Even though individual identification is not necessary for those studies, it adds information about individuals' variations in behaviour, movement patterns, and habitat use, for example (e.g., Chen, Hung, Qiu, Jia, and Jefferson, 2010; De Moura, Cantor, Broadhurst, and Domit, 2021; Mueller and Fagan, 2008; Strickland, Mann, Foroughirad, Levengood, and Frère, 2021). In this way, in cases where dolphins have whistles unique to the individual, the so-called signature whistle, that sound has the potential to be used in passive acoustic protocols to monitor individuals.

Signature whistles were reported for captive bottlenose dolphins (*Tursiops truncatus*) for the first time in 1965 (Caldwell and Caldwell, 1965) and since then, for other dolphins species (e.g.; Caldwell and Caldwell, 1970; Cheng et al., 2017; Duarte de Figueiredo and Simão, 2009; Fearey, Elwen, James, and Gridley, 2019; Parijs and Corkeron, 2001). However, identifying signature whistles in free-ranging animals was not a simple task until Janik et al. (2013) propose the Signature Identification method (SIGID). This conservative method allows for identifying the signature whistles and, therefore, recognizing free-ranging dolphins' individuals by their sounds. Only in the last years, the use of this sound emission has been proposed to explore different ecological questions (e.g.; Bailey et al., 2021; Fearey, Elwen, Dines, and James, 2021; Fearey, Elwen, Distiller, and Gridley, 2022; Gordigiani et al., 2019; Longden et al., 2020; Rashley, Gridley, Elwen, Bastian, and Jacobs, 2016). Here, we tested the application of signature whistles, recorded in static passive acoustic monitoring, to estimate the density of a population and investigate its spatial distribution. Since these acoustic data have a different character in the collection process than photo-identification, we explore a method not used yet in association with signature whistles, the spatial capture-recapture (see Efford, 2004; Royle, Chandler, Sollmann, and Gardner, 2013). The population in our study is the resident bottlenose dolphin of Laguna, southern Brazil, which has its abundance and home range well-known.

These dolphins have been studied since the end of the 1980s (Simões-Lopes, 1991; Simões-Lopes, Fábian, and Menegheti, 1998). It is a small population, around 54-60 individuals, with a high site fidelity (Bezamat, Simões-Lopes, Castilho, and Daura-Jorge, 2019; Daura-Jorge, Ingram, and Simões-Lopes, 2013; Simões-Lopes and Fabian, 1999), characteristics that result in a genetic isolation from other populations (Costa et al., 2015; Fruet et al., 2014). This population belongs to a recently recognized subspecies *Tursiops truncatus gephyreus*, endemic to the Southwestern Atlantic Ocean (Costa et al., 2019; Vermeulen, Fruet, Costa, Coscarella, and Laporta, 2019). In Laguna, these dolphins interact positively with artisanal fishers (cooperative fishery; Simões-Lopes, 1991; Simões-Lopes, Fábian, and Menegheti, 1998) at specific sites in the lagoon system where they inhabit (Daura-Jorge et al., 2013). Some dolphins interact more frequently (known as cooperative dolphins) than others (noncooperative dolphins), and such individual variations define their home ranges (Cantor et al., 2018) and other ecological and biological aspects such as acoustic behaviour and population parameters (Bezamat et al., 2019; Romeu, Cantor, Bezamat, Simões-Lopes, and Daura-Jorge, 2017). That well-known dolphin population is ideal for replicating ecological studies using new approaches. In this way, our main objective is to investigate how effective can be using signature whistles combined with spatial capture-recapture methods for ecologic studies. Then, using preliminary data we: 1) estimate the encounter probabilities at pre-defined sites, evaluating heterogeneity in the individual spatial distribution; 2) estimate population density and then abundance, comparing the result with abundance estimated by traditional mark-recapture methods based on photo-identification data reported in the literature; 3) and compare the spatial distribution between daytime and night, and between seasons.

4.3 MATERIAL AND METHODS

4.3.1 Data collection

The bottlenose dolphins population inhabits the lagoon system located in Laguna, southern Brazil. That lagoon system has three lagoons interconnected, Mirim, Imaruí, and Santo Antônio (Figure 1a). The last lagoon has an average depth of 1.8m (0.4-13m) and is linked with the ocean. This lagoon is the area most used by the dolphins (see Cantor et al., 2018) and where the acoustic data were collected.

Four to six sites were chosen in the lagoon to deploy the recorders (Figure 1b). The data were collected once by season in 2020: 11th – 13th February (summer), 16th – 18th May (autumn), 23rd – 25th August (winter), and 14th – 16th October (spring). In the summer, the recorders were deployed in four sites (Figure 1b: numbers 1-5, including 2.3 and excluding 2 and 3). However, for the data collected in autumn, one of the collecting sites (Figure 1b: number 2.3) needed to be replaced by two other sites covering the same area (Figure 1b: numbers 2 and 3). Site 2.3 was at one of the most important cooperative fishery sites, and the replacement was due to a request from fishers. Also, an additional recorder was used in the interior of the lagoon in autumn and winter (Figure 1b: number 6). That recorder was also deployed in the summer, but there were technical problems. This recorder was not deployed in spring because of the low tide condition.

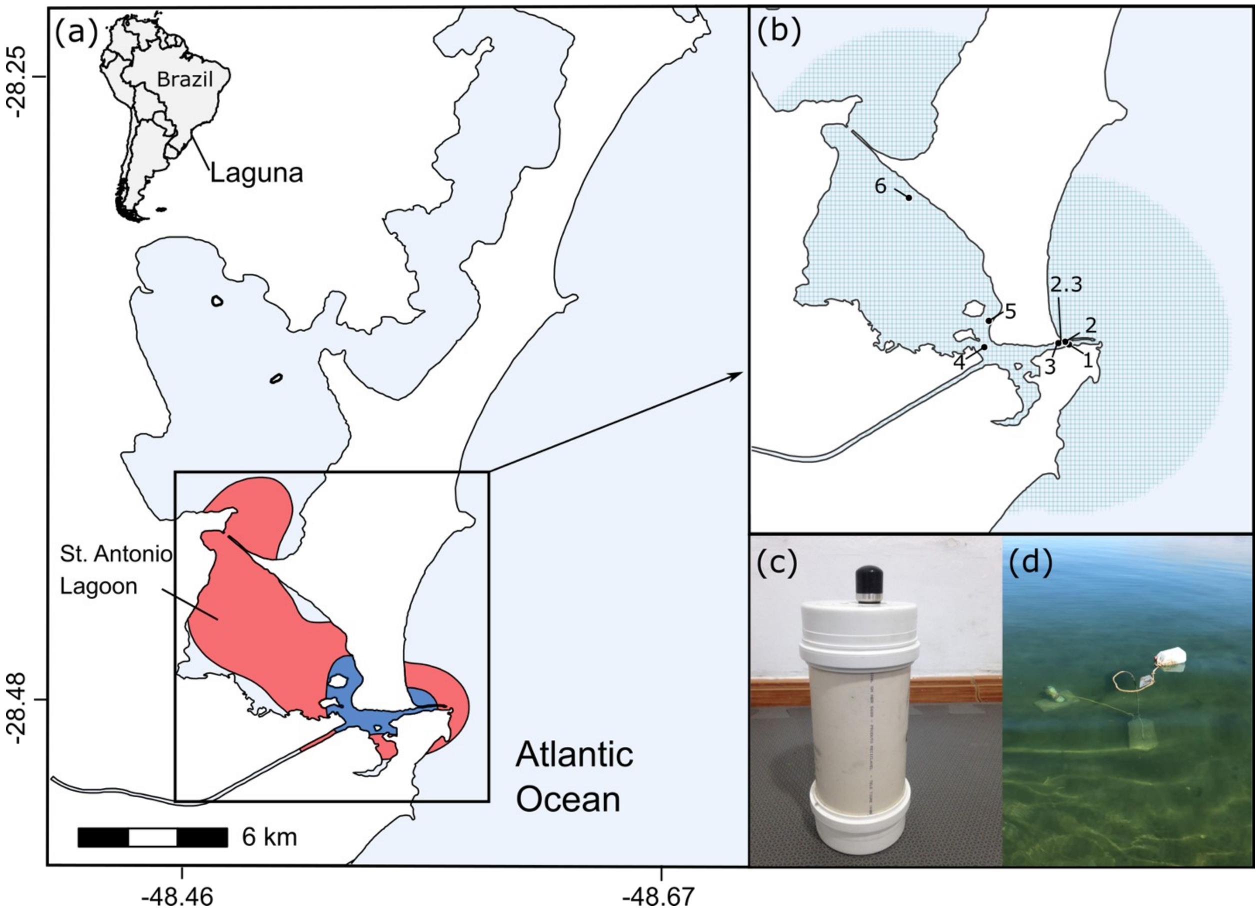

Figure 1: (a) Map of the study area with the home range of the dolphins that tend to forage independently of fishers (red, noncooperative dolphins) and the home range of dolphins that tend to forage with fishers (blue, cooperative dolphins). (b) Inset showing the location of each recorder deployment site represented by numbers (1-6) and the state-space used in the spatial capture-recapture models (green grid); (c) The custom-made waterproof housing for the Solo audio records; (d) A recorder deployed at site 6.

Solo audio recorders (Whytock and Christie, 2017) were used, operating in a duty cycle of 5 min on/5min off for 2-3 days. The recorders worked with a sampling rate of 48 kHz/16 bits (Nyquist frequency of 24 kHz), connected in hydrophones Aquarian H2c (sensitivity -180 dB re: 1V/µPa). The recorders were enclosed in PVC pipe cases, used as waterproof cases (Figure 1c and Figure S1, Supplementary Material), and were attached to a mooring system for deployment (Figure 1d). The depth of each deployment site varied between 1-5 m, depending on the site and tide condition.

4.3.2 Data processing

To find the signature whistles all the recordings made by the four recorders during the summer were checked visually, looking for whistles. For these recordings, every whistle with a good signal-to-noise ratio (SNR), which means whistles with time and frequency parameters distinguishable from background noise (e.g., Kriesell, Elwen, Nastasi, and Gridley, 2014; La Manna et al., 2020) was catalogued. In this catalogue, for each whistle was registered their identification number (a crescent numerical sequence, according to the order that each whistle was added in the catalogue), the initial and final time of the whistle in the recording, and if it were like another catalogued whistle in terms of frequency modulation (contour). An image catalogue of all whistles was also kept, to facilitate the contour comparison among whistles.

Only the first author has compared the contour similarity among whistles visually. Instead of automated comparison, we have chosen the visual one because that is the most accurate method to compare and cluster whistles spectrograms (Janik, 1999; Kershenbaum, Sayigh, and Janik, 2013). We have decided on only one person to compare the whistles considering that when this is done by more people (observers), even by non-specialists in dolphins' whistles, there is a high agreement among the observers about the classification according to the contour similarity (Janik, 1999; Janik and Slater, 1998).

Signature whistles were looked for in parallel with cataloguing the whistles, using the Signature Identification method (SIGID; Janik, King, Sayigh, and Wells, 2013), which proposes to identify the signature whistles by a bouts analysis. The whistle shall belong to a bout, where it is followed or preceded by another similar whistle, which means one with similar contours, within a time window of 1-10s. In addition, these whistles must compose 75% or more of all whistles in the bout, counting at least four whistles (Janik et al., 2013). Thus, the signature whistles present in the recordings made in the summer were identified.

In the next step, these signature whistles were looked for in the recordings of the other seasons. First, the Whistle and Moan Detector module of Pamguard software (Gillespie, Caillat, Gordon, and White, 2013) was used to identify the recordings with whistles. Then, the Raven Pro 1.4 software was used to check each recording detected with whistles (sample rate: 48 kHz, encoding: 16-bit, Hann window, 512 FFT, 50% overlap), looking for the signature whistles previously identified. From this moment on, even though a whistle recorded was not in a bout pattern described by the method SIGID, if it was like a signature whistle previously identified, we considered it a ‘recapture’ of that signature whistle. For each recording signature whistle was registered: the identification number of the signature whistle, site, season, day, and recording start time. We analysed only the recordings made when all recorders were operating.

4.3.3 Analysis: spatial capture-recapture models

The signature whistle data were organized in an encounter history with the following information: whistle’s identification number, which recorder recorded the whistle (according to the site), season, and hour of the day when the whistle was recorded. Each hour was considered a recapture occasion. Since our recordings are 5 min long for each 10 min, the six recordings belonging to the same hour were considered one recapture occasion. Then, if a signature whistle occurred in a recording, the hour when the recording was made was considered an occasion with a recapture. However, the same signature whistle could be recorded more than once on the same occasion, in the same or different recorders. In these cases, that signature whistle was added in the encounter history as many times as the recordings with it. And, in some rare cases when the same whistle was recorded at the same time in more than one recorder, it was considered just the recording which had the whistle with the stronger signal (Efford, Dawson, and Borchers, 2009), easily identified visually.

In addition to the encounter history, deployment files were organized by season, with information about the recorders’ identification (like in Figure 1b) and coordinates of each deployment. For each recorder, information about the deployment site and if each occasion was daytime or night was added. All the seven recorders presented in Figure 1b were included in the deployment file of all seasons, defining as “off” the recorders which were not working in each season (see Royle, Chandler, Sollmann, et al., 2013; Sutherland, Royle, and Linden, 2019), according to the previous description in the *Data collection* section.

These data tables (encounter history and deployment files) were used to estimate the encounter probability and density by spatial capture-recapture (SCR) models, using the “oSCR” R package (Sutherland et al., 2019). In SCR models, the encounter probability (p) depends on the distance between the individuals’ activity centre and the traps (recorders, in our case), decreasing with increasing distance. The spatial scale parameter (σ), or spatial decay, represents that decrease (Dupont, Royle, Nawaz, and Sutherland, 2021; Efford, 2004; Sutherland et al., 2019). The density (D) is estimated according to the state-space area (Royle, Chandler, Sollmann, et al., 2013).

The state-space is the area where the individuals that might be captured are, including all potential activity centres (Royle, Chandler, Sollmann, et al., 2013; Royle, Fuller, and Sutherland, 2018). Such area is defined by a buffer from the recorders’ location. Buffer is the sampled area or a polygon that includes all recorders, where the individuals in it are exposed to them and might be sampled at some time (Efford, 2004; Royle et al., 2013). That buffer is divided into grid cells, representing the possible activity centres (Efford, 2004; Sutherland et al., 2019). Considering that it is difficult to know a priori a specific value for the buffer and grid cells resolutions, some authors suggest values for them. Buffer can be 3-4 times the spatial scale (σ) value estimated by SCR models (Efford, 2004; Sutherland et al., 2019) or ½ value of the mean maximum distance moved (MMDM) among the recorders (Royle, Chandler, Sollmann, et al., 2013). The grid cell size may be an average activity centre, or ½ σ (Royle, Chandler, Sollmann, et al., 2013; Sutherland et al., 2019).

We have defined the state-space with a buffer of 5825m and the resolution of the grid cells at 158m. For the buffer, the area equivalent to the mean individual home range of this dolphins’ population was considered, estimated at ~34 km² (Bezamat et al., 2019). Thereby, the sum of the buffers built around each recorder covered all the lagoon area and part of the sea (Figure 1b), complying with the requirement that the buffer must be as large as possible (Royle, Chandler, Sollmann, et al., 2013) to guarantee the inclusion of all individuals exposed to the recorders. For the grid cells, it was defined the size of 158m for two reasons. First, our initial model resulted in an underestimated σ of around 2500m (see *Results* section), which means a grid cell size of 1250m, according to the suggestion of Sutherland et al. (2019). That value would result in a buffer with few cells since our buffer has 5825m, which means a low resolution to analyse the spatial heterogeneity. Then, considering that the area where most of the recorders were deployed is the area where occurs cooperative fishery, we have decided to use a grid cells size similar to the area of the main site of the cooperative fishery, the Tesoura and Quarto's beaches (between the deployment sites 2 and 3, in Figure 1b; Cantor et al., 2018; Simões-Lopes and Fabian, 1999). To find the exact value of the grid cell, we estimate the true σ that represents a home range of $34km^2$ by using the following analytical solution (Royle, Chandler, Sollmann, et al., 2013):

$$\sqrt{(34/\pi)}/(\sqrt{5.99}), \qquad (1)$$

and then found the resolution value that equals the true and the estimated σ. In the end, also the area corresponding to the land was excluded from the state-space to adjust the density estimated (Borchers and Efford, 2008).

Finally, our data were analysed using General Linear Models (GLMs) approach (see Royle, Chandler, Sollmann, et al., 2013). Models with D and σ with constant values and varying by season (session, in the models), and p0 with a value constant and varying by session, deployment site, and/or period of the day (daytime/night) were tested. Considering that each recorder can capture more than one individual on the same occasion, and the same individual can be captured more than once on the same occasion in the same or different recorders, a Poisson distribution was used for the encounter and density model (Efford, Dawson, and Borchers, 2009; Sutherland et al., 2019). The Euclidian distance was used to measure moved distances among the recorders because it was not possible to define precise values to specify the least-cost path, and then use the Ecological distance (Royle, Chandler, Gazenksi, and Graves, 2013), because the lagoon has many sites with shallow water due to sand banks and tidal variation, where the dolphins cannot pass.

4.4 **RESULTS**

As preliminary results, eight signature whistles were identified in 180 hours of recordings made in the summer, summing all the recorders. The recordings made by all the recorders in the other seasons totalized 889 hours. Of those signature whistles, four were recaptured in every season. However, at least five signature whistles were recaptured in each season (Table S1). The average number of times that an individual was recaptured in each season was 5.40-7.33 (winter and spring, respectively), and the average number of sites where an individual was recaptured was 2.14-2.40 (autumn and winter, respectively). The mean maximum distance moved by individuals varied from 1,959 to 2,737 meters (summer and autumn, respectively; Table S1). However, these latter values are underestimated by the Euclidian distance used in the models. The model selection procedure indicates that the model with density and sigma (σ) constant and encounter probability (p) varying according to the deployment site (site), period of the day (period), and session better supported the data (Table 1 and Table S2).

Table 1: SCR candidate models for density (D), capture probability (p), and the spatial scale parameter (σ) are ranked by AICc. AICc weight indicates the support of the selected model over the others (see the complete list in the Table S2, Supplementary Material). Notation: (.) constant, (site) deployment sites, if daytime of night (period), season (session); k represents number of parameters.

model	model specification	k	AIC	dAIC	weight	Deviance
7	D(.) p(site+period+session) σ(.)	13	1350.921	0	0.639	662.461
4	D(.) p(site+period) σ(.)	10	1353.547	2.626	0.172	666.774
23	D(.) p(site+period+session) σ(session)	16	1354.559	3.638	0.104	661.279
15	D(session) p(site+period+session) σ(.)	16	1356.361	5.44	0.042	662.18
12	D(session) p(site+period) σ(.)	13	1358.47	7.549	0.015	666.235
20	D(.) p(site+period) σ(session)	13	1358.488	7.567	0.015	666.244
31	D(session) p(site+period+session) σ(session)	19	1359.205	8.284	0.01	660.603
5	D(.) p(site+session) σ(.)	12	1362.48	11.559	0.002	669.24
28	D(session) p(site+period) σ(session)	16	1363.479	12.558	0.001	665.739
1	D(.) p(site) σ(.)	9	1365.313	14.392	0	673.657

That model that better supported the data (model 7) estimated a density of 0.08 individuals/km² (SE = 0.02; 95% CI = 0.05-0.12; Table S3). Considering that the estuarine area used by the dolphins has around 200 km² (see Cantor et al., 2018), this density suggests an abundance of 16 dolphins (95% CI = 10-24). There is a greater encounter probability for site 4 in all seasons, and higher at night: p= 0.36 (SE = 0.18; 95% CI = 0.10-0.71) and p= 0.50 (SE = 0.19; 95% CI = 0.18-0.81), for daylight and night respectively (Figure 2, Table S3). The σ was estimated in 2,534m (SE = 291; 95% CI = 2022-3175; Table S3), which is underestimated as is the MMDM calculated for not considered the least-cost path where the dolphins can pass.

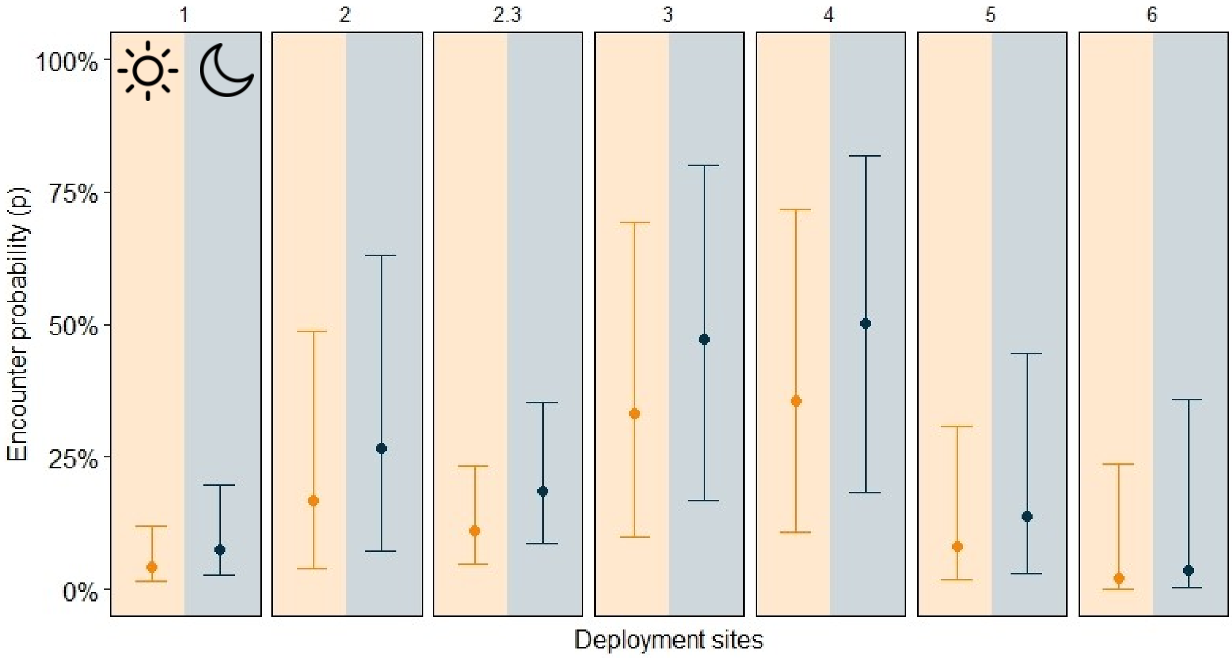

Figure 2: Encounter probability (p) by site, daytime (yellow), and night (grey). Points indicate p probabilities, and lines indicate a 95% confidence interval.

4.5 DISCUSSION

Our findings reveal that signature whistles can help ecological studies when associated with the spatial capture-recapture method. Our data are preliminary, resulting in underestimated abundance compared with the abundance estimates for this population by photo-identification data. However, our results confirm the heterogeneity in the spatial distribution and show that dolphins use their core area in the same way at night as in daylight. Even with many other variables influencing the emission and record of signature whistles, they show the potential to represent ecological aspects of populations correctly.

Abundance estimates for this population have been estimated since the beginning 1990s using long-term photo-identification data, and indicate a population size of around 54-60 individuals in the least years (Bezamat et al., 2019; Simões-Lopes and Fabian, 1999). Around 18 to 21 individuals are cooperative dolphins (Daura-Jorge et al. 2013), those that consistently engage in cooperative foraging with fishers. When we compare the abundance estimated by using the signature whistles—16 individuals—it represents less than one-third of the population size previously estimated, but it is very similar to the previous estimates of cooperative dolphins. As the recorders were predominantly deployed at the home range of the cooperative dolphins, perhaps our sampling was adequate to estimate this subset of the population. In addition, although we partially corrected density estimates by removing land areas of the state-space (see *Analysis: spatial capture-recapture models* in Material and Methods section; Borchers and Efford, 2008), it can be slightly underestimated by the use of the Euclidian distance to estimate capture probabilities (see Royle, Chandler, Gazenksi, et al., 2013; Sutherland, Fuller, and Royle, 2015).

We expect that with more signature whistles identified, the abundance estimates for this population from the spatial capture-recapture will be more accurate and similar to the previous estimate by photo-identification To identify more signature whistles, we can analyse more recordings using the SIGID method or investigate how this population predominantly emits such whistles. The SIGID is a conservative method, assuming a miss-identification rate of around 50% because the dolphins do not always emit the signature whistle in the bout pattern defined (Janik et al., 2013; Kriesell, Elwen, Nastasi, and Gridley, 2014). However, until that moment, the SIGID is the most used non-invasive method to identify signature whistles in wild dolphin populations (e.g., Erbe, Salgado-Kent, Winter, Marley, and Ward, 2020; Fearey, Elwen, James, and Gridley, 2019; King et al., 2018; Kriesell, Elwen, Nastasi, and Gridley, 2014; Longden et al., 2020). Another option to find more signature whistles is a long-term study about such sounds of bottlenose dolphin population in Laguna to understand the emission pattern of signature whistles in this population (e.g., Kriesell, Elwen, Nastasi, and Gridley, 2014).

Regarding spatial distribution, our results reinforce the spatial heterogeneity of this population (Cantor et al., 2018). The area where we deployed all recorders, except one, represents not only the home range of cooperative dolphins but the core area of the population. The model that better supported the data suggests that encounter probabilities (p) varied by site, period (daylight/night), and session. The latter result probably reflects the difference in sampling effort across seasons (sessions). The main p variations were between sites and when comparing daylight and night periods. The two highest p were for sites 4 and 3, respectively (Figure 2; Table S3), which represent the central area in the core area of this population. Since we cannot match the dolphins with their signature whistles yet, these results can be biased if all the whistles belong to cooperative dolphins, who have a smaller home range than the noncooperative dolphins in that area (Cantor et al., 2018). Even so, with only a few signature whistles identified we could represent a spatial distribution of the dolphins similar to the pattern described by long-term studies based on longitudinal photo-identification efforts. Of course, since we have sampled almost only the core area, we cannot compare the p values within this area and the adjacent ones. However, the p values decrease from the centre to the margin of the core area.

In addition to being consistent with the known spatial distribution of the population, our data bring a piece of new information. Our knowledge about these dolphins until now came from data collected only during the daytime, the photo-identification data. The acoustic monitoring data allow us to analyse the ecological aspects of the dolphins also at night. Thus, we could confirm that the spatial distribution of the individuals apparently kept equal to daytime among the monitoring sites. Although the model indicates a variation of p between day and night, with higher values at night for all sites, the variation between sites was consistent between periods, suggesting the same spatial distribution. Such information is particularly important for this population, seriously threatened by the trammel nets used to catch catfish (Bezamat, Hammond, Castilho, Simões-Lopes, and Daura-Jorge, 2021; Peterson, Hanazaki, and Simões-Lopes, 2008). That fishery occurs at night, and to avoid bycatch events a local law prohibited the use of trammel nets in the core area of the dolphins (Laguna, municipal law number 1998/2018). Interesting, our results show higher values of p at night. This can be a result of two processes:

the area is used mainly at night, or the signature whistles are emitted more frequently during the night. Considering the consistence of p values across sites between daylight and night, maybe the second explanation is the most probable.

Whether to describe the spatial distribution of the dolphins or to use signature whistles as an individual mark in acoustic monitoring, we need to understand the context in which these sounds are emitted. In our case study, we had expected a higher encounter probability (p) at sites 2, 2.3, and 3 (Figure 1) since they are within the area where cooperative fishery consistently happens. Then, dolphins tend to spend more time there, which would increase the chance to recapture a signature whistle (Fearey, Elwen, Distiller, and Gridley, 2022). However, dolphins do not necessarily use signature whistles during that specialized foraging strategy, as suggested by other studies that found a reduced emission of these whistles in the feeding context (Cook, Sayigh, Blum, and Wells, 2004). There are reports of signature whistles in situations like isolation or voluntary separation from other individuals (Watwood, Owen, Tyack, and Wells, 2005), groups meet and cohesion (Janik and Slater, 1998; Quick and Janik, 2012), mother and calf contact (Kuczaj, Eskelinen, Jones, and Borger-Turner, 2015; Smolker, Mann, and Smuts, 1993), and, recently, to keep the weaker social bonds with individuals of the population whom dolphins spend less time (Chereskin et al., 2022). None of these seem to be the case in the cooperative fishery context (except mother and calf contact), which is a foraging tactic performed by dolphins who have stronger social relationships among themselves than with the others that do not use the same tactic (Daura-Jorge, Cantor, Ingram, Lusseau, and Simões-Lopes, 2012; Machado et al., 2019). In this way, the higher p values at night could be a result of an increase in the emission of signature whistles during the period when the cooperative fishing does not happen because the fishers are absent and, then, dolphins spend more time in other social activities. Alternatively, signature whistles can be more used to recognize the others when there is not light enough to see the other individuals.

Even if used only in specific contexts, it still seems valid to use signature whistles as an individual mark in acoustic monitoring. There are reports of a percentage of around 32-52% of signature whistles emitted in whistle emission in general (Cook et al., 2004; Luís, Couchinho, and Santos, 2016; Watwood et al., 2005), which may allow consistent ‘recapture’ events to fit population models. However, such context-dependence of signature whistles can bias estimates and should be considered when describing ecological aspects of the studied population. Also, dolphins may mimic the signature whistle of another individual. However, this probably does not cause bias in the data collection since that mimicry is not much frequent, and it is used to address the other to which belongs the signature whistle (Janik and Slater, 1998; Janik, 2000; Tyack, 1986), then the dolphin owner of the whistle probably is present in the context of such emission.

Other important factors are the record and the sampling. The record of the whistles depends on the distance and position of the dolphin relative to the recorder. Whistles can be not recorded or, if recorded, they can be in a not good SNR. In the first case, if the signature whistle is emitted in bouts, the chance to record at least one of them increases. For the second scenario, there is not an easy solution. Some alternatives are using just the whistles with good SNR, losing some records, or trying to confirm the whistle by observing the previous or posterior when it is emitted in bouts if some are in a better SNR. In addition, the duty cycle chosen to sample also influences the chance to recapture the signature whistles, being the best result from the full-time recordings and the duty cycle of 10 min on/5min off for the bottlenose dolphins' population in Walvis Bay, Namibia, for example (Fearey et al., 2022).

Besides those limitations, there are advantages in signature whistles, compared with photoidentification, which are the possibility to monitor individuals even in bad weather conditions, at night, in more than one site simultaneously, and for a long time, like days. Also, compared with other sound emissions recorded in passive acoustic monitoring that are not specific for individuals, signature whistles dispense additional information about the sound recorded. For example, if the sound used in SCR is not individual-specific, it is necessary to record the same sound emission in more than one recorder to estimate the location of the sound source (individual) in the way to avoid super estimate the density, and guarantee that is being estimated individuals density, not calls density (e.g., Efford et al., 2009; Marques et al., 2012; Stevenson et al., 2015; Stevenson, van Dam-Bates, Young, and Measey, 2021). Additionally, using signature whistles is possible estimate other parameters beyond abundance or density.

Here, we focus on density and encounter probability estimates. Besides these parameters, another piece of information can be explored using signature whistles associated with SCR: the distance covered by the "marked" individuals. The mean maximum distance moved (MMDM) and the spatial parameter (σ), which estimates the distance between the individual’s activity centre and the recorder, can be used to describe movements and population home range area. We do not explore these results because our distance values are underestimated since we have used the default Euclidian distance in our models.

In conclusion, signature whistles collected in static acoustic monitoring are feasible for studying dolphins’ populations and answering questions about the population’s density and spatial distribution, taking some advantages compared with photoidentification and other kinds of sounds recorded by acoustic monitoring. Even a few whistles, when with a considerable recapture in different sites (Royle, Chandler, Sollmann, et al., 2013; Royle et al., 2018), can be used for a preliminary estimate of population density. The results about spatial distribution represent well the habitat use, even with a few signature whistles and considering the bias caused by the behavioural context of that sound emissions. For resident populations and long-term studies, where many signature whistles are identified, such emissions can be a precise tool to study those populations.

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4.8 CONFLICTS OF INTEREST/COMPETING INTERESTS

Authors declare that they have no competing interests.

4.9 AVAILABILITY OF DATA AND MATERIAL

For transparency, we provide all the data in the open-access repository: https://zenodo.org/badge/DOI/10.5281/zenodo.7166937

4.10 CODE AVAILABILITY

For transparency, we provide all the (customized) R code to replicate the analyzes and figures in the open-access repository: https://zenodo.org/badge/DOI/10.5281/zenodo.7166937

4.11 AUTHOR CONTRIBUTIONS

Conceptualization: BR, FGDJ; Data curation: BR; Formal Analysis: BR; Funding acquisition: FGDJ; Methodology: BR, FGDJ, PSH; Investigation: BR, FGDJ, PSH, PC, PCSL; Project administration: BR, FGDJ; Resources: BR, FGDJ; Supervision: FGDJ, PSH, PCSL; Visualization: BR, FGDJ; Writing–original draft: BR; Writing–supplementary material: BR; Writing–review & editing: BR, FGDJ, PSH, PC, PCSL.

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4.13 SUPPLEMENTARY MATERIAL

(Chapter 3)

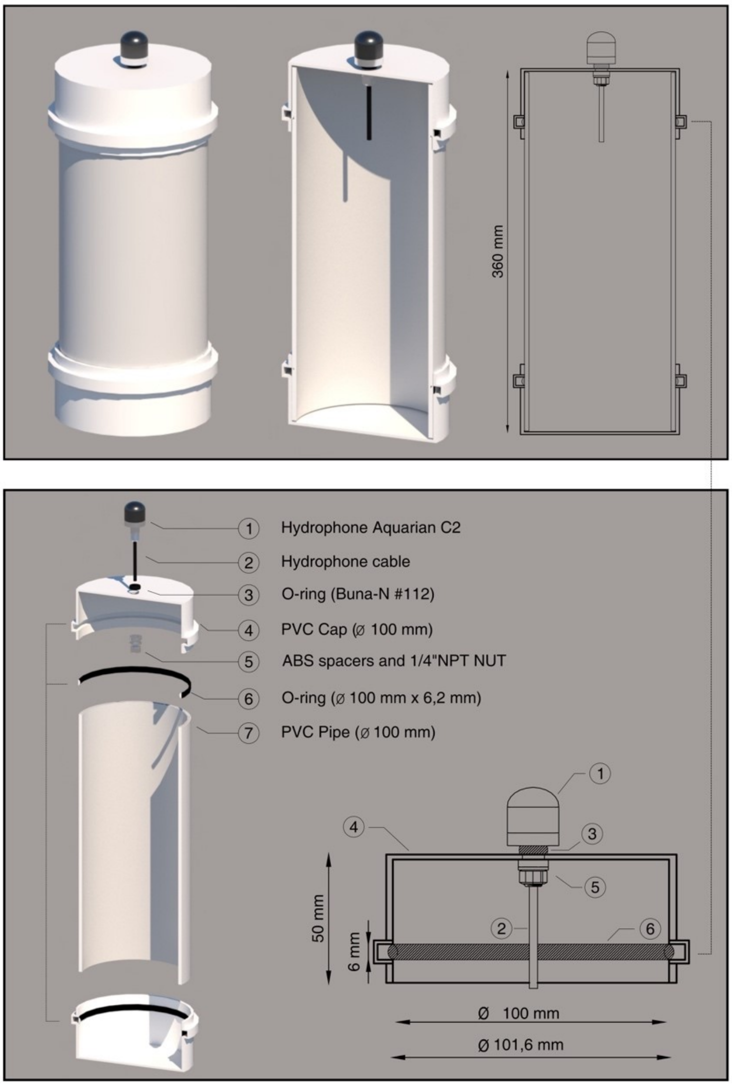

Figure S1: Custom made waterproof housing. Top panel shows the 3D model of a waterproof housing fully assembled, a half section view in 3D and dimensioning of the section view. The bottom panel shows the half-section view of a disassembled waterproof housing and all the components used, with a dimensioning section view of the PVC cap with the hydrophone. Dashed lines connecting parts show in detail the groove with O-rings in PVC caps.

Table S1: Summary information, for each season, about the number of individuals recaptured (individuals), number of recorders (traps), and number of hours sampled (occasions), the average number of times that an individual was recaptured (captures), the average number of sites where an individual was recaptured (spatial captures), the mean maximum distance moved (mmdm); and, the mmdm pooled across sessions (MMDM).

	S1	S2	S3	S4
individuals	8	7	5	6
traps	7	7	7	7
occasions	45	52	52	53
captures	5.75	6.00	5.40	7.33
spatial captures	2.25	2.14	2.40	2.17
mmdm	1959.57	2737.34	2493.37	2374.45
MMDM	2392.07			

Table S2: Complete list of SCR candidate models for density (D), capture probability (p) and the spatial scale (σ) parameter (σ) ranked by AICc. ranked AIC. AICc weight indicates the support of the selected model over the others (see the complete list in the Supplementary Material). Notation: (.) constant, (site) recorder sites/location, (period) if daytime of night, (session) samples; k represents number of parameters.

model	Model specification	k	AIC	dAIC	weight	Deviance
7	D(.) p(site+luz+session) sig(.)	13	1350.921	0	0.639	662.461
4	D(.) p(site+luz) sig(.)	10	1353.547	2.626	0.172	666.774
23	D(.) p(site+luz+session) sig~session	16	1354.559	3.638	0.104	661.279
15	D(session) p(site+luz+session) sig(.)	16	1356.361	5.44	0.042	662.18
12	D(session) p(site+luz) sig(.)	13	1358.47	7.549	0.015	666.235
20	D(.) p(site+luz) sig(session)	13	1358.488	7.567	0.015	666.244
31	D(session) p(site+luz+session) sig(session)	19	1359.205	8.284	0.01	660.603
5	D(.) p(site+session) sig(.)	12	1362.48	11.559	0.002	669.24
28	D(session) p(site+luz) sig(session)	16	1363.479	12.558	0.001	665.739
1	D(.) p(site) sig(.)	9	1365.313	14.392	0	673.657
21	D(.) p(site+session) sig(session)	15	1366.118	15.197	0	668.059
13	D(session) p(site+session) sig(.)	15	1367.92	16.999	0	668.96
9	D(session) p(site) sig(.)	12	1370.23	19.309	0	673.115

17	D(.) p(site) sig(session)	12	1370.277	19.356	0	673.138
29	D(session) p(site+session) sig(session)	18	1370.764	19.843	0	667.382
25	D(session) p(site) sig(session)	15	1375.271	24.35	0	672.635
6	D(.) p(luz+session) sig(.)	7	1436.281	85.36	0	711.141
18	D(.) p(luz) sig(session)	7	1437.887	86.966	0	711.943
2	D(.) p(luz) sig(.)	4	1438.279	87.358	0	715.14
22	D(.) p(luz+session) sig(session)	10	1438.773	87.852	0	709.386
14	D(session) p(luz+session) sig(.)	10	1441.111	90.19	0	710.555
10	D(session) p(luz) sig(.)	7	1442.227	91.306	0	714.113
26	D(session) p(luz) sig(session)	10	1443.374	92.453	0	711.687
30	D(session) p(luz+session) sig(session)	13	1444.216	93.295	0	709.108
3	D(.) p(session) sig(.)	6	1447.84	96.919	0	717.92
16	D(.) p(.) sig(session)	6	1449.634	98.713	0	718.817
0	D(.) p(.) sig(.)	3	1450.02	99.099	0	722.01
19	D(.) p(session) sig(session)	9	1450.332	99.411	0	716.166
11	D(session) p(session) sig(.)	9	1452.67	101.749	0	717.335
8	D(session) p(.) sig(.)	6	1453.963	103.042	0	720.982
24	D(session) p(.) sig(session)	9	1455.126	104.205	0	718.563
27	D(session) p(session) sig(session)	12	1455.775	104.854	0	715.887

Table S3: Density (D), capture probability (p) and the spatial scale parameter (σ) predicted from the most parsimonious model. Density is individuals per pixel (in this case, individual per 150x150 m²). The spatial scale parameter is in meters. For encounter probability and σ, the occasions are identified according to the period of the day as daytime (d) or night (n). The higher encounter probabilities are identified by *.

Parameter	estimate	se	lwr	upr	Site
Density (D)	0.001991	0.000437	0.001295	0.003061	
Sigma (sig)	2534.55	291.5258	2022.988	3175.474	
p (d)	0.042650	0.023438	0.014256	0.120674	1
p (d)	0.111640	0.045025	0.049083	0.234283	2.3
p (d)	0.166203	0.110351	0.040174	0.486996	2
p (d)	0.331561	0.170696	0.098793	0.691777	3
p (d)*	0.356116	0.177785	0.107941	0.716552	4
p (d)	0.081175	0.061606	0.017202	0.308409	5
p (d)	0.021066	0.028045	0.001495	0.236256	6
p (n)	0.074758	0.039194	0.025921	0.196995	1
p (n)	0.185616	0.067210	0.087049	0.352677	2.3
p (n)	0.265527	0.154263	0.071239	0.630166	2
p (n)	0.473577	0.190644	0.167336	0.801077	3
p (n)*	0.500771	0.192475	0.181543	0.819371	4
p (n)	0.138103	0.097708	0.031067	0.444668	5
p (n)	0.037562	0.049052	0.002724	0.358003	6

5 CONCLUSÃO GERAL

Os botos-da-tainha estão presentes, ao longo de todo o ano na área de estudo e foram detectados em todos os dias amostrados. Porém, sua distribuição e o uso que fazem desta área são heterogêneos, variando conforme o fotoperíodo e fatores ambientais tais como período do dia, maré e vento. A pesca cooperativa, que ocorre principalmente na área de vida dos botos cooperativos, não parece ser um fator determinante para a presença dos animais, visto que eles permanecem ali à noite, quando a pesca cooperativa não ocorre. Além disso, nem todos os locais em que a pesca cooperativa acontece são os locais onde os botos passam mais tempo. A porção central da área de estudo é, aparentemente, a área que estes animais usam com mais frequência.

Estas conclusões foram possíveis a partir do monitoramento acústico passivo (MAP) estático, que pela primeira vez foi aplicado nesta população. Assim, os resultados encontrados corroboram e complementam o que já se conhecia para estes animais através dos métodos de estudo visuais, principalmente a fotoidentificação. Porém, para implementar o MAP, foi necessária a adaptação de um equipamento que fosse de baixo custo, mas efetivo para o registro das emissões sonoras dos botos. Isto porque, uma das limitações de equipamentos de menor custo é o limite de frequência (kHz) das gravações. Neste sentido, fez-se necessário primeiro testar se a frequência de amostragem a ser utilizada é capaz de registrar os cliques de ecolocalização, devido à alta frequência que estes sinais podem atingir. Sabe-se que os cliques, apesar de atingirem frequências muito altas, também apresentam componentes em frequências mais baixas, porém não havia uma estimativa da proporção de cliques que podem ser registrados nestas frequências mais baixas. Então, utilizando gravações feitas com taxa de amostragem de 192 kHz e observando os cliques de ecolocalização que também eram registrados em frequências abaixo de 48 e 24 kHz (taxa de amostragem de 96 e 48 kHz, respectivamente), foi possível concluir que, apesar da perda de alguns cliques, estas frequências são efetivas para o registro da ecolocalização nas gravações. Ou seja, tais frequências podem ser usadas em estudos que trabalham com dados de presença e ausência dos animais. Isto possibilita o emprego de equipamentos de menor custo que, mesmo apresentando restrições em suas taxas de amostragem, não inviabilizam a implementação de MAP para estudar populações de golfinhos, ao menos *Tursiops truncatus*, para o qual as frequências foram testadas.

Confirmada a efetividade da taxa de amostragem de 48 kHz (frequência de Nyquist de 24 kHz) para gravar os sons de *T. truncatus*, pudemos implementar o MAP de baixo custo para. Nossos resultados, utilizando o registro de todas as emissões sonoras dos botos ─ cliques e assobios ─ mostraram que os animais não só se mantêm na mesma área à noite, como aumentam a ocupação desta área ou intensificam seu comportamento acústico neste período, em comparação ao dia. Apesar de não podermos concluir qual destas duas alternativas melhor representa a resposta para o aumento das emissões sonoras à noite, tal resultado nos indica que a pesca cooperativa não é necessariamente um fator determinante para a presença dos botos nesta área. Porém, a altura da maré e a velocidade do vento têm certa influência nos locais que os botos mais utilizam em cada condição destas variáveis ambientais.

Após ter o panorama geral da distribuição da população na área de estudo, voltamos a atenção para os indivíduos, através do levantamento e análise de alguns assobios assinatura. Pela primeira vez, até onde se tem conhecimento dos registros na literatura, analisou-se dados de recaptura de assobios assinatura, nos diferentes locais monitorados, a partir do método de marcação-recaptura espacial. Os resultados da probabilidade de captura possibilitaram identificar os locais que os botos provavelmente usam com mais frequência e por mais tempo. Com apenas oito assobios assinatura, resultantes de uma avaliação preliminar, este método de análise permitiu identificar a distribuição heterogênea, em nível individual, dos botos na área e confirmar a sua importância para a população inclusive à noite, quando a probabilidade de captura pelo registro dos assobios assinatura é maior.

Neste ponto, é importante destacar que tanto os resultados do monitoramento que utilizaram o repertório acústico dos botos no geral para registrar sua ocupação da área, quando os resultados que focaram apenas nos assobios assinatura, foram concordantes quanto ao aumento do uso da área, ou do comportamento acústico, à noite. Esta informação é relevante para duas conclusões. Primeiro, a área de vida dos botos aparentemente não é definida pelos locais de pesca cooperativa. O contrário parece ser o mais provável: a pesca cooperativa acontece principalmente nesta área pelas características que a área apresenta e que fazem ela ser interessante para os botos. Esta é uma informação nova que pode ajudar a entender como surgiu a estratégia de forrageio especializada que é a pesca cooperativa. Segundo, sabendo que os botos permanecem na mesma área à noite, medidas de conservação que foquem nesta área tem maiores chances de serem efetivas. Isto vem sendo observado com a redução do *bycatch* após a proibição da pesca com redes de emalhe nesta parte da área de vida dos botos.

A manutenção de um monitoramento acústico passivo da população de botos-da-tainha de Laguna, com a identificação de mais assobios assinatura e a distribuição de gravadores por outros locais da área de vida dos botos, ao longo do complexo estuarino, contribuirá com os estudos de longo prazo. Ampliando os métodos de estudo desta população geramos informações mais abrangentes para as tomadas de decisão quanto à conservação da população, além de adicionar peças ao quebra-cabeça que leva ao entendimento do desenvolvimento e manutenção da pesca cooperativa.