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DINÂMICA E VIABILIDADE DA POPULAÇÃO DE BOTOS-DATAINHA *Tursiops truncatus gephyreus* EM LAGUNA, SUL DO BRASIL

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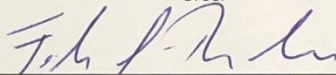
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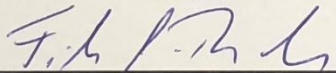
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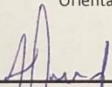


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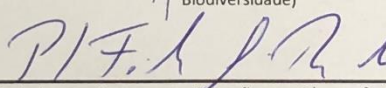
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Para meus avós e meus sobrinhos

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RESUMO

A pequena população de botos-da-tainha *Tursiops truncatus gephyreus* encontrada em Laguna, sul do Brasil, é conhecida por interagir com pescadores artesanais através de uma tática de forrageio especializada – a pesca cooperativa. Esta população encontra-se exposta a diversos impactos provenientes de atividades antrópicas, principalmente capturas acidentais em rede de pesca. Esta tese busca estimar parâmetros populacionais e reprodutivos dos botos de Laguna, analisar a viabilidade desta população e sugerir estratégias de manejo e conservação. A sobrevivência anual dos adultos foi de 0,95 (SE = 0,015), levemente influenciada pelo tamanho da área de vida individual, sexo e frequência de interação com os pescadores. A probabilidade de sobrevivência ligeiramente maior para indivíduos com área de vida menor pode ser um resultado dos benefícios de requisitos espaciais reduzidos implicados pela pesca cooperativa. Não houve emigração temporária ou permanente, confirmando a alta taxa de residência na área de estudo. A abundância flutuou sutilmente ao longo dos anos (2007-2016), de 54 a 60 indivíduos, sem uma tendência populacional evidente. A reprodução é sazonal, com a maioria dos nascimentos ocorrendo no final da primavera e verão. A taxa bruta de natalidade média foi de 0,09 (SD = 0,04), e a fecundidade estimada foi de 0,17 (SD = 0,06). O intervalo médio entre nascimentos variou de 2,09 a 2,43, dependendo do método usado. A probabilidade de sobrevivência dos filhotes no primeiro e no segundo ano de vida foi de 0,74 e 0,82, respectivamente. O mês de nascimento foi um preditor significativo para a sobrevivência dos filhotes até os dois anos. Ao dar à luz perto da temporada de tainhas, as fêmeas lactantes dispõem de uma alta disponibilidade de recursos, o que poderia aumentar a sobrevivência dos filhotes. Fêmeas que frequentemente cooperam com pescadores apresentaram uma maior fecundidade e sobrevivência dos filhotes do que aquelas que tendem a forragear de forma independente. A simulação do cenário atual, que inclui duas mortes por emalhe acidental ao ano, resultou em uma população em declínio ($r = -0,022$) com alta probabilidade de extinção nos próximos 100 anos (PE = 0,88). Se o número de emalhes aumentar, a população estará fadada à extinção. Ações de manejo parecem promissoras, mas somente o manejo com zero emalhe possibilitaria um crescimento populacional. Combinados, nossos resultados indicam que o nível atual de mortes por emalhe é insustentável

e este fator de mortalidade deve ser eliminado imediatamente. A pesca da tainha também deve ser monitorada para garantir a disponibilidade de recursos, uma vez que ela influencia o sucesso reprodutivo. Essas ações combinadas devem garantir a persistência a longo prazo da população de botos-da-tainha em Laguna e conseqüentemente da pesca cooperativa.

Palavras-chave: *Tursiops truncatus* *gephyreus*, boto-da-tainha, abundância, sobrevivência, reprodução, Análise de Viabilidade Populacional, conservação.

ABSTRACT

The small bottlenose dolphin *Tursiops truncatus gephyreus* population found in Laguna, southern Brazil, is known for interacting with artisanal fishermen through a specialized foraging tactic—the so-called “cooperative fishery”. This population faces several impacts from human activities in the area, mainly incidental bycatch in fishing gear. This thesis aims to estimate population and reproductive parameters of Laguna dolphins, to analyze the viability of this population and to suggest management and conservation strategies. We estimated adult survival to be 0.95 (SE = 0.015), weakly influenced by home range size, sex or the frequency of interaction with fishermen. The slightly higher survival probability for individuals with smaller home ranges could stem from the benefits of reduced spatial requirements implied by the specialized foraging. There was no temporary or permanent emigration, confirming the high site fidelity to the area. Abundance fluctuated slightly over the years (2007-2016) from 54 to 60 individuals, with no evident population trend. Calving was found to be seasonal, with most births occurring in late spring/summer. The average crude birth rate was 0.09 (SD = 0.04), and estimated fecundity was 0.17 (SD = 0.06). The mean inter-birth interval ranged from 2.09 to 2.43 years, depending on the method used. First and second year calf survival rates were 0.74 and 0.82, respectively. Timing of birth was a significant predictor of 2 years calf survival rates. Giving birth close to the local mullet season, provided lactating females with increased seasonal prey resources, leading to increased calf survival. Females that often cooperate with fishermen showed slightly higher fecundity and calf survival than those that tended to forage independently. The simulation of the current scenario, which includes two bycatches a year, yielded a declining population ($r=-0.022$) with a high probability of extinction within 100 years (PE=0.88). If bycatch increases, the population is doomed to extinction. On the other hand, management actions seem promising, but only the zero-bycatch management would make the difference between a declining and increasing population. Combined, our results indicate that the current level of bycatch is unsustainable, and it must be eliminated immediately. Moreover, habitat degradation should be reduced and the impacts of planned development in the area should be mitigated, once these factors influence calf survival. The mullet fishery should also be monitored to ensure resource

availability, due to its influence on the reproductive success. These combined actions should guarantee the long-term persistence of bottlenose dolphins in Laguna and their specialized foraging tactic.

Keywords: *Tursiops truncatus* *gephyreus*, bottlenose dolphin, abundance, survival, reproduction, Population Viability Analysis, conservation

LISTA DE FIGURAS

INTRODUÇÃO GERAL

Figura 1: Registros da pesca cooperativa entre botos e pescadores artesanais em Laguna, sul do Brasil. Os botos conduzem os cardumes em direção aos pescadores, que aguardam o momento exato para lançar as tarrafas. 32

Figura 2: Nas duas fotos acima, dois indivíduos com rede de pesca presa ao corpo. Abaixo à esquerda, um filhote neonato morto devido à colisão com embarcação. Abaixo à direita, um indivíduo com lesão de pele semelhante à Lobomicose. 33

Figura 3: Área de estudo em Laguna, sul do Brasil. Em vermelho está representada a rota pré-definida percorrida em cada dia de amostragem. As estrelas azuis marcam os principais locais onde ocorre a interação entre botos e pescadores. 37

CAPÍTULO 1

Figure 1: Frequency of interaction (bars) and home range (red circles) for each marked bottlenose dolphin in Laguna (x-axis; dark gray bars are females and light gray bars are males). Imputations for home range were omitted. 61

Figure 2: Survival rate and individual home range (HR; Model 1 Table 2A) and frequency of interaction (f_i ; Model 3 Table 2A) (predicted values and 95% confidence intervals) for bottlenose dolphins in Laguna. 63

Figure 3: Relationship between capture probability and individual frequency of interaction (predicted values and 95% confidence intervals) for bottlenose dolphins in each year of the study in Laguna. 64

CAPÍTULO 2

Figure 1: Birth seasonality for bottlenose dolphins in Laguna based on a long-term monitoring study (2007–2009 and 2013–2017) in relation to the peak of the mullet season in June. Light gray bars express the number of births estimated from mark-recapture surveys conducted in the lagoon system, while the dark grey bar expresses the number of neonates found stranded during beach surveys. 91

CAPÍTULO 3

Figure 1: Population Viability Analysis predictions for the six scenarios of annual bycatch mortality (‘harvest’) of bottlenose dolphins in Laguna, southern Brazil. Numbers refer to models in Table 2. Simulation of an annual bycatch of: (1) one juvenile (male/female) and one adult male–baseline scenario; (2) one juvenile (male/female) and two adult males; (3) one juvenile (male/female) and one adult (male/female); (4) one adult male; (5) one juvenile (male/female); and (6) zero bycatch. 122

Figure 2: Sensitivity analysis. Effect of additional adult (A) male and (B) female bycatches and (C) different first year calf survival rates on stochastic growth rate (r) forecasts. 125

LISTA DE TABELAS

CAPÍTULO 1

Table 1: Sampling effort used in Robust Design: number of secondary periods (capture occasions), number of marked dolphins identified, and number of new dolphins identified within each primary period. 57

Table 2: (A) Robust Design and (B) Pradel's temporal symmetry candidate models for survival probability (ϕ), capture probability (p), recapture probability (c), temporary emigration probability (γ'') and population growth rate (λ) ranked by AICc. AICc weight indicates the support of the selected model over the others. Deviance is a measure of model fit. Notation: (.) constant, (t) time-dependence between primary periods, (s) time-dependence within primary periods, (γ'') probability of temporary emigration, (γ') probability of remaining outside the study area, ($p=c$) no recapture effect, ($\gamma'' = \gamma' = 0$) no emigration, ($\gamma'' = \gamma'$) random emigration, (γ'' , γ') Markovian emigration, (f_i) frequency of interaction, (HR) home range size, (sex) sex of individuals. Akaike information criterion corrected for small sample size (AICc)..... 65

Table 3: Estimates of abundance for each year from Robust Design models. Shown are: abundance of marked individuals (N), theta estimates (θ), the total population size adjusted by theta method (N_{Total}), the CVs adjusted using the delta method [$CV(N_{Total})$], the confidence intervals [$CI(N_{Total})$], and the number of recovered carcasses. 66

CAPÍTULO 2

Table 1: Sightings of reproductive females (ID# = individual photo-ID catalogue number) and their calves from 2007 to 2009 and 2013 to 2017 in Laguna, including sightings of females without a calf (marked with a “•”) and their first (1), second (2), third (3),

), or fourth (4) calves. Calf ages were categorized as young-of-year (< 1 year old; YC), calves (1–3 year old; C) and juveniles (> 3 year old; J). The number of reproductive females in each year (#F) and the number of calves born in each year (#YOY) are also shown. 89

Table 2: Summary of reproductive rates of bottlenose dolphins in Laguna, Southern Brazil, estimated from mark-recapture studies; Fecundity = ratio between the number of female calves (assuming a calf sex ratio of 1:1) and the number of mature females in Laguna (cf. Fruet et al. 2015)..... 90

Table 3: Summary of age-structured Cormack–Jolly–Seber models for survival (ϕ) and recapture (p) probabilities of calves (c) from Laguna bottlenose dolphin population based on a mark-recapture study (2013–2017). Models are ranked according to the lowest QAIC. Notation: (·) constant, (t) time-dependence. Slash distinguishes age classes. 92

Table 4: Summary of the GLMM for factors influencing calf survival to 1 and 2 years. Fixed input parameters include mother frequency of interaction with fishermen (Motherfi), home range size (MotherHR) and age (Motherage), time between birth and the peak of the following mullet season (Tmullet) and fishery yield of the mullet season following the birth (Nmullet). The null model (i.e. no fixed effects), contains the random effect of mother ID (Calfsurvival~1). Models are ranked according to the lowest Akaike information criterion corrected for small sample size (AICc). Notation: delta AICc (Δ AICc), Log-likelihood (logLik), delta Log-likelihood (Δ logLik), degrees of freedom (df) and AICc model weight (weight). 94

CAPÍTULO 3

Table 1: Summary of demographic parameters used as input data in the modeling of the viability of the bottlenose dolphin population in Laguna, Brazil. Standard deviations due to environmental variation are shown in parenthesis. 116

Table 2: Summary of the results of the Population Viability Analysis for six scenarios of bycatch mortality (‘harvest’) of bottlenose dolphins in Laguna, Brazil. Stochastic growth rate

(stoch- r), standard deviation (SD), N_{100} : population size in 100 years, probability of extinction (PE), mean time at extinction (mean TE), M: male and F: female. 121

Table 3: Fixed-proportion and observed-variation sensitivity analyses. Effects of parameter variation on stochastic growth rate (r) and 100-year population size (N_{100}) forecasts for the bottlenose dolphins in Laguna, Brazil. 124

Table 4: Sensitivity and elasticity of population growth rate (λ) to small changes (-1%) in life history traits of bottlenose dolphins in Laguna, Brazil. 124

SUMÁRIO

INTRODUÇÃO GERAL	23
OS PARADIGMAS POPULACIONAIS	23
CONSIDERANDO O ACASO	24
HISTÓRIAS DE VIDA: MAMÍFEROS MARINHOS	24
O DESAFIO DE GERAR OS <i>INPUTS</i>	25
VARIAÇÃO INDIVIDUAL E O COMPORTAMENTO	26
BOTO-DA-TAINHA: O MODELO BIOLÓGICO	28
O ESTUDO DE CASO E AMEAÇAS LOCAIS	31
OBJETIVOS.....	34
DESENHO AMOSTRAL E PROCESSAMENTO DOS DADOS	36
REFERÊNCIAS	38
CAPÍTULO 1	
THE INFLUENCE OF COOPERATIVE FORAGING WITH FISHERMEN ON THE DYNAMICS OF A BOTTLENOSE DOLPHIN POPULATION	51
ABSTRACT	52
INTRODUCTION	53
METHODS.....	55
DATA SAMPLING	55
ROBUST DESIGN	56
MODEL VALIDATION AND SELECTION PROCEDURES	58
TOTAL ABUNDANCE	59
RESULTS.....	60
MODEL SELECTION	62
PARAMETER ESTIMATES.....	62
DISCUSSION.....	67
ACKNOWLEDGEMENTS	70

REFERENCES	71
-------------------------	-----------

CAPÍTULO 2

REPRODUCTIVE PARAMETERS AND FACTORS INFLUENCING CALF SURVIVAL OF BOTTLENOSE DOLPHINS THAT ENGAGE IN A UNIQUE COOPERATION WITH FISHERMEN	79
--	-----------

ABSTRACT	80
-----------------------	-----------

INTRODUCTION	81
---------------------------	-----------

METHODS	83
----------------------	-----------

DATA COLLECTION	83
------------------------------	-----------

REPRODUCTIVE PARAMETERS	84
--------------------------------------	-----------

CALF SURVIVAL.....	85
---------------------------	-----------

FACTORS INFLUENCING REPRODUCTIVE SUCCESS	86
---	-----------

RESULTS.....	88
---------------------	-----------

REPRODUCTIVE PARAMETERS	88
--------------------------------------	-----------

CALF SURVIVAL.....	91
---------------------------	-----------

FACTORS INFLUENCING REPRODUCTIVE SUCCESS	92
---	-----------

DISCUSSION	95
-------------------------	-----------

REPRODUCTIVE PARAMETERS	95
--------------------------------------	-----------

CALF SURVIVAL AND FACTORS INFLUENCING REPRODUCTIVE SUCCESS	96
---	-----------

ACKNOWLEDGEMENTS.....	99
------------------------------	-----------

REFERENCES	100
-------------------------	------------

CAPÍTULO 3

DOLPHIN POPULATION SPECIALIZED IN FORAGING WITH FISHERMEN REQUIRES ZERO BYCATCH MANAGEMENT TO PERSIST	109
--	------------

ABSTRACT	110
-----------------------	------------

INTRODUCTION	111
---------------------------	------------

METHODS.....	114
STUDY AREA.....	114
POPULATION VIABILITY ANALYSIS INPUTS.....	115
ALTERNATIVE SCENARIOS	117
SENSITIVITY AND ELASTICITY ANALYSES.....	117
ASSESSING IMPACTS AND EVALUATING MANAGEMENT	
OPTIONS.....	118
RESULTS.....	119
POPULATION VIABILITY ANALYSIS OUTPUTS	119
SENSITIVITY AND ELASTICITY ANALYSES.....	123
ASSESSING IMPACTS AND EVALUATING MANAGEMENT	
OPTIONS.....	123
DISCUSSION.....	126
ACKNOWLEDGEMENTS	130
REFERENCES	130
CONSIDERAÇÕES FINAIS E CONCLUSÕES	139

INTRODUÇÃO GERAL

Os paradigmas populacionais

Na Biologia da Conservação, emergiram dois conjuntos de ideias: o paradigma das populações em declínio, que foca em maneiras de detectar, diagnosticar e deter o declínio de determinada população, e o paradigma das pequenas populações, que lida com o risco de extinção inerente ao baixo número de indivíduos na população (CAUGHLEY, 1994). O paradigma das populações em declínio compreende principalmente investigações ecológicas caso a caso, visando identificar as causas determinísticas de declínio da população em questão, e alternativas para modificar este cenário. Por este paradigma, o problema ocorre quando uma população está em risco devido a algum agente externo a ela, e o tamanho atual da população não é de grande relevância, mas sim sua tendência temporal. Já o paradigma das pequenas populações considera os efeitos teóricos do reduzido tamanho populacional nas chances de persistência de pequenas populações, incorporando o acaso em uma abordagem que avalia a viabilidade populacional em um tempo específico.

Em termos teóricos, pequenas populações são mais propensas a serem extintas do que populações numerosas (GILPIN; SOULÉ, 1986). Quanto menor a população, mais suscetível ela está à extinção por fatores diversos, em particular processos estocásticos, que podem ser intrínsecos à sua dinâmica, ou motivados por mudanças ambientais. Perturbações estocásticas que podem extinguir populações pequenas incluem variação natural nas taxas de sobrevivência e reprodução individual (estocasticidade demográfica), e sua maior vulnerabilidade à perda de variabilidade genética e depressão por endogamia (estocasticidade genética). Além disso, a estocasticidade pode ser gerada por flutuações naturais ou antropogênicas nas condições ambientais (estocasticidade ambiental) ou, em situações extremas, como catástrofes ambientais (SHAFFER, 1981; CAUGHLEY, 1994). Ao combinar esse paradigma das pequenas populações com o paradigma das populações em declínio, combinamos a ecologia teórica com a ecologia aplicada, e adicionamos os efeitos da estocasticidade aos processos determinísticos que regem a

dinâmica populacional. Assim, tem-se a possibilidade de uma leitura mais completa sobre as possíveis trajetórias populacionais, facilitando o entendimento de como ameaças não naturais afetam a viabilidade de pequenas populações e quais estratégias de conservação seriam mais efetivas para a redução de riscos de extinção.

Considerando o acaso

Do ponto de vista instrumental, a combinação dos dois paradigmas populacionais mencionados anteriormente se dá pela Análise de Viabilidade Populacional (AVP). Esta é uma ferramenta de modelagem que utiliza modelos estatísticos (incorporando estocasticidades) e teóricos/matemáticos (descrevendo determinismos) para avaliar riscos relativos à persistência populacional em uma escala de tempo pré-definida, considerando diferentes cenários. No processo de comparação destes cenários, que podem representar múltiplas ameaças não naturais às trajetórias populacionais, pode-se avaliar a eficácia de alternativas de manejo (BOYCE, 1992; AKÇAKAYA; SJÖGREN-GULVE, 2000; BEISSINGER; MCCULLOUGH, 2002), e assim orientar a tomada de decisões estratégicas que sejam de fato efetivas na redução dos riscos de extinção (DRECHSLER; BURGMAN, 2004). Em termos funcionais, a AVP estima o risco de extinção de uma população (ou espécie) em cada cenário pré-definido por meio de simulações estocásticas de parâmetros demográficos e de história de vida (BEISSINGER; WESTPHAL, 1998). Um dos resultados mais interessantes de uma AVP é a identificação dos principais parâmetros do histórico de vida que influenciam a dinâmica da população em estudo (e.g. MANLIK et al., 2016; LACY et al., 2017).

Histórias de vida: mamíferos marinhos

A história de vida de mamíferos marinhos combina elementos que os tornam especialmente vulneráveis a impactos antropogênicos (e.g. baixo potencial reprodutivo e baixa taxa de crescimento populacional; MERRICK; SILBER; DEMASTER, 2018), principalmente em populações pequenas, que são mais afetadas pela estocasticidade

demográfica, ambiental e genética (CAUGHLEY, 1994). Nesses casos, a AVP é uma ferramenta valiosa, que vem sendo aplicada para várias espécies de mamíferos marinhos, incluindo peixes-boi *Trichechus manatus latirostris* (MARMONTEL; HUMPHREY; O'SHEA, 1997), elefantes-marinhos-do-sul *Mirounga leonina* (MCMAHON et al., 2005), orcas *Orcinus orca* (LACY et al., 2017), botos-da-tainha *Tursiops truncatus* (THOMPSON et al., 2000; GASPARG, 2003; FORTUNA, 2007) e *Tursiops aduncus* (MANLIK et al., 2016). Além da utilização de AVP para a construção de cenários e avaliação de riscos de extinção, diferentes parâmetros populacionais foram identificados como determinantes para a dinâmica de populações de mamíferos marinhos; por exemplo, o modelo de simulação gerado para os peixes-boi da Flórida identificou a mortalidade de indivíduos adultos como sendo uma taxa vital chave (MARMONTEL; HUMPHREY; O'SHEA, 1997), enquanto estudos com botos-da-tainha na Austrália e orcas no nordeste do Pacífico descobriram que a variabilidade na reprodução teve uma influência maior sobre o crescimento populacional do que a mortalidade (MANLIK et al., 2016; LACY et al., 2017). A variação do parâmetro chave depende do contexto em que a espécie está inserida, bem como sua história de vida. A AVP da população de botos-da-tainha em Moray Firth, na Escócia, combinada a uma análise de poder, ilustra como esta análise pode influenciar na tomada de decisões, de modo a antecipar possíveis ações de manejo, uma vez que a perda de indivíduos durante o período anterior à detecção de uma tendência pode ser capital para a viabilidade da população (Thompson et al. 2000).

O desafio de gerar os *Inputs*

A crescente acessibilidade e utilização de ferramentas computacionais permitiu uma rápida popularização das Análises de Viabilidade Populacional nas últimas décadas. Com esta popularização emerge também uma série de recomendações para se evitar o mau uso e interpretação dos modelos (WHITE, 2000; COULSON et al., 2001; REED et al., 2002). Um dos desafios de uma AVP é a entrada de dados de qualidade, dados estes que, dependendo da biologia da espécie-alvo,

vão exigir um esforço considerável para serem gerados/estimados acuradamente. Um monitoramento de longo prazo de uma população, com base no acompanhamento de cada indivíduo, pode gerar informações valiosas sobre a história de vida e parâmetros reprodutivos, dados essenciais para uma AVP. Tais informações requerem muitos dados de campo primários, mas são fundamentais para permitir avaliações da dinâmica, estado de conservação e viabilidade de uma população (BEISSINGER; MCCULLOUGH, 2002). Em geral, os parâmetros reprodutivos são particularmente difíceis de serem obtidos, exigindo longos períodos em campo e um esforço sistemático de acompanhamento da história de vida do indivíduo. Diante do desafio de se estimar alguns parâmetros, é comum a utilização de dados secundários obtidos de diferentes populações da mesma espécie (REED et al., 2002). No entanto, diferentes populações podem estar expostas a diferentes condições e pressões ecológicas (BAKER et al., 2018), criando incertezas e limitando a utilidade e confiabilidade das projeções geradas quando estas incluem dados secundários. Portanto, estimativas confiáveis sobre parâmetros específicos da população de interesse, como sobrevivência, fecundidade e abundância, são de grande importância para avaliar seu estado de conservação, bem como detectar e investigar mudanças ou tendências no tamanho da população, fornecendo assim as melhores informações para ações de manejo efetivas (e.g. KRAUS et al., 2001; RUNGE; LANGTIMM; KENDALL, 2004; CURREY et al., 2011).

Variação individual e o comportamento

A dinâmica de populações animais é sensível a variações entre os indivíduos e, portanto, traços individuais, como idade, sexo, ou mesmo aspectos comportamentais, devem ser considerados nas estimativas dos parâmetros populacionais (ESTEBAN et al., 2016; SPROGIS et al., 2016; TIXIER et al., 2017; BEZAMAT et al., 2018; ARSO CIVIL et al., 2019). Indivíduos diferem quanto à sua genética (HUGHES et al., 2008), tolerância a fatores abióticos (MEYER et al., 2009), resistência a parasitas (GANZ; EBERT, 2010) e uso dos recursos (BOLNICK et al., 2003), bem como defesas contra predadores (DUFFY, 2010) e táticas de forrageio (ESTES et al., 2003; TORRES; READ, 2009). Quando indivíduos da mesma população diferem no uso de recursos e investem em diferentes

táticas de forrageio, eles podem experimentar níveis variados de competição intraespecífica (ARAÚJO; BOLNICK; LAYMAN, 2011), o que em última análise pode moldar as estruturas sociais (DAURAJORGE et al., 2012) e influenciar os parâmetros demográficos (TIXIER et al., 2015, 2017; ESTEBAN et al., 2016).

Os mamíferos marinhos são bons modelos para explorar as implicações da variação individual, em especial o comportamento intraespecífico, pois seus repertórios comportamentais são variáveis e diversos. Por exemplo, especializações de forrageio são bem conhecidas entre lontras *Enhydra lutris* (ESTES et al., 2003) e leões-marinhos-do-sul *Otaria flavescens* (BAYLIS et al., 1992), entre ecótipos simpátricos de orcas (BAIRD et al., 1992; PITMAN; DURBAN, 2012), populações de baleias-jubarte *Megaptera novaeangliae* (WEINRICH, SCHILLING; BELT, 1992; WILEY et al., 2011) e baleias-minke *Balaenoptera acutorostrata* (HOELZEL et al., 1989). Mais recentemente, as implicações ecológicas de especializações de forrageio dentro de uma população, no nível de indivíduos ou unidades sociais, vem sendo relatadas na literatura. Um exemplo clássico é a coexistência de duas formas de orcas no nordeste do Pacífico, conhecidas como “residentes” e “transeuntes”, que diferem quanto ao comportamento de forrageio, uso do habitat e dinâmica de grupo (BAIRD et al., 1992). A especialização de forrageio individual de lontras na Califórnia parece influenciar seu sucesso reprodutivo e a dinâmica da rede alimentar local (ESTES et al., 2003). Alguns botos-da-tainha do Indo-Pacífico (*Tursiops aduncus*), na Austrália, se aproveitam da pesca de arrasto para obter alimento e são socialmente segregados de outros botos residentes que não utilizam essa tática de forrageio (CHILVERS; COKERON, 2001). Assim, é importante considerar possíveis efeitos e variações comportamentais na dinâmica populacional.

Monitoramentos que visem a estimativa de parâmetros populacionais podem ser realizados combinando técnicas de reconhecimento individual, com um desenho amostral que permita a construção de históricos de captura e utilização de modelos de marcação-recaptura. Modelos de marcação-recaptura têm sido amplamente utilizados para estimar parâmetros demográficos, como abundância e probabilidade de sobrevivência (WILLIAMS; NICHOLS; CONROY, 2002), e como trabalham em nível individual permitem avaliar o efeito de

características dos indivíduos na probabilidade do mesmo ser capturado, ou ainda nos parâmetros populacionais que estão sendo estimados. Modelos de população aberta, como Cormack-Jolly-Seber (CORMACK, 1964; JOLLY, 1965; SEBER, 1965; LEBRETON et al., 1992), por exemplo, podem ser utilizados para estimar taxas de sobrevivência aparente específicas para diferentes classes de idade (e.g. FRUET et al., 2015). Já a abordagem do Desenho Robusto (POLLOCK, 1982; KENDALL; POLLOCK; BROWNIE, 1995; KENDALL; NICHOLS; HINES, 1997) combina modelos de população fechada e aberta sob uma estrutura de amostragem aninhada. Além de estimar abundância, probabilidade de captura e sobrevivência, essa abordagem inclui a possibilidade de emigração temporária (KENDALL; NICHOLS; HINES, 1997), que indiretamente pode revelar mudanças nas condições ambientais ou padrões sazonais de comportamento (DWYER et al., 2014). Também é possível pelo Desenho Robusto – ou mesmo outras parametrizações disponíveis – incluir covariáveis individuais nas estimativas, o que, como dito, possibilita investigar a influência da variação individual nos parâmetros estimados, como as variações resultantes de diferenças comportamentais que podem influenciar a dinâmica populacional através de benefícios individuais distintos. Por exemplo, algumas orcas nos arredores das Ilhas Crozet e do Estreito de Gibraltar se especializaram em depredar a pesca de espinhel, e essa tática de forrageio apresentou uma influência positiva na sobrevivência individual e na reprodução, com consequências para a dinâmica da população como um todo (TIXIER et al., 2015, 2017; ESTEBAN et al., 2016).

Boto-da-tainha: o modelo biológico

Os botos-da-tainha, como são conhecidos no sul do Brasil, pertencem ao gênero *Tursiops* que apresenta uma ampla distribuição em águas temperadas e tropicais, e utiliza uma grande diversidade de habitats como baías, lagoas, estuários e desembocaduras de rios (WELLS; SCOTT, 1999). Eles têm sido objeto de vários esforços de pesquisa de longa duração no mundo todo (por exemplo, WELLS; SCOTT, 1990; MANN et al., 2000; FRUET et al., 2015; ARSO CIVIL et al., 2019; CHENEY; THOMPSON; CORDES, 2019), permitindo estudos de

muitos aspectos da sua história de vida e biologia reprodutiva na natureza. São animais de vida longa que se reproduzem através de um sistema poligâmico (WELLS; SCOTT, 1990); fêmeas em Sarasota (Flórida, EUA) podem viver por mais de 50 anos e machos mais de 40 anos (HOHN et al., 1989; WELLS, SCOTT; 1999). As fêmeas começam a reproduzir entre cinco e dez anos de idade e, geram apenas um filhote após uma gestação de 12 meses, que permanece junto à sua mãe por vários anos (WELLS et al., 1987). Machos começam a reproduzir um pouco mais tarde, entre oito e doze anos de idade (WELLS et al., 1987). Os nascimentos podem ocorrer o ano todo (FÉLIX 1994, URIAN et al., 1996) ou sazonalmente (THAYER et al., 2003), variando geograficamente. Picos na estação reprodutiva têm sido descritos para várias populações, principalmente aquelas encontradas em altas latitudes (WELLS et al., 1987; BEARZI et al., 1997; HENDERSON et al., 2014), mas também em águas tropicais (FEARNBACH et al., 2011). O intervalo médio entre nascimentos, fecundidade e sobrevivência dos filhotes varia bastante entre populações (MANN et al., 2000; ROBINSON et al., 2017; BAKER et al., 2018), e o sucesso reprodutivo individual das fêmeas também pode variar dentro das populações (HENDERSON et al., 2014; FRUET et al., 2015; BROUGH et al., 2016). As taxas de sobrevivência também variam entre populações, dependendo das características ambientais e ameaças antrópicas locais, mas geralmente são altas para indivíduos adultos e menores para filhotes (WELLS; SCOTT, 1990; STOLEN; BARLOW, 2003), sendo este padrão típico para mamíferos (CAUGHLEY, 1977).

São particularmente conhecidos por sua plasticidade comportamental, reflexo de uma complexa habilidade cognitiva (MARINO et al., 2007), e apresentam diversas táticas de forrageio especializadas que podem variar tanto entre populações como dentro de uma mesma população, como por exemplo suspender o sedimento através de batidas de cauda (LEWIS; SCHROEDER, 2003), ou utilizar esponjas como ferramenta para auxiliar no forrageio (KOPPS et al., 2014). Os botos-da-tainha também são conhecidos por explorar recursos alimentares em torno de atividades humanas, como os descartes de barcos de pesca (CORKERON; BRYDEN; HEDSTROM, 1990) e a pesca cooperativa com pescadores artesanais em Laguna e Tramandaí, no sul do Brasil (SIMÕES-LOPES; FABIÁN; MENEGHETI, 1998; SIMÕES-

LOPES; DAURA-JORGE; CANTOR, 2016). Outros relatos de interações entre pequenos cetáceos e pescadores podem ser encontrados na literatura, porém longe da complexidade observada no sul do Brasil. Na costa da Mauritània, oeste da África, pescadores nômades realizavam uma espécie de pesca de cerco da tainha e se beneficiavam da colaboração de golfinhos-corcunda-do-atlântico *Sousa teuszii* e eventualmente botos-da-tainha *Tursiops truncatus* (BUSNEL, 1973). Mais recentemente, surgiu o relato de pesca também interativa entre o golfinho de Irrawaddy (*Orcaella brevirostris*) e pescadores locais de Myanmar, sul da Ásia (SMITH et al., 2009). Apesar dessa plasticidade comportamental dos botos-da-tainha ser bem documentada, pouco se sabe sobre as implicações disso na dinâmica populacional. Em Shark Bay na Austrália, alguns botos-da-tainha do Indo-Pacífico são alimentados por turistas. Filhotes de fêmeas que são alimentadas tiveram um cuidado parental reduzido e, consequentemente, maior mortalidade no primeiro ano de vida em relação a filhotes de fêmeas que forrageiam independentemente (MANN et al., 2000).

A presença de marcas de longa duração, naturais ou adquiridas, na nadadeira dorsal dos botos permite o reconhecimento e acompanhamento dos indivíduos ao longo da vida a partir da técnica de foto-identificação (WÜRSIG; JEFFERSON, 1990; WILSON; HAMMOND; THOMPSON, 1999; URIAN et al., 2015). A combinação dessa técnica com outras abordagens permite, por exemplo, estimar parâmetros demográficos a partir dos modelos de marcação e recaptura supracitados (e.g. SPROGIS et al., 2016; ARSO CIVIL et al., 2019); descrever padrões de distribuição individual, como área de vida e área de concentração, através do uso de análises espaciais, além de movimentos em escala regional (e.g. CHILVERS; CORKERON; PUOTINEN, 2003; WILSON et al., 2004); e descrever padrões sociais a partir das associações entre indivíduos (e.g. WELLS; SCOTT; IRVINE, 1987; MACHADO et al., 2019).

Diversas espécies globalmente abundantes estão expostas a impactos humanos que ameaçam a viabilidade de populações locais. *Tursiops truncatus* é uma dessas espécies, com ampla distribuição e estado de conservação global classificado como de menor preocupação pela Lista Vermelha da IUCN (HAMMOND et al., 2012). No entanto, muitas populações que habitam águas costeiras estão em declínio (GASPAR, 2003; CURREY et al., 2009; FÉLIX et al., 2017). As populações costeiras são especialmente vulneráveis pois tendem a ter uma distribuição restrita, que frequentemente se sobrepõe a atividades

humanas diversas (REEVES; REIJNDERS, 2002; REEVES et al., 2003). No sudoeste do Oceano Atlântico, as distinções morfológicas e genéticas entre duas formas de boto-da-tainha—costeira e *offshore*—sugerem adaptações a diferentes habitats (COSTA et al., 2016; WICKERT et al. 2016). Consequentemente, o Comitê de Taxonomia (2017) reconheceu recentemente esses botos costeiros como a subespécie *Tursiops truncatus gephyreus*, que consiste em pequenas unidades populacionais discretas, com alta fidelidade a estuários e a foz de rios (FRUET et al., 2014). Devido à falta de dados suficientes, no entanto, o estado de conservação regional desta subespécie ainda não foi avaliado.

O estudo de caso e ameaças locais

Uma dessas populações costeiras representante da subespécie *T. t. gephyreus* é encontrada em Laguna, no sul do Brasil. É uma população pequena e residente (SIMÕES-LOPES; FABIÁN, 1999; DAURA-JORGE; INGRAM; SIMÕES-LOPES, 2013) e geneticamente discreta (FRUET et al., 2014). Alguns indivíduos dessa população interagem com pescadores artesanais em uma rara tática de forrageio, aparentemente cooperativa, que parece beneficiar ambas as espécies: botos e pescadores (SIMÕES-LOPES; FABIÁN; MENEGHETI, 1998; SIMÕES-LOPES; DAURA-JORGE; CANTOR, 2016). Os botos cooperativos conduzem os cardumes, principalmente tainhas, em direção aos pescadores que aguardam de pé em águas rasas ou em canoas; os pescadores reconhecem comportamentos estereotipados dos botos como pistas que indicam quando e onde devem lançar suas tarrafas (SIMÕES-LOPES; FABIÁN; MENEGHETI, 1998; SIMÕES-LOPES; DAURA-JORGE; CANTOR, 2016; PETERSON; HANAZAKI; SIMÕES-LOPES, 2008; Fig. 1). Em função da grande relevância ecológica e socioeconômica dessa interação, e dos próprios botos-da-tainha, eles foram reconhecidos como Patrimônio Natural do Município de Laguna em 1997 (Laguna, lei municipal número 521/97). Os botos que compartilham essa tática de forrageio associam-se mais frequentemente uns aos outros do que ao resto da população, dividindo a população em unidades sociais de botos cooperativos — que interagem frequentemente com pescadores — e não-cooperativos — que

não interagem ou interagem ocasionalmente com pescadores (DAURA-JORGE et al., 2012). Essa tática de forrageio influencia o padrão de distribuição e comportamento espacial — os botos que cooperam com mais frequência têm áreas de vida menores (CANTOR; SIMÕES-LOPES; DAURA-JORGE, 2018) — e o repertório acústico dos indivíduos — os parâmetros acústicos dos assobios variam durante a cooperação (ROMEU et al., 2017). No entanto, sua influência na dinâmica populacional não foi totalmente compreendida.



Figura 1: Registros da pesca cooperativa entre botos e pescadores artesanais em Laguna, sul do Brasil. Os botos conduzem os cardumes em direção aos pescadores, que aguardam o momento exato para lançar as tarrafas.

Apesar dessa interação aparentemente positiva com pescadores artesanais, a população de botos em Laguna está exposta a diversos impactos provenientes de outras atividades humanas locais, incluindo capturas acidentais em rede de emalhe, efeitos cumulativos de poluentes, colisões com embarcações e ruído antropogênico (DAURA-JORGE et al., 2013, PELLEGRINI, 2018; RIGHETTI et al., 2019; Fig. 2). Nos últimos anos, vários botos morreram emalhados em aparatos de pesca, principalmente redes de emalhe colocadas próximas à área de cooperação entre botos e pescadores (BEZAMAT et al., 2018). Em resposta a essa mortalidade, recentemente o uso de redes de emalhe foi proibido na área de concentração dos botos (Laguna, lei municipal número 1.998/2018).

No entanto, pela escassez de recursos para uma fiscalização efetiva, novos casos de emalhe acidental ocorreram mesmo após a definição da área de exclusão de pesca de emalhe.



Figura 2: Nas duas fotos acima, dois indivíduos com rede de pesca presa ao corpo. Abaixo à esquerda, um filhote neonato morto devido à colisão com embarcação. Abaixo à direita, um indivíduo com lesão de pele semelhante à Lobomicose.

Poluentes como PCBs (bifenilas policloradas) também podem afetar a população de botos de Laguna; as concentrações de PCBs em alguns botos biopsiados excederam os limites de toxicidade (RIGHETTI et al., 2019). Sabe-se que os PCBs reduzem a sobrevivência de filhotes (REDDY et al., 2001; WELLS et al., 2005), afetam o sistema imunológico e, conseqüentemente, aumentam a suscetibilidade a doenças (DESFORGES et al., 2016). De fato, temos observado um número crescente de botos com lesões na pele semelhantes à lobomicose, uma infecção dérmica crônica, de origem fúngica, que afeta pequenos cetáceos (DAURA-JORGE; SIMÕES-LOPES, 2011; VAN BRESSEM et al., 2015; SACRISTÁN et al., 2016). A colisão com embarcações também é uma ameaça reconhecida. O ruído oriundo do tráfego diário de embarcações e empreendimentos locais (por exemplo, dragagens e a construção da ponte Anita Garibaldi) tem o potencial de mascarar a

comunicação entre mães e filhotes e, conseqüentemente, aumentar a mortalidade de filhotes (PARSONS; DOLMAN, 2004). O ruído também pode afetar o sucesso do forrageio, uma vez que os botos usam a ecolocalização para detectar presas (LACY et al., 2017). Na presença de embarcações, foi observada uma redução nas taxas de emissão de assobios e cliques de ecolocalização durante a interação com os pescadores (PELLEGRINI, 2018).

Objetivos

Nos últimos 11 anos (2007-2018), a população de botos de Laguna foi monitorada sistematicamente através de um esforço amostral por foto-identificação que nos permitiu acompanhar 65 indivíduos adultos marcados e 45 filhotes. Embora o monitoramento não tenha sido contínuo (não ocorreu esforço entre os anos de 2010 e 2012), o banco de dados existente permite um refinamento nas estimativas de parâmetros populacionais, como sobrevivência e abundância, por marcação-recaptura, bem como a estimativa de novos parâmetros relacionados ao comportamento reprodutivo. Permite também a utilização destes parâmetros para a projeção populacional em diferentes cenários de manejo, além de uma avaliação da influência de variáveis individuais nos parâmetros populacionais — em especial a hipótese de que o uso diferenciado da tática de forrageio com pescadores poderia estar interferindo na probabilidade de sobrevivência e na reprodução dos indivíduos, com conseqüências para a dinâmica populacional.

Assim, o objetivo geral desta tese é avaliar a viabilidade da população de botos-da-tainha *Tursiops truncatus gephyreus* em Laguna, sul do Brasil, nos próximos 100 anos e avaliar o fator que mais interfere na viabilidade para subsidiar as decisões de manejo. Para alcançar este objetivo, foram realizadas estimativas de parâmetros populacionais e reprodutivos, e os dados gerados foram incluídos em uma Análise de Viabilidade Populacional.

A tese está estruturada em três capítulos, sendo que em cada um deles foram propostos objetivos específicos. No primeiro capítulo, utilizamos modelos de marcação-recaptura aplicados a dados de foto-identificação individual visando testar a hipótese de influência da tática de forrageio de cooperar com pescadores nos parâmetros populacionais

dos botos. Modelamos abundância, sobrevivência, taxa de emigração temporária e probabilidade de captura em função do sexo, e de duas características individuais que representam os efeitos dessa tática de forrageio—frequência de interação com os pescadores e tamanho da área de vida.

No segundo capítulo, registramos o histórico reprodutivo de fêmeas conhecidas na população visando: 1) estimar parâmetros reprodutivos como sazonalidade de nascimentos, fecundidade, intervalo entre nascimentos e sobrevivência de filhotes; 2) testar a hipótese de influência da tática de forrageio nos parâmetros reprodutivos; 3) investigar fatores que podem influenciar na sobrevivência de filhotes, incluindo características das mães, como frequência de interação com os pescadores, tamanho da área de vida e idade, distância entre o nascimento e o pico da temporada de tainha, e total de tainha capturada na temporada após o nascimento.

No terceiro capítulo, realizamos uma Análise de Viabilidade Populacional baseada no monitoramento de longo prazo dos indivíduos e nos dados gerados nos capítulos anteriores visando: 1) modelar a viabilidade dessa população nos próximos 100 anos sob diferentes níveis de mortalidade por captura acidental em rede de pesca, incluindo o cenário atual e cenários de manejo; 2) identificar os parâmetros da história de vida para os quais a dinâmica populacional é mais sensível; 3) explorar como cenários de com ameaças adicionais relacionadas a atividades humanas (isto é, capturas acidentais e dragagem) afetariam a dinâmica populacional.

O primeiro capítulo foi publicado na revista *Marine Mammal Science*, o segundo capítulo foi submetido para a revista *Marine Biology* e o terceiro capítulo está em fase de preparação para submissão para a revista *Animal Conservation*. No corpo da tese os artigos estão pré-formatados para as respectivas revistas. Ao final, apresentamos conclusões gerais que, com base nos resultados dos três capítulos, resumam as principais recomendações para a conservação desta pequena população de botos e dessa interação única entre botos e pescadores.

Desenho amostral e processamento dos dados

O sistema lagunar costeiro adjacente à cidade de Laguna, no sul do Brasil, (28°20'S – 48°50'O) abrange uma área de cerca de 200 km² e é formado por três subunidades: as lagoas Santo Antônio, Imaruí e Mirim (Fig. 3). Em geral, o sistema lagunar é raso, com uma profundidade média de 2 metros, com exceção pro canal de ligação com o mar, com profundidade de até 10 metros. A hidrodinâmica local é influenciada pelo regime de marés, ventos predominantes (SE e NE) e pluviosidade (MEURER; NETTO, 2007).

Para alcançar os objetivos deste trabalho, nós realizamos um esforço sistemático de saídas embarcadas para foto-identificação dos botos, de setembro de 2007 a setembro de 2009 (mesmo conjunto de dados de DAURA-JORGE; SIMÕES-LOPES; INGRAM, 2013), e de abril de 2013 a dezembro de 2017, utilizando um barco de 5 m com um motor de popa de 15 hp. Durante cada dia de amostragem, foi percorrida uma rota pré-definida de cerca de 30 km para cobrir de maneira uniforme a principal área usada pelos botos (CANTOR et al., 2018) durante aproximadamente cinco horas. Nosso esforço de busca foi restrito a condições climáticas favoráveis (boa visibilidade e vento < 10 nós) para aumentar a chance de localizar os botos e obter fotos de boa qualidade.

Um grupo de botos foi definido como o número total de indivíduos em um raio de 50 m uns dos outros e engajados em um comportamento similar (como em DAURA-JORGE; SIMÕES-LOPES; INGRAM, 2013). Para cada grupo avistado, foi feita uma sessão de fotos para a identificação dos indivíduos e foram registrados horário, localização, tamanho do grupo e tática de forrageio. Nós definimos duas táticas de forrageio: “forrageio cooperativo”, quando os botos interagem com os pescadores (ou seja, direcionavam os cardumes para os pescadores e realizavam comportamentos estereotipados associados à interação, conforme descrito em SIMÕES-LOPES; FABIÁN; MENEGHETI, 1998) e “forrageio não-cooperativo”, quando os botos estavam forrageando independentemente (isto é, mergulhando com frequência e de forma assíncrona e em várias direções). Nós tentamos fotografar a nadadeira dorsal de todos os botos no grupo, de ambos os lados e sem preferências individuais, seguindo protocolos bem estabelecidos para pequenos cetáceos (WÜRSIG; JEFFERSON, 1990; URIAN et al., 2015).

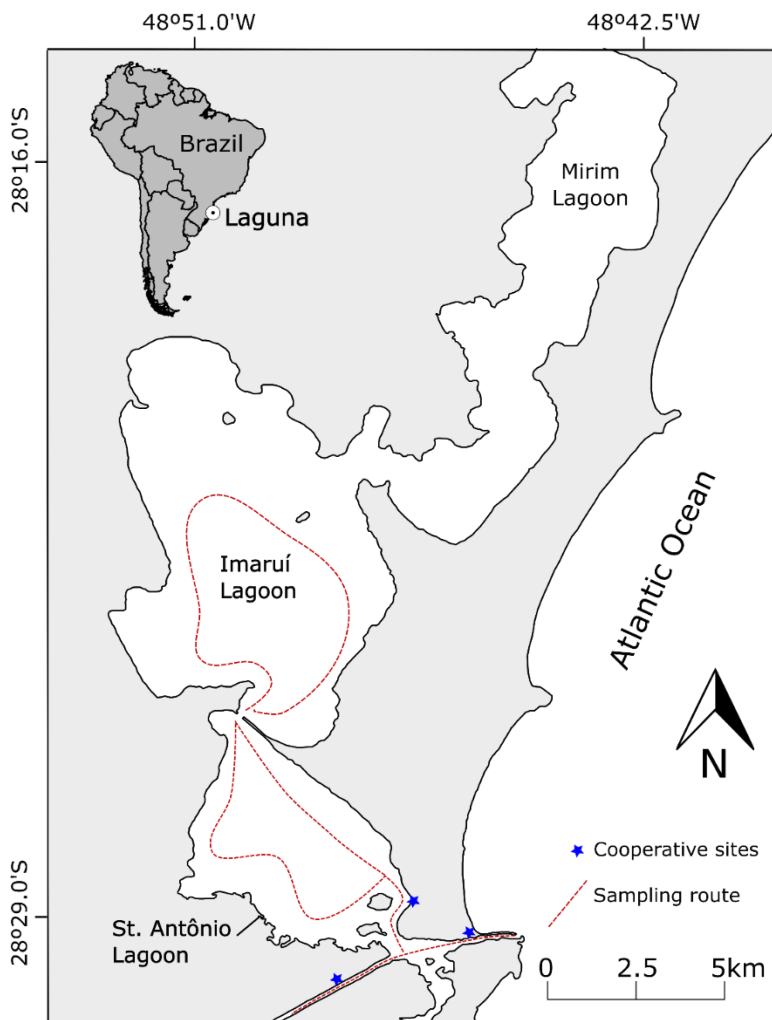


Figura 3: Área de estudo em Laguna, sul do Brasil. Em vermelho está representada a rota pré-definida percorrida em cada dia de amostragem. As estrelas azuis marcam os principais locais onde ocorre a interação entre botos e pescadores.

Para minimizar erros na identificação individual, esta foi baseada apenas em marcas de longa duração na nadadeira dorsal, como cortes e cicatrizes (WILSON; HAMMOND; THOMPSON, 1999). Para minimizar o efeito da heterogeneidade individual na distinção de marcas, utilizamos apenas fotos de alta qualidade (de uma escala de A a C, em termos de ângulo, foco e exposição; WILLIAMS; DAWSON; SLOOTEN, 1993). Filhotes tipicamente não possuem marcas e foram acompanhados até o desmame por meio da identificação das suas mães. Marcas temporárias, como arranhões, na nadadeira dorsal e no corpo, também auxiliaram na identificação individual dos filhotes. A partir do banco de dados de foto-identificação, nós extraímos um registro detalhado das avistagens de todos os indivíduos, e do nascimento de filhotes para todas as fêmeas reprodutivamente ativas identificadas ao longo do estudo (ou seja, aquelas que sabidamente deram à luz a filhotes viáveis). E então, construímos dois históricos de captura, um para indivíduos adultos e outro para filhotes, que serviram de base para todas as análises realizadas na tese.

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CAPÍTULO 1

THE INFLUENCE OF COOPERATIVE FORAGING WITH FISHERMEN ON THE DYNAMICS OF A BOTTLENOSE DOLPHIN POPULATION

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ABSTRACT

Recent years have seen an increasing interest in individual behavioral variation. However, the implications of such variation for population dynamics are often unknown. We studied the dynamics of a bottlenose dolphin (*Tursiops truncatus gephyreus*) population from southern Brazil, where some individuals forage cooperatively with artisanal fishermen. We fitted mark-recapture models to 10 years of photo-identification data to investigate the influence of this foraging specialization on dolphins' population parameters, controlling for sex and ranging behavior. We estimated adult survival to be high (0.949 ± 0.015 SE), weakly influenced by home range size, sex or the frequency of interaction with fishermen. The slightly higher survival probability for individuals with smaller home ranges could stem from the benefits of reduced spatial requirements implied by the specialized foraging. Foraging also influenced the probability of re-sighting individuals, and there was no temporary or permanent emigration. Abundance fluctuated slightly over the years from 54 (95% CI = 49-59) to 60 (95% CI = 52-69) individuals, with no evident population trend. Despite such apparent population stability, we confirm this population remains small and geographically isolated which may threaten its viability and the viability of its unusual, localized foraging specialization. Our study also illustrates how accounting for individual variation can portray animal population dynamics more realistically.

Keywords: *Tursiops truncatus gephyreus*, mark-recapture models, foraging behavior, survival probability, abundance, individual variation, artisanal fishermen.

INTRODUCTION

The dynamics of animal populations are sensitive to variation among individuals. When individuals of the same population differ in resource use (Bolnick *et al.* 2003) and invest in different foraging tactics (Estes *et al.* 2003, Torres and Read 2009), they may experience varying levels of intraspecific competition (Araújo *et al.* 2011), which ultimately can shape social structures (Daura-Jorge *et al.* 2012) and influence demographic processes (Bolnick *et al.* 2011). For instance, foraging specializations may improve individual survival or reproductive output, which in turn can have broader consequences for the dynamics of the population as a whole (Esteban *et al.* 2016, Tixier *et al.* 2017).

Bottlenose dolphins are particularly well known for their behavioral plasticity and display numerous specialized foraging techniques that vary within and between populations—*e.g.*, mud plume feeding (Lewis and Schroeder 2003), crater feeding (Rossbach and Herzing 1997), and sponge feeding (Kopps *et al.* 2014). Bottlenose dolphins are also known to exploit food resources around human activities, such as discards from fishing boats (Corkeron *et al.* 1990), and cooperative fishing with artisanal fishermen (Simões-Lopes *et al.* 1998). Despite the well-documented behavioral plasticity of bottlenose dolphins, whether this has real implications for their population dynamics remains relatively unknown. In Shark Bay, Australia, calves born to provisioned females of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) experienced reduced care and higher first year mortality relative to calves of non-provisioned mothers (Mann *et al.* 2000).

In Laguna, southern Brazil, a very distinctive foraging tactic of free-living Lahille's bottlenose dolphins (*Tursiops truncatus gephyreus*¹) involves synchronized interaction with net-casting fishermen (Simões-Lopes *et al.* 1998, 2016). A subset of dolphins from this small, resident (see Daura-Jorge *et al.* 2013) and apparently isolated population (see Fruet *et al.* 2014) frequently herd mullet shoals towards a line of

¹ The Society for Marine Mammalogy's Committee on Taxonomy (2017) recognized the coastal bottlenose dolphins from Southwest Atlantic as the subspecies *Tursiops truncatus gephyreus*.

fishermen and ‘signal’ with specific behavioral displays when and where fishermen should cast their nets (Simões-Lopes *et al.* 2016). Dolphins that share this foraging tactic associate more often with each other than with the rest of the population, dividing the society into social units of cooperative and noncooperative dolphins (Daura-Jorge *et al.* 2012). This foraging tactic influences spatial habitat use (dolphins that cooperate more often have smaller home ranges; Cantor *et al.* 2018); and acoustic repertoires (whistle acoustic parameters vary during the cooperation; Romeu *et al.* 2017), but its influences on the population dynamics have not previously been entirely explored.

Assessing population parameters and dynamics for long-lived marine species is challenging, expensive and time-consuming (see Williams and Thomas 2009), but necessary for robust conservation and management plans. Mark-recapture modeling techniques have been widely used to estimate demographic parameters (Williams *et al.* 2002). One of these techniques, the robust design (RD; Pollock 1982, Kendall and Nichols 1995, Kendall *et al.* 1997), combines closed and open population models under a nested sampling framework to bring realism to the complex biological system. This approach accounts for temporary emigration (Kendall *et al.* 1997), which may reveal changes in environmental conditions or seasonal behavioral patterns (Dwyer *et al.* 2014), reducing the bias in the estimated survival parameters (Peñaloza *et al.* 2014). Temporary emigration should be considered for the study population, since movements of individuals from Laguna to neighboring communities have been recorded (Simões-Lopes and Fábian 1999). This approach also allows for the inclusion of individual covariates, which is important to investigate the influence of individual variation in population parameters, for example behavioral differences that might influence population dynamics through individual benefits (see Esteban *et al.* 2016, Tixier *et al.* 2017).

Here, we used mark-recapture techniques applied to photo-identification data to test the influence of the foraging tactic of cooperating with fishermen on population parameters. Using the robust design, we modeled abundance, survival, temporary emigration rates, and capture probabilities as a function of two individual traits that typify the effects of this cooperative foraging tactic: the frequency of interaction with fishermen and the home range size. Since dolphin foraging and ranging behavior can be sex-specific (*e.g.*, Sprogis *et al.* 2016), we also included sex as a covariate in our models. We hypothesize that foraging

in cooperation with fishermen (1) increases dolphin survival probabilities; and (2) influences temporary emigration and capture probabilities, and should be taken into account when estimating survival and abundance. Our final goal was to assess population change over a ten year period, comparing our results with a previous mark-recapture analysis of data collected between 2007-2009 (see Daura-Jorge *et al.* 2013).

METHODS

Data sampling

We studied the bottlenose dolphin population resident within the 200 km² coastal lagoon system in Laguna, southern Brazil (28°20'S–48°50'W), which comprises three shallow lagoons connected to the Atlantic Ocean by a deep canal (see Fig. 3–Thesis' Introduction, page 37). The lagoon system is tidally dynamic and strongly influenced by prevailing winds (SE and NE) and rainfall (Meurer and Netto 2007). As fishing is the major local economic activity, accidental bycatch is probably one of the main causes of dolphin mortality (see Peterson *et al.* 2008).

We carried out systematic photo-identification surveys from September 2007 to September 2009 (same data set in Daura-Jorge *et al.* 2013) and from April 2013 to October 2016 using a 5-meter boat powered by an outboard engine. During each daily sampling occasion, we followed a 30-kilometer predefined route (see Fig. 3–Thesis' Introduction, page 37) to evenly cover the main area used by the dolphins (Cantor *et al.* 2018) over approximately 5 h. Our search effort was restricted to good weather conditions (*i.e.*, good visibility, wind < 10 knots) to reduce the chance of missing dolphins and increase the chance of recognizing individuals (capture) *via* photo-identification.

A group of dolphins was defined as the total number of individuals encountered within a 50 m radius of each other and engaged in similar behavior (as in Daura-Jorge *et al.* 2013). For all sighted groups, we collected data on individual photo-identification, time, location, group size and foraging behavior. We defined two foraging tactics: 'cooperative

foraging’, when dolphins were interacting with fishermen (*i.e.*, driving prey schools towards fishermen and performing stereotyped behaviors associated with the interaction, as described in Simões-Lopes *et al.* 2016); and ‘noncooperative foraging’, when dolphins were foraging by themselves (*i.e.*, diving frequently and asynchronously and in various directions). We attempted to photograph the dorsal fin of all dolphins in the group, taking as many photos as possible of both sides and without individual preferences, following protocols for small cetaceans (Würsig and Jefferson 1990). To minimize errors, individual identification was based only on long-lasting natural marks (nicks and marks on the leading and trailing edges; Wilson *et al.* 1999). To minimize the effect of individual heterogeneity from mark distinctiveness, we used only pictures classified as high quality (from a scale of A to C in terms of angle, focus, exposure; Williams *et al.* 1993). Calves (<1y old) and nonidentifiable individuals (intact or indistinctive dorsal fin, or captured only on low-quality photographs) were not included in our analyses.

Robust Design

We analyzed mark-recapture histories under the robust design (RD; Pollock 1982, Kendall and Nichols 1995, Kendall *et al.* 1997), considering two hierarchical sampling periods: seven annual primary periods composed of 13 to 18 secondary periods each (*i.e.*, daily capture occasions) (Table 1). For each primary period (year), we estimated capture probabilities (p) and abundance of marked individuals (\hat{N}). From the intervals between primary sampling periods, we estimated apparent survival probability (ϕ); the probability of temporary emigration (γ'') or being unavailable for capture, given that the individual was available during the previous sampling occasion; and the probability that an emigrated individual remained outside the study area unavailable for capture during subsequent sampling (γ') (Kendall *et al.* 1997). Capture (p) and recapture (c) probabilities were set as equal, as photo-identification is not known to cause a trap response.

We developed a set of 13 candidate models from the classical closed and open population models (Lebreton *et al.* 1992) to test different effects on the estimated parameters (survival and capture probabilities) and then evaluated multiple ecological hypotheses: no variation (.); time-dependent effect between primary periods (t); time-dependent effect between and within primary periods ($t*s$). A model with no emigration

($\gamma'' = \gamma' = 0$) was used as a basis to investigate time-dependence effect on capture probabilities. Temporary emigration models were fitted using constant random (classical, $\gamma'' = \gamma'$) and Markovian (γ'' , γ') emigration parameters (see Kendall *et al.* 1997). Emigration models with time-dependence effects were over-parameterized and were not considered.

Previous studies have proposed that interaction with fishermen may benefit dolphins in terms of resource accessibility (Simões-Lopes *et al.* 1998). An earlier mark-recapture analysis for the period 2007-2009 considered the effect of the foraging behavior, classifying dolphins into two categories of cooperatives and noncooperatives (Daura-Jorge *et al.* 2013). However, we noticed that all dolphins seem to have a degree of engagement in the interaction with fishermen. Therefore, we accounted for the effect of the following three individual covariates on the apparent survival and capture probabilities: (1) the frequency of interaction of each dolphin with fishermen; (2) the home range size of each dolphin; and (3) sex. When possible, sex was determined by genetic analyses of biopsied skin samples (data from Costa *et al.* 2015); for completion, we assumed individuals consistently observed in close association with a calf to be females (*e.g.*, Mann *et al.* 2000), and highly-scarred individuals with well-marked dorsal fin nicks to be males (Rowe and Dawson 2009), validated for Laguna population from molecular sexing of 23 individuals (14 males and 9 females).

Table 1: Sampling effort used in Robust Design: number of secondary periods (capture occasions), number of marked dolphins identified, and number of new dolphins identified within each primary period.

Primary period	Secondary periods (capture occasions)	Dolphins identified	New dolphins identified
2007	13	45	45
2008	18	47	3
2009	16	43	0
2013	14	45	13
2014	13	46	2
2015	16	45	0
2016	15	45	2

We calculated the frequency of interaction (f_i) as the number of independent events each dolphin was observed foraging with fishermen divided by the total number of observation events. Individual home ranges (HR; *sensu* Burt 1943) were estimated using the fixed kernel method (Worton 1989) in R (R Core Team 2017) using the `adehabitatHR` package (Calenge 2006). To minimize any potential spatial autocorrelation bias for home range analyses, we randomly selected a single record per individual per sampling day. The resolution of the smoothing parameter (*i.e.*, the bandwidth value) was estimated using the *ad hoc* method, choosing the optimum smoothing parameter (h) value for some standard distribution (details in Worton 1989). Individual home ranges were defined using the 95% probability contour (excluding land). We could not fit individual home ranges for 13 dolphins because we had less than five relocations for each of them. For these individuals, we assigned the average home range size for cooperative and noncooperative dolphins according to previous classification (Daura-Jorge *et al.* 2013). Since collinearity between these individual covariates was identified (investigated by a Pearson-rank correlation coefficient), models including both predictors for the same parameter (*e.g.*, survival or capture probability) were not built. To estimate population parameters, we used the Huggins' parameterization method (Huggins 1991), which in general seems to be more stable with small sample sizes and applicable to models with individual covariates.

Model validation and selection procedures

Since there is no goodness-of-fit (GOF) test available to validate the assumptions for RD models (see Williams *et al.* 2002), we used program Release (Burnham *et al.* 1987) to test the fit of the Cormack-Jolly-Seber model to our data, previously pooled into primary periods (*cf.* Daura-Jorge *et al.* 2013). We used the TEST 2 and TEST 3 to evaluate potential violations of the assumptions of equal probabilities of capture and survival between individuals (Pradel *et al.* 1997). We tested the assumption of population closure across all sampling occasions within a primary period using the Otis closure test (Otis *et al.* 1978) in program CloseTest (Stanley and Richards 2005).

To select the most parsimonious models, we relied on the lowest Akaike Information Criterion corrected for small sample size (AICc, Burnham and Anderson 2002). Since the use of covariates already

accounts for some variability, we did not correct AIC for overdispersion by the estimated \hat{c} value, to avoid over-simplified models. We used a step-down model selection procedure (Lebreton *et al.* 1992). First, we tested for capture probability to be constant or variable between or within primary periods, in models with constant survival and no emigration ($\gamma'' = \gamma' = 0$). From the most parsimonious model for capture probability, we tested whether survival probabilities changed between annual primary periods, also considering no emigration. From the resultant best fitting model for survival, we then fitted models with constant random ($\gamma'' = \gamma'$) or Markovian (γ'' , γ') temporary emigration. Additionally, we investigated the effects of three individual covariates (frequency of interaction, home range and sex) on capture and survival probabilities. Models within $\Delta\text{AIC} \leq 2$ show considerable support from the data (Burnham and Anderson 2002). However, to account for uncertainty across models, our final parameter estimates were averaged across the most supported models based on the AICc weights (Burnham and Anderson 2002). All mark-recapture analyses were performed using program MARK (White and Burnham 1999).

Total Abundance

Because the abundance estimates (\hat{N}) refer exclusively to the marked animals in the population, we corrected our estimates to include unmarked individuals (\hat{N}_{Total}). To do so, we divided the abundance of marked individuals (\hat{N}) by the proportion of marked individuals in the population (θ , see Wilson *et al.* 1999). We estimated theta (θ) for each year as the number of marked individuals divided by the total number of individuals observed on each capture occasion, averaged over all capture occasions in that period. Calves were considered as unmarked individuals. The standard errors (SE) of the total abundance (\hat{N}_{Total}) were calculated using the method proposed by Urian *et al.* (2015):

$$SE(\hat{N}_{Total}) = \sqrt{\hat{N}_{Total}^2 \left(\frac{SE(\hat{N})^2}{\hat{N}^2} + \frac{SE(\theta)^2}{\theta^2} \right)}$$

We then estimated log-normal confidence intervals for total abundance following Burnham *et al.* (1987), dividing or multiplying the total abundance by a factor C calculated as:

$$C = \exp \left[z \frac{\alpha}{2} \times \sqrt{\ln \left\{ 1 + [CV(\hat{N}_{Total})]^2 \right\}} \right]$$

where z is the normal deviate, $\alpha = 0.05$ and CV is the coefficient of variation.

We estimated the realized population growth rate (λ) by a parameterization of Pradel's (Pradel 1996) temporal symmetry model (ϕ and λ parameterization). We modelled population growth rate by testing whether it was constant or changed yearly, while keeping constant survival and capture probability varying between primary periods. We selected the most supported model using the same procedure as described for RD.

Finally, we considered the number of bottlenose dolphin carcasses recovered in or near Laguna (up to 35 km) by a systematic beach monitoring program carried out since 2013. To quantify carcasses that potentially belong to the Laguna population, we disregarded the bottlenose dolphin specimens of the offshore ecotype (identified based on skull morphology in Costa *et al.* 2016), and the individuals whose dorsal fins could not be matched with the Laguna photo-identification catalog.

RESULTS

We analyzed photo-identification data collected systematically during 105 capture occasions in 2007-2009 and 2013-2016 (Table 1). We analyzed a total of 26,649 dorsal fin photos (66% of which were adequate for individual recognition) which resulted in encounter histories of 65 individuals with long-lasting natural marks. On average, 90% of individuals released at primary occasion i were recaptured at primary occasion $i+1$, except for the interval between 2009 and 2013 when the recapture rate was 74%. Out of the 65 marked dolphins, 37 were females and 28 were males. Twenty-three individuals were sexed through genetic analysis, 19 were females with calves, and 23 were sexed based on the

rate of scarring and dorsal fin nicks. Forty-eight individuals (74%) were identified during 2007-09, and 51 (78%) during 2013-16. Thirty-four dolphins (52%) were sighted in both periods, 14 (22%) were sighted exclusively in 2007-09, and 17 (26%) only in 2013-16. The proportion of marked individuals using the area (*i.e.*, the average proportion of marked individuals on all capture occasions within each year) ranged from 0.721 in 2009 to 0.866 in 2014. Individual frequencies of foraging interaction with fishermen ranged from 0% to 69%, and individual home range sizes ranged from 4.1 to 101.5 km² (Fig. 1).

Results from Otis closure test indicated that all primary (annual) periods could be considered closed with no gains or losses of individuals ($P > 0.05$ for all primary periods). The goodness-of-fit test indicated that assumptions of equal capture (TEST 2) and survival (TEST 3) probabilities were not violated (Global TEST: $X^2 = 0.365$, $P = 0.947$, $df = 3$).

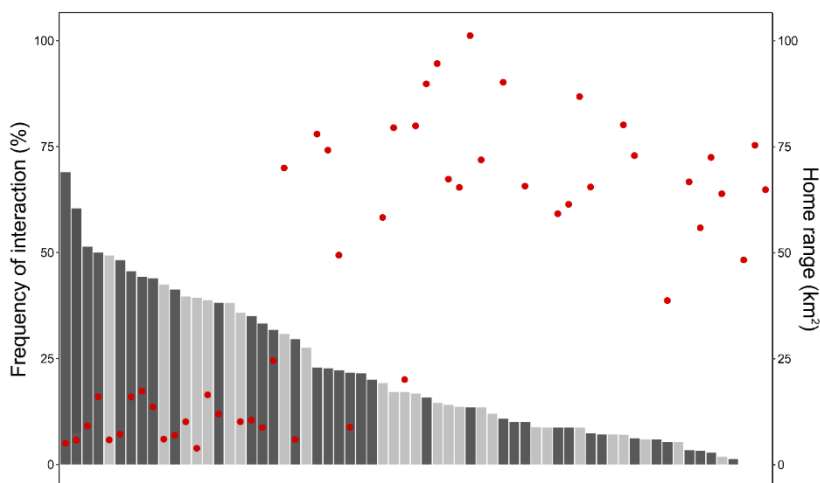


Figure 1: Frequency of interaction (bars) and home range (red circles) for each marked bottlenose dolphin in Laguna (x-axis; dark gray bars are females and light gray bars are males). Imputations for home range were omitted.

Model selection

The best-ranked model before incorporating individual covariates had constant survival probability over time, no emigration and capture probability constant within primary periods but varying between them (Model 8 in Table 2A). With the incorporation of individual covariates, the model with the most support from the data had constant survival probability influenced by individual home range size (HR), no emigration and capture probability constant within primary periods but varying between them, with time variation in the relationship between capture probability and frequency of interaction (\bar{f}_i) (37% of AICc weight; Model 1 in Table 2A). The next three models also had considerable support from the data ($\Delta\text{AICc} < 2$; Table 2) and differed from the top model only in that survival was invariant (Model 2), dependent on the frequency of interaction (\bar{f}_i ; Model 3), or dependent on the sex of individuals (Model 4).

Parameter estimates

The survival rate (weighted over the best fitting models) was 0.949 (SE = 0.015, 95%CI = 0.914 – 0.970). The predicted survival decreased slightly with increasing home range from 0.972 (SE = 0.018; 95%CI = 0.901 – 0.993) for the dolphin with the smallest home range to 0.901 (SE = 0.053; 95%CI = 0.741 – 0.969; Fig. 2) for the dolphin with the largest home range; and increased slightly with the frequency of interaction with fishermen from 0.932 (SE = 0.032; 95%CI = 0.835 – 0.972) for the dolphin with the lowest frequency of interaction to 0.975 (SE = 0.025; 95%CI = 0.834 – 0.997; Fig. 3) for the dolphin with the highest frequency of interaction. The estimated survival was slightly higher for females (0.957; SE = 0.013; 95%CI = 0.921 – 0.977) than for males (0.936; SE = 0.019; 95%CI = 0.885 – 0.965). Capture probabilities varied between 0.30 and 0.52 among primary periods. The relationship between capture probability and frequency of interaction with fishermen varied within and between primary occasions (Model 1, Table 2), increasing or decreasing with frequency of interaction in different years (Fig. 3).

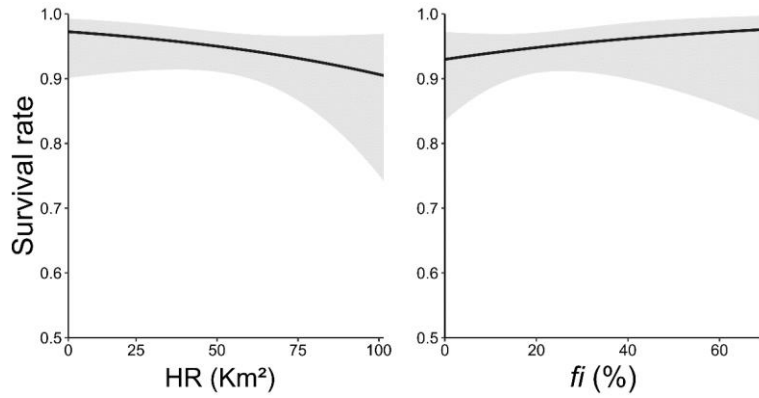


Figure 2: Survival rate and individual home range (HR; Model 1 Table 2A) and frequency of interaction (*fi*; Model 3 Table 2A) (predicted values and 95% confidence intervals) for bottlenose dolphins in Laguna.

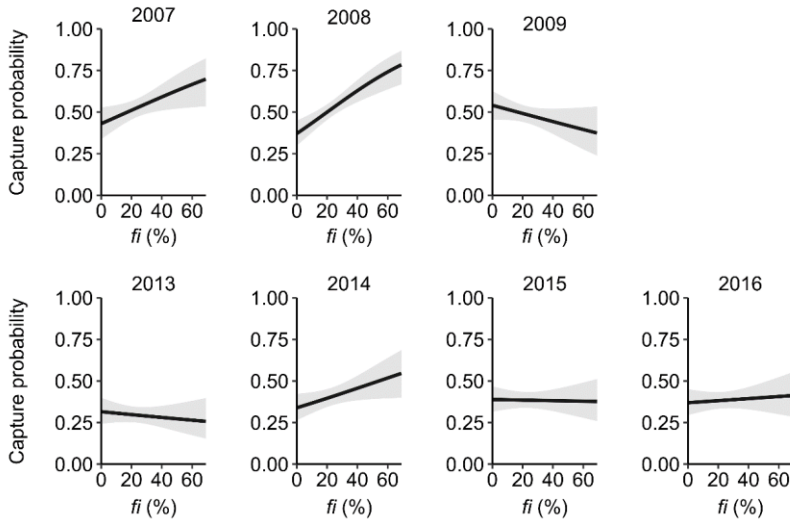


Figure 3: Relationship between capture probability and individual frequency of interaction (predicted values and 95% confidence intervals) for bottlenose dolphins in each year of the study in Laguna.

The abundance of marked dolphins using the area did not vary markedly throughout the study period. The averaged RD model yielded annual abundance estimates ranging from 43 to 47 marked dolphins (Table 3). Due to differences in the number of calves (range: 2 - 7) and juveniles (range: 2 - 10) each year, the total population size (\hat{N}_{Total}) corrected for unmarked individuals fluctuated from 54 (95%CI = 49-59) in 2007 to 60 (95%CI = 52-69) in 2016 (Table 3). The Pradel model (Table 2B) estimated a constant annual population growth rate of 0.999 (SE = 0.014; 95% CI = 0.971 - 1.027). We could not model λ with time-variation due to unsuccessful numerical convergence. From the 15 stranded carcasses recovered on the beach from 2013 to 2016 potentially belonging to the Laguna population (Table 3), we identified six adult known individuals: four dolphins that rarely or never interacted with fishermen and two that routinely foraged with artisanal fishermen

Table 2: (A) Robust Design and (B) Pradel's temporal symmetry candidate models for survival probability (ϕ), capture probability (p), recapture probability (c), temporary emigration probability (γ'') and population growth rate (λ) ranked by AICc. AICc weight indicates the support of the selected model over the others. Deviance is a measure of model fit. Notation: (.) constant, (t) time-dependence between primary periods, (s) time-dependence within primary periods, (γ'') probability of temporary emigration, (γ') probability of remaining outside the study area, ($p=c$) no recapture effect, ($\gamma'' = \gamma' = 0$) no emigration, ($\gamma'' = \gamma'$) random emigration, (γ'' , γ') Markovian emigration, (f_i) frequency of interaction, (HR) home range size, (sex) sex of individuals. Akaike information criterion corrected for small sample size (AICc).

Model	AICc	Δ AICc	AICcWeight	Likelihood	Npar	Deviance
(A) Robust Design						
1 $\{\phi(\text{HR}) \gamma''=\gamma'=0 \ p=c(t*f_i)\}$	6506.9	0.00	0.37	1.00	16	6474.67
2 $\{\phi(.) \ \gamma''=\gamma'=0 \ p=c(t*f_i)\}$	6507.4	0.49	0.29	0.78	15	6477.20
3 $\{\phi(f_i) \ \gamma''=\gamma'=0 \ p=c(t*f_i)\}$	6508.3	1.33	0.19	0.51	16	6476.01
4 $\{\phi(\text{sex}) \ \gamma''=\gamma'=0 \ p=c(t*f_i)\}$	6508.7	1.73	0.15	0.42	16	6476.40
5 $\{\phi(.) \ \gamma''=\gamma'=0 \ p=c(t+f_i)\}$	6538.7	31.72	0.00	0.00	9	6520.57
6 $\{\phi(.) \ \gamma''=\gamma'=0 \ p=c(t+\text{sex})\}$	6541.8	34.87	0.00	0.00	9	6523.72
7 $\{\phi(.) \ \gamma''=\gamma'=0 \ p=c(t+\text{HR})\}$	6543.3	36.34	0.00	0.00	9	6525.19
8 $\{\phi(.) \ \gamma''=\gamma'=0 \ p=c(t)\}$	6548.8	41.84	0.00	0.00	8	6532.71
9 $\{\phi(.) \ \gamma''=\gamma' \ p=c(t)\}$	6550.6	43.63	0.00	0.00	9	6532.48
10 $\{\phi(.) \ \gamma'', \ \gamma' \ p=c(t)\}$	6552.6	45.65	0.00	0.00	10	6532.48
11 $\{\phi(t) \ \gamma''=\gamma'=0 \ p=c(t)\}$	6555.6	48.70	0.00	0.00	13	6529.46
12 $\{\phi(.) \ \gamma''=\gamma'=0 \ p=c(t*s)\}$	6577.9	70.95	0.00	0.00	106	6354.22
13 $\{\phi(.) \ \gamma''=\gamma'=0 \ p=c(.)\}$	6654.7	147.80	0.00	0.00	2	6650.73
(B) Pradel's temporal symmetry model						
1 $\{\phi(.) \ \lambda(.) \ p=c(t)\}$	3762.7	0.00	1.00	1.00	9	3441.37
2 $\{\phi(.) \ \lambda(.) \ p=c(.)\}$	3816.9	54.17	0.00	0.00	3	3507.62

Table 3: Estimates of abundance for each year from Robust Design models. Shown are: abundance of marked individuals (\hat{N}), theta estimates (θ), the total population size adjusted by theta method (\hat{N}_{Total}), the CVs adjusted using the delta method [$CV(\hat{N}_{Total})$], the confidence intervals [$CI(\hat{N}_{Total})$], and the number of recovered carcasses.

Year	\hat{N}	$CV(\hat{N})$	θ	$CV(\theta)$	\hat{N}_{Total}	$CV(\hat{N}_{Total})$	$CI(\hat{N}_{Total})$	Recovered carcasses
2007	45	0.002	0.832	0.047	54	0.047	49-59	-
2008	47	0.001	0.787	0.057	60	0.057	53-67	-
2009	43	0.001	0.721	0.086	60	0.086	50-71	-
2013	45	0.018	0.818	0.077	55	0.079	47-65	4
2014	46	0.009	0.866	0.064	53	0.065	47-60	6
2015	45	0.004	0.864	0.066	52	0.066	46-59	0
2016	45	0.005	0.750	0.071	60	0.072	52-69	5

DISCUSSION

Our study incorporated sex and individual variation in foraging tactics and ranging area in mark-recapture models to assess whether these covariates influenced apparent survival and capture probabilities. Results showed that individual variation in foraging behavior weakly affected demographic parameters of dolphins using the lagoon system in Laguna. We found that dolphins that routinely forage with fishermen and have reduced home ranges tend to have slightly higher survival and variable capture probabilities. In addition, our sampling effort over ten years strengthens the evidence that this population is small, highly resident and apparently stable.

The four RD models with the most support from the data suggested that survival probabilities were weakly influenced by individual home range size, sex and the frequency with which individuals interact with fishermen. We hypothesized that cooperative foraging could affect survival positively, since dolphins may have access to more abundant prey when interacting with fishermen than when foraging by themselves (Simões-Lopes *et al.* 1998). This increase in food intake with apparent lower cost – *e.g.*, by reducing home range size (Cantor *et al.* 2018) – could, in turn, increase their probability of survival. Similar cases support this hypothesis; for example, within killer whale populations where individuals actively hunt or depredate on drop-line fisheries, depredation provides access to larger prey and may result in a lower energy cost, increasing survival probabilities and population growth rate (Esteban *et al.* 2016, Tixier *et al.* 2017). However, as aforementioned, the influence of home ranges size on survival probabilities was not that clear. The restricted home ranges of cooperative dolphins and an eventual dependence on the interaction with fishermen could make these dolphins more vulnerable to local events (*e.g.*, accidental bycatch in trammel nets used to catch catfish in channels close to the fishermen-dolphin cooperation area: see Peterson *et al.* 2008) –, nulling, at least partially, any positive ecological benefits to cooperative dolphins. Therefore, potential benefits from the cooperative interaction with fishermen in terms of survival probabilities might be masked by nonnatural mortalities. Six out of the 12 carcasses recovered from 2015 to 2018 and analyzed by

veterinarians presented evidence of entanglement in fishing gear (nets and ropes attached to the body and signs of drowning²). Nevertheless, the annual adult survival rate estimated here (0.949 ± 0.015 SE) is within the range of survival estimates for other bottlenose dolphin populations inhabiting coastal-estuarine waters (*e.g.*, Bunbury, Western Australia [0.95 ± 0.02 SE] by Smith *et al.* 2013; Patos Lagoon, Brazil [0.93; 95% CI: 0.89–0.95] by Fruet *et al.* 2015; Coffin Bay, South Australia [0.98 ± 0.04 SE] by Passadore *et al.* 2017).

Our results also confirm the high site fidelity of dolphins to Laguna and the apparent geographic closure (see also Simões-Lopes and Fábian 1999; Daura-Jorge *et al.* 2013), which may challenge this small population exposed to multiple human impacts. Likely, only a few animals move between Laguna and neighboring communities (Simões-Lopes and Fábian 1999). For instance, an identified male from Laguna population was sighted in Itajaí, and then sighted back in Laguna within six weeks, covering a distance of about 200 km³. The short duration of these occasional movements relative to an annual sampling might be the reason why temporary emigration models did not fit well with our data. Unlike the low emigration probability between seasons found previously (Daura-Jorge *et al.* 2013), emigration was not evident on an annual scale during our study. The high recapture rates of marked individuals also tally with high site fidelity and residency patterns. Our apparent survival estimate was also high (0.949), indicating an almost complete lack of permanent emigration during our study. Moreover, this population has remarkably low genetic diversity (comprising only one haplotype) and very low gene flow with adjacent communities, apparently constituting a more closed genetic unit (Fruet *et al.* 2014).

The specialized foraging influenced the capture probability but in different ways each year. We hypothesized that capture probability would

² Personal communication from Pedro Volkmer de Castilho, Universidade do Estado de Santa Catarina, Rua Cel. Fernandes Martins 270, Laguna, Brazil, May 2018

³ Personal communication from Leonardo Liberali Wedekin, Socioambiental Consultores Associados, Avenida Rio Branco 380, Florianópolis, Brazil, January 2017

increase with higher frequency of interaction with fishermen, since dolphins that often interact with fishermen tend to spend more time inside the lagoon system, increasing our chances of capturing them, whereas dolphins that only occasionally interact with fishermen tend to have larger home ranges (see Cantor *et al.* 2018) and probably forage beyond the study area. We observed this pattern in some years but not in others, which could reflect variation in the availability of the dolphins' main prey: in years with lower abundance of mullet fish, dolphins may have interacted less with fishermen or used the external area more intensively (see Daura-Jorge *et al.* 2013). Data on mullet fishing each year is required to test this hypothesis. However, the main point raised here is that models including the effect of a behavioral trait on capture probability received more support from the data, producing more robust estimates of apparent survival and abundance (White *et al.* 1982).

The estimated number of marked dolphins equaled the number of animals identified in each year. Therefore, our effort was large enough to capture all marked individuals in the study area within each primary period, suggesting we did not need to fit mark-recapture models to estimate population size. However, we believe it is crucial to maintaining RD protocols for a long-term monitoring program, since photo-identification effort in the future may not be enough to capture all dolphins. In addition, the RD provides other demographic parameters such as survival and temporary emigration probabilities, and allows for the possibility of assessing the influence of covariates on these. The total annual abundance, corrected for unmarked individuals, ranged between 52 and 60 individuals, similar to previous estimates for this population (Simões-Lopes and Fábian 1999; Daura-Jorge *et al.* 2013). Most coastal bottlenose dolphin populations are relatively small (*e.g.*, 63-139 individuals in Bunbury, Western Australia; Smith *et al.* 2013; 88 individuals in Patos Lagoon Estuary, Brazil; Fruet *et al.* 2015; 40-83 individuals in Bahía San Antonio, Argentina; Vermeulen and Bräger 2015). The number of new marked dolphins being identified every year suggests this dolphin population depends heavily on the entry of new individuals *via* reproduction to maintain a seemingly constant population size. In addition, the stability in the number of individuals could be an indication of the carrying capacity of the ecosystem, a hypothesis to be investigated by a longer monitoring program.

Using data from 2007 to 2009, Daura-Jorge *et al.* 2013 estimated that a sampling effort over nine years should be sufficient to detect abundance changes in order of 5% with 95% of certainty (Daura-Jorge *et al.* 2013). Results from this study do not indicate any marked trend in population size, which suggests this population remained stable over this 10-year period. Despite the stability in the population size, this small, resident and apparently isolated population (Daura-Jorge *et al.* 2013, Fruet *et al.* 2014) may be extremely vulnerable to local decline due to limited resilience to mortality resulting from stochastic environmental disturbances (Shaffer 1981). For cetacean populations of less than 100 individuals the death of a single reproductive individual can be unsustainable (Slooten *et al.* 2006). To ensure the conservation of these dolphins in Laguna, therefore, any anthropogenic stressors that impact survival need to be mitigated. In addition, if the specialization in foraging with fishermen ultimately improves individual fitness (see Whitehead *et al.* 2004), the demographic consequences of this interaction between dolphins and the fishing community should also be considered for conservation purposes. Although our analytical approach identified that the foraging tactic of cooperating with fishermen had only a slight influence on survival, further studies, with a longer time-series and accounting for other individual traits – *i.e.*, social position, diet, health condition – might provide more details on the ecological role this tactic represents at the individual and population levels. Finally, although this dolphin population seems to be geographically closed, a metapopulation mark recapture study (as proposed by Fruet *et al.* 2014), including neighboring communities, is important in order to make a regional assessment for *Tursiops truncatus gephyreus* following IUCN Red List criteria (IUCN 2012a, b, 2017).

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CAPÍTULO 2

REPRODUCTIVE PARAMETERS AND FACTORS INFLUENCING CALF SURVIVAL OF BOTTLENOSE DOLPHINS THAT ENGAGE IN A UNIQUE COOPERATION WITH FISHERMEN

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ABSTRACT

A subset of the bottlenose dolphin *Tursiops truncatus gephyreus* population in Laguna, southern Brazil, specialize in foraging cooperatively with fishermen. In this study, we describe reproductive parameters for these dolphins and investigate whether this specialized tactic generates reproductive advantages for females that frequently use this unusual behavior. We analyzed photo-identification data collected during 233 boat-based surveys during 2007-2009 and 2013-2017. From 27,808 high-quality photographs, we identified and tracked the fate of 24 reproductive females and 45 of their calves. Calving was found to be seasonal, with most births occurring in late spring/summer. The average crude birth rate was 0.09 (SD = 0.04), and estimated fecundity was 0.17 (SD = 0.06). The mean inter-birth interval ranged between 2.09 and 2.43 years, depending on the method used. Based on Cormack–Jolly–Seber population models, first and second year calf survival rates were 0.74 (95%CI = 0.53-0.88) and 0.82 (95%CI = 0.49-0.95), respectively. Generalized linear mixed models assessed how birth timing, resource availability, maternal age, home range size and frequency of interaction with fishermen contributed to variation in calf survival. Timing of birth was a significant predictor of 2 years calf survival rates. Giving birth close to the local mullet season, provided lactating females with increased seasonal prey resources, leading to increased calf survival. Females that often cooperate with fishermen showed slightly higher fecundity and calf survival than those that tended to forage independently. We emphasize the importance of long-term monitoring of populations in order to understand regional life history characteristics and provide accurate information for viability analyses.

Keywords: reproduction; *Tursiops truncatus gephyreus*; long-term monitoring; life-history parameters; reproductive success; calf survival

INTRODUCTION

Long-term, individual-based monitoring of a population can generate valuable information on life-history and reproductive parameters. Such information requires lots of primary field data but is critical to assessments of a population's dynamics, status, and viability (Beissinger and McCullough 2002). In general, reproductive parameters are particularly difficult to obtain, requiring extended periods of extensive and systematic field effort. As a result, it is common to rely on secondary data obtained from different populations of the same species (Reed et al. 2002) and since different populations might be exposed to different ecological conditions and pressures (Baker et al. 2018), such assessments have limited utility. There are clear benefits to local conservation outcomes, therefore, to use regionally specific demographic parameters in order to produce reliable population viability analyses (Manlik et al. 2016, Arso Civil et al. 2017).

Moreover, understanding the factors influencing female reproductive success, in terms of calf survival, provides valuable insights into the causes of low population sizes, declines and even extinction risks (Craig and Ragen 1999, Baker et al. 2007). Reproductive success may be driven by ecological (Thompson et al. 2007), socio-behavioural (Cameron et al. 2009), environmental (Frick et al. 2010) or morphological factors (Blueweiss et al. 1978; Pomeroy et al. 1999). For cetaceans, in particular, calf survival seems to vary with birth timing due to the influence of environmental conditions such as water temperature and resource availability (Brough et al. 2016); in parallel, the mother's experience, age, and size are also reported as a key factor for calf survival (Elwen and Best 2004; Brough et al. 2016). The influence of behavioural tactics, such as foraging specializations, or other ecological drivers, such as resource availability, on the reproductive success in cetacean populations needs further investigation.

Bottlenose dolphins (*Tursiops* spp.) show a wide distribution in temperate and tropical waters, in a variety of habitats (Wells and Scott 1999). They have been the subject of several long-term research efforts worldwide (e.g. Wells and Scott 1990; Mann et al. 2000; Fruet et al. 2015; Arso Civil et al. 2019; Cheney et al. 2019), enabling studies of many aspects of their life-history and reproductive biology in the wild. Life-

history traits, such as female reproductive parameters, may vary considerably throughout its distribution. Births can occur year-round (Félix 1994, Urian et al. 1996) or seasonally (Thayer et al. 2003), varying geographically. Peaks in calving season have been described for several bottlenose dolphin populations, mainly those found in high latitudes (Wells et al. 1987, Bearzi et al. 1997, Mann et al. 2000, Henderson et al. 2014), but also in tropical waters (Fearnbach et al. 2011). Average inter-birth interval (IBI), fecundity and calf survival vary greatly among populations (Mann et al. 2000, Robinson et al. 2017, Baker et al. 2018), and reproductive success of individual females may vary within populations as well (Henderson et al. 2014, Fruet et al. 2015, Brough et al. 2016), due to natural individual heterogeneity. However, from the best of our knowledge, only a few studies have investigated the potential factors influencing female reproductive success within a population of bottlenose dolphins (e.g. Fruet et al. 2015; Brough et al. 2016).

The bottlenose dolphins in Laguna, southern Brazil, are a small, resident (Simões-Lopes and Fabian 1999; Daura-Jorge et al. 2013, Bezamat et al. 2018) and genetically discrete population (see Fruet et al. 2014). Some individuals from this population interact with artisanal fishermen in a rare cooperative foraging tactic, which seems to benefit both species (Simões-Lopes et al. 1998, 2016). Dolphins herd schools of fish, mainly mullet, towards fishermen, who stand in shallow water waiting to cast their nets in response to the dolphins' stereotyped behavioural cues (Simões-Lopes et al. 1998, Peterson et al. 2008). This specialized foraging tactic influences the social structure (Daura-Jorge et al. 2012), space use (Cantor et al. 2018) and acoustic repertoire (Romeu et al. 2017) of the dolphins. The interaction has also been shown to influence survival with slightly higher survival rates among dolphins that regularly interact with fishermen (Bezamat et al. 2018). Although in recent years we have investigated many aspects of the dynamic behaviour and social organization of this small dolphin population, there is currently no information on reproductive parameters and their influence on population viability.

Furthermore, the Society for Marine Mammalogy's Committee on Taxonomy (2017) has recently recognized the coastal bottlenose dolphins from Southwest Atlantic (southern Brazil, Uruguay and central Argentina), which includes the bottlenose dolphin population from Laguna, as the subspecies *Tursiops truncatus gephyreus*. This subspecies is endemic to the area and is comprised by only a few small and discrete

population units (at least five; see Fruet et al. 2014), probably totaling no more than a few hundred individuals. It is noteworthy that at least two of these populations specialize in foraging with fishermen (Simões-Lopes et al. 1998). There is limited information on the reproduction of this subspecies and only two of these units have reproductive parameters estimated: the community in the Patos Lagoon estuary (Fruet et al. 2015), about 520 km south of Laguna, southern Brazil; and the population in Bahía San Antonio, Argentina (Vermeulen and Bräger 2015). As a regional assessment of this subspecies is needed, we should focus now on estimating such life history traits for other population units and investigating which factors may influence heterogeneity in female reproductive success, so we can examine variability of reproductive rates and calf survival among and within populations.

In this study we used eight years of mark-recapture photo-identification data to estimate female reproductive parameters for the Laguna bottlenose dolphin population, including calving seasonality, fecundity, IBI, and calf survival rates. We investigated potential factors influencing reproductive success, such as the mother's foraging specialization and home range, and timing of birth in relation to the mullet *Mugil liza* season, a key local prey species. We also investigated the influence of the foraging specialization on reproductive parameters, by comparing parameters for females that frequently cooperate with fishermen and those that tend to forage independently. Understanding the life history characteristics of the Laguna bottlenose dolphin population is essential to evaluate its status and viability, improving conservation and management actions for this population and the subspecies *Tursiops truncatus gephyreus*.

METHODS

Data collection

From 2007-2009 and 2013-2016 we carried out boat-based surveys of a small and resident bottlenose dolphin population in the Santo-Antônio-Imaruí-Mirim lagoon system, an area of approximately 200 km² in Laguna, southern Brazil (28°20'S–48°50'W; (see Fig. 3–Thesis'

Introduction, p. 35). During each survey, we followed a 30 km predefined route using a 5 m boat powered by an outboard engine aiming to cover the main area used by the dolphins (Cantor et al. 2018). A group of dolphins was defined as all individuals within a 50 m radius of each other and engaged in similar behaviour (as in Daura-Jorge et al. 2013; Bezamat et al. 2018). During encounters with dolphins, we attempted to photograph both sides of the dorsal fin of all individuals and then, using only high quality pictures (on a scale of A to C in terms of angle, focus, exposure; Williams et al. 1993), we identified them from the nicks and marks on their dorsal fins (Würsig and Jefferson 1990). During encounters we also recorded time, location, group size and whether or not dolphins were interacting with artisanal fishermen (see Daura-Jorge et al. 2012).

Individually identified adults seen in close association with a calf — individuals with small size, dark grey in colouration or visible foetal folds — for two or more subsequent and independent encounters (i.e. different surveys) were assumed to be mothers. Calves were typically tracked until weaning via identification of their accompanying mothers. Temporary marks on the dorsal fin and body (*e.g.* scratches) also assisted in identifying calves individually. From the photo-identification database, we extracted a detailed record of sightings and calving histories for all reproductively active females identified throughout the study (*i.e.* those known to have given birth to viable calves).

Reproductive parameters

The annual number of births was obtained from counts of neonatal calves recorded each calendar year. The annual crude birth rate was calculated as the total number of documented births divided by the total abundance of Laguna dolphins, estimated each year using mark-recapture models (see Bezamat et al. 2018).

We assumed females become reproductively active the year before the production of the first known calf, given that pregnancy lasts about a year for the species (*e.g.* Perrin and Reilly 1984). We used longitudinal photo-identification data to verify the minimum number of mature females seen each year (including those that were no longer reproductively active), and then estimated fecundity as the number of female calves (assuming a calf sex ratio of 1:1 for mammals; Caughley 1977) produced by mature females in a given year (after Fruet et al. 2015):

$$\hat{F}_i = \frac{1}{2n} \times \sum_{i=1}^n \frac{N_{ci}}{N_{mi}}$$

where \hat{F}_i is the estimated fecundity in year i ; n is the total number of years; N_{ci} is the number of calves born in year i ; and N_{mi} is the number of mature females alive in year i .

The seasonality of births and the peak birth period were examined based on the estimated calendar month of parturitions. For calves classified as newborns — with obvious foetal fold marks, floppy fins, and less than half the length of their mothers (Urian et al. 1996, Mann and Smuts 1999) —, birth was assigned to the month of their first sighting. Otherwise, month of birth was estimated as the midpoint between the date of the last sighting of a mother without the calf and the date of the first sighting of the mother with the new calf (adapted from Wells et al. 1987), when this interval was ≤ 60 days. Additionally, two neonate cadavers found stranded during systematic beach surveys were included in the estimates of calving seasonality and number of calves born in 2016 and 2017.

Inter-birth interval (IBI) was estimated as the time elapsed between subsequent births for individual mothers with two consecutive births where the estimated breeding season of birth (rather than month of birth) was available for both calves. We used two approaches to calculate IBIs: (a) considering only the intervals in which the first calf survived to age 2 (minimum age at weaning *cf.* Fruet et al. 2015), (b) considering intervals in which the first calf died before 1 year of age as well.

Calf survival

We used Cormack–Jolly–Seber (CJS) open population models (Cormack 1964; Jolly 1965; Seber 1965; Lebreton et al. 1992) to estimate the annual survival probability for calves born to individually known females from 2013 to 2016 ($n = 23$). If a mother was sighted without her calf before it turned 2 years old (minimum age at weaning *cf.* Fruet et al. 2015), the calf was assumed to have died. We estimated age-specific survival by fitting age models to calf sighting history data (collapsed for each year). Our models included three age classes: 0-1, 1-2, and > 2 years.

We modeled annual survival to be constant (.) or to vary with time (t), and recapture probability to be constant for all candidate models due to intense field work and high encounter rates for adult females (Bezamat et al. 2018). We also modeled calf survival as age-invariant but varying with time.

As the CJS goodness-of-fit (GOF) test neglects age effects, model fit was assessed by estimating the median variance inflation factor (\hat{c}). We estimated the variance inflation factor (\hat{c}) to measure of potential over- or under-dispersion of the data using a parametric bootstrapping goodness-of-fit approach with 1,000 iterations (White et al. 2001). When \hat{c} was >1 , we used the estimated value to adjust the CJS models and account for overdispersion (Hurvich and Tsai 1989). To select the most parsimonious models, we relied on the lowest Quasi-Akaike Information Criterion corrected for overdispersion and small sample size (QAICc, Burnham and Anderson 2002). All mark-recapture analyses were performed using program MARK (White and Burnham 1999).

Factors influencing reproductive success

In Laguna, there is a marked seasonality in prey availability related to a peak in the abundance of mullet from May to July, when mullet migrate from Argentina to southern Brazil to spawn (Lemos et al. 2014). Taking this into account, reproductive histories were used to assign a fate (i.e. survival to 1 and 2 years) to each calf ($n = 38$) along with the following covariates: (1) mother frequency of interaction with fishermen (\hat{f}_i) — estimated as the number of independent events each female was observed foraging with fishermen divided by the total number of foraging records (see Bezamat et al. 2018) —; (2) mother home range size — estimated from location data using the fixed kernel method with a 95% probability contour, excluding land, and selecting the smoothing parameter by the ad hoc method (Worton 1989) in R (R Core Team 2017) using the `adehabitatHR` package (Calenge 2006; see Bezamat et al. 2018) —; (3) mother age, classified into two age classes (cf. Brough et al. 2016): the “older” females which have been seen with calves since 2007-2008 at least, and the “younger” females which have been seen with calves since 2013; (4) the time (in months) between birth and the peak of the following mullet season (defined as June by Lemos et al. 2014); (5) the regional fishery yield of the mullet season following the birth (FEPESC –

Federation of Fishermen of Santa Catarina, unpublished data), as a proxy for prey availability for lactating females.

To model calf survival as a function of these covariates we used binomial generalized linear mixed models (GLMM) with log link function (*cf.* protocol in Zuur and Ieno 2016). Mother covariates were included as fixed factors and calf survival to 1 or 2 years was the binary response variable (1 = survived; 0 = did not survive) in two different sets of modelling procedure. Mother ID was included as a random intercept to account for dependency among siblings. Interaction terms were not incorporated in the model to avoid overparameterization. Prior to model development, data exploration was carried out and explanatory variables were log transformed when appropriate. Each set of models was fitted in R, using the ‘glmmTMB’ package (Magnusson et al. 2017). To avoid convergence issues, we started from a model with the three maternal covariates and then selected those variables by stepwise backwards elimination, using Akaike’s information criterion (AIC) and Akaike weight to rank and find the most parsimonious model. In a second round, we included the other two covariates related to resource availability. For calculations of AIC, Akaike weight and other parameters based on model averaging (see Burnham and Anderson, 2002), we used the R package ‘MuMin’ (Barton 2009). Model assumptions were assessed by plotting residuals versus fitted values using the DHARMA package (Zuur et al. 2016; Hartig 2019).

In addition, we assumed that a female reproduced successfully if her calf survived from birth to the minimum age at weaning (2 years *cf.* Fruet et al. 2015; Mann et al. 2000). We then estimated female annual reproductive success as the proportion of calves born in a given year that survived to weaning. We estimated the length of time a calf remains with its mother based on the estimated month of birth and the date of the last sighting of the calf closely associated to its mother. We also classified each female as cooperative or non-cooperative (*cf.* Cantor et al. 2018). We used Kernel density estimation to fit a probability density function to the continuous distribution defined by the frequency each individual interacts with fishermen. The minimum value in this distribution, $\min(x)$, was then used as the cut-off frequency of interaction to classify individual dolphins as “cooperative” (i.e. $f_i > \min(x)$) or “non-cooperative” ($f_i <$

min(x)). Finally, we estimated mean fecundity, IBI and reproductive success for the cooperative and non-cooperative females.

RESULTS

Reproductive parameters

We analyzed photo-identification data collected systematically during 233 boat-based surveys in 2007-2009 and 2013-2017. From 27,808 high-quality photographs, we identified and tracked the reproductive history of 24 females (Table 1). The maximum number of documented calves per female was four (mode = 1). During the study, we documented 40 births and five one-year-old calves first sighted in 2007 and 2013, as well as two dead neonates stranded on the beach. The annual number of reproductive females (range: 12-20) and births (range: 2-7) varied throughout the study (Table 2). The average crude birth rate was 0.09 (SD = 0.04) and estimated fecundity was 0.17 (SD = 0.06). We successfully assigned the month of birth for 26 newborns of 17 known females, and both dead neonates. Births occurred from September to April, but the majority (79%) from December to March (late spring and summer months; Fig. 2).

Inter-birth interval for females with surviving calves was either 2 or 3 years, and the mean IBI was 2.43 years ($n = 7$). Including intervals in which the first calf died before one year of age, mean IBI was 2.09 years ($n = 11$). Females that have lost their calves within the first weeks of life had a 1-year calving interval ($n = 2$).

Weaning age was documented for four calves. Separation of the mother and calf occurred after 2 or 3 years. Older siblings left their mothers probably few weeks (1 to 3 months) before the new calf was born. In one case, the older sibling, after nursing for 2 years, continued to associate with its mother ID#42 and her new calf eventually for at least another year. Her new calf died before weaning.

We managed to track only one female ID#51 from birth until her first calving. She gave birth for the first time in 2017 at age 10, and her calf survived the first year of life. The female ID#15 has been seen in the study area for at least 30 years and gave birth to a calf in the late 1980's (personal communication from Paulo C. Simões-Lopes). However, after

2007, we have never seen her with a calf again, which could be a sign of reproductive senescence.

Table 4: Sightings of reproductive females (ID# = individual photo-ID catalogue number) and their calves from 2007 to 2009 and 2013 to 2017 in Laguna, including sightings of females without a calf (marked with a “•”) and their first (1), second (2), third (3), , or fourth (4) calves. Calf ages were categorized as young-of-year (< 1 year old; YC), calves (1–3 year old; C) and juveniles (> 3 year old; J). The number of reproductive females in each year (#F) and the number of calves born in each year (#YOY) are also shown.

ID#	Years							
	2007	2008	2009	2013	2014	2015	2016	2017
2	•	•	•	C1	•	YC2	C2	C2
8	•	YC1	C1	C2	C2	YC3	C3	C3
9	C1	C1	J1					
10	•	•	YC1	•	YC2	•	YC3	C3
11	YC1	C1	C1	•	YC2	C2	C2	YC3
12	YC1	C1	C1	YC2	•	•	•	•
14	YC1	C1	C1					
18	YC1	C1	C1	C2	C2	•	•	•
19	C1	C1	J1					
21	•	•	•	YC1	YC2	C2	C2	J2
23	•	•	•	•	•	•	•	YC1
24	•	•	•	•	•	YC1	C1	C1
27	•	•	•	•	•	•	YC1	C1
28	•	•	•	YC1	C1	C1	YC2	
31	YC1	C1	C1	•	•	•	•	•
36	YC1	C1						
40	•	•	YC1	YC2	C2	C2	J2/YC3	C3
42	•	YC1	C1	YC2	C2	C2+YC3	J2+C3	•
44		•	•		•	•	•	YC1
50	YC1	C1	C1	•	YC2	YC3	C3	YC4
51	•	•	•	•	•	•	•	YC1
52	•	YC1	C1	•	YC2	C2	YC3	C3
56				•	•	YC1	C1	C1
63				•	YC1	C1	YC2	C2
#F	12	14	13	14	16	17	20	20
#YOY	7	3	2	5	6	6	6	5

Table 5: Summary of reproductive rates of bottlenose dolphins in Laguna, Southern Brazil, estimated from mark-recapture studies; Fecundity = ratio between the number of female calves (assuming a calf sex ratio of 1:1) and the number of mature females in Laguna (*cf.* Fruet et al. 2015).

	2007	2008	2009	2013	2014	2015	2016	2017
Photo-ID surveys	25	49	31	51	15	25	23	14
Abundance ^a	54	60	60	55	53	52	60	-
Reproductive females	12	14	13	14	16	17	20	20
Newborn calves	7	3	2*	5	6	6	7	6*
Calves surviving to age 1	6	3	-	3	3	5	6	-
Calves surviving to weaning (age 2)	6	-	-	3	2	4	-	-
Reproductive success	0.86	-	-	0.60	0.17	0.67	-	-
Crude birth rate	0.13	0.05	0.03	0.09	0.11	0.12	0.12	-
Fecundity	0.29	0.11	0.08	0.18	0.19	0.18	0.175	0.15

^a Extracted from Bezamat et al. 2018

*Number of births could be underestimated, since we conducted few surveys in the end of these years.

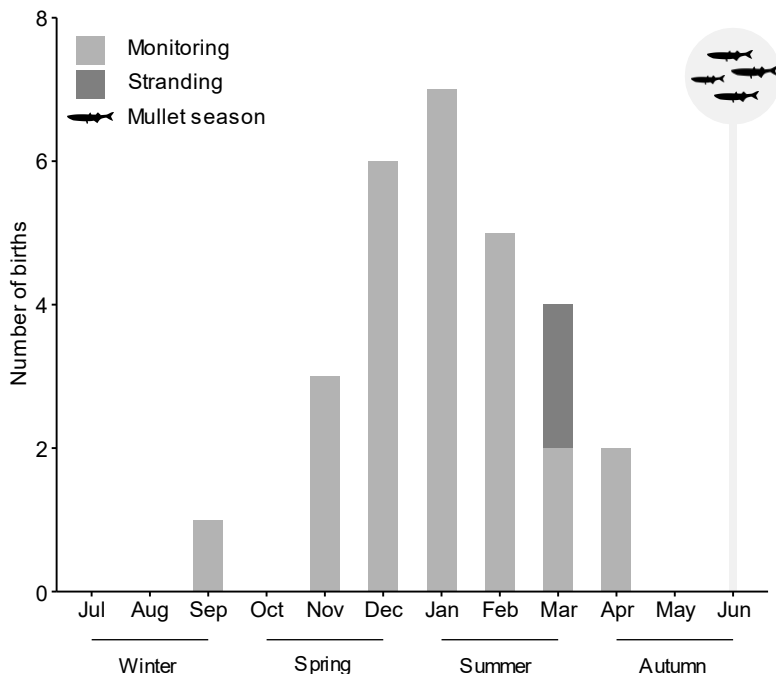


Figure 4: Birth seasonality for bottlenose dolphins in Laguna based on a long-term monitoring study (2007–2009 and 2013-2017) in relation to the peak of the mullet season in June. Light gray bars express the number of births estimated from mark-recapture surveys conducted in the lagoon system, while the dark grey bar expresses the number of neonates found stranded during beach surveys.

Calf survival

Our estimated variance inflation factor $\hat{c} = 2.27$ indicated a subtle overdispersion in our data, which could result from individual heterogeneity. Thus, we used the \hat{c} -value to adjust the CJS models. The model with the most support from the data had constant survival for each age class and constant recapture probability (Table 3). The estimated first- and second-year calf survival rates were 0.74 (SE = 0.09, 95%CI = 0.53

– 0.88) and 0.82 (SE = 0.12, 95%CI = 0.49 – 0.95), respectively. The second model also had considerable support from the data ($\Delta\text{QAICc} < 2$); this model had survival varying with time, disregarding age effect. Estimated survival for each year was: a) 2013: 0.60 (SE = 0.22, 95%CI = 0.20 – 0.90); b) 2014: 0.67 (SE = 0.16, 95%CI = 0.33 – 0.89); c) 2015: 0.83 (SE = 0.11, 95%CI = 0.52 – 0.96); and d) 2016: 0.87 (SE = 0.08, 95%CI = 0.61 – 0.97). For all candidate models, capture probability was estimated to be 1. The proportion of calves surviving to weaning (reproductive success) varied among years, from 0.86 in 2007 to 0.17 in 2014 (Table 2). Fifteen out of the 24 calves (62.5%) born in 2007, 2013, 2014 and 2015 have survived until age 2. We could not assess individual female reproductive success due to the small sample size.

Table 6: Summary of age-structured Cormack–Jolly–Seber models for survival (ϕ) and recapture (p) probabilities of calves (c) from Laguna bottlenose dolphin population based on a mark–recapture study (2013–2017). Models are ranked according to the lowest QAIC. Notation: (·) constant, (t) time-dependence. Slash distinguishes age classes.

Model	QAICc	ΔQAICc	QAICc weight	Model Likelihood	N. Par.	QDev.
$\{\phi(c_{0-1(\cdot)}/c_{1-2(\cdot)}/c_{>2(\cdot)}) p(\cdot)\}$	27.96	0.00	0.71	1.00	4	4.76
$\{\phi(t) p(\cdot)\}$	29.75	1.79	0.29	0.41	5	3.97
$\{\phi(c_{0-1(t)}/c_{1-2(t)}/c_{>2(\cdot)}) p(\cdot)\}$	39.18	11.21	0.00	0.00	9	1.43
$\{\phi(c_{0-1(t)}/c_{1-2(t)}/c_{>2(t)}) p(\cdot)\}$	42.20	14.24	0.00	0.00	10	0.98

Factors influencing reproductive success

Overparameterization issues prevented the inclusion of all five explanatory variables in the same model to examine their influence on calf survival. Therefore, in both sets of models, we first built models with the three variables related to mothers, including the frequency of interaction with fishermen ($Mother_{fi}$), home range size ($Mother_{HR}$), and age ($Mother_{age}$). None of these covariates explained the variance in calf survival to 1 or 2 years, and the null models in both cases were selected by AIC ($\text{Calf}_{\text{survival}} \sim 1$; Table 4). Then, we included, one at a time, covariates related to resource availability, including the time between

birth and the peak of the following mullet season (T_{mullet}) and the fishery yield of the mullet season following the birth (N_{mullet}). For calf survival to 1 year, the most supported model suggests the influence of birth timing on calf survival ($Cal_{survival} \sim -12.04.T_{mullet}$; SE = 7.25; z = -1.66; p = 0.097; Table 4). For calf survival to 2 years, this model was also the most parsimonious, and calves born closer to the peak of the following mullet season have significantly higher chance of survival ($Cal_{survival} \sim -11.88.T_{mullet}$; SE = 5.93; z = -2.044; p = 0.045; Table 4).

Out of the 24 individually identified females, we classified nine as cooperatives and 15 as non-cooperatives. Reproductive parameters were slightly different between these groups. Mean annual fecundity was 0.18 (SD = 0.14) for cooperatives and 0.15 (SD = 0.05) for non-cooperatives. Mean IBI (including intervals in which the first calf died before one year of age) was 2 years for cooperative females (n = 4) and 2.14 years for non-cooperative females (n = 7). Seventy percent (7/10) of cooperative females' calves and 57% (8/14) of non-cooperative females' calves born in 2007, 2013, 2014 and 2015 survived to age 2.

Table 7: Summary of the GLMM for factors influencing calf survival to 1 and 2 years. Fixed input parameters include mother frequency of interaction with fishermen ($Mother_{fi}$), home range size ($Mother_{HR}$) and age ($Mother_{age}$), time between birth and the peak of the following mullet season (T_{mullet}) and fishery yield of the mullet season following the birth (N_{mullet}). The null model (i.e. no fixed effects), contains the random effect of mother ID ($Calf_{survival} \sim 1$). Models are ranked according to the lowest Akaike information criterion corrected for small sample size (AICc). Notation: delta AICc ($\Delta AICc$), Log-likelihood (logLik), delta Log-likelihood ($\Delta \log Lik$), degrees of freedom (df) and AICc model weight (weight).

Survival to 1 year	AICc	$\Delta AICc$	logLik	$\Delta \log Lik$	df	weight
$Calf_{survival} \sim T_{mullet}$	13.6	0	-3.5	14.6	3	0.76
$Calf_{survival} \sim T_{mullet} + N_{mullet}$	15.9	2.4	-3.5	14.6	4	0.24
$Calf_{survival} \sim 1$	40.5	26.9	-18.1	0	2	<0.001
$Calf_{survival} \sim Mother_{HR}$	42.1	28.5	-17.8	0.3	3	<0.001
$Calf_{survival} \sim Mother_{fi} + Mother_{HR}$	44.3	30.7	-17.7	0.4	4	<0.001
$Calf_{survival} \sim Mother_{fi} + Mother_{HR} + Mother_{age}$	46.7	33.1	-17.7	0.4	5	<0.001
Survival to 2 years	AICc	$\Delta AICc$	logLik	$\Delta \log Lik$	df	weight
$Calf_{survival} \sim T_{mullet}$	17.8	0	-5.7	13.7	3	0.90
$Calf_{survival} \sim T_{mullet} + N_{mullet}$	22.1	4.3	-6.6	12.7	4	0.10
$Calf_{survival} \sim 1$	42.9	25.1	-19.3	0	2	<0.001
$Calf_{survival} \sim Mother_{HR}$	45.1	27.3	-19.3	0	3	<0.001
$Calf_{survival} \sim Mother_{fi} + Mother_{HR}$	46.3	28.5	-18.7	0.6	4	<0.001
$Calf_{survival} \sim Mother_{fi} + Mother_{HR} + Mother_{age}$	48.3	30.5	-18.5	0.8	5	<0.001

DISCUSSION

This study extends our knowledge on bottlenose dolphin reproduction, especially on a small and resident population, representative of the recently recognized subspecies *Tursiops truncatus gephyreus* endemic to the Southwest Atlantic, and with a very specialized foraging behavior. Using longitudinal sighting data from dedicated boat surveys in Laguna, southern Brazil, we established long-term reproductive histories of known females and investigated calf production, IBIs and calf survival. We evaluated the potential factors influencing calf survival, including the mothers' features, and the timing of birth in relation to prey availability. Moreover, we compared reproductive parameters of females that often cooperate with fishermen, with those females that tend not to cooperate.

Calving season in Laguna was the same as in the Patos Lagoon estuary (Fruet et al. 2015), as expected due to the proximity of the two populations (520 km). Crude birth rate and mean IBI were also similar. Although the Laguna population is apparently genetically isolated from other population units (Fruet et al. 2014), they share similar reproductive traits, suggesting consistence among populations of the subspecies. Fecundity in Laguna was marginally higher, but on the other hand, calf survival rates in the first and second years were lower than in the Patos Lagoon estuary (Fruet et al. 2015). Differences in life-history parameters may reflect the different ecological and environmental conditions and pressures to which each population or community is subject. Threats faced by calves in Laguna include entanglement in fishing gear, boat collision, pollution and the cumulative effects of persistent organic pollutants (Daura-Jorge et al. 2013; Bezamat et al. 2018; Righetti et al. 2019), which will be discussed later.

Reproductive parameters

Calving in Laguna was highly seasonal, with most births occurring in late spring and summer. Bottlenose dolphins show a great variability in the seasonality of their reproduction in different areas (Urian et al. 1996). Birth seasonality might be influenced by seasonal changes in the environment, including water temperature (Wells et al. 1987; Henderson

et al. 2014), food availability (Urian et al. 1996; Mann et al. 2000) and predation pressure (Mann and Watson-Capps 2005; Fearnbach et al. 2011). Females tend to give birth when the water is warm, which is thermally efficient for small calves, apparently increasing calf survival. A high abundance of food is also important to support the costs of lactation, the most energetic demanding time of reproduction (Kastelein et al. 2002; Rechsteiner et al. 2013).

Forty-two calves were born to resident females between 2007-2009 and 2013-2017, and the average crude birth rate was 0.09, which is similar to that found for other bottlenose dolphin populations. As reported by other studies (e.g. Steiner and Bossley 2008, Kogi et al. 2004, Cheney et al. 2019), some births may have gone unnoticed, particularly for females that have lost their calves very soon after birth, before we were able to observe them. As a result, the number of calves born each year may be biased low, especially in 2009 and 2017, when we conducted fewer surveys during the calving season. To offset this bias, we included the two newborns we found dead on the beach in the estimates, even though we could not tell from which females they were born. Nevertheless, the mean annual crude birth rate of 0.09 for Laguna dolphins fall within the range reported for other bottlenose dolphins populations, from 0.04 in Doubtful Sound, New Zealand (Henderson et al. 2014) and Bafa San Antonio, Argentina (Vermeulen and Bräger 2015) to 0.12 in the North Sea, Scotland (Robinson et al. 2017).

The mean IBI of 2.0 and 2.4 years estimated here is similar to those reported for the Shannon Estuary, Ireland (Baker et al. 2018) and the Adriatic Sea, Croatia (Bearzi et al. 1997), but at the lower range reported from elsewhere (see Baker et al. 2018). However, we probably missed longer IBIs since the study period was relatively short when compared to dolphins' life span, and we had a gap in data collection from 2010 to 2012. For example, female ID#31 had a calf in 2007, which stayed with her until the beginning of 2010 at least, from 2013 to 2017 she was never seen with a calf, and in 2018 she gave birth again. The shortest IBIs of 1 year involved females whose calves died within the first weeks of life, making them receptive for another pregnancy (as in Kogi et al. 2004).

Calf survival and factors influencing reproductive success

The first-year survival rate estimated here (0.74) is similar to that reported for Shark Bay (0.71; Mann et al. 2000) and the Port River

estuary, Australia (0.70; Steiner and Bossley, 2008). Elsewhere, rates of between 0.89 (Shannon Estuary, Ireland; Baker et al. 2018) and 0.37 (Doubtful Sound, New Zealand; Currey et al. 2009) have been reported. The latter is the lowest recorded for free-ranging bottlenose dolphins, apparently due to the increased freshwater discharge into the fjord by a hydroelectric power station, resulting in decreased water temperature that may exceed the physiological tolerance of newborn calves (Currey et al. 2009). The cumulative impacts on individuals <3 years old resulted in a reduced recruitment, which is probably the cause of population decline in Doubtful Sound (Currey et al. 2011). First-year survival rate is likely to have been slightly overestimated here, given that some calves probably died before being sighted (as in Mann et al. 2000; Kogi et al. 2004). Second-year calf survival rate (0.82) is comparable to other estimates obtained for bottlenose dolphins in the wild: in Shark Bay, Australia (0.82; Mann et al. 2000) and Bay of Islands, New Zealand (0.78; Tezanos-Pinto et al. 2015).

The causes of calf mortality in Laguna are uncertain. Probably one of the main causes is the bycatch in illegal trammel netting in the dolphins' core area (Peterson et al. 2008, Laguna municipal law number 1.998/2018). Several deaths caused by entanglements or injuries from fishing gear have been recorded in the last few years, of both adults and calves (Bezamat et al. 2018). From December 2017 to November 2018, a live calf was seen entangled in marine debris wrapped tightly around its head. Boat collision is another direct impact that threatens calf survival. In December 2018, a one-month-old calf was found dead and the necropsy revealed a blunt trauma injury on its cervical spine, an evidence that it was probably hit by a boat. The predation pressure in Laguna seems to be very low, since predators of bottlenose dolphins (*i.e.* large sharks and killer whales, *Orcinus orca*) were never seen in the estuary and rarely seen in the surroundings, and we have never observed shark scars or wounds in the dolphins.

Less obvious human impacts could also be affecting calf survival, such as PCB contamination. Blubber PCB concentrations in some biopsied dolphins in Laguna exceeded the PCB toxicity threshold for the species (Schwacke et al. 2002; Righetti et al. 2019). PCBs are known to bioaccumulate in dolphins and are passed on to calves via the female, through gestation and lactation, increasing the chances of foetal and calf

mortality, particularly for first-born calves (Reddy et al. 2001, Wells et al. 2005). Some small or declining populations of bottlenose dolphins and killer whales in the NE Atlantic were associated with low recruitment, consistent with PCB-induced reproductive toxicity (Jepson et al. 2016).

Other potential human impact is the acoustic disturbance from daily boat traffic and the construction of a 2.8 km bridge, from late 2012 to early 2015, in a core area for the dolphins at that time. Disturbance during the bridge construction included dredging (see Pirota *et al.* 2013; Todd *et al.* 2014), pile-driving (see Bailey *et al.* 2010) and increased boat traffic (see Bejder *et al.* 2006; Pérez-Jorge *et al.* 2016). Since acoustic communication between mothers and calves is essential to their associations, if anthropogenic noise disrupts the communication it could lead to the severe debilitation and even death of a dependent calf (Parsons and Dolman 2004). Indeed, calf mortality was higher in 2013 and 2014.

Survival to 2 years seems to be affected by timing of birth. Calves born closer to the peak of the following mullet season have a higher chance of survival to 2 years relative to calves born in other periods. As aforementioned, when giving birth close to the mullet season, lactating females can take advantage of seasonally abundant resources for raising offspring. Synchronizing time of birth with high food abundance has been correlated with reproductive success in other bottlenose dolphin populations (Urian et al. 1996; Fruet et al. 2015). However, timing of birth was not shown to be a significant predictor of survival to 1 year. On the first year of life, other factors may be contributing to calf survival and then masking the influence of birth timing, such as congenital malformations and the effects of PCBs. About 80% of the mother's body burden of PCBs and t-DDT is transferred to the calf through lactation within seven weeks post-partum, with the first-born offspring receiving the majority of the mother's body burden (Cockcroft et al. 1989).

Regarding different foraging tactics within the population, females classified as cooperatives showed slightly higher fecundity and calf survival than those classified as non-cooperatives. Over multiple generations, these differences may show clear benefits of the cooperation. A small difference in survival may represent a selective advantage and contribute to the evolution and maintenance of the cooperative fishing specialization. Differences in first-year calf survival were reported for bottlenose dolphins at Monkey Mia (Shark Bay, Australia) based on exposure to human provisioning (provisioned: 0.44; not provisioned: 0.76; Mann et al. 2000). In Shark Bay as well, there was a decline in

bottlenose dolphin survival and reproductive rates after the 2011 marine heatwave (Wild et al. 2019); interestingly, dolphins that use tools to forage—known as spongers—were less affected, suggesting that this specialized tactic plays an ecological role that reduces the negative effects of the heatwave. Differences in calving rate within populations of killer whales due to different foraging specializations were also described (Tixier et al. 2015; Esteban et al. 2016). Despite the differences reported here, our small sample size prevents strong conclusions on the influence of the cooperative tactic on female reproductive success; a longer time series is required to state that this forage specialization increases individual fitness.

Besides estimating reproductive parameters crucial for a population assessment, our findings reveal that resource availability may influence reproduction success of bottlenose dolphins in Laguna, and the cooperative tactic may influence fecundity and calf survival. Moreover, this study emphasizes the importance of long-term, individual-based monitoring of populations to understand regional life history characteristics and provide accurate information towards effective conservation and management. This is especially critical for this dolphin population in Laguna, that retains the tactic of cooperating with fishermen, but also faces several human threats that put them at local and regional risk of extinction.

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CAPÍTULO 3

DOLPHIN POPULATION SPECIALIZED IN FORAGING WITH FISHERMEN REQUIRES ZERO BYCATCH MANAGEMENT TO PERSIST

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ABSTRACT

The small population of bottlenose dolphins *Tursiops truncatus gephyreus* that resides in Laguna, southern Brazil, and have specialized in foraging with artisanal fishermen faces high levels of bycatch and other human threats. Using Vortex, we modeled the viability of this population within 100 years under different levels of bycatch, including the current scenario of two bycatches every year, two worst-cases and three management scenarios. The current scenario yielded a declining population ($r = -0.022$) with a high probability of extinction ($PE = 0.88$). If bycatch increases, the population is doomed to extinction. On the other hand, management actions seem promising, but only the zero-bycatch management would make the difference between a declining and an increasing population. Based on sensitivity analyses, we found that growth rate is most sensitive to small and proportional changes in adult female and juvenile survival. However, observed temporal variation indicated that population dynamics were more influenced by reproduction. We also compared the relative effects of human impacts (*i.e.*, additional bycatches and reduced calf survival due to increased underwater noise or pollution) on population dynamics. We found that growth rate was most sensitive to changes in adult bycatch (especially females) than to a reduction in calf survival. Combined, our results indicate that the current level of bycatch is unsustainable, and it must be eliminated immediately. Moreover, habitat degradation should be reduced and the impacts of planned development in the area should be mitigated. The mullet fishery should also be monitored to ensure resource availability. These combined actions should guarantee the long-term persistence of bottlenose dolphins in Laguna.

Keywords: bottlenose dolphins, Population Viability Analysis, *Tursiops truncatus gephyreus*, bycatch, conservation, population dynamics, sensitivity analysis, wildlife management.

INTRODUCTION

In conservation biology, two paradigms have emerged (Caughley 1994): the declining population paradigm and the small population paradigm. The declining population paradigm focuses on environmental or demographic factors associated with population declines (Akçakaya and Raphael 1998). The small population paradigm focuses on population-level processes, importing concepts from theoretical ecology, to primarily identify minimum viable population sizes (Shaffer 1981) in face of both demographic and environmental stochasticity (May, 1973). To determine the reason why a population is declining, one needs to extrapolate multiple population parameters, such as recruitment, demographic stochasticity and extinction. However, this is a challenging task, which may require a long-term study of the population. To evaluate the viability of small populations, several population parameters are also required to project reliable population trends in a given number of years.

The small population paradigm deals with extinction risk. Small populations are more likely to go extinct than large populations (Gilpin and Soulé 1986). The smaller the population, the more susceptible it is to extinction from various causes, in particular stochastic processes, which may be intrinsic to their dynamics or motivated by environmental changes. Stochastic perturbations that may extinguish small populations include natural variation in individual reproductive and survival rates (demographic stochasticity), and their greater vulnerability to loss of genetic variability and inbreeding depression (genetic stochasticity). In addition, stochasticity can be generated by natural or anthropogenic fluctuations in environmental conditions (environmental stochasticity) or, in extreme situations, by environmental catastrophes (Shaffer 1981; Caughley 1994). When combining the declining and the small population paradigms, we link applied and theoretical ecology, and include stochasticity in population-level processes. Thus, we can better understand how current threats affect the viability of small populations, and guide more effective conservation strategies.

Population viability analysis (PVA) is a powerful mathematical modeling tool for examining the relative risks posed by different threats to the persistence of small populations over time and evaluating the

effectiveness of management alternatives for their recovery (Boyce 1992; Akçakaya and Sjögren-Gulve 2000; Beissinger and McCullough 2002). The latter can be helpful in assisting conservation decision-making (Drechsler and Burgman 2004). PVA estimates a population's (or species') risk of extinction through stochastic simulations of demographic and life-history parameters in different scenarios (Beissinger and Westphal 1998). Therefore, reliable demographic estimates are essential to assess a population's status and viability, and thus to provide consistent information towards powerful management actions (e.g. Kraus et al. 2001; Runge et al. 2004; Currey et al. 2011). One of the most interesting output of a PVA is the identification of the key life-history parameters that influence the dynamics of the population under study (e.g. Manlik et al. 2016; Lacy et al. 2017).

PVA has been used for several marine mammal species, including manatees *Trichechus manatus latirostris* (Marmontel et al. 1997), southern elephant seals *Mirounga leonina* (McMahon et al. 2005), killer whales *Orcinus orca* (Lacy et al. 2017) and bottlenose dolphins *Tursiops truncatus* (Thompson et al. 2000; Gaspar 2003; Fortuna 2007) as well as *Tursiops aduncus* (Manlik et al. 2016). The simulation model of the Florida manatee identified changes in adult mortality as being a key vital rate (Marmontel et al. 1997), whereas studies with bottlenose dolphins off Australia and killer whales in the northeastern Pacific Ocean found that variability in reproduction had a greater influence on population growth than mortality (Manlik et al. 2016; Lacy et al. 2017). PVA in the bottlenose dolphin population from the Moray Firth, Scotland, illustrates how it can be influential to stakeholders, so that precautionary management actions are implemented (Thompson et al. 2000).

Several globally abundant species are exposed to human impacts that threaten the viability of local populations. The common bottlenose dolphin *Tursiops truncatus* is one of these species, with widespread distribution and its global conservation status classified as of least concern by the IUCN Red List (Hammond et al. 2012). However, many populations inhabiting coastal waters have been declining lately (Gaspar 2003; Currey et al. 2009; Félix et al. 2017). Coastal populations are especially vulnerable because they tend to have small and restricted distributional ranges that often overlap with human activities (Reeves and Reijnders 2002; Reeves et al. 2003). In the Southwest Atlantic Ocean, morphological and genetic distinctions between two bottlenose dolphin forms (i.e., coastal and offshore) suggests adaptation to different habitats

(Costa et al. 2016; Wickert et al. 2016). Consequently, the Committee on Taxonomy (2017) has recently recognized these coastal bottlenose dolphins as the subspecies *Tursiops truncatus gephyreus* which consists of small discrete populations—no more than 300 individuals in total—with high site fidelity to estuaries and river mouths (Fruet et al. 2014). Due to lack of relevant data, its regional conservation status has not been assessed yet.

One of these coastal populations that comprises the subspecies is found in Laguna, southern Brazil. It is a resident population of about 60 individuals (Bezamat et al. 2018), and some of them often interact with artisanal fishermen in an apparently cooperative foraging, mainly during the mullet fishing season (Simões-Lopes et al. 1998, 2016). Cooperative dolphins drive the schools of fish towards the fishermen that are waiting in shallow waters; fishermen recognize dolphins' stereotyped behaviors as cues indicating when and where they should cast their nets (Simões-Lopes et al. 1998, 2016). Although the role of this specialized behaviour on individual fitness and population dynamics was not fully investigated, this foraging tactic influences individual and population aspects in many ways, such as in population social structure (Daura-Jorge et al. 2012), acoustic behavior (Romeu et al. 2017) and space use (Cantor et al. 2018). The frequency of use of this foraging tactic varies among individuals. However, all dolphins interact with each other and their home ranges overlap, which may contribute to a mild effect of the foraging tactic on population and reproductive parameters (Bezamat et al. 2018; Bezamat et al. in prep). Calving is seasonal, with most births occurring during late spring and summer, and calf survival seems to be affected by the calf being born close to the peak of mullet fishing season, when resource availability is high (Bezamat et al. in prep). Dolphin distribution in Laguna overlaps considerably with human activities, which is a cause of concern as to the viability of this small population.

Immediate threats to the survival of the bottlenose dolphins in Laguna include bycatch, pollutants, boat collisions, and anthropogenic noise (Daura-Jorge et al. 2013; Bezamat et al. 2018; Righetti et al. 2019; Bezamat et al. in prep). Over the past years, several dolphins have died from entanglement in fishing gear, mostly trammel nets placed near the fishermen-dolphin cooperation area overnight to catch catfish (Peterson et al. 2008; Bezamat et al. 2018). Recently, this fishery was banned in the

dolphins' core area (Laguna, municipal law number 1.998/2018), but unfortunately, it continues to occur because inspection is insufficient due to lack of resources. Pollutants other than PCBs might affect the population; blubber PCB concentrations in some biopsied dolphins exceeded toxicity thresholds (Righetti et al. 2019). PCBs are known to reduce infant survival (Reddy et al. 2001; Wells et al. 2005) and affect the immune system and consequently disease susceptibility (Desforges et al. 2016). In fact, we have been observing an increasing number of dolphins with Lobomycosis-like disease, a chronic dermal infection that affects small cetaceans (Daura-Jorge and Simões-Lopes 2011). Boat collision is also a recognized threat. Recently, a one-month-old calf was found dead and the necropsy revealed a blunt trauma injury on its cervical spine, an evidence that it was probably hit by a boat (Bezamat et al. in prep). Anthropogenic noise from daily boat traffic and local enterprises (e.g., dredging and bridge construction) have the potential to mask communication between mothers and their calves, and consequently increase calf mortality (Bezamat et al. in prep). Noise could also affect foraging success once dolphins use echolocation to detect prey (Lacy et al. 2017).

In this study, we applied a PVA modelling framework for the small bottlenose dolphin population in Laguna, Brazil. Based on estimates of demographic rates from a long-term individual-based monitoring of this population, we used PVA aiming to: 1) model the viability of this population within 100 years under different levels of annual bycatch mortality, including the baseline (current conditions), worst-cases and management scenarios; 2) identify the life-history parameters to which the population dynamics is most sensitive; 3) explore how additional threat scenarios of recognized human activities (*i.e.* bycatch and dredging) would affect population dynamics. Finally, based on the PVA results, we recommend priorities for conservation management of this unique dolphin population that interacts with fishermen, to prevent it from extinction in the near future.

METHODS

Study area

We studied the year-round, resident population of common bottlenose dolphins in Laguna (28°20'S, 48°50'W; (see Fig. 3–Thesis'

Introduction, p. 35), one of the largest lagoon systems in southern Brazil. Fishing is the major local economic activity, and incidental bycatch in trammel nets is one of the main causes of dolphin mortality in the area (Peterson et al. 2008; Bezamat et al. 2018). Other local threats to the survival of these dolphins include the cumulative effect of pollutants, boat collisions, and anthropogenic noise (Daura-Jorge et al. 2013; Righetti et al. 2019; Bezamat et al. in prep.).

Population Viability Analysis Inputs

We conducted population viability analyses (PVAs) and sensitivity analyses with the computer software Vortex (version 10, available at www.vortex10.org/Vortex10.aspx) (Lacy 1993, 2000; Lacy and Pollak 2018). Vortex is an individual-based simulation package designed to model the effects of deterministic factors and demographic, environmental, and genetic stochasticity on population dynamics (Lacy 1993). Vortex has been widely used for many threatened species (Maehr et al. 2002; Carroll et al. 2013; Fante-lepczyk et al. 2018), including marine mammals (Marmontel et al. 1997). To provide the most likely forecast, we used the best demographic parameters estimates (*i.e.* population size, survival and reproductive rates) available for the bottlenose dolphin population in Laguna based on photo-identification surveys between September 2007 and December 2017 (Daura-Jorge et al. 2013; Bezamat et al. 2018; Bezamat et al. in prep.; Table 1).

We estimated first and second year calf survival (Bezamat et al. in prep), sex-specific adult survival and abundance (Bezamat et al. 2018) by fitting mark-recapture models to individual sighting histories. Since we could not estimate post-weaning survival, we used the adult survival estimates for juveniles as well. Age at first offspring for females and males were set at 10 and 11 years, respectively (Fortuna 2007; Bezamat et al. in prep.), and reproductive lifespan and maximum lifespan were set at 45 and 50 years, respectively (Hohn et al. 1989; Wells and Scott 1999). We estimated the number of females breeding in a given year as a percentage of all adult females sighted during that period, which will be called the ‘reproductive rate’ from now on. We used standard error values as standard deviations due to environmental variance (SD_{EV}) for survival and reproductive rates, since the standard error is the standard deviation

of the estimated parameter. These variances were used to define the distributions of demographic rates from which values are sampled in each year of the simulation model. We assumed that the population was demographically isolated and that the initial population had a stable age structure. The carrying capacity was set at 90 dolphins, which is the size of the largest known population of the subspecies (Fruet et al. 2015). However, this carrying capacity could be overestimated and hence, our scenarios could be optimistic. The Patos Lagoon estuary is larger (10,000 km²) than Laguna (200 km²) and therefore supports a larger fishing productivity. All mature males were assumed to be in the breeding pool. We do not have data on inbreeding (Frère et al. 2010) in Laguna, thus we omitted inbreeding depression from the standard models, but evaluated its potential effect with sensitivity analyses by varying the number of lethal equivalents—a common measure of the severity of inbreeding depression (Lacy et al. 2018).

Table 8: Summary of demographic parameters used as input data in the modeling of the viability of the bottlenose dolphin population in Laguna, Brazil. Standard deviations due to environmental variation are shown in parenthesis.

Parameter	Value	Reference
Percent of females breeding yr ⁻¹	32.8 (± 10.0)	Bezamat et al. in prep.
1 st year calf survival (%)	73.9 (± 9.2)	Bezamat et al. in prep.
2 nd year calf survival (%)	81.8 (± 11.6)	Bezamat et al. in prep.
Adult = Juvenile survival (%)	95.7 (± 1.3)	Bezamat et al. 2018
Females		
Males	93.6 (± 6.4)	Bezamat et al. 2018
Initial population size	60	Bezamat et al. 2018
Age at first offspring (females/males)	10/11	Bezamat et al. in prep., Fortuna 2007
Maximum age of reproduction	45	Hohn et al. 1989,
Maximum lifespan	50	Wells and Scott 1999
Sex ratio at birth (males)	50	(Caughley 1977)
Carrying capacity	90	

Alternative scenarios

Systematic beach surveys have been conducted in the area since 2013, allowing the recovery of stranded carcasses of dolphins that potentially belong to the Laguna population, and their cause of death has been analyzed by veterinarians since 2015 (Projeto de Monitoramento de Praias da Bacia de Santos; Bezamat et al. 2018). The number of dolphins bycaught in recent years was: one juvenile male in 2016; one juvenile female and one adult male in 2017; two juveniles (one male and one female) and one adult male in 2018. Therefore, we examined six different levels of annual bycatch mortality. The (1) baseline scenario represents the current level of bycatch based on the annual average of the last three years, with no conservation actions. We simulated an initial population size of 60 individuals (Bezamat et al. 2018) and, since adult survival estimates used as inputs did not include these recent bycatch mortalities, we included two bycatches every year: one juvenile from 2 to 3 years (taking turns between a male and a female) and one adult male. To examine the impacts of additional bycatch or the effectiveness of management actions, we modeled other five scenarios including: (2) baseline scenario plus one adult male killed every year; (3) baseline scenario, but the adult bycatch is of a male in one year and a female the following year; (4) one adult male bycatch every year; (5) one juvenile bycatch every year; (6) zero bycatch. For each model we ran 1000 simulations over a 100-year projection.

Sensitivity and Elasticity Analyses

Sensitivity analysis was used in combination with the PVA to evaluate which parameters would most affect population dynamics (Akçakaya 2000; Akçakaya and Sjögren-Gulve 2000). Based on the baseline scenario, we conducted fixed-proportion and observed-variation sensitivity analyses by varying each vital rate by $\pm 1\%$ or $\pm 1 \text{ SD}_{EV}$, respectively, while holding all other parameters constant. Selected vital rates were survival of all age stages and reproductive rates. The number of lethal equivalents also varied from 0 to 3.14 (the median value reported for 38 mammalian species; Ralls et al. 1988) and 6.29 (the combined mean effect of inbreeding on fecundity and first year survival; O'Grady

et al. 2006) to evaluate the potential effect of inbreeding depression. For good statistical results, 1000 samples of each parameter were taken.

Sensitivity (S_X) of stochastic mean population growth rate (λ) to a -1% change in a particular vital rate (X) was calculated as the slope of the tangent line describing the population growth rate as a function of the parameter (Morris and Doak 2002):

$$S_{ij} = \frac{\partial \lambda}{\partial a_{ij}}$$

$$S = \frac{\lambda_{new} - \lambda_{baseline}}{X_{new} - X_{baseline}} = \frac{\Delta \lambda}{\Delta X}$$

where stochastic mean growth rate is presented as lambda (λ) which results from the transformation of r as follows:

$$\lambda = e^r$$

We also calculated elasticity values, which measure the proportional change in mean population growth rate resulting from a proportional change in each of the parameters of interest (de Kroon et al. 2000; Morris and Doak 2002):

$$e_{ij} = \left(\frac{\partial \lambda}{\partial a_{ij}} \right) \left(\frac{a_{ij}}{\lambda} \right)$$

$$e = \frac{(\lambda_{new} - \lambda_{current})/\lambda_{current}}{(X_{new} - X_{current})/X_{current}} = \frac{S * X_{current}}{\lambda_{current}}$$

Assessing impacts and evaluating management options

We also used sensitivity analysis to determine the most effective management action by simulating a human impact or disturbance and assessing its influence on population dynamics. We assessed the impacts of additional adult bycatches and regular dredging operations or intense boat traffic (assuming the underwater noise would disturb mother-calf bonds and consequently decrease calf survival; Parsons and Dolman 2004) by comparing the baseline scenario with the results of models that incorporate the effects of the simulated impacts on model parameters. We

simulated the effects of bycatch on population dynamics by adding to the baseline scenario up to four adult male or female removals every year. Moreover, we simulated the potential impact of increased underwater noise by reducing first-year calf survival rate by 10, 20, 30, 40, 50, 60, 70, 80 and 90%. Survival rate reduced by 10 and 20% was similar to the lowest survival rates estimated in Laguna, 0.669 in 2014 and 0.600 in 2013 (Bezamat et al. in prep), during the construction of a bridge in the lagoon system, when there was noise from pile driving and intense boat traffic. Survival rate reduced by 50% was similar to the lowest calf survival rate recorded for free-ranging bottlenose dolphins (0.375; Currey et al. 2009). We evaluated whether adult survival or first-year calf survival would have the greatest influence on population growth rate, and determined which vital rate we should focus on in management and conservation efforts.

RESULTS

Population Viability Analysis Outputs

The baseline model yielded a declining population ($r = -0.022$; Model 1, Figure 1, Table 2). Probability of extinction was high (0.876), and the mean time of extinction was 48.8 years with a mean population size of 7.25 dolphins. Compared to the baseline model, models with one additional male adult bycatch every year or the replacement of one adult male bycatch with one adult female bycatch every other year (Models 2 and 3, respectively), presented decreased population growth rates and population sizes, and increased probabilities of extinction, with all or nearly all simulated populations going extinct within 100 years. Overall, the three management models (avoiding either a juvenile or an adult bycatch, or both bycatches every year) showed great success when compared to the current conditions; they indicated increases in population growth rate, population size and time to extinction, and lower probabilities of extinction (Models 4, 5 and 6, Table 2) over the baseline model. Although avoiding the bycatch of one juvenile or one adult every year (Models 4 and 5, respectively) were a considerable improvement

over baseline, the 'zero bycatch' (Model 6) was the only model that exhibited a positive growth rate and zero risk of extinction.

Table 9: Summary of the results of the Population Viability Analysis for six scenarios of bycatch mortality ('harvest') of bottlenose dolphins in Laguna, Brazil. Stochastic growth rate (stoch-r), standard deviation (SD), N_{100} : population size in 100 years, probability of extinction (PE), mean time at extinction (mean TE), M: male and F: female.

Harvest scenarios	stoch-r	SD (r)	N_{100}	SD (N_{100})	PE	Mean TE
(1) Baseline:						
1 Juvenile M/F + 1 Adult M yr ⁻¹	-0.0222	0.0849	7.25	19.65	0.876	48.8
(2) 1 Juvenile M/F + 2 Adults M yr ⁻¹	-0.0453	0.0798	0.00	0.00	1.000	26.0
(3) 1 Juvenile M/F + 1 Adult M/F yr ⁻¹	-0.0467	0.1187	1.50	8.60	0.957	53.7
(4) 1 Adult M yr ⁻¹	-0.0017	0.0749	41.77	38.09	0.426	55.2
(5) 1 Juvenile M/F yr ⁻¹	-0.0007	0.0741	54.39	25.09	0.020	86.9
(6) Zero bycatch	0.0110	0.0629	80.55	11.55	0.000	0.0

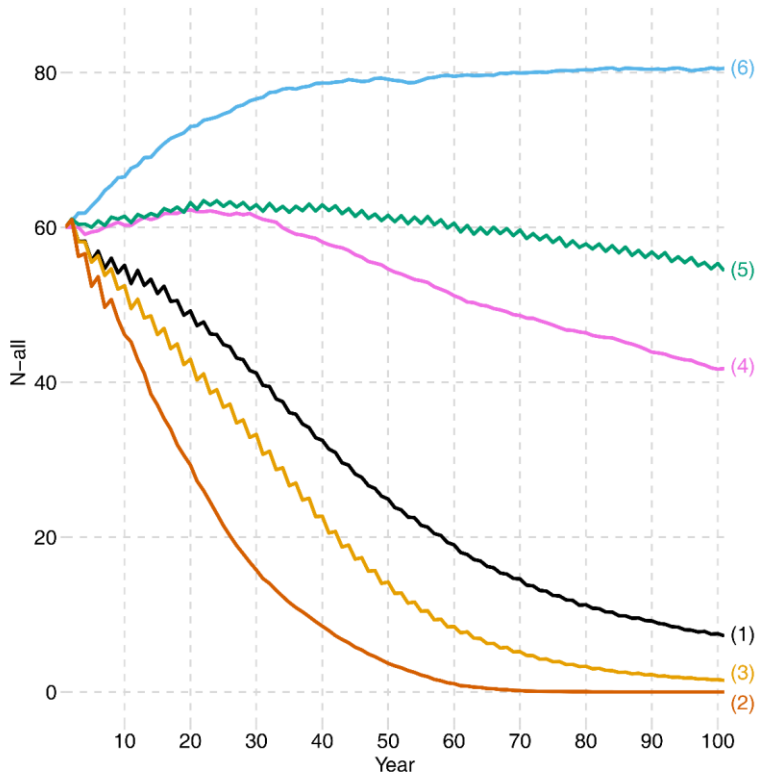


Figure 5: Population Viability Analysis predictions for the six scenarios of annual bycatch mortality ('harvest') of bottlenose dolphins in Laguna, southern Brazil. Numbers refer to models in Table 2. Simulation of an annual bycatch of: (1) one juvenile (male/female) and one adult male—baseline scenario; (2) one juvenile (male/female) and two adult males; (3) one juvenile (male/female) and one adult (male/female); (4) one adult male; (5) one juvenile (male/female); and (6) zero bycatch.

Sensitivity and Elasticity Analyses

The effects of fixed-proportion ($\pm 1\%$) and observed-variation changes ($\pm 1 \text{ SD}_{\text{EV}}$) in the input parameters—reproductive rates, calf, juvenile, and adult survival rates, and inbreeding—on population growth and population size are shown in Table 3. Inbreeding had a very small and non-significant effect (Table 3). Growth rate and population size forecasts after 100 years (N_{100}) were more sensitive to proportional changes in adult female and juvenile survival rates; these parameters showed the highest sensitivity and elasticity values (Tables 3 and 4). Proportional changes of reproductive rates, calf and adult male survival rates had relatively little effect on growth rate and N_{100} -forecasts (Tables 3). Low sensitivity and elasticity values indicate that the model is less sensitive to small changes in these parameters (Table 4). On the other hand, the observed-variation analysis showed that population viability was most affected by variation in reproductive rates, followed by adult female and calf survival rates (Table 3). Observed temporal variation in adult male survival rates had the least influence on population dynamics (Table 3).

Assessing impacts and evaluating management options

The effects of additional bycatches and the potential impact of regular dredging operations and intense boat traffic (*i.e.*, reduced first-year calf survival) on growth rate are presented on Figure 2. Sensitivity analyses showed that growth rate was most sensitive to changes in adult female bycatches. The removal of one more female annually resulted in a growth rate ($r = -0.1003$) over two times lower than the addition of one male bycatch every year ($r = -0.0451$), and similar to a reduction in 90% in calf survival ($r = -0.1071$; Figure 2). The impact on population dynamics caused by the addition of one male bycatch every year ($r = -0.0451$) corresponded to a 30% reduction in calf survival ($r = -0.0446$; Figure 2), and the addition of two male bycatches annually ($r = -0.0516$) was equivalent to a 40% reduction in calf survival ($r = -0.0512$; Figure 2). Therefore, the influence of adult survival rates (especially of females) on population growth was greater than the influence of first-year calf survival rate.

Table 10: Fixed-proportion and observed-variation sensitivity analyses. Effects of parameter variation on stochastic growth rate (r) and 100-year population size (N_{100}) forecasts for the bottlenose dolphins in Laguna, Brazil.

	Growth rate (r)			Population size (N_{100})		
	Low	Baseline	High	Low	Baseline	High
Inbreeding	-0.0212	-0.0212	-0.0213	8.65	8.74	8.66
Fixed-proportion Analysis						9.95
Reproduction	-0.0223	-0.0213	-0.0201	7.57	8.56	
1st year calf survival	-0.0223	-0.0212	-0.0200	7.59	8.65	9.98
2nd year calf survival	-0.0224	-0.0212	-0.0200	7.48	8.75	10.10
Juvenile survival						16.23
Females	-0.0280	-0.0213	-0.0145	3.66	8.67	
Males	-0.0237	-0.0213	-0.0194	5.52	8.61	11.69
Adult survival						22.93
Females	-0.0326	-0.0212	-0.0095	1.99	8.68	
Males	-0.0220	-0.0212	-0.0210	7.66	8.63	9.19
Observed-variation Analysis						58.19
Reproduction	-0.0439	-0.0212	0.0067	0.01	8.74	
1st year calf survival	-0.0326	-0.0212	-0.0087	1.12	8.73	27.26
2nd year calf survival	-0.0346	-0.0213	-0.0059	0.63	8.68	33.02
Juvenile survival						19.14
Females	-0.0301	-0.0212	-0.0123	2.70	8.74	
Males	-0.0265	-0.0213	-0.0175	2.86	8.60	15.26
Adult survival						29.79
Females	-0.0362	-0.0213	-0.0054	1.08	8.63	
Males	-0.0228	-0.0212	-0.0204	6.86	8.64	10.02

Table 11: Sensitivity and elasticity of population growth rate (λ) to small changes (-1%) in life history traits of bottlenose dolphins in Laguna, Brazil.

	Sensitivity	Elasticity
Reproduction	0.0029	0.0978
1st year calf survival	0.0015	0.1099
2nd year calf survival	0.0014	0.1199
Juvenile survival		
Females	0.0068	0.6678
Males	0.0025	0.2397
Adult survival		
Females	0.0116	1.1335
Males	0.0008	0.0800

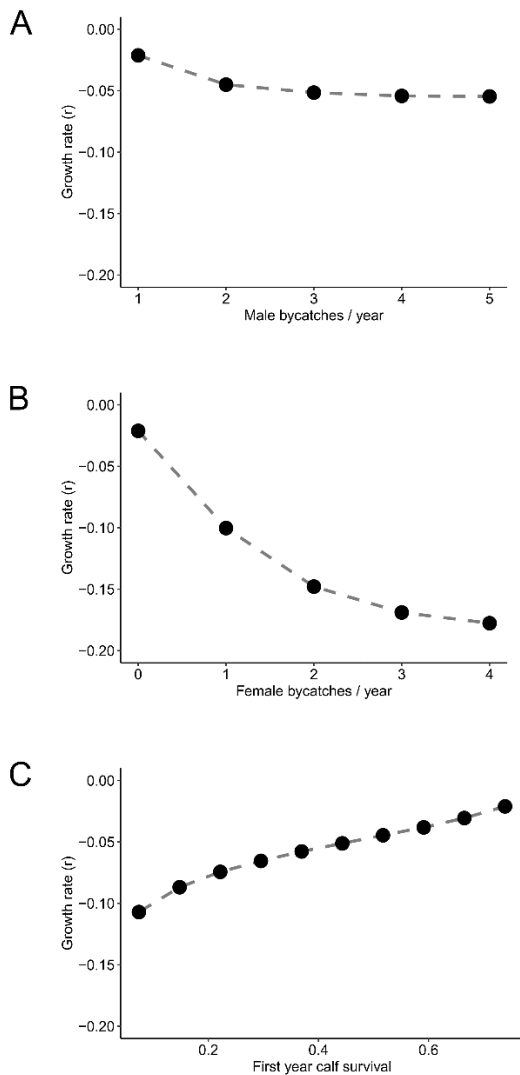


Figure 6: Sensitivity analysis. Effect of additional adult (A) male and (B) female bycatches and (C) different first year calf survival rates on stochastic growth rate (r) forecasts.

DISCUSSION

We evaluated the viability of the small bottlenose dolphin population in Laguna using the best demographic parameters estimates available. The baseline scenario yielded a declining population ($r = -0.022$) under current conditions, with high probability of extinction in the next 100 years ($PE = 0.876$). If bycatch increases, the population is doomed to extinction. On the other hand, management actions seem promising: avoiding bycatch would increase population growth and lower probabilities of extinction. Growth rate was most sensitive to small and proportional changes in adult female and juvenile survival. However, observed temporal variation indicated that population dynamics were more influenced by reproduction. We also compared the relative effects of human impacts (*i.e.*, additional bycatches and reduced calf survival) on population dynamics. We found that the growth rate was most sensitive to changes in adult bycatch (especially females) than to a reduction in calf survival. Combined, our results indicate that only a zero-bycatch management strategy can guarantee the persistence of this dolphin population.

Population size has remained apparently stable in the last decade (Bezamat et al. 2018). However, the level of bycatch has been increasing since 2016, and, under current conditions (two bycatches every year on average: one juvenile and one adult male), population is expected to decline. The estimated survival rates we used as inputs in the PVA did not include these mortalities from entanglement in fishing gear from 2016. Thus, we included this current level of harvest in the baseline model to account for this major threat. Our monitoring effort has been intense in recent years and estimates of abundance and survival are precise and appears accurate. Nevertheless, a longer time series is required to validate our estimates of reproductive parameters, which were based on eight discontinuous data years. Additional efforts are also required for a real assessment of the carrying capacity, which is likely overestimated here. Moreover, the possibility of inbreeding depression in the studied population should be accounted for in future forecasts—although sensitive analysis suggests this parameter is not so relevant to population dynamics, this small dolphin population exhibit remarkably low genetic variability and low gene flow with adjacent communities, which may, in the long-term, be detrimental to its viability (Fruet et al. 2014). However,

regardless of whether this population is stable or declining, it is dangerously small and highly vulnerable to the wide range of potential threats as well as stochastic events.

Population viability was greatly affected by incidental bycatch. Projections indicated that the current level of bycatch mortality in Laguna is unsustainable. Several recovered carcasses have shown evidences of entanglement in fishing gear (Bezamat et al. 2018). We have also photographed many individuals with scars or nets and lines around their bodies, including a young calf in early December 2017 (Bezamat et al. in prep) and two adults that died that same year, 20 and 27 months after being entangled. Incidental bycatch is probably the major conservation issue for small cetaceans worldwide (Reeves et al. 2003). Unsustainable bycatch in local fisheries was probably the main cause of the extinction of the baiji *Lipotes vexillifer* in the Yangtze River (Turvey et al. 2007). Numerous other populations and species are seriously threaten by entanglement mortality, such as the vaquita *Phocoena sinus* (Rojas-Bracho et al. 2006), the North Island (New Zealand) population of Hector's dolphin *Cephalorhynchus hectori* (Dawson et al. 2001) and the Mahakam River (Indonesia) population of Irrawaddy dolphins *Orcaella brevirostris* (Smith et al. 2003). For small populations, even the removal of a single individual each year, especially females in this study, may have a great impact on the population dynamics (Araújo et al. 2014). The most optimistic mitigation of bycatch would make the difference between a declining and increasing population, securing the long-term persistence of bottlenose dolphins in Laguna.

Although growth rates were more sensitive to proportional changes in adult and juvenile survival, long-term observed variations in reproductive rates had a greater impact on growth rates than survival. This finding is similar to studies of bottlenose dolphin *Tursiops aduncus* populations off Australia (Manlik et al. 2016) and a killer whale *Orcinus orca* population of the northeastern Pacific Ocean (Lacy et al. 2017). While the fixed-proportion sensitivity and elasticity analyses have been commonly used to evaluate the importance of vital rates for population viability, the observed-variation analysis reflects variability likely to occur in wild populations, offering insight into feasibility and effectiveness of wildlife management options (Manlik et al. 2016). In Laguna, adult survival rates were relatively constant over the last decade

(2007-2016), whereas reproductive rates showed a large temporal variation. Moreover, since adult survival is already close to one, there is more potential for improving reproduction than for improving survival. Therefore, in order to reverse or prevent population declines, the best long-term management strategy should aim at both reproduction and survival, rather than just one vital rate at a time.

Our assessment of the potential impact of additional bycatches and a dredging operation (decreasing calf survival) showed that bycatch of female adults had the greatest influence on growth rate. Even the removal of a single female annually can greatly increase the probability of extinction. The influence on probability of extinction is also biased towards females in the critically endangered eastern Taiwan Strait population of Indo-Pacific humpback dolphins *Sousa chinensis* (Araújo et al. 2014). The sensitivity analysis showed that breeding females are extremely important in the Laguna population and that a higher recruitment rate is needed in order to increase population growth rate. The influence of additional male mortality was lower. As for other mammals with a polygynous mating system, a single male can mate with multiple receptive females in a given year (Breed and Moore 2012).

Although the influence of reduced calf survival as a potential impact of dredging operations was lower than an increase in adult female bycatch, it was not negligible. A dredging operation associated with the maintenance of the Laguna harbour is expected to take place shortly to increase the channel depth, which is a passing and core area for the dolphins, where most cooperative sites are located. We assumed a dredging operation would decrease calf survival due to communication masking between mothers and their calves (Parsons and Dolman 2004), but we do not know exactly to what extent and whether this would be the only impact on population dynamics. Calf survival was 20% lower during the construction of a bridge in the lagoon system, when there was acoustic disturbance from pile driving and intense boat traffic (Bezamat et al. in prep). A reduction of 20% in first year calf survival would generate an 81% reduction in growth rate in Laguna. Effects of dredging on marine mammals varies with species, location and dredging equipment type (Todd et al. 2014). Overall, more likely effects include acoustic masking, avoidance and short-term changes to behavior, and prey availability (Todd et al. 2014). Higher intensities of dredging caused bottlenose dolphins to spend less time in a foraging patch in Aberdeen harbor, Scotland (Pirodda et al. 2013). Planned developments in Laguna, including

this dredging operation and the construction of a wind farm, will probably cause an increase in boat traffic with a risk of dolphins being killed or injured by boat collisions, and an increase in acoustic disturbance compromising habitat quality.

Nevertheless, increased underwater noise—from intense boat traffic and regular dredging operations and constructions—is not the only factor that could contribute to a reduction in calf survival. Increased levels of persistent organic pollutants, especially PCBs, and decreased resource availability could add in reducing calf survival as well. Dolphins in Laguna are exposed to contaminants and some biopsied individuals showed high blubber PCB levels (Righetti et al. 2019). Females transfer PCBs to their calves through the placenta and during lactation, which may increase chances of fetal and first-year calf mortality (Reddy et al. 2001; Wells et al. 2005), and potentially depress population growth rates (Hall et al. 2006). Moreover, since lactation is the most energetic demanding time of reproduction, females need a high abundance of food at this stage (Kastelein et al. 2002; Rechsteiner et al. 2013). Thus, a decrease in resource availability could compromise calf nutrition and reduce its chances of survival. In fact, we found that calves born right after the peak of the mullet season had higher chances of survival (Bezamat et al. in prep).

Management actions to reduce the current threats to this small bottlenose dolphin population are needed immediately. Our most important conclusion is that the present level of bycatch in Laguna is unsustainable, thus a reduction in associated mortality is an urgent priority. The responsible institutions should reinforce surveillance to ensure that trammel net fishery does not occur in the dolphins' core area. Moreover, fishermen who cooperate with dolphins perceive multiple values from their occurrence in Laguna and the interaction with them, and therefore could be engaged in an alternative co-management strategy to help monitoring the banned fishery (Machado et al. 2019). They should be warned that a zero-bycatch management strategy must be implemented right away for this dolphin population to persist in the long-term. The area of restriction of trammel net fishery is essential and should be expanded in the near future, to include not only the dolphins' core area, but their entire distribution area in the lagoon system. Regarding planned developments in the area, several mitigation measures have been used

elsewhere (e.g. Jefferson et al. 2009) and should be considered here, such as reducing underwater noise of pile driving using air bubble curtains (Würsig et al. 2000). Habitat degradation (e.g. acoustic disturbance and pollution) must be reduced in order to improve habitat quality for this population. The mullet fishery should also be monitored to ensure resource availability for the dolphins. These combined actions should ensure the long-term persistence of bottlenose dolphins in Laguna.

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CONSIDERAÇÕES FINAIS E CONCLUSÕES

No primeiro capítulo, incorporamos variações individuais relacionadas à tática de forrageio, tamanho da área de vida e sexo em modelos de marcação-recaptura para avaliar se essas covariáveis influenciaram a sobrevivência aparente e probabilidade de captura dos botos. Os resultados mostraram que a variação individual no comportamento de forrageio afetou sutilmente os parâmetros demográficos dos botos em Laguna. Descobrimos que os botos que interagem frequentemente com os pescadores e apresentam áreas de vida reduzidas tendem a ter probabilidades de sobrevivência ligeiramente mais altas e probabilidade de captura variáveis. Além disso, nosso esforço de amostragem ao longo de dez anos fortalece a evidência de que essa população é pequena, altamente residente e aparentemente estável. Apesar da estabilidade observada nos últimos anos, essa pequena população pode ser extremamente vulnerável ao declínio local devido à limitada resiliência à mortalidade resultante de distúrbios ambientais estocásticos. Portanto, para garantir a conservação dos botos em Laguna, quaisquer fatores antropogênicos que impactem sua sobrevivência devem ser mitigados. Além disso, se a pesca cooperativa, em última análise, melhora o fitness individual, as consequências demográficas dessa interação entre botos e pescadores também devem ser consideradas para fins de conservação.

No segundo capítulo, nós estimamos parâmetros reprodutivos para as fêmeas conhecidas na população, cruciais para uma avaliação populacional, e investigamos fatores que poderiam influenciar no sucesso reprodutivo, incluindo características das mães e disponibilidade de recurso. Vimos que a reprodução em Laguna é sazonal e os filhotes que nasceram mais próximos da temporada de tainha apresentaram uma sobrevivência maior, provavelmente devido à grande demanda energética das fêmeas durante o período de lactação. Fêmeas que frequentemente interagem com os pescadores apresentaram fecundidade e sobrevivência dos filhotes ligeiramente maiores do que fêmeas que tendem a forragear independentemente. Ao longo de várias gerações, essas diferenças podem mostrar benefícios claros da pesca cooperativa. Uma pequena diferença na sobrevivência dos filhotes pode representar uma vantagem seletiva e contribuir para a evolução e manutenção da tática de forrageio

especializada. Esse estudo enfatiza a importância do monitoramento de longo prazo das populações, baseado nos indivíduos, para compreender as características regionais de história de vida e fornecer informações precisas para ações de manejo e conservação eficazes. Isso é especialmente crítico para essa população de botos em Laguna, que mantém a tática de forrageio especializada, mas também enfrenta várias ameaças humanas que a colocam em risco local e regional de extinção.

No terceiro capítulo, nós avaliamos a viabilidade da pequena população de botos em Laguna utilizando os parâmetros demográficos estimados nos capítulos anteriores. O cenário que simula as condições atuais, com duas mortes por emalhe ao ano, gerou uma população em declínio, com alta probabilidade de extinção nos próximos 100 anos. Se o número de mortes por emalhe aumentar, a população estará fadada à extinção. Por outro lado, as ações de manejo parecem promissoras: evitar mortes por emalhe aumentaria a taxa de crescimento populacional e diminuiria a probabilidade de extinção. A taxa de crescimento foi mais sensível a mudanças pequenas e proporcionais na sobrevivência de fêmeas adultas e de juvenis. Entretanto, quando avaliamos a variação temporal observada, a reprodução teve uma influência maior na dinâmica populacional. Também comparamos os efeitos relativos dos impactos humanos (isto é, aumento das capturas acidentais e redução da sobrevivência de filhotes) na dinâmica populacional, e vimos que a taxa de crescimento foi mais sensível a mudanças no número de emalhes de adultos, especialmente as fêmeas. Combinados, nossos resultados indicam que apenas uma estratégia de manejo de zero capturas acidentais pode garantir a persistência desta população de botos e da pesca cooperativa.

A implementação efetiva e imediata de ações de manejo para reduzir as ameaças atuais à essa pequena população de botos é necessária. Nossa principal conclusão é que o nível atual de capturas acidentais em Laguna é insustentável, e uma redução na mortalidade associada é uma prioridade. Os órgãos responsáveis devem reforçar a fiscalização para garantir que não ocorra a pesca de emalhe na área de concentração dos botos. Além disso, os pescadores que cooperam com os botos poderiam ser incluídos em uma estratégia alternativa de manejo para ajudar no monitoramento dessa pesca proibida no local. A área de restrição da pesca de emalhe é essencial e deve ser ampliada no futuro próximo, para incluir não só a área de concentração dos botos, mas toda a área de distribuição deles no complexo lagunar. Quanto à futuros empreendimento na área,

medidas de mitigação, como o uso de cortinas de bolhas para reduzir o ruído proveniente da bate estacas, devem ser consideradas. De modo geral, a degradação do habitat (por exemplo, distúrbio acústico e poluição) deve ser reduzida a fim de melhorar a qualidade do habitat para essa população, pois influencia principalmente a sobrevivência dos filhotes. A pesca da tainha também deve ser monitorada para garantir a disponibilidade de recursos para os botos, uma vez que isso influencia o sucesso reprodutivo. Essas ações combinadas devem garantir a persistência a longo prazo dos botos de Laguna e dessa interação singular entre botos e pescadores.