UFRGS
UNIVERSIDADE FEDERAL
DO RIO GRANDE DO SUL

PPGBAN
PROGRAMA DE PÓS-GRADUAÇÃO EM BIOLOGIA ANIMAL

INSTITUTO DE BIOCIÊNCIAS
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ALÉM DAS RAÍZES CULTURAIS: AS HABILIDADES DE CAÇA DE GOLFINHOS COOPERATIVOS DO SUL DO BRASIL

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Dissertação apresentada ao Programa de Pós-Graduação em Biologia Animal, Instituto de Biociências da Universidade Federal do Rio Grande do Sul, como requisito parcial à obtenção do título de Mestre em Biologia Animal.

Área de concentração: Biologia e Comportamento animal
Orientador(a): Prof. Dr. Ignacio Benites Moreno

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Aprovada em 08 de abril de 2019.

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AGRADECIMENTOS

Loucura é pensar que sozinho se chega longe. Reconhecer e valorizar quem caminha junto é capaz de dissolver uma realidade ideológica onde a individualidade e a soberba são fortemente incentivadas. Hoje olho pra trás e, com muitos rostos cruzando minhas lembranças, vejo como meu caminho foi construído a muitas mãos.

Agradeço às instituições que colaboraram com este trabalho: a Transpetro, pelo suporte financeiro; ao CNPq pela bolsa concedida; ao PPG-Biologia Animal pela formação e constante aprimoramento na construção de profissionais qualificados; e ao Ceclimar, pelo suporte logístico e por ter sido minha segunda morada ao longo de tantos anos, aos seus profissionais, professores e técnicos, que compartilharam seus saberes comigo.

Muito obrigada aos colegas do Projeto Botos da Barra, principalmente por construirmos em equipe um trabalho tão gratificante; aos pescadores artesanais da barra, por me levarem a conhecer outro mundo e me fazerem ver o mundo todo de forma diferente; a todos os voluntários que me auxiliaram nas atividades de campo e que dividiram todas as emoções de fazer um robô planar no céu. Realmente voar não é uma missão fácil. Ao meu orientador e amigo, Ignacio, pelo incentivo constante, pela confiança, e pela parceria e entusiasmo por bons registros fotográficos durante a realização dos campos na barra.

O meu agradecimento mais profundo a minha base emocional tão sólida: a minha família, a que escolhi ao longo da vida e a que eu tive a sorte de nascer. Minhas amigas-irmãs que tanto me ensinam sobre respeito, união, compreensão e acolhimento. A família Frainer pelo espaço de amor, apoio e alegria pura que ela representa na minha vida.

Aos meus pais, minhas maiores fontes de amor, que com muita dedicação e carinho me proporcionaram uma vida privilegiada, da qual possibilitou que eu chegasse ao final dessa etapa. Agradeço do fundo do meu coração a preocupação diária com meus sentimentos e conforto, a todas as oportunidades que vocês plantaram por mim e a liberdade de seguir no que acredito. Ao meu irmão, meu fiel escudeiro dessa vida, por me ensinar sobre perseverança, força e o mais verdadeiro companheirismo, mesmo de tão longe. A todos meus ramos genealógicos, principalmente ao meu avô Darlan, que com sua luta me ensinou sobre humildade, e as minhas avós e bisa, mulheres fortes guardiãs de vivências profundas e dos olhares mais carinhosos.

A Manu, minha estrelinha da sorte mais preciosa, quem fez nascer em mim uma nova forma de amar. A ela e as crianças da minha vida, Heleninha e Matheus, que com toda sua pureza me lembram sobre a importância de questionar, de simplificar e colorir a vida.

Agradeço especialmente ao companheiro que escolhi pra me embalar na dança da vida, o Gui: pela pareceria no trabalho e na viagem do dia a dia, pelas nossas histórias, pela construção diária de uma realidade feliz, por sonharmos e caminharmos unidos e livres nesse mundão.

Por fim, a todos que buscam uma forma de viver em maior equilíbrio com o planeta e anseiam uma sociedade mais justa e empática, muito obrigada!

SUMÁRIO

RESUMO

A diversidade comportamental de golfinhos selvagens pode ilustrar o processo de transformação dos ambientes naturais. No entanto, a investigação de seus comportamentos é limitada às condições de detectabilidade e, por isso, seus repertórios podem ser subestimados. Por expandir o campo observacional, de forma segura e não invasiva, o uso de drones vem ampliando o conhecimento acerca dos aspectos sociais e comportamentais desses animais. Seus dados visuais (e.g. vídeos), além de serem reinterpretáveis, recriam o ambiente no contexto temporal e espacial, o que facilita acompanhar a dinâmica das paisagens naturais e de seus componentes biológicos. Apesar de ser um grupo estudado há quase três décadas, as atividades de caça dos botos ainda não foram analisadas de forma ampla - até o presente momento, os esforços pesquisa concentraram-se nas culturais táticas associadas à pesca cooperativa. Neste trabalho investigamos o repertório comportamental dos botos (*Tursiops gephyreus*) do estuário do rio Tramandaí a partir da perspectiva aérea. Também exploramos suas relações sociais e analisamos a influência de seu repertório na prática de pesca dos pescadores artesanais. Ao longo de um ano (jun/17-mai/18) sobrevoamos o canal estuarino utilizando um Veículo Aéreo Não Tripulado (hexacoptero S550), totalizando cerca de 10 h de filmagem. Buscando evitar possíveis reações dos animais, estabelecemos uma altura mínima para os voos de 20 m de altura. Simultaneamente aos sobrevoos, os botos foram identificados a partir da técnica de foto-identificação. As filmagens foram analisadas no software de livre acesso BORIS (*Behavioral Observation Research Interactive Software*). Os repertórios individuais foram comparados em relação a sua dissimilaridade e a análise foi conduzida no software R (pacote Vegan). Já os padrões de associação (*simple ratio index*, SRI) entre os animais foram obtidos com o software SOCPROG. Foi possível identificar que os golfinhos estuarinos de Tramandaí possuem um repertório diverso, apresentando mais de 20 táticas de caça. A análise de agrupamento, baseada na dissimilaridade entre os indivíduos (*Bray-Curtis index*), evidenciou a variabilidade intrapopulacional e padrões relacionados à modulação comportamental ao longo da ontogenia. Também identificamos traços de personalidade individuais e particularidades do grupo residente em relação a um animal visitante, das quais sugerem a adaptação da população residente ao ambiente. A exceção do par mãe-filhote, a associação dos animais com outros indivíduos ocorreu de forma aleatória durante as atividades de caça. Uma ampla gama (n=16) de táticas influenciou as tentativas de captura pelos pescadores artesanais, no entanto poucas delas (n=4) influenciaram positivamente sua produtividade. Os resultados obtidos neste estudo revelaram padrões ainda mais complexos do que já se conhecia acerca da plasticidade e especialização comportamental dos botos do estuário do rio Tramandaí, dos quais representam uma prática cultural de pesca singular do mundo contemporâneo.

Palavras chave: Diversidade comportamental, relações sociais, repertório especializado, cultura

Abstract

The behavioral diversity of wild dolphins may illustrate the transformation process of natural ecosystems. However, the behavior repertoire seems to be underestimated due to logistical constraints such as detectability. The use of drone has been increased our knowledge on social and behavioral traits of these animals since it expand the observational field in a safe and non invasive manner. Visual data (e.g. filming) are reinterpretable, and can characterize the environment in a temporal and spatial perspective, which allowed us monitoring the environment dynamic. This unique dolphin population has been studied for almost three decades, but its hunting behaviors have not yet been widely analyzed so far because research efforts have focused on the cultural tactics associated with cooperative fishing. Here we have investigated the behavioral repertoire of Lahille´s bottlenose dolphins (*Tursiops gephyreus*) in the Tramandaí estuary from the aerial perspective. We also have explored their social relationships, as well as the influence of their repertoire on the fishing activities of artisanal fishermen. We flew over the estuary using an Unmanned Ariel Vehicle (hexacoptero S550) to record dolphin behaviors in the rio Tramandaí estuary between June 2017 and May 2018, totalizing almost 10 hours of footage. The minimum altitude of flight was set in 20 m for avoiding behavioral responses of dolphins. Simultaneously, individuals were identified by photo-identification technique. Footages were analyzed in BORIS (Behavioral Observation Research Interactive Software), and statistical analysis was performed in the R (Vegan package) to compare the variability among individual repertoires. Association pattern (simple ratio index, SRI) was explored in the software SOCPROG. We identified that estuarine dolphins performed a diverse repertoire, using more than 20 hunting strategies. The cluster analysis, based on their behavioral dissimilarity (Bray-Curtis index), emphasize the intrapopulational variability as well as modulation patterns related to ontogeny. We also identified personality traits of individuals and particularities of the resident group relative to the transient animal, suggesting local adaptation of residents in this unique environment. Inside estuary, dolphins seem to present no association preference, instead of the mother-calf pair. Several dolphin behaviors (n=16) led artisanal fishermen to throw their nets, but few (n=4), in fact, have increased their fishing productivity. Our results revealed the complexity involved in plasticity and specialization of Tramandaí estuary dolphins, which represent a unique fishing cultural practice of the contemporary world.

Keywords: Behavioral diversity, social relationships, specialized repertoire, culture

CAPÍTULO I

ASPECTOS CULTURAIS DOS GOLFINHOS COOPERATIVOS

Golfinhos (Odontoceti: Delpihinidae) apresentam uma ampla diversidade comportamental associada ao forrageamento (Baird, 2000; Rendell & Whitehead, 2001; Nowacek, 2002; Mann & Sargeant, 2003). A particularidade das histórias de vida, a distribuição e a disponibilidade de alimento são alguns dos principais fatores que influenciam o desenvolvimento de determinada tática de caça (Partridge & Green, 1985). Estratégias ecológicas moldadas por processos evolutivos influenciam como as espécies exploram o ambiente, incluindo a qualidade da dieta e custo energético do estilo de vida (Spitz *et al.*, 2012). Esses mamíferos marinhos também desenvolvem técnicas voltadas à otimização das atividades de caça, como por exemplo, o uso de barreiras físicas e a parceria com outros animais durante o cerco do cardume (Leatherwood, 1975; Connor & Norris, 1982; Quérouil *et al.*, 2008; Coscarella & Crespo, 2010; Zaeshmar *et al.*, 2013). Fatores ambientais específicos, bem como habitats com características peculiares (e.g. regiões com fundo vegetado e presença de bancos de areia), favorecem o investimento e estabelecimento de estratégias especializadas de caça em populações restritas e/ou residentes (Guinet, 1991; Hoelzel, 1991; Rossbach & Herzing, 1997; Connor *et al.*, 2000a). O aprendizado social parece ser um fator importante no estabelecimento e perpetuação dessas táticas específicas dentro das populações de golfinhos (Mann & Sargeant, 2003; Sargeant *et al.*, 2005).

Os cercos colaborativos de peixe em direção à costa e envolvendo a espécie humana representam uma das peculiares táticas especializadas utilizadas pelo grupo (Fairholme, 1856; Pryor & Lindbergh, 1990; Smith *et al.*, 2009; Kumar *et al.*, 2012). A interação positiva entre golfinhos e pescadores artesanais possui um longo histórico (Lockyer, 1990; Orams, 1997). Sua documentação mais antiga remonta ao século I na Província Romana da Gália, atual França (Busnel, 1973; Parsons *et al.*, 2013). Apesar da relação dos animais com a pesca artesanal da tainha (*Mugil* sp.) ser conhecida há bastante tempo, ela se restringe a poucas espécies de golfinhos e comunidades tradicionais (Northbridge, 2009). Desde o século XIX, o ritual já foi registrado em restritas regiões da África, Oceania, Ásia e América (Lockyer, 1990). Atualmente, é um patrimônio cultural (não reconhecido formalmente) associado a comunidades tradicionais específicas da costa do Brasil, Mauritânia, Myanmar e Índia (Fig. 1) (Simões-Lopes, 1991; Campredon & Cuq, 2001; Smith *et al.*, 2009; Kumar *et al.*, 2012). A maneira como humanos e golfinhos interagem durante a pesca varia nas diferentes localidades, sendo uma técnica diversificada (Ginsberg & Clode, 1994; Whitehead & Rendell, 2014a).

O conhecimento empírico dos pescadores tradicionais sobre a caça costeira dos golfinhos é a origem comum dessa prática nas diferentes culturas (Zappes *et al.*, 2011). Os pescadores, dispostos na costa, observam a aproximação dos animais e aguardam o momento certo para cercar parte do cardume (Busnel, 1973; Simões-Lopes *et al.*, 1998; Smith *et al.*, 2009; Kumar *et al.*, 2012). A partir de comportamentos executados pelos golfinhos, pescadores artesanais localizam os peixes, aumentando assim sua produtividade pesqueira (Simões-Lopes *et al.*, 1998; Smith *et al.*, 2009; Kumar *et al.*, 2012). Tendo em vista que essa interação é voltada à captura da tainha, a ocorrência do fenômeno é associada ao ciclo migratório da espécie-alvo na maioria das localidades (Lemos *et al.*, 2014; Crosseti & Blaber, 2016). No entanto, a prática conhecida como pesca cooperativa é frequente ao longo de todo ano em dois sistemas estuarinos brasileiros: os animais entram espontaneamente durante todas as estações nos estuários de Laguna (SC) e Tramandaí (RS). Assim, a interação favorece a captura de outros peixes pelos pescadores nessas localidades (Simões-Lopes *et al.*, 1998; Santos *et al.*, 2018). A interação nos complexos estuarinos brasileiros destaca-se pela execução de comportamentos especializados, ritualizados e coordenados por ambas as espécies (Pryor & Lindbergh, 1990; Simões-Lopes *et al.*, 1998).

Figura 1. Atual diversidade das práticas artesanais de pesca envolvendo golfinhos selvagens ao longo do mundo (**A**, El Memghar, Mauritânia; **B**, Estuário Ashtamudi, Índia; **C**, Rio Ayeyarwady, Myanmar; **D**, Estuário de Laguna, Brasil; **E**, Estuário de Tramandaí, Brasil). Pescadores tradicionais relacionam-se com os animais a partir do uso de técnicas de captura ativa. Imagem adaptada de Busnel, 1973; Smith *et al*., 2009; Kumar *et al.,* 2012; Catão & Barbosa, 2018; e Acervo Projeto Botos da Barra do Rio Tramandaí.

Pescadores e botos precisam aprender como se comportar durante a caça estuarina (Simões-Lopes *et al.*, 2016). Enquanto essa cultura vem sido mantida pelos humanos principalmente por linhagens masculinas, a transmissão materna é a principal fonte de conhecimento para os golfinhos (Simões-Lopes *et al.*, 1998; Ilha *et al*., 2018). Além de aprender, é necessário praticar como se movimentar durante a pesca (Catão & Barbosa, 2018). Embora essa cultura venha mantendo certo padrão ao longo das gerações, a aprendizagem é um processo contínuo do qual cada indivíduo é moldado por suas diferentes experiências (van Schaik, 2010). Assim, a pesca cooperativa de Laguna e Tramandaí, apesar de compartilhar muitas semelhanças, apresenta uma série de particularidades relacionadas à característica de cada estuário, bem como dos diferentes pescadores e botos que atuam em cada região (Simões-Lopes *et al.*, 1998). Em ambos os locais são os golfinhos de Lahille (*Tursiops gephyreus*, ver Wickert *et al.* (2016)) que se envolvem na interação, e uma das diferenças mais marcantes entre os dois sistemas é a proporção em que o ritual ocorre: em Tramandaí a população residente de botos e o tamanho do estuário são, respectivamente, cerca de cinco e 20 vezes menor em relação a Laguna.

Dentre alguns visitantes sazonais, dez botos residem atualmente no estuário do rio Tramandaí, sendo cinco deles habitantes há mais de duas décadas (Tabajara, 1992; Giacomo & Ott, 2016; Ilha *et al.*, 2018). A ocorrência dos animais dentro do estuário representa uma fração das suas áreas de vida, ocorrendo assim uma variabilidade intra e interanual dos indivíduos no interior do sistema estuarino (Giacomo & Ott, 2016). Dados moleculares e de foto identificação indicam que os botos distribuídos nos diferentes estuários do sul do Brasil (i.e. Laguna, Mampituba, Tramandaí e Lagoa dos Patos) compõem uma metapopulação (Simões-Lopes & Fabian, 1999; Fruet *et al.*, 2014). Mesmo sendo próximos e os animais possuindo ampla mobilidade, a movimentação entre os locais, a diversidade e o fluxo gênico entre as comunidades é baixo (Simões-Lopes & Fabian, 1999; Costa *et al.*, 2015). A restrição e a independência demográfica dos grupos, bem como suas características biológicas e ecológicas (e.g. grande longevidade, taxa reprodutiva baixa), restringem a probabilidade de reabastecimento no caso de um declínio demográfico (Fruet *et al.*, 2014; Costa *et al.*, 2015).

A fragilidade da população do estuário do rio Tramandaí ainda é agravada devido a sua inserção na região de maior crescimento urbano do Rio Grande do Sul (IBGE, 2017). A degradação do habitat, sobre-exploração dos recursos pesqueiros, captura acidental em redes de pesca, poluição sonora e química da água são alguns dos fatores que ameaçam o grupo, bem como os outros botos costeiros do sul brasileiro (Plaganyi & Butterworth, 2005; van Bressem *et al.*, 2009; Zappes *et al.*, 2011; Fruet *et al.*, 2012). No estado do Rio Grande do Sul, comunidades costeiras e estuarinas do gênero *Tursiops* já se encontram oficialmente ameaçadas de extinção, devido principalmente ao seu tamanho populacional muito restrito (Decreto Estadual No. 51.797, 2014). Assim como na perspectiva dos golfinhos, a manutenção da cultural prática de pesca também é ameaçada pelo lado dos pescadores artesanais (Ilha *et al.*, 2018). O processo de urbanização que hoje ameaça a preservação dos botos originou-se a partir da descaracterização do habitat da comunidade tradicional costeira da região (Fig. 2).

Figura 2. Vista do canal do estuário de Tramandaí visto de cima da desembocadura. O processo de urbanização, que já levou a descaracterização total de uma de suas margens (Tramandaí à esquerda, Imbé à direita), ainda é crescente, assim como seus impactos sobre o ecossistema.

O sistema urbano e econômico contemporâneo vem ameaçando patrimônios culturais imateriais, a exemplo da interação entre botos e pescadores. Considerando que culturas são resultantes da transmissão de comportamentos típicos ao longo das gerações a partir de interações sociais (Laland & Galef, 2009), destaca-se a importância desse processo para a conservação de tais patrimônios (Brakes *et al.*, 2019a). Nesse sentido, a documentação dos padrões comportamentais e das relações sociais de ambas as espécies envolvidas na pesca cooperativa pode revelar aspectos relacionados a transformação cultural ocorrida ao longo do tempo. A partir da documentação de Simões-Lopes (1991) é possível, por exemplo, perceber que o modo como os pescadores se organizam e movimentam durante a interação com o boto mudou completamente nas últimas décadas (Zappes *et al.*, 2011). Observar e entender a dinâmica dos humanos envolvidos nesta prática (e.g. produtividade a partir da interação, repertório comportamental) é mais fácil comparado aos botos. Nesse sentido, o repertório comportamental dos botos de Tramandaí ainda não foi analisado de maneira sistematizada e sob uma ampla perspectiva, apesar de ser um grupo estudado desde a década de 90.

Além das táticas de caça dos golfinhos fundamentarem um patrimônio cultural, sua diversidade pode representar um repositório de informações adaptativas (Brakes *et al.*, 2019a). Seus comportamentos voltados à pesca da tainha são conhecidos (Simões-Lopes *et al.*, 1998), porém, o estuário possui uma ampla diversidade de presas disponíveis, das quais possivelmente também moldam o repertório de caça dos botos. Assim, nesta dissertação investigamos os padrões envolvidos na dinâmica comportamental da população de botos Tramandaí, principalmente das atividades de forrageamento, a partir de uma metodologia replicável. Também buscamos relacionar tais comportamentos com a prática de pesca dos pescadores artesanais, identificando quais foram interpretados como o momento certo para jogar a tarrafa e quais precederam o sucesso de captura pelos pescadores. Considerando que os botos são animais sociais e que isso influencia a aprendizagem dos comportamentos de caça (Connor *et al.*, 2000b), as relações sociais dos botos também foram analisadas.

A partir da observação aérea com o uso de Veículo Aéreo Não Tripulado (VANT) foi possível observar que a população amostrada apresenta um repertório diverso. Os animais utilizaram mais de 20 comportamentos distintos durante suas atividades de caça. Tamanha riqueza comportamental está provavelmente associada à plasticidade alimentar do gênero. A análise de agrupamento, baseada nas semelhanças comportamentais entre os indivíduos, evidenciou aspectos relacionados ao desenvolvimento: i) até o final da infância, a companhia materna influencia diretamente na forma como o filhote se comporta, assemelhando-se a sua progenitora; ii) a fase juvenil parece ser um momento onde os animais ajustam seu comportamentos aprendidos até ali, adaptando seus usos a nova vida como recém independentes; e iii) tal período de adaptação possivelmente desencadeia a variabilidade intrapopulacional observada na fase adulta. A partir da identificação de traços de personalidade individuais, também identificamos particularidades do grupo residente em relação ao animal visitante.

Embora populações do gênero *Tursiops* tendam a estabelecer relações sociais preferenciais, os botos não seguiram esse padrão. A associação aleatória dos animais durante a caça rejeitou nossa hipótese de que os animais escolheriam parceiros específicos, principalmente em relação às semelhanças compartilhadas entre os indivíduos (i.e. homofilia), como por exemplo, a faixa etária e ao repertório comportamental. Grande parte do repertório comportamental dos botos influenciou a dinâmica de pesca dos pescadores artesanais: 64% dos eventos foram interpretados pelos pescadores como o momento certo de jogar a tarrafa, no entanto poucas delas (n=4) levaram ao sucesso de captura. Considerando que nossa análise trouxe uma visão ampla acerca da resposta dos pescadores, sem diferencia-los em relação a suas habilidades, é possível que essa baixa eficiência de interpretação reflita seus diferentes níveis de experiência na pesca com os botos. Os resultados obtidos neste estudo ampliam a percepção sobre uma prática cultural de pesca singular do mundo contemporâneo, revelando padrões ainda mais complexos do que já se conhecia.

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CAPÍTULO II

BEYOND CULTURAL ROOTS: FORAGING SKILLS OF FISHER-COOPERATIVE DOLPHINS FROM SOUTHERN BRAZIL

"Of course mama's gonna help build the wall"
Pink Floyd, 1979

Manuscrito redigido nas normas do periódico *Animal Behaviour*
(Disponível em https://www.elsevier.com/journals/animal-behaviour/00033472/guide-for-authors)

Beyond cultural roots: foraging skills of fisher-cooperative dolphins from Southern Brazil

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ABSTRACT

Cetaceans are well known for their high cognitive abilities that enable them to develop complex behavioural skills in the wild environment. In southern Brazil, two wild populations of Lahille's bottlenose dolphins (*Tursiops gephyreus*) have evolved typical-group behaviours for coastal hunting, which are the foundation of a traditional fishing art known as cooperative fishing. Here, using the innovative technology of an Unmanned Aerial Vehicle, we examined the behavioural repertoire of the dolphins from the Tramandaí estuary -an urban, highly dynamic and biodiverse environment. We also have explored their social relationships and some clues about the influence of their repertoire on the fishing activities of cast net fishers. We flew over the estuary between June 2017 and May 2018, totalling almost 10 hours of footage. Our findings suggest that behavioural dynamics of cooperative dolphins are much more complex than researchers have been assumed in recent years. We identified that dolphins (n=11) exploit resources under generalized and specialized tactics, both in groups and alone, using more than 20 behaviours during hunting. The cluster analysis, based on their behavioural dissimilarity (Bray-Curtis index), emphasized the intrapopulational variability, the variation between developmental stages and resident and visitor individuals. The overall mean of group's connections was about six and they did not choose specific partners during foraging, what may be related to the familiar scenario they face in the region (historical average of 9 residents). Sixteen behaviours of the dolphins (64%) led fishers to throw their nets, but few (n=4), in fact, resulting in fish capture. The maintenance of the plasticity and behavioural diversity of cooperative dolphins, as well as their social structure, can be crucial not only for their adaptation to a changing environment, but also for the conservation of a traditional and unique fishing practice of the contemporary world.

Keywords: Behavioural diversity, specialized repertoire, learning, social relationship, tradition

INTRODUCTION

Whales and dolphins (Cetartiodactyla: Cetacea) have sophisticated cognitive abilities that allow them to perform complex behaviours, to socialize, to learn and evolve cultural identities (Marino et al., 2007). Specialized feeding tactics traditionally used by some populations have been preserved from the combination of all these factors (Rendell & Whitehead, 2001), as for example: the lobtail feeding of humpback whales (*Megaptera novaeangliae*) in the Gulf of Maine (USA) (Allen et al., 2013); the beach hunting of bottlenose dolphins (*Tursiops truncatus*) in the Shark Bay (AUS) (Sargeant et al., 2005); of orcas (*Orcinus orca*) in Patagonia (ARG) (Lopez & Lopez, 1985) and Crozet Archipelago (Guinet & Bouvier, 1995); the tool use by bottlenose dolphins, also in Shark Bay (Krützen et al., 2005; Mann et al., 2012); and the cooperative-fishing between Lahille's bottlenose dolphins (*T. gephyreus*) and artisanal fishermen in Laguna and Tramandaí lagoons (BRA) (Simões-Lopes et al., 1998; Simões-Lopes et al., 2016).

The interspecific relationship of hunting involving wild dolphins and humans developed independently only in few places around the world (Moreton Bay, AUS (Fairholme, 1856); El Memghar, MTN (Busnel, 1973); Laguna and Tramandaí lagoons, BRA (Pryor & Lindbergh, 1990; Simões-Lopes, 1991); Ayeyarwady River, MYA (Smith et al., 2009); Ashtamudi estuary (Kumar et al., 2012)). The phenomenon in southern Brazil distinguishes itself from other records documented since the 19^{th} century, because in Brazilian waters it involves peculiar characteristics: it is initiated by the Lahille's bottlenose dolphins (hereafter dolphin) and is based on stereotyped behaviours, both by dolphins and artisanal fishermen (Pryor & Lindbergh, 1990; Simões-Lopes et al., 1998; Peterson et al., 2008). Fishers perceive some typical behaviours from dolphins (e.g. head slap and back presentation) as a signal which indicate the location of fish shoals (Pryor & Lindbergh, 1990; Simões-Lopes et al., 1998).

Although the behaviours of dolphins traditionally related to the fishermen interaction are well known in science, their general repertoire is still undisclosed. Thus, we aimed to get an overview of cooperative dolphins' skills, from the observation of the behavioural repertoire of the Tramandaí estuary population. From aerial observation, we explored hypothesis concerning: i) the behavioural diversity of the dolphins; ii) their social bonds; and iii) the response of fishers to the dolphins' performance.

Behavioural diversity

Dolphins of genus *Tursiops* are opportunistic predators that can adapt their diet in relation to prey availability (Barros & Clarke, 2009; Milmann et al., 2016; Secchi et al., 2016). Such plasticity requires that they develop different foraging strategies (Barros & Wells, 1998; Sargeant et al., 2006; Torres & Read, 2009), what may be especially advantageous for whoever lives in greatly dynamic environments. Thus, we predicted the group has a rich repertoire considering this study population lives in a highly dynamic estuary (Hoeinghaus et al., 2011), where several fishes of different ecological groups coexist (Ramos & Vieira Sobrinho, 2001).

Social bonds

Social mammals, such as dolphins, have their juvenility marked by the shift of preference from maternal company towards social expansion (Sachser & Kaiser, 2010; Krzyszczyk et al., 2017). Independent animals (i.e. juveniles and adults) tend to establish preferential associations based on the similarities shared with other individuals, in relation to age, gender, kinship and behavioural traits (i.e. homophily principle) (Hinde, 1976). These social experiences represent opportunities for individuals to learn with others and the homophily tend to reinforce the traditions and social structure within the group (Cantor et al., 2015). As the *Tursiops* genus follows this pattern (Gero et al., 2005; Wiszniewski et al., 2009; Daura-Jorge et al., 2012; Diaz-Aguirre et al., 2018; Genov et al., 2018; Zanardo et al., 2018; Machado et al., 2019), we hypothesized that at least juveniles and adults of the study group had preferred associations, especially among age peers in foraging activities.

Fishers' response

The hunting of dolphins near off the coastline facilitates the fish capture by the cast net fishers (Simões-Lopes et al., 1998; Santos et al., 2018). Besides herding the shoal near to where fishers dispose themselves, their fishing tactics evidence the fish location (Zappes et al., 2011). Identifying the right moment from the dolphins behaviour is a learned skill (Peterson et al., 2008) that guarantee the fisher success during the interaction and over generations (Simões-Lopes et al., 1998). Four main patterns (i.e. back presentation, head slap, partial emersion and tail slap) are identified as dolphins' signals by traditional fishers (Simões-Lopes et al., 1998; Zappes et al., 2011). According to local fishers active in the interaction, outsiders and non-professional fishers do not know how it works and, thus, tend to ignore the effective behaviours presented by dolphins, disrupting the traditional fishing (Peterson et al., 2008; Zappes et al., 2011). As our study did not focus on the interaction itself, but in the general hunting repertoire of dolphins, fishers were not differentiated by their experience. Thus, we predicted that, throughout our sampling, a greater variety of behaviours was interpreted by fishers as the right moment to cast their nets.

MATERIAL AND METHODS

Study site and population

Southern Brazil has a peculiar hydrographic system of interconnected lagoons that extend for 115 km parallel to the coastline (Fig. 1) (Viero & Silva, 2010). This fluvial network (Tramandaí River Basin) flows into the Tramandaí river estuary (29°58'33.7"S 50°07'10.0"W) where it connects with the south-western Atlantic Ocean through a narrow and relatively shallow canal (average depth = 2.9 m). The estuarine system is surrounded by an increasing urban environment (Fig. 1) (da Silva et al., 2017) and this wild-urban scenario is one of the priority areas for Brazilian biodiversity conservation (MMA, 2007).

There have been only a few Lahille's dolphins inhabiting the estuary mouth for the last 60 years (Tabajara, 1992). Among some seasonal visitors, resident dolphins with high fidelity to the region have been using the area for decades (Simões-Lopes et al., 1998; Simões-Lopes & Fabian, 1999; Giacomo & Ott, 2016). Their presence in the Tramandaí estuary is only a portion of a wider home-range so their frequency in the area have intra and inter-annual variability (Giacomo & Ott, 2016). An average of nine individuals have been recorded since the 90's (from calves to adults), whereas some of them are still residents of this region (Simões-Lopes & Fabian, 1999; Giacomo & Ott, 2016).

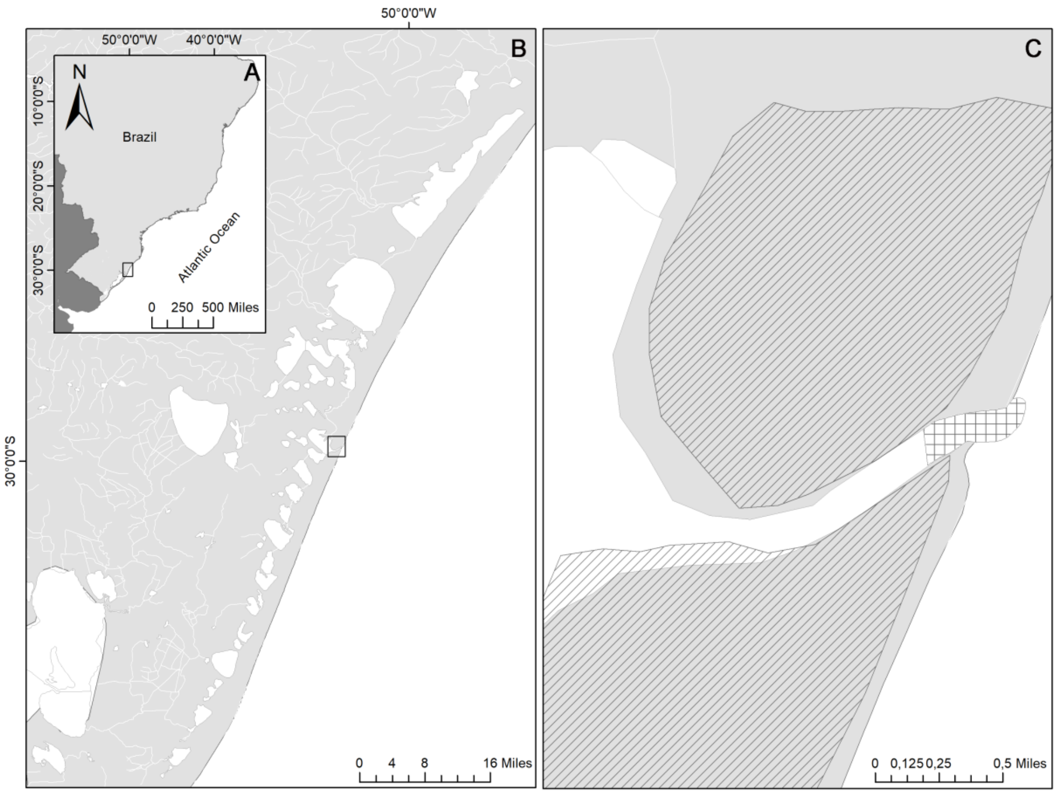

Figure 1. The study area (Tramandaí estuary) is located in southern Brazil (A). One of the singularities of the region is the extensive chain of lagoons (B) from which flows into the Tramandaí estuary (C), where a small population of dolphins have been living for decades. The hatched area in image C indicates the urbanized area surrounding estuary mouth and the squared region indicates where dolphins were sampled.

Data sampling

Behavioural investigation of the local dolphins was based on continuous records (Lehner, 1996) acquired with an Unmanned Aerial Vehicle (UAV). The flights over the mouth of the Tramandaí Estuary were conducted over the period of one year (June/2017 - May/2018) in days with favourable weather conditions:

wind speed < 20 km/h and no rain or fog. Before starting an aerial survey, we located the animals, from the estuary margin, to identify them by photo-identification (variability of dorsal fin shapes and markings) (Würsig & Würsig, 1977). A trained operator would start the UAV operations, once an individual or group (i.e. spatial aggregation over a time scale sufficiently short that there are few changes in composition, see Whitehead (2009)) was detected. Considering that the canal is relatively small and dolphins frequently enter in the estuary spontaneously, all flights were conducted manually (Verfuss et al., 2019) from a terrestrial platform located on the shore. We used a Dragon Fly hexacopter (S550) equipped with a HD camera connected on a gimbal with 3-axis stabilization for aerial surveys.

Aiming to avoid behavioural responses by the equipment approach, the first step of all overflights was the stabilization of UAV in a safe altitude to hover above the animals (Ramos et al., 2018). Once over the dolphins, the UAV was maintained at the same altitude during all surveys. Considering the potential noise effects of UAVs below the water surface (Christiansen et al., 2016), the minimum height for operations was set at 20 m. Flight altitude varied between 20-35 m being adjusted based on daily wind, wave dynamics and dolphins' location within the estuary. During all operations we monitored live video and flight parameters (e.g. altitude, battery level, trajectory and pilot distance) via a mobile device (tablet or smartphone). Direct observations of dolphins' behaviour as well as identification of group composition were conducted from the shore simultaneously to all UAV time effort. To complement behavioural information recorded from aerial perspective, photographic sequences (10 frames per second using Canon 7D Mark II using Lens EF 300mm f2.8) and *ad libitum* observations (Altmann, 1974; Mann & Smuts, 1999) at surface level were implemented.

Data analyses

Behavioural repertoire

We identified, characterized and quantified the dolphins' behavioural repertoire (Table 1) from aerial footage using the free software BORIS (Behavioural Observation Research Interactive Software v. 7.4, see Friard and Gamba (2016)). For each video (i.e. a flight) an initial and final point was set where the sampling period was defined as the time when we were focusing on the animals. It would begin when the UAV had stabilized its altitude to hover over dolphins and finish just before starting to come down to the ground. Only this sampling period was explored in each video to determine the frequency and duration of behaviours and activities listed in Table 1.

To investigate which dolphins behaved similarly during hunt activities, we conducted a hierarchical cluster analysis (Morgan et al., 1976; Lehner, 1996) based on behavioural dissimilarity among individuals (Bray-Curtis index). We used in this analysis a presence-absence matrix of individuals by behavioural states and events, which included the movement states -milling, against-current and prowling- and all events present in Table 1 with the exception of courtship. Using the mean dissimilarity across all pairs of elements contained within group, the Unweighted Pair-Group Average (UPGMA) method grouped elements based on the average distance between all members in the two groups (Sokal & Michener, 1958). The test was carried out using package Vegan for R 2.5-3 (Oksanen et al., 2018).

Also from an aerial perspective, two variables related to the practice of artisanal fishermen were quantified: number of thrown nets and the events of fishery success. They were quantified using BORIS in combination with foraging tactics of dolphins and behavioural strings obtained from BORIS were posteriorly explored in Behatrix (www.boris.unito.it/pages/behatrix). From the total number of times that dolphins performed each event described in Table 1, behavioural strings revealed the frequency that such behaviours

(i) were understood as a signal by fishers to cast their nets as well as (ii) collaborated to their catch success (i.e. which preceded events of fish catch by cast net fishers).

Table 1. Behavioural repertoire of Lahille's bottlenose dolphins (*Tursiops gephyreus*) identified from aerial perspective. The right column present the number of times each behaviour was identified.

Behavior	Description	Source	Number of observation from aerial images (frequency and states duration in sec)
States			
Foraging	Rapid energetic surfacing, frequent directional changes, fish chases and fish fleeing. Peduncle and tail-out dives can be common	Shane et al. (1986); Shane (1990); Mann and Sargeant (2003); Mann and Watson-Capps (2005); Lusseau (2006)	76 (21 012.516)
Socializing	Dolphins in almost constant physical contact with one another, oriented toward one another, and often displaying surface behaviors. Individuals often change their position in the school and the school could split in small subgroups that are spread over a large area.	Shane *et al*. (1986); Shane, (1990); Mann and Sargeant (2003); Mann and Watson-Capps (2005); Lusseau (2006)	17 (901.587)
Travelling	Dolphins moving steadily in one. They may meander, but still move in a general direction	Shane *et al*. (1986); Shane (1990); Mann and Sargeant (2003); Mann and Watson-Capps (2005); Lusseau (2006)	2 (105.016)
Milling	No net movement. Individuals are surfacing facing different directions. The school often changes direction. Dive intervals are variable but short	Shane *et al*. (1986); Shane (1990); Mann and Sargeant (2003); Lusseau (2006)	50 (21 299.689)
Against-current	Dolphins faced against a current and remained in one place except when chasing and catching fish	Shane (1990)	23 (4 180.757)
Prowling	Dolphins swim in normal speed surrounding a specific area, generally near of shoreline	This study	13 (2 449.525)
Events			
Regular dive	Only the blowhole, part of the back, and the dorsal fin are exposed. Dolphin leaves surface by sinking at end of a breathing series without arching peduncle or raising flukes out of water	Shane,(1990); Mann and Sargeant (2003)	702
Peduncle dive	The dolphin arches its back and exposes its peduncle arched at dive but not its flukes as it submerges after breathing (or becomes partially submerged).	Shane (1990), as tail-stock dive; Mann and Sargeant (2003); Lusseau (2006), as tail-stock dive	99
Head slap	Dolphin exposes its head and hits the surface with its throat	Würsig and Würsig (1979); Simões-Lopes *et al.* (1998)	80
Side slap	Dolphin exposes its head and hits the surface with the lateral portion of the head	Shane (1990)	70
Fast swim	A dolphin rapidly accelerates and/or swims fast along or below the water surface	Mann and Sargeant (2003)	65
Sharking	Dolphin swims horizontally at the water surface with its dorsal fin visible above water	Lusseau (2006)	63
Active surfacing	Rapid surfacing with spray (horizontal posture), the dolphin's ventrum does not clear the water surface	Shane (1990), as racing dive; Mann and Sargeant (2003), as rapid surface; Lusseau (2006)	62
Side swim	Dolphin swims on its side	Leatherwood (1975)	40
Humping surface	A normal speed surface in which the dolphin "humps up" its posterior half to break its forward motion as it descends. Often seen when dolphins are driving and pursuing the prey in shallow waters	Mann and Sargeant (2003)	29
Underwater tail-slap	A dolphin slaps the herring fish with their flukes	Smolker and Richards (1988)	27
Rooster tailing	Fish chase with fast swim along the surface of the water which causes a sheet of water to trail off the dorsal fin. After that, the dolphin descends rapidly, often opposite to the direction of the swim	Mann and Sargeant (2003)	25
Bubble-blow	Exhaling underwater, producing a stream of bubbles	Lusseau (2006)	22

Porpoise	Rapid surfacing whereby dolphin almost clears surface in horizontal position but ventrum remains on surface. The dolphin's entire body does leave the water surface in the course of the dive	Mann and Sargeant (2003)	18
Side-roll	Head and body slightly turned to one side	Shane (1990); Ramos *et al.* (2018)	17
Macrophyte-carrying	Dolphin carries a macrophyte with its rostrum down of the water surface	This study	11
Eye-out	Dolphin lifts its head above water until its eye is exposed	Würsig and Würsig (1979), as noseout; Shane (1990), as nose out; Lusseau (2006)	10
Tail slap	Dolphin barely clears the surface with its flukes before it brings them down	Würsig and Würsig (1979); Shane (1990); Lusseau (2006), as lobtail; Simões-Lopes *et al*. (1998)	9
Horizontal circle	Dolphin swims rapidly in a circle on its side with body bent forward, much like a cat chasing its tail	Shane (1990)	9
Pinwheeling	Dolphin increases its speed suddenly (often with its fin constantly exposed) for 10-20m toward shoreline. Just before it reaches the shore, the dolphin leans on its side and spin in a circle or makes a hairpin turn	Leatherwood (1975); Smolker and Richards (1988); Shane (1990)	8
Tail-out dive	The dolphin arches its back and exposes its flukes as it dives. Usually used for deep dives	Shane (1990), as flukes-up dive; Mann and Sargeant (2003); Lusseau (2006)	7
Leap	Dolphin jumps out of the water with entire body clears (any height)	Würsig and Würsig (1979); Shane (1990); Mann and Sargeant (2003)	5
Backward slap	Dolphin emerges from the water as far as about mid-body and then slaps its back against the water	Shane (1990)	5
Vertical position	Dolphin in vertical position with the head or caudal fin perpendicular to the surface	Kuczaj and Eskelinen (2014)	4
Carousel	Dolphins swam in circles around the fish, gradually tightening the school. Animals surround the school forcing fish to swim in a concentrated ball. Occasionally, one of the dolphins would perform agile movements against the surface.	Bel'Kovich et al. (1991)	3
Spy-hop	Dolphin raises out of the water vertically, with only a part of the body	Lusseau (2006)	1
Fish toss	Fish thrown into the air by dolphins	Würsig and Würsig (1979); Shane (1990)	1
Courtship	The animals display several bouts of rapid swimming side by side while in physical contact interchanging their relative position. One individual also can stay stationed below each other maintaining some physical contact (genital region of both in contact, peak-to-genital propulsion, ventral presentations and chases)	Wells (1984); dos Santos and Lacerda (1987)	1

Social relationships

Considering the easiness to identify individuals, due to their proximity to the shoreline, we explored their relationships, quantifying the proportion of time each dyad (i.e. pair of individuals) spent together, using the simple ratio index (SRI) (Hoppitt & Farine, 2018). Dolphins were considered associated when they were using the same site (maximum of 30 m of distance between them) simultaneously (Whitehead, 2008a), and usually engaged in the same activity pattern (Shane, 1990). All animals were sighted in more than 5% of the sample units (i.e. each flight with distinct group composition), hence all of them were included in this analysis. To verify if SRIs reflect the true sociality and the variability of the association index within the population, we calculated, respectively, the correlation coefficient (r) and the social differentiation estimate (S) (Whitehead, 2008b). For the first, values range on a scale of 0 to 1, where 0 represents a poor accuracy and 1 a perfect representation of the social structure; whereas the latter indicates that relationships within a population are well-differentiated if estimate has value greater than 0.5 (Whitehead, 2008b).

We used the multiple regression quadratic assignment procedure (MRQAP) to verify the influence of structural factors (i.e. gregariousness, age and gender) on group association pattern (Whitehead & James, 2015). In order to test if individuals tend to associate randomly (i.e. without preference for specific members) we used a null model that permutes the incidence matrix of groups for each sample unit to create randomized SRI matrices (in our case 20 000 iterations, 1000 flips per permutation), maintaining the original group size and sighting frequency (Bejder et al., 1998; Whitehead et al., 2005). Preferred companionships were considered when standard deviation (SD) and coefficient of variation (CV) of the observed SRI was significantly higher than those expected by the chance (Whitehead, 2008a).

A weighted network was built from association index to illustrate the social relationships among individuals (network metrics (Whitehead, 2008a) of all elements of social diagram are present in supplementary material 1). Tests were performed in SOCPROG v. 2.8 (Whitehead, 2009), and the social diagram was also explored in Gephi v. 0.9.2 (Bastian et al., 2009) mainly for configuration of visual features.

Ethical note

Our study was entirely observational from a land platform. The unmanned aircraft used to capture images and fly over dolphins is register under the National Civil Aviation Agency (PR-437497387) and maximum care was taken to minimize any disturbance to animals during approaching and hovering (e.g. to set a safer altitude for each sampling occasion, to not approach animals directly, minimize UAV movements, permanent attention for any response signal).

RESULTS

We performed 78 flights in which 11 Lahilles's bottlenose dolphins from the Tramandaí estuary were recorded, totalling more than 9h of aerial footage (09:05:01). Flights lasted on average 6.98 min (SD = 2.23 min) ranging from 1.83 to 11.26 min. Out of the 48 different group compositions observed, the mean size was 2.25 dolphins (SE = 0.14), ranging from 1 to 4. Even with estuary not having very clear water (turbidity mean ± SE = 101.46 ± 6.64 cm), unprecedented behaviours for the population, that were undetectable from surface level observations (e.g. courtship, carousel and vertical swim; see Table 1), could be identified from an aerial perspective.

Behavioural repertoire

Out of the total time of aerial filming, behavioural information was obtained from 07:41:06 (sampling period). Only in one flight a possible behavioural response to the presence of the UAV was noticed. This response consisted of a briefly upward-directed behaviour (side-roll with open mouth, see Ramos et al. (2018)) where no activity change was observed. Focal groups spent most of their time foraging (78.8%), followed by socializing (3.4%). About 90% of socialization occasions were performed simultaneously to feeding activities. Since our surveys mainly recorded information of dolphins while foraging, Table 1 essentially presents hunting tactics used by them.

We identified dolphins moving within the estuary using three different patterns: milling, prowling and against-current (Table 1, Fig. 2). The first was the most frequent (79%) through all sampling periods. When performed during feeding activities, these movements seem to be related with prey search and they differed, in general, in habitat use, since dolphins explored respectively: (A) a wide area of the estuary moving in varied directions; (B) a specific and restricted zone as the waters near of sandbank; and (C) few regions adjacent to the point where dolphins swim maintaining their position. Dolphins engaged in prowling and against-current predominantly in autumn (respectively, 59.6% and 46.1%).

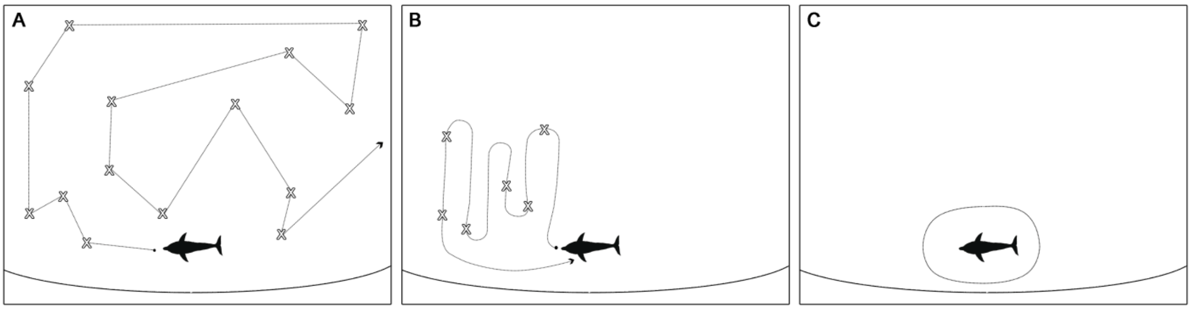

Figure 2. Schematic drawing of the three movement patterns performed by Lahille's bottlenose dolphins inside of the Tramandaí estuary. Milling (A), prowling (B) and against-current (C) differ from each other in relation to the amplitude of the area used by them as well as the regularity of their movements. Curved line at the bottom of images represents the shoreline.

Dolphins used several behaviours during foraging (Table 1, supplementary material 2), including some high performance tactics as fast swimming and turning movements (i.e. rooster tailing, horizontal circle, pinwheeling and side-swimming). Such behaviours were useful to explore the water column widely for preying on a wide variety of resources. The capture of mullets (*Mugil* sp.), a pelagic prey, involve mainly head slaps (i.e. head and side slap), agile tactics just below and along surface, as horizontal circles and rooster tailing. On the other hand, in the benthic fishing, dolphins spent more time below the water surface performing underwater tail-slaps and other movements at the estuary bottom, causing sand to rise towards the surface above the area where they had dived. The exploitation of epipelagic waters involved mainly side swimming at surface and vertical position (supplementary material 2). It is worth to highlight that the calf (I26) was the only one who was recorded hunting in the entire water column, fishing from benthic (i.e. flounder, *Paralichthys* sp.) to epipelagic (i.e. pompano, *Trachinotus* sp.) preys (Fig. 3). While it fished in epipelagic waters in the few moments where it was without its mother, the benthic hunt was developed in the presence of its mother. Despite the main behaviour used for these activities also being used by other animals, none of them performed them with these purposes (i.e. flounder and pompano hunt). Additionally, juveniles and adults were not recorded with these preys on the mouth, contrary to calves.

Figure 3. Lahille's bottlenose dolphins exploring different prey types. They fished pelagic preys, such as pompano (*Trachinotus* sp.) (A) and mullet (*Mugil* sp.) (B), as well as flounder (*Paralichthys* sp.) (C), a benthic species.

Most of the time (69.7% including head and side slap) when dolphins performed head slaps was when they were fishing near the shore (< 10 m), where fishermen usually positioned themselves. However, we have also observed them behaving in this way while they were hunting alone in the middle of the canal and close to the shoreline when fishers were not present. In addition, dolphins hit the surface with head while they were hunting cooperatively with other dolphins. Dolphins cooperated between themselves also performing the behaviour known as carousel (Table 1, supplementary material 2). This tactic was rare (n=3) and was developed only by a calf (I26, Ligeirinho) and a juvenile (17) dolphins. Carousels were preceded and succeeded by active surfacing, sharking and tail slaps. Other cooperative tactic consisted of one dolphin positioning itself in front of another individual, which would be performing a pinwheel (supplementary material 2). Just one group out of the six that foraged cooperatively did not include some calf or juvenile. Dolphins also optimised their fishing effort using the waves of the estuary mouth as well as the estuary margins, formed by a mix of sandbank and permanent constructions. High speed movements, as fast swims and rooster tailing, were observed in these occasions (supplementary material 2).

The clustering analysis enlightened the intrapopulational variability, the variation between developmental stages as well as resident and visitor individuals (Fig. 4). The majority of dolphins present in the estuary for more than 20 years (I7, I16, I11 and I14), in general, behaved similarly. The calf (I26, Ligeirinho, see Fig. 5), which was still partially dependent on its mother (I11, Geraldona, see Fig. 5) during our sampling, was the dolphin that behaved most similar to these experienced dolphins. Over this stage of partial dependency, only in 5 out of the 16 sampling groups, we could observe the calf in a few moments of mother-independence while within the estuary. Some residents, including all juveniles (I17, I20 and I22) and two adults (I6 and I15), present a certain variation in their repertoire in relation to other residents mentioned previously, even though they are related (Figure 5). The transient dolphin (I21) was the most behaviourally distinguished from all residents (Fig. 4) being the only one who did not use head slap in its fishing activities, suggesting that the behaviour is actually typical of the resident group. Our findings show evidence of a typical-group method, since all animals employed this tactic during fishing, with the exception of the single visitor (I21) being one of the dolphins with more associations (see the social network in following section, supplementary material 1).

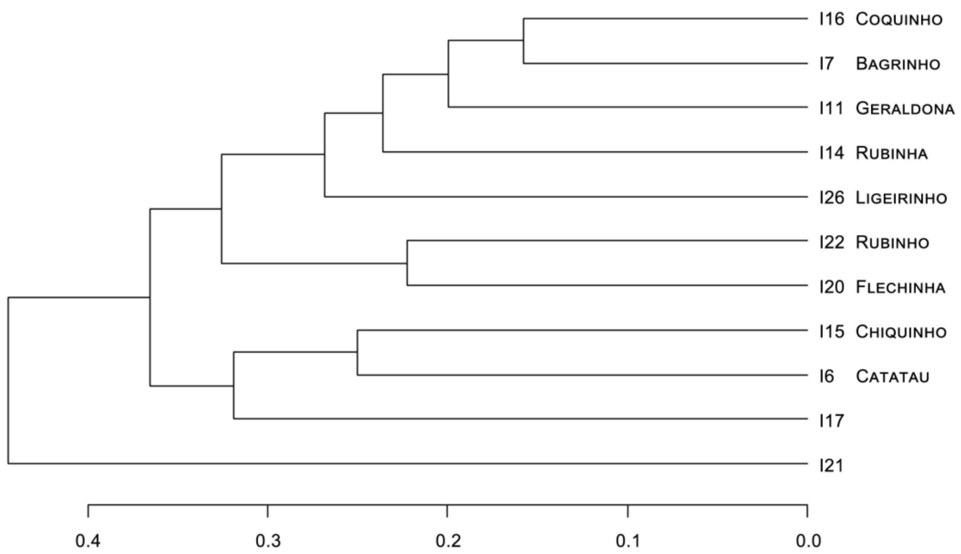

Figure 4. Foraging similarity of Lahille’s bottlenose dolphins (n=11) in the Tramandaí estuary. Dendrogram resulted from a hierarchical cluster analysis (cophenetic correlation = 0.743) based on behavioural similarity revealed by Bray-Curtis index.

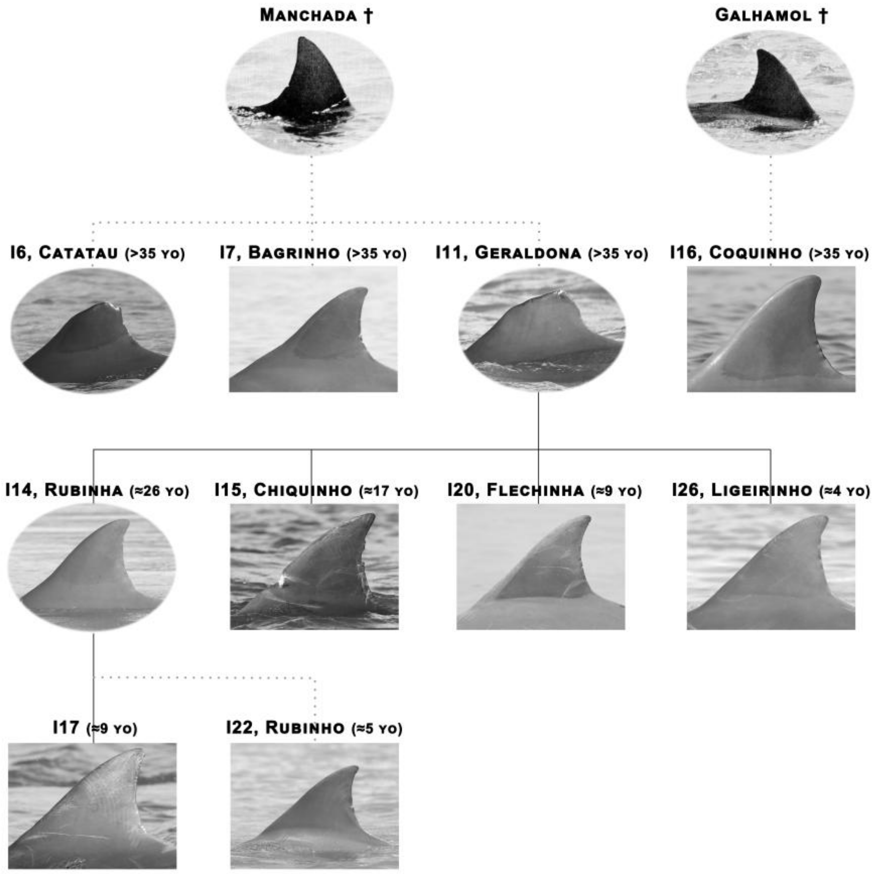

Figure 5. Kinship and resident dolphins' profile of Tramandaí estuary. Names, ages and family relationship were constructed from both the traditional knowledge of artisanal fishermen active in the cooperative fishing for a long time (> 30 years), evidences of dolphins history present in literature (Tabajara, 1992; Simões-Lopes et al., 1998; Hoffmann, 2004; Kleinz, 2012; Giacomo & Ott, 2016) and records obtained during the field work done since 2004. Circles represent females and squares males. Dotted grey lines indicate relations with weak evidence considering the sources mentioned before.

We identified 16 dolphins behaviours that led fishers to throw their nets (n=496) during dolphins fishing activities (Fig. 6). In relation to the total number of times each behavioural event was performed by animals (Table 1), rapid and turning movements, such as fast swim, pinwheeling and horizontal circle, frequently were read by the fishers as a signal for the right moment to cast their nets toward the shoal (Fig. 6). In addition, slaps with head (i.e. head and side slap) and leaps also were recognized as a signal. Out of these 16 behavioural "signals", only head slaps, regular dives, fast swims and active surfacing resulted in fish catch by fishermen (Fig. 6).

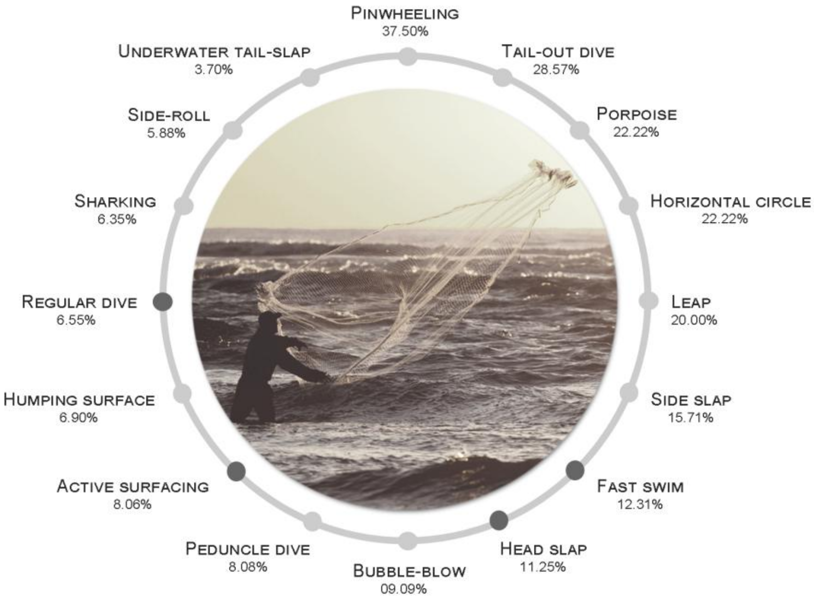

Figure 6. Dolphins' behaviours recognized by artisanal fishermen as a signal to locate the shoal. Only the four indicated by dark grey resulted in successful catch by cast net fishermen.

Social relationships

The social relationships established by dolphins during foraging activities were analysed based on forty-nine sample units (i.e. total flights with distinct group membership). Considering the correlation between true and estimated association index (r ± SE = 0647 ± 0.059, based on bootstrap with 10 000 replications), we validated the reliability of our data for a good description of this social system (Whitehead, 2008b). The estimate of social differentiation using the likelihood method (S ± SE = 0.808±0.077) revealed that dolphins did not relate homogeneously with all others (Whitehead, 2008b). Despite the association pattern was variable within group, animals did not possess preferred companionships. We rejected our hypothesis that dolphins had established preferred associations, mainly based on age similarity, since the permutation test suggested that individuals associated randomly with others (CVreal = 1.24, CVrandom = 1.14, p > 0.01; SDreal = 0.16, SDrandom = 0.15, p > 0.01).

None of the predictor variables (gregariousness, age and gender: p > 0.01) were useful for explaining social structure of the group over our sampling period. Association index (SRI) ranged from 0.00 to 0.89 and the overall mean was 0.13 (SD = 0.05). The mother-calf pair (Geraldona, I11, and Ligeirinho, I26) had the strongest association index, following by a juvenile (Rubinho, I22) and a female (Rubinha, I14) residents of the estuary (SRI = 0.67) (Fig. 7, supplementary material 1). In general, the other three most experienced dolphins (Catatau, I6, Bagrinho, I7, and Coquinho, I16) maintained the weaker associations (strength mean < 1.00) (Fig. 7, supplementary material 1).

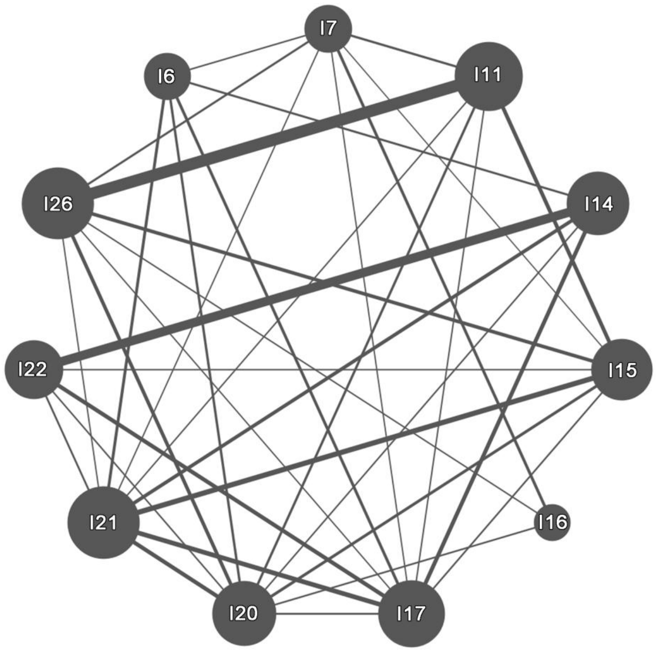

Figure 7. Social network of Lahille's bottlenose dolphins relative to their foraging associations in the Tramandaí estuary. Nodes represent individuals and their sizes correspond to their weighted degree. It considers the number of edges for each node ponderated by the weight of each edge. The thickness of lines linking nodes indicates the strength of associations (SRI) between them.

DISCUSSION

Behind the scenes of a singular and complex repertoire

With the assistance of the novel technology of UAV, we have been able to present in this study the foraging skills used by Lahille's bottlenose dolphins in an urban estuary. Our findings suggest that behavioural dynamics of cooperative dolphins are much more complex than researchers have assumed in recent years (Simões-Lopes, 1991; Simões-Lopes et al., 1998; Simões-Lopes et al., 2016; Cantor et al., 2018). The acquisition and use of certain behavioural repertoire are thus intimately connected with the environmental context in which they are inserted (Duckworth, 2008) and Tramandaí estuary has a high fish richness of different ecological groups (Ramos & Vieira Sobrinho, 2001). Dolphins had several tactics to exploit such resource diversity using both specialized (e.g. head slap) (Simões-Lopes et al., 2016) and universal tactics common to other coastal bottlenose dolphins around the world (e.g. leap, porpoise, active surfacing, fish toss) (Shane, 1990; Mann & Sargeant, 2003; Lusseau, 2006).

Dolphins, such as other social mammals, learn how to exploit environmental resources from their personal experiences and through social transmission (Rendell & Whitehead, 2001; Jablonka & Lamb, 2005). As well as tactics, offspring may also learn about habitat use patterns with elders, mainly with their mothers (Sargeant et al., 2006). Social learning plays an important role in the evolution of complex and specialized behaviours (Galef & Laland, 2005; Thornton & Clutton-Brock, 2011) as well as in the development of costly generalized tactics (Rapaport & Brown, 2008). The foraging activities of the mother-calf pair evidence both applications of social learning. Parental care can boost expertise acquisition (Dukas, 2017), often implying in a specialization development (Dukas, 2019).

Resident dolphins of the Tramandaí estuary have a specialized behaviour that differentiates their repertoire from other populations of the world. The head slap, using the throat (head slap) or lateral portion (side slap), is a specialized technique to capture mullets against the sandbank, where fishermen usually position themselves, thus also related to fishermen interaction (Simões-Lopes, 1991; Whitehead & Rendell, 2014; Simões-Lopes et al., 2016). This typical behaviour has been maintained mainly through inter-generational vertical transmission and dolphins begin to practice it in the first months of life (Simões-Lopes et al., 1998; Simões-Lopes et al., 2016). In a similar way to what has been reported by Simões-Lopes et al. (1998), we could see calf-mother pair performing head slaps sequentially. The same mother-dolphin (Geraldona, I11) observed in the 1990s, with an offspring of 4 months old, was reported in this study assisting her late calf. This fact indicate that group typical behaviour may last until the final stages of infancy as well as other specialised foraging tactics of cetaceans (e.g. sponge tool use, Patterson et al. (2015); beach hunting, Guinet and Bouvier (1995)). A prolonged period of practicing these tactics may be of high importance so dolphins can become experts in coastal fishing at the same time they learn about the risks of fishing in proximity to the sandbank and fishers.

Animals with high tolerant social systems and prolonged development, as bottlenose dolphins, tend to evolve the longer ways of social learning while young (van Schaik & Burkart, 2011), and this period may be a critical time for improving special foraging skills that probably will be useful when they become juveniles and adults (Connor et al., 2000). The development of this stereotyped pattern for mullet fishing seems to be highly adaptive, mainly for the resident group. Every year during their reproductive season, mature mullets cross the Tramandaí lagoon canal to migrate from the estuary into the ocean, having high concentration of large fishes along certain months (Vieira & Scalabrin, 1991; Santos et al., 2018). In addition, mullet is one of the main resources exploited by bottlenose dolphins along the Brazilian southern coast (Laporta et al., 2016; Milmann et al., 2016; Secchi et al., 2016). Acquiring a specialized repertoire is costly, thus dolphins tend to conserve their learned behavioural traits over their lifetimes (Sargeant & Mann, 2009).

Some universal tactics (e.g. deep dives) also require great energy expenditure in order to be developed, such as the deep dives. To explore deeper environments they must first improve their hunting skills and diving capacity (Mann & Sargeant, 2003; Miketa et al., 2018). Although calves do not require social input to learn how to exploit deeper waters (Sargeant & Mann, 2009), vertical transmission (i.e. from mothers) may represent a shortcut along their asocial learning process (Laland, 2004). The engagement of the calf in the benthic fishing associated with its mother, as well as the use of specific behaviours by them, such as underwater tail-slaps, illustrates this optimization for a costly hunting. The *copy-when-asocial-learning-is-costly* strategy (Laland, 2004) is adaptive for situations that information is costly to acquire and/or utilize, thus individuals may take advantage of the knowledge provided by others (Boyd & Richerson, 1988). The benthic practice of the calf from flounder fishing is particularly interesting since this prey is usually readily available in estuaries and on the coast of southern Brazil, being one of the resources exploited by bottlenose dolphins along youth and adulthood in these regions (Secchi et al., 2016).

On the other hand, the pompano fishing seems to be not a cost-effective practice for independent dolphins of the Tramandaí estuary. The exclusively engagement of the calf in epipelagic hunting, in one of the few occasions when its mother was absent, may exemplify a transient habit of immature dolphins, possibly related both to its nutrition and enhancement of feeding skills. The transitory nature of this fishing pattern is supported by the following facts: i) juveniles and adults did not participate in the pompano hunt through our sampling; ii) epipelagic tactics declines as dolphins age (Mann & Smuts, 1999; Mann & Sargeant, 2003); and iii) the genus *Trachinotus* (pompanos) is almost nonexistent in the diet of coastal bottlenose dolphins around the world (Cockroft & Ross, 1990; Barros & Wells, 1998; Amir et al., 2005; Ganon & Waples, 2006; McCabe et al., 2010; Pate & McFee, 2012; Gladilina & Gol'din, 2014), being absent in juveniles and adults on the Brazilian southern coast (Laporta et al., 2016; Milmann et al., 2016; Secchi et al., 2016). The low cost-benefit of pompano hunting may be related to the pattern of prey occurrence in turbid waters, such as surf zones and estuary mouths, where they live essentially when they are young (Rodrigues et al., 2015).

Dolphins of genus *Tursiops* have high ecological plasticity of feeding habits (Leatherwood, 1975; Mead & Potter, 1990). The dolphins studied by us presented more than 20 foraging tactics, retracting the behavioural diversity involved in such plasticity in a very restrict and familiar social system. Such behavioural and social conditions tend to lead social animals to established preferred companions for hunting, since it would maximize their catch efficiency (Gero et al., 2005). Similar to dolphins, it also happens with humans (Haun & Over, 2014) and non-humans primates (de Waal & Luttrell, 1986). Dolphins from Tramandaí estuary contradicted this pattern. Excepting only 2 dyads, dolphins spent less than 40% of their time associated with other animals. We believe that it may be related to the behavioural similarity of the group, particularly of resident individuals. They behave so similarly that they probably do not need to preferred specific hunting-partners. The shared framework allows them to associate randomly inside of estuary, as most of them, at least juveniles and adult residents, learned and know how the estuarine fishing works.

The context faced by resident dolphins inside the Tramandaí estuary is extremely rare in the wild. This population is very restricted, basically composed by one matrilineal lineage which has been living in a small and high productive open system, without predators, for decades. These conditions may influence the fact that the group have characteristics outside of expected patterns, such as the absence of preferred associations. Even without partner preference, immature dolphins frequently involved themselves in intraspecific cooperative fishing. About 83% of intraspecific cooperative fishing of Tramandaí dolphins involved groups with calves and/or juveniles. This agrees with the fact that immature dolphins spend considerable time socializing, learning and practicing its foraging techniques (Connor et al., 2000). Their behavioural profile tend to be strongly shaped by social experience (Sachser et al., 2013). We believe that our results indicate both the strong influence of maternal company during infancy and the behavioural adjustment of juveniles, since the cluster analysis evidenced the high behavioural similarity between mother-calf pair, as well as the performance of juveniles as external groups in relation to other resident dolphins.

Learning is a complex mechanism for acquisition of behaviours throughout ontogeny (Laland et al., 2000). The social transmission is able to spread new information very quickly (Whitehead, 2010), being a strong mechanism maintaining specialized and cultural techniques of many social mammals, including primates (Whiten et al., 1999; van Schaik et al., 2003) and cetaceans (Rendell & Whitehead, 2001). The typical characteristics of the populations are responsible for differentiating them from the others of the same species, influencing directly on how they will interact with their habitats as well as with the human world (Whitehead, 2010). To consider these features, in addition to the behavioural variability within the population and its social connections, is essential for the conservation of the dolphin group studied here (Whitehead et al., 2004; Wolf & Weissing, 2012; Brakes et al., 2019), since it is a unit of a metapopulation already under threat which has restricted size, low diversity and gene flow (Fruet et al., 2014; Costa et al., 2015).

Sociocultural perspective on cooperative-dolphins

Before scientists turning their attention to these wild dolphins, traditional fishermen of the Tramandaí estuary had already developed their own perspective about behavioural dynamics of this population (Simões-Lopes, 1991; Tabajara, 1992). Fishers acquired the ability to identify and integrate their modus operandi in relation to dolphins' movements towards the sandbank learning mainly with their fathers and other elders (Ilha et al., 2018). In addition to the typical head slap, the key feature of dolphin interaction, we observed that fishermen casted their nets in response to other 15 behaviours, but only 26% of 'signals' led to successful catches. The low number of tactics (n=4) preceding the catch success of fishers indicate that capture behaviours performed by dolphins are overestimated by the fishers. This is probably related to the large difference in their individual experiences fishing together with the dolphins.

Traditional fishers see the dolphins as 'good' and 'bad' ones regarding to individual fishing abilities, and according to them, good ones show the exact location of the school (Zappes et al., 2011). Geraldona, the mother dolphin reported in this study, is one of the better examples of a 'good' animal: besides her precision and expertise in estuarine fishing, she also is appreciated by fishermen due to her resourceful offspring. At least two of her sons, Flechinha and Ligeirinho, have names that in the Portuguese language refer to agility and velocity. These names were chosen by the fishers based on dolphins profile, and this practice also compose the fishing culture associated with dolphins (Ilha et al., 2018). Kinship, ages, behaviours and dolphins' dynamic (e.g. differentiation of residents and visitors) are all knowledge that emerged naturally from experienced fishers who have been involved in this traditional fishing for several years.

CONCLUSION

Our findings support the potential for UAVs to enhance behavioural studies of cetaceans (Nowacek et al., 2016; Hodgson et al., 2017; Smultea et al., 2018; Torres et al., 2018; Weir et al., 2018). This tool had already optimized the ability to observe behaviour of gray (*Eschrichtius robustus*) (Torres et al., 2018), humpback whales (*Megaptera novaeangliae*) (Hodgson et al., 2017), dusky (*Lagenorhynchus obscures*) (Weir et al., 2018) and risso's dolphins (*Grampus griseus*) (Smultea et al., 2018). Our findings about Lahille's bottlenose dolphins were similarly useful and novel. From this tool we documented their diversity and plasticity, even identifying both subtle and unknown patterns for the group.

To know how animals behave is crucial for managing and conserving wild populations efficiently, since it can reveal how they are shaped by ecosystem changes (Brakes et al., 2019). The Tramandaí estuary is a cultural nursery site in which dolphins learn and develop their foraging and social skills, and all this functional diversity is related to the health of the ambient. Diversity and tradition of behavioural repertoire of the Tramandaí dolphins is a regional culture essence. While we still see new generations of dolphins practicing hard the estuarine fishing, the fishermen culture side of the equation is not so prominent anymore. Just as fishers are already responding to the ongoing environmental changes, depending on how urbanization processes will be managed from now on, the disfigurement of the Tramandaí dolphins repertoire also can also become a lost patrimony, thus threatening one the most peculiar socio-cultural heritage of the world.

Acknowledgments

We are grateful to colleagues from the Projeto Botos da Barra (CECLIMAR/UFRGS Litoral, including scientists and artisanal fishermen, and to all volunteers for helping during fieldwork. Our special thanks to Felipe Serpa for comments and language help; to Rodrigo Wiebbelling for all support with the equipment during the entire sampling. We also are grateful to Luke Rendell, Maria João Ramos and Fábio Daura-Jorge for proof reading and improving the manuscript. N.S. was supported by *Conselho Nacional de Desenvolvimento Científico e Tecnológico* - CNPq (grant number 130940/2017-8). This study was partially funded by Petrobras Transporte S.A. (TRANSPETRO). This is a contribution of the Research Group "Evolução e Biodiversidade de Cetáceos/CNPq".

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CAPÍTULO III

CONSIDERAÇÕES FINAIS

Até recentemente, acreditava-se que cultura era uma característica exclusiva dos seres humanos (Laland & Janik, 2006). No entanto, a ampliação de conceitos e perspectivas da ciência tornou evidente que outras espécies do reino animal também são moldadas pela herança cultural. A capacidade de aprender, memorizar e transmitir socialmente hábitos comportamentais típicos de grupo, ao longo das gerações, é o elemento fundamental desse mecanismo (Rendell & Whitehead, 2001; Laland & Galef, 2009). Peixes, aves e mamíferos ilustram exemplos de culturas desenvolvidas por vertebrados não-humanos (Laland & Hoppitt, 2003). Além das informações fornecidas pelo genoma e pelas interações com o ambiente, a capacidade de aprender socialmente configura uma fonte adicional de conhecimento para alguns grupos (Laland *et al.*, 2000). Porém, ao contrário dos genes, culturas não são mecanismos fisicamente replicáveis, uma vez que são baseadas no processo de aprendizagem ao longo da ontogenia de cada indivíduo (Kline, 2015). Assim, o uso de técnicas capazes de replicar aspectos comportamentais, na escala temporal e espacial, permite que cientistas acompanhem como populações se especializam em seus ambientes ao longo do tempo, bem como desenvolvem culturas e comportam-se frente a possíveis atividades antropogênicas.

Com o estudo nesta dissertação, sugere-se que o uso de filmagens a partir da perspectiva inovadora do Veículo Aéreo Não Tripulado (VANT) pode ser uma alternativa eficiente e segura para o monitoramento desses processos. Além de recriar o ambiente e seus componentes biológicos fidedignamente, os dados podem ser analisados repetidas vezes de forma detalhada. Ainda, a expansão do campo observacional a partir do VANT também pode contribuir para a ampliação do conhecimento sobre a dinâmica dos golfinhos. A população de botos (*Tursiops gephyreus*) do estuário do rio Tramandaí, conhecida popularmente como botos da barra, possui um longo histórico como foco de pesquisa, devido principalmente a sua íntima relação com a pesca artesanal local (Simões-Lopes, 1991; Simões-Lopes *et al*., 1998). No entanto, a abordagem trazida neste trabalho sobre os botos da barra revelou que sua relação com o ambiente estuarino é ainda mais complexa do que se considerava. Desde a década de 90 o grupo vem sido tradicionalmente associado à pesca cooperativa da tainha. Porém, muito além do interesse na interação com os pescadores, os golfinhos utilizam o estuário de forma diversificada, sendo capazes de se adaptar a diferentes tipos de atividades e condições ambientais.

O repertório do grupo inclui mergulhos profundos, movimentos ágeis e de batida na superfície, manobras de giro no próprio eixo, em direção à margem do estuário ou a outro animal ativo na pescaria. Na tentativa de capturar a presa, os botos combinam comportamentos universais (aqueles realizados por outros grupos do gênero pelo mundo) e táticas tradicionais (as batidas de cabeça). Apesar desses animais apresentarem uma ampla plasticidade comportamental, suas descrições na literatura, até este momento, retratavam basicamente sua interação com os pescadores (Simões-Lopes *et al*., 1998). O enfoque de nas táticas relacionadas à interação acarretou na subestimação de tal repertório por quase três décadas, principalmente em relação aos seus produtos associais. É inegável a relação cultural no desenvolvimento de alguns comportamentos típicos dos botos, como a batida de cabeça, porém, a influência do DNA e do ambiente são elementos indissociáveis no desenvolvimento comportamental, mesmo em populações especializadas em técnicas complexas (Sacher & Kaiser, 2010). Sabendo que alguns elementos do repertório não possuem relação direta com a aprendizagem social (i.e. comportamentos universais), é possível evidenciar que mais mecanismos estão atuando no desenvolvimento comportamental. Essa variedade de táticas, por exemplo, também pode ser resultante da plasticidade alimentar característica da espécie. Embora ainda seja necessário aprofundar a investigação sobre os processos atuantes na plasticidade comportamental dos botos, características biológicas e ecológicas da espécie, associadas a tamanha diversidade de comportamentos, evidenciam que o repertório analisado não é somente produto da herança cultural.

Assim como a variabilidade comportamental do grupo como um todo, um conjunto de fatores deve atuar na variação entre o comportamento individual dos botos. Tal variação intrapopulacional revelou a ocorrência de personalidades em um grupo de golfinhos selvagens. Atualmente, é reconhecido que essas diferenças podem afetar a estabilidade, resiliência e persistência das populações, influenciando ecossistemas inteiros na perspectiva ecológica e evolutiva (Wolf & Weissing, 2012). Traços de personalidade podem influenciar diretamente na forma como os animais interagem com o ambiente e tal variabilidade pode ser de extrema importância para a adaptação do grupo frente a novas condições ambientais (Wolf & Weissing, 2012). Especialmente para populações inseridas em ambientes antropizados, como os botos de Tramandaí, a ocorrência de diferentes personalidades pode representar um amplo repositório referente as especializações do grupo.

Os padrões de personalidade evidenciaram aspectos relacionados a ontogenia comportamental. A semelhança entre o comportamento de caça do filhote em relação sua mãe e outros animais experientes, a modulação comportamental dos juvenis e sua possível influência na performance dos animais adultos foram nossas principais interpretações. É válido ressaltar que a população de golfinhos analisada é restrita, tanto em relação ao tamanho de grupo (o máximo já registrado foi 16 indivíduos), quanto a dinâmica social, uma vez que é formada basicamente por animais aparentados (Ilha *et al*., 2018). Embora diversos fatores influenciem o estabelecimento do comportamento animal, a manutenção da diversidade comportamental típica e especializada está intimamente relacionada a aprendizagem social (Laland & Galef, 2009). O padrão comportamental das atividades de caça envolvendo a mãe e o filhote de botos, conhecidos respectivamente como Geraldona e Ligeirinho, bem como sua forte associação, indicam o longo período de prática, principalmente, em comportamentos de alto custo energético e culturais (i.e. batida de cabeça). A prática prolongada dos filhotes pode ser crítica para o seu desenvolvimento, pois adquirir experiência é custoso e tende a influenciar diretamente nas habilidades da fase adulta (Connor *et al*., 2000; Sargeant & Mann, 2009). Assim, acreditamos que o período de aprendizagem ilustrado pelo par mãe-filhote retrata como a cultura da pesca costeira do grupo vem sendo transmitida e praticada durante o final da infância. A aprendizagem, assim como a plasticidade comportamental, possibilita aos indivíduos desenvolver táticas voltadas a otimização dos ambientes explorados ao longo da vida (Thornton & Clutton-Brock, 2011).

A dinâmica comportamental e a estrutura social dos botos da barra de Tramandaí ilustra um cenário singular. A ausência de predadores, a riqueza de presas disponíveis e a predominância de somente uma linhagem materna vêm possivelmente assegurando a estabilidade da área como local restrito de aprendizagem, desenvolvimento e especialização. O ambiente natural amostrado neste estudo mais se assemelha a um experimental, uma vez que tais condições são raras na natureza. Até a forma como os animais interagem entre si foge do padrão visto em grupos coespecíficos (Gero *et al*., 2005; Wiszniewski *et al*., 2009; Daura-Jorge *et al*., 2012; Genov *et al*., 2018). Ao contrário do esperado, os botos associam-se de forma aleatória, não possuindo preferência por parceiros de caça específicos, com exceção do par mãe-filhote. No entanto, espécies sociais, como cetáceos e primatas, humanos e não-humanos, tendem a interagir com outros animais de acordo com as semelhanças compartilhadas, em relação a faixa etária e aos hábitos (de Waal & Luttrell, 1986; Gero et al., 2005; Haun & Over, 2014). A ausência desse padrão, conhecido como homofilia, na população amostrada é provavelmente resultado do contexto familiar vivenciado dentro do estuário pelos animais. Não possuir restrições nas relações interindividuais, pelo menos dentro de um ambiente relativamente estável socialmente, pode potencializar o aprimoramento de habilidades sociais e comportamentais, bem como otimizar as atividades em grupo.

Assim como a diversidade comportamental dos botos vem sendo observada a partir da perspectiva científica, seu repertório também é interpretado sob o olhar dos pescadores artesanais. A dinâmica de pesca de alguns pescadores respondeu diretamente a mais de 15 movimentos utilizados pelos botos durante suas atividades de caça. Considerando a ampla gama de táticas lidas pelos pescadores como sinalizadores de cardume, é provável que a diferença entre suas experiências pessoais influenciem na eficiência da pescaria com o boto. Sabe-se que a transmissão social é intimamente relacionada ao conhecimento e manutenção dessa prática pelos pescadores (Ilha *et al*., 2018). Tendo que driblar diversos desafios enfrentados pela classe profissional em resposta ao intenso crescimento urbano, as principais fontes de conhecimento dos pescadores (i.e. pais e pescadores experientes) já não incentivam as novas gerações a dar continuidade a essa cultural prática de pesca (Ilha *et al*., 2018). A quebra no fluxo do conhecimento, que já ameaça a cultura de pescadores tradicionais, também é passível de atingir os botos da barra, dependendo do padrão de desenvolvimento investido na região.

De forma oposta a interação conhecida como pesca cooperativa, diversas atividades humanas influenciam negativamente a dinâmica natural dos golfinhos. O trânsito intenso de embarcações (Bejder *et al*., 2006; Mattson *et al*., 2005; Pirotta *et al*., 2015; Stensland & Berggren, 2007), a ocorrência de esportes náuticos que se movimentam erraticamente (Buckstaff , 2004), operações de dragagem e construções (Thompson *et al*., 2010; Pirotta *et al*., 2013; Weaver, 2015) podem alterar o padrão de uso dos animais em seus ambientes naturais. Suas consequências incluem desde a mudança no comportamento em curto prazo até o abandono da área. Além disso, fêmeas tendem a ser mais impactadas negativamente (Constantine, 2001; Weaver, 2015), o que é ainda mais preocupante, pois golfinhos mantém suas culturas principalmente a partir do aprendizado materno (Connor *et al*., 2000). Embora o repertório dos botos da barra não seja exclusivamente uma herança cultural, sua influência na diversidade, plasticidade e especialização configura não só uma rara população selvagem, como também fundamenta uma cultura humana já ameaçada de extinção. Seguindo o rumo do desenvolvimento insustentável, projetos de planejamento urbano da região vêm buscando ampliar a mobilidade náutica e automobilística via/sobre o estuário de Tramandaí, ignorando completamente os riscos e a fragilidade do cenário apresentado nesta dissertação. Assim como o amplo repertório comportamental dos botos, seus aspectos mais sutis, como personalidades e relações sociais, devem ser necessariamente considerados na previsão dos impactos ambientais gerados pelos projetos apresentados. Caso contrário, patrimônios culturais baseados em “fontes primárias” de conhecimento, como a Geraldona, serão preservados somente em dissertações científicas.

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