



**Dolphin population specialized in foraging with artisanal fishers requires zero-bycatch management to persist**

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3 1 Dolphin population specialized in foraging with artisanal fishers requires zero-bycatch  
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33 14 Abstract  
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35 15 1. The small population paradigm assumes that populations with low numbers of  
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37 16 individuals intrinsically have a high probability of extinction. The small  
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39 17 population of Lahille's bottlenose dolphins *Tursiops truncatus gephyreus* that  
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41 18 specializes in foraging with artisanal fishers in Laguna, southern Brazil, faces  
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43 19 human pressures including bycatch in fishing gear. The viability of this population  
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45 20 was modelled over 30 and 100 years under different levels of bycatch, including  
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47 21 the current scenario of two bycatches every year, two scenarios with higher  
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49 22 incidence of bycatches, and three management scenarios. The sensitivity of  
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51 23 predicted growth rates to fixed-proportion and observed-variation changes in life  
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53 24 history parameters was explored.  
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3 25 2. The current scenario predicted a declining population ( $r=-0.014$ ;  $\lambda=0.986$ ) with a  
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5 26 high probability of extinction in the long term ( $PE=0.71$ ). A small increase in  
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7 27 bycatches, would result in a marked increase in the probability of extinction.  
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10 28 Management scenarios seem promising, but only the zero-bycatch management  
11  
12 29 would make the difference between a declining and an increasing population.  
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14 30 3. As expected for slow-growing species, population growth rate was most sensitive  
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16 31 to proportional changes in adult female and juvenile survival. However,  
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18 32 considering observed variation in vital rates, population dynamics were most  
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20 33 influenced by variation in reproductive rates.  
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23 34 4. To determine the highest priority for management action, another simulation was  
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25 35 made of how additional threat scenarios of recognized human activities (i.e.  
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27 36 bycatch influencing adult survival and increased underwater noise or pollution  
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29 37 influencing calf survival) would affect population dynamics. Population growth  
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31 38 rate was very sensitive to changes in adult bycatch (especially females), as  
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33 39 expected, and only subtly sensitive to a reduction in calf survival.  
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36 40 5. The current level of bycatch is unsustainable. Bycatch needs to be eliminated to  
37  
38 41 maximize the probability of long-term persistence of this dolphin population. Still,  
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40 42 this population's persistence could be threatened by natural variation in  
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42 43 reproductive rates.  
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45 Keywords: bottlenose dolphins, Population Viability Analysis, *Tursiops truncatus*  
46 *gephyreus*, bycatch, conservation, sensitivity analysis, wildlife management.

## 48 Introduction

49 In conservation biology, the small population paradigm focuses on population-  
50 level processes primarily to identify minimum viable population sizes and extinction risk

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3 51 (Shaffer, 1981; Gilpin & Soulé, 1986) in face of both demographic and environmental  
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5 52 stochasticity (May, 1973). The smaller the population, the more susceptible it is to  
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7 53 extinction from stochastic processes. Stochastic perturbations include natural variation in  
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9 54 reproductive and survival rates (demographic stochasticity), and reduction of genetic  
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11 55 variability and inbreeding depression (genetic stochasticity). Stochasticity can also be  
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13 56 generated by natural or anthropogenic fluctuations in environmental conditions  
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15 57 (environmental stochasticity) or, in extreme situations, by environmental catastrophes  
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17 58 (Shaffer, 1981; Caughley, 1994). By including stochasticity in population-level  
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19 59 processes, it is possible to better predict how current threats affect the viability of small  
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21 60 populations.  
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26 61 Population viability analysis (PVA) is a powerful modelling tool for examining  
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28 62 the risks posed by different threats to the persistence of small populations over time  
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30 63 (Boyce, 1992; Akçakaya & Sjögren-Gulve, 2000). PVA is helpful in evaluating the  
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32 64 effectiveness of management alternatives, which can assist conservation decision-making  
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34 65 (Drechsler & Burgman, 2004). PVA estimates a population's (or species') risk of  
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36 66 extinction through stochastic simulations of demographic and life-history parameters in  
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38 67 different scenarios (Beissinger & Westphal, 1998). With robust estimates of life history  
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40 68 parameters, a challenging task that requires long-term studies, PVA can reliably assess a  
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42 69 population's status (e.g. Kraus et al., 2001; Runge, Langtimm & Kendall, 2004; Currey  
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44 70 et al., 2011).  
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49 71 An additional valuable output of a PVA is the identification of the key life history  
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51 72 parameters that influence the dynamics of the population under study (e.g. Manlik et al.,  
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53 73 2016; Lacy et al., 2017). Traditionally, for slow-growing populations, including  
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55 74 cetaceans, several studies have shown that female survival tends to influence population  
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57 75 growth more significantly than reproduction (e.g. Caughley, 1966; Heppell et al., 2000;  
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3 76 Young & Edward, 2011). Therefore, conservation strategies should aim to increase adult  
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5 77 survival in order to be more effective (van de Kerk et al., 2013). However, a number of  
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7 78 studies has questioned this generalization (e.g. Mills, Doak & Wisdom, 1999; Morris &  
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9 79 Doak, 2002), suggesting that the importance of vital rates for conservation depends on  
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11 80 their observed variation and chance of being manipulated by management actions. In this  
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13 81 context, even for slow-growing population with long life expectancy, investigating the  
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15 82 influence of each vital parameter on population growth is then crucial for making wildlife  
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17 83 management decisions.

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21 84 PVA has been used to assess a number of marine mammal species, including  
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23 85 manatees *Trichechus manatus latirostris* (Marmontel, Humphrey & O'Shea, 1997),  
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25 86 southern elephant seals *Mirounga leonina* (McMahon et al., 2005), killer whales *Orcinus*  
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27 87 *orca* (Lacy et al., 2017), Indo-Pacific humpback dolphins *Sousa chinensis* (Araújo et al.,  
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29 88 2014), Hector's dolphins *Cephalorhynchus hectori* (Burkhart & Slooten, 2003), and  
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31 89 common bottlenose dolphins *Tursiops truncatus* (Thompson et al., 2000) and Indo-  
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33 90 Pacific common dolphins *Tursiops aduncus* (Manlik et al., 2016). Adult survival is,  
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35 91 indeed, as observed for many slow breeding and slow growing species, a key vital rate  
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37 92 for marine mammals, as shown in the modelling of the Florida manatee (Marmontel,  
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39 93 Humphrey & O'Shea, 1997). However, natural variability in birth rate can also influence  
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41 94 cetacean's population growth more than natural variability in mortality, as found in PVAs  
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43 95 of Indo-Pacific common dolphins off Australia and killer whales in the northeastern  
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45 96 Pacific Ocean (Manlik et al., 2016; Lacy et al., 2017).

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51 97 Several globally abundant species are exposed to human pressures that threaten  
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53 98 local populations. The common bottlenose dolphin *Tursiops truncatus* is one of these  
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55 99 species, with its global conservation status classified as Least Concern on the IUCN Red  
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57 100 List (Hammond et al., 2012). However, although some populations inhabiting coastal  
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3 101 waters are stable or increasing (e.g. Arso-Civil et al., 2019), others have declined (Currey  
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5 102 et al., 2009; Félix et al., 2017). Coastal populations are especially vulnerable because their  
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7 103 distributional ranges overlap with human activities (Reeves & Reijnders, 2002; Reeves et  
8  
9 104 al., 2003). PVA of the bottlenose dolphin population from eastern Scotland illustrates  
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11 105 how it can be informative to stakeholders in consideration of precautionary management  
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13 106 actions to deal with human pressures that threaten local populations (Thompson et al.,  
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15 107 2000).

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19 108 In the Southwestern Atlantic Ocean, morphological and genetic distinctions  
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21 109 between coastal and offshore bottlenose dolphins suggests adaptation to different habitats  
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23 110 (Costa et al., 2016; Wickert et al., 2016; Fruet et al., 2017; Costa et al., 2019).  
24  
25 111 Consequently, the Society for Marine Mammalogy has recognized the coastal bottlenose  
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27 112 dolphins as the subspecies *Tursiops truncatus gephyreus* (Lahille's bottlenose dolphin),  
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29 113 consisting of small discrete populations with high site fidelity to estuaries (Fruet et al.,  
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31 114 2014). Although robust data on these regional coastal populations are limited, the small  
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33 115 number of individuals (likely no more than 600 individuals in total), evidence of  
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35 116 declining, and the low genetic variability, motivated a recent regional assessment that  
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37 117 classified the subspecies as Vulnerable (Vermeulen et al., 2019). In fact, the first risk  
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39 118 assessment for Lahille's bottlenose dolphins confirms that its largest population in the  
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41 119 Patos Lagoon estuary, southern Brazil, is vulnerable to any increase in non-natural  
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43 120 mortality (Fruet, Möller & Secchi, 2021). The other smaller populations of this subspecies  
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45 121 are probably in the same situation.

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51 122 One of these coastal populations of this subspecies is found in Laguna, southern  
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53 123 Brazil. It is a resident population of about 60 animals (Bezamat et al., 2019)—one of the  
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55 124 largest populations among all population units (*sensu* Fruet et al. 2014) of the  
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57 125 subspecies—, in which some individuals specialize in interaction with artisanal net-  
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3 126 casting fishers in apparently cooperative foraging (Simões-Lopes, Fabián & Menegheti,  
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5 127 1998; Simões-Lopes, Daura-Jorge & Cantor, 2016). Cooperative dolphins drive the  
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7 128 schools of fish towards the fishers that are waiting in shallow waters; fishers recognize  
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9 129 dolphins' stereotyped behaviours as cues indicating when and where they should cast  
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11 130 their nets (Simões-Lopes, Daura-Jorge & Cantor, 2016). Fishers benefit from this  
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13 131 interaction by catching more fish and, apparently, dolphins accrue similar benefits  
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15 132 (Simões-Lopes, Fabián & Menegheti, 1998).

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19 133 This foraging tactic influences the dolphins in a number of ways at both individual  
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21 134 and population level, such as in population social structure (Daura-Jorge et al., 2012),  
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23 135 acoustic behaviour (Romeu et al., 2017) and spatial habitat use (Cantor, Simões-Lopes &  
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25 136 Daura-Jorge, 2018). The frequency of use of this foraging specialization varies among  
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27 137 individuals. However, all dolphins interact with each other and their home ranges overlap,  
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29 138 which may contribute to only a mild effect of cooperative foraging on survival and  
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31 139 reproduction (Bezamat et al., 2019; Bezamat et al., 2020). Calving is seasonal, with most  
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33 140 births occurring during late spring and summer, and calf survival seems to be affected by  
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35 141 the proximity of birth to the peak of the mullet fishing season, when resource availability  
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37 142 is high (Bezamat et al., 2020). Dolphin distribution in Laguna overlaps considerably with  
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39 143 human activities, which is a cause of concern for the viability of this small population.

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43 144 The dolphins in Laguna are subject to multiple anthropogenic pressures including  
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45 145 bycatch, the cumulative effect of pollutants, boat collisions, and anthropogenic noise  
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47 146 (Daura-Jorge, Ingram & Simões-Lopes, 2013; Bezamat et al., 2019; Righetti et al., 2019;  
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49 147 Bezamat et al., 2020). Dolphins are often accidentally entangled, injured, or killed in  
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51 148 trammel nets placed near the fishers-dolphin cooperation area overnight to catch catfish  
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53 149 *Genidens barbatus* (Simões-Lopes, 1991; Peterson, Hanazaki & Simões-Lopes, 2008;  
54  
55 150 Bezamat et al., 2019). Recently, this fishery was banned in the dolphins' core area  
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3 151 (Laguna, municipal law number 1.998/2018) but it continues to occur because  
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5 152 enforcement is insufficient due to lack of resources. Incidental bycatch is probably the  
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7 153 major conservation issue for small cetaceans worldwide (Reeves et al., 2003).  
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9 154 Unsustainable bycatch in local fisheries was probably the main cause of the extinction of  
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11 155 the baiji *Lipotes vexillifer* in the Yangtze River (Turvey et al., 2007). Other populations  
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13 156 and species are seriously threatened by entanglement mortality, such as the vaquita  
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15 157 *Phocoena sinus* (Taylor et al., 2017; Jaramillo-Legorreta et al., 2019), the Māui dolphin  
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17 158 subspecies *Cephalorhynchus hectori maui* (Slooten, 2007) and the Mahakam River  
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19 159 (Indonesia) population of Irrawaddy dolphins *Orcaella brevirostris* (Smith, Beasley &  
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26 161         Pollutants such as PCBs might also affect dolphins in Laguna; blubber PCB  
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28 162 concentrations in some biopsied dolphins exceeded toxicity thresholds (Righetti et al.,  
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30 163 2019). PCBs are known to reduce infant survival (Reddy et al., 2001; Wells et al., 2005)  
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32 164 and affect the immune system and consequently disease susceptibility (Desforges et al.,  
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34 165 2016). In fact, an increase in the number of dolphins with Lobomycosis-like disease, a  
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36 166 chronic dermal infection that affects small cetaceans, has been observed (Daura-Jorge &  
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38 167 Simões-Lopes, 2011). Susceptibility to Lobomycosis-like disease could be enhanced by  
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40 168 the very low genetic variability of this population (Fruet et al., 2014). Boat collision is  
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42 169 also a recognized threat. Recently, a one-month-old calf was found dead, and the necropsy  
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44 170 revealed a blunt trauma injury on its cervical spine, evidence that it was probably hit by  
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46 171 a boat (Bezamat et al., 2020). Anthropogenic noise from daily boat traffic and local  
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48 172 activities (e.g. pile driving) also have the potential to mask communication between  
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50 173 mothers and their calves, and consequently increase calf mortality (Bezamat et al., 2020).  
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52 174 Noise could affect foraging success because dolphins use echolocation to detect prey  
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54 175 (Papale et al., 2015).  
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3 176 In this study, a PVA modelling framework was applied to investigate the long-  
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5 177 term viability of the small Lahille's bottlenose dolphin population in Laguna, Brazil.  
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7 178 Based on estimates of demographic rates from long-term individual-based monitoring of  
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9 179 this population (Bezamat et al., 2019; Bezamat et al., 2020), PVA was used to: 1) model  
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11 180 the viability of this population over 30 and 100 years under different levels of annual  
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13 181 bycatch mortality, including the baseline (current conditions), two scenarios that assume  
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15 182 realistic higher incidence of bycatches (based on the bycatch records in recent years), and  
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17 183 a number of management scenarios to limit bycatch; 2) identify the life history parameters  
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19 184 to which the population dynamics were most sensitive; and 3) determine the highest  
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21 185 priority management action by simulating how additional threat scenarios of recognized  
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23 186 human activities (i.e. bycatch influencing adult survival and increased underwater noise  
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25 187 or pollution influencing calf survival) would affect population dynamics. Based on the  
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27 188 PVA results, recommendations are made on priorities for the management of human  
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29 189 activities and protection of this dolphin population that interacts with fishers from  
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31 190 extinction in the near future.  
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## 40 192 Methods

### 41 193 *Population Viability Analysis Inputs*

42 194 Population viability analyses (PVAs) and sensitivity analyses of the year-round,  
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44 195 resident population of common bottlenose dolphins in Laguna (28°20'S, 48°50'W; Figure  
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46 196 1), southern Brazil, were conducted using software Vortex (version 10, available at  
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48 197 [www.vortex10.org/Vortex10.aspx](http://www.vortex10.org/Vortex10.aspx)) (Lacy, 1993; Lacy, 2000; Lacy & Pollak, 2018).  
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50 198 Vortex runs individual-based simulations to model the effects of deterministic factors and  
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52 199 demographic, environmental, and genetic stochasticity on population dynamics (Lacy,  
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54 200 1993). Essentially, Vortex creates a representation of each animal and follows the fate of  
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3 201 the animal throughout its life. The population dynamics are then modelled as discrete,  
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5 202 sequential events (e.g. births, deaths, catastrophes, etc.) that occur according to defined  
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7 203 probabilities, which can be constants or random variables that follow specified theoretical  
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9 204 distributions. These probabilities come from population parameters (survival  
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11 205 probabilities, reproduction rate, migration rate, etc.), and their uncertainty (defined by  
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13 206 their observed standard errors) defines the random effect, or the environmental  
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15 207 stochasticity. Uncertainty in parameter estimates is implemented using Monte Carlo  
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17 208 methods (Manly, 1997) when running multiple iterations. Each iteration randomly selects  
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19 209 parameter values from a theoretical distribution (e.g. binomial, beta, normal) defined by  
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21 210 the standard errors of the parameters.  
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26 211 Vortex has been widely used to assess the viability of many threatened species  
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28 212 (Maehr et al., 2002; Carroll et al., 2013; Lacy et al., 2017; Fantle-Lepczyk et al., 2018).  
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30 213 To provide the most robust predictions, we used the best demographic parameters  
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32 214 estimates (i.e. population size, survival and reproductive rates) available for the Lahille's  
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34 215 bottlenose dolphin population in Laguna based on photo-identification surveys between  
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36 216 September 2007 and December 2017 (Daura-Jorge, Ingram & Simões-Lopes, 2013;  
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38 217 Bezamat et al., 2019; Bezamat et al., 2020).  
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44 219 *Add figure 1 here*  
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49 221 Estimates of first-, and second-year calf survival, sex-specific adult survival and  
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51 222 abundance were available for modelling (Bezamat et al., 2019; Bezamat et al., 2020;  
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53 223 Table 1). Since post-weaning survival could not be estimated, juvenile survival was  
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55 224 assumed to be the same as adult survival. Age at first offspring for females and males  
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57 225 were set at 10 and 11 years, respectively (Bezamat et al., 2020), and maximum age of  
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3 226 reproduction and maximum observed age (referred to as ‘maximum lifespan’ in Vortex)  
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5 227 were set at 45 and 50 years, respectively, which are the highest known values for the  
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7 228 species *Tursiops truncatus* (following Hohn et al., 1989 and Wells & Scott, 1999).  
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9 229 Although there is some information on the maximum observed age of Lahille’s bottlenose  
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11 230 dolphins (44 years - see Fruet et al., 2015a; Venuto et al., 2020), we chose to use the  
12  
13 231 higher value to be conservative. This decision can make our model optimist; however,  
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15 232 the annual mortality rates likely prevent most individuals from reaching this maximum  
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17 233 age and therefore, this variable should have little effect on population dynamics.  
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21 234 Longitudinal photo-identification data were used to estimate the number of  
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23 235 females breeding (i.e. known to have given birth) in a given year as a percentage of all  
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25 236 adult females sighted during that period (see Bezamat et al., 2020 for more details), which  
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27 237 we refer to as ‘reproductive rate’ from now on. Some births may have gone unnoticed,  
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29 238 particularly for females that have lost their calves very soon after birth, before we were  
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31 239 able to observe them. We incorporated environmental stochasticity ( $SD_{EV}$ , environmental  
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33 240 variance in Vortex) in our simulations by randomly selecting, for each iteration, values  
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35 241 for mortality and reproduction rates from a beta distribution defined by the standard errors  
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37 242 of these parameters.  
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42 243 The population was assumed to be demographically isolated, and the initial  
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44 244 population was assumed to have a stable age structure (i.e. since it was not possible to  
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46 245 specify the number of individuals within each age-sex class at the start of the simulation,  
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48 246 Vortex calculated the expected age distribution based on the input parameters and  
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50 247 allocated the initial population size accordingly). As we do not have data to sustain the  
51  
52 248 hypothesis of intraspecific competition, we set the carrying capacity at 90 dolphins, which  
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54 249 is the size of the largest known population of the subspecies in the Patos Lagoon estuary,  
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56 250 ~400 km south of our study area (Fruet et al., 2015b). We set this value—about 30%  
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3 251 higher than the maximum population size estimated for dolphins in Laguna—not to  
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5 252 restrict population growth by intraspecific competition. This decision can make our  
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7 253 scenarios optimistic; thus, further studies should investigate the effects of competition in  
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10 254 this system to suggest more appropriate K values in future predictions. All males were  
11  
12 255 assumed to be in the breeding pool. Due to the lack of data on inbreeding in Laguna,  
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14 256 inbreeding depression was omitted from the standard models, but its potential effect was  
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17 257 evaluated with sensitivity analyses by varying the number of lethal equivalents, a  
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19 258 common measure of the severity of inbreeding depression (Lacy, Miller & Traylor-  
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21 259 Holzer, 2018). The inputs to the PVA are summarized in Table 1.  
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25  
26 261 *Add table 1 here*  
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30  
31 263 *Modelled scenarios*  
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33 264 The baseline scenario (1) represented the current level of annual bycatch (based  
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35 265 on the annual average from 2016 to 2018 reported by a systematic carcass recovery  
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37 266 programme in the study area), with no management of bycatch. An initial population size  
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39 267 of 60 individuals (Bezamat et al., 2019) was modelled and, since survival estimates used  
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42 268 as inputs were estimated for a previous period (2007-2016; Bezamat et al., 2019) with no  
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44 269 bycatch records, two bycatches were included every year: one juvenile from 2 to 3 years  
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47 270 (alternating between a male and a female) and one adult male (only adult males were  
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49 271 bycaught from 2016 to 2018). To examine the impacts of additional bycatch or the  
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51 272 effectiveness of management actions, five other realistic scenarios were modelled based  
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53 273 on the bycatch records in recent years: (2) baseline scenario plus one adult male killed  
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55 274 every year; (3) baseline scenario, but the annual adult bycatch alternated between a male  
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57  
58 275 and a female; (4) one adult male bycatch every year; (5) one juvenile bycatch every year,  
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3 276 alternating between male and female; (6) zero bycatch. For each model, 1000 simulations  
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5 277 were carried out in a 100-year projection. Model outputs are also presented for a shorter-  
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7 278 term (30 years).  
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### 11 280 *Sensitivity Analyses*

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14 281 Sensitivity analysis was conducted to evaluate which of the survival and  
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16 282 reproductive rate parameters most affected population dynamics (Akçakaya, 2000;  
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18 283 Akçakaya & Sjögren-Gulve, 2000). Based on the baseline scenario, fixed-proportion and  
19  
20 284 observed-variation sensitivity analyses (*sensu* Manlik et al., 2016) were conducted by  
21  
22 285 varying each vital rate by  $\pm 1\%$  or  $\pm 1 \text{ SD}_{\text{EV}}$ , respectively, while holding all other  
23  
24 286 parameters constant, to evaluate the effects of parameter variation on stochastic growth  
25  
26 287 rate ( $r$ ). Each parameter was sampled 1000 times.  
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30 288 For the  $\pm 1\%$  fixed-proportion scenarios, the relative sensitivity ( $S_X$ ) of population  
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32 289 growth rate ( $\lambda = e^r$ ) was calculated to changes in each vital rate, one at a time. Relative  
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34 290 sensitivity was calculated as:

$$35 \quad 291 \quad S_X = \frac{(\lambda_+ - \lambda_-)}{(0.02 \times \lambda_0)}$$

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43 293 where  $\lambda_+$  and  $\lambda_-$  are the population growth rates from the adjusted parameter values,  $\lambda_0$   
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45 294 is the population growth rate of the baseline model, and 0.02 defines the total perturbation  
46  
47 295 of the parameter values ( $\pm 1\%$ ) (see Mortensen & Reed, 2016). For the  $\pm 1 \text{ SD}_{\text{EV}}$   
48  
49 296 observed-variation scenarios, the low-to-high range of population growth rate was  
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51 297 calculated to changes in each vital rate.  
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54 298 The number of lethal equivalents was also varied from 0 to 3.14 (the median value  
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56 299 reported for 38 mammalian species; Ralls, Ballou & Templeton, 1988) and 6.29 (the  
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3 300 combined mean effect of inbreeding on fecundity and first year survival; O'Grady et al.,  
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5 301 2006) to evaluate the potential effect of inbreeding depression.  
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10 303 *Assessing impacts and evaluating management options*  
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12 304 Sensitivity analysis was also used to determine the highest priority management  
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14 305 action by simulating the impacts on population growth rate of decreased adult survival  
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16 306 caused by a hypothetical increase in adult bycatches, and decreased calf survival, which  
17  
18 307 could result from future construction in the lagoon system, if the increased underwater  
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20 308 noise (e.g. pile driving and intense boat traffic) acted to disturb mother-calf bonds  
21  
22 309 (Parsons & Dolman, 2004). The effects of an increase in bycatch on population dynamics  
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24 310 were simulated by gradually adding to the baseline scenario up to four adult male or  
25  
26 311 female removals every year. The potential impact of increased underwater noise was  
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28 312 simulated by reducing first-year calf survival rate by 10, 20, 30, 40, 50, 60, 70, 80 and  
29  
30 313 90%. Survival rate reduced by 50% was similar to the lowest calf survival rate recorded  
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32 314 for free-ranging bottlenose dolphins (0.375; Currey et al., 2009). We evaluated whether  
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34 315 these modelled effects on adult survival or first-year calf survival would have the greatest  
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36 316 influence on population growth rate and thus which vital rate should be a focus for future  
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38 317 management actions.  
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49 319 Results

50 320 *Population Viability Analysis Outputs*

51 321 The baseline model yielded a declining population ( $r = -0.014$ ; Model 1, Figure  
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53 322 2, Table 2). Probability of extinction within 30 years was low (0.058), but within 100  
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55 323 years was high (0.714), and the mean time to extinction was 52.9 years. Mean population  
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57 324 size was 48 dolphins within 30 years (20% reduction) and 20 dolphins within 100 years  
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3 325 (33.3% reduction). Compared to the baseline model, models with one additional male  
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5 326 adult bycatch every year or the replacement of one adult male bycatch with one adult  
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7 327 female bycatch every other year (Models 2 and 3, respectively), resulted in decreased  
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9 328 population growth rates and population sizes, and increased probabilities of extinction,  
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11 329 with all or nearly all populations going extinct within 100 years. Overall, the three  
12  
13 330 management models (avoiding either a juvenile or an adult bycatch, or both bycatches  
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15 331 every year) showed a marked improvement compared to the current conditions, resulting  
16  
17 332 in increases in population growth rate, population size and time to extinction, and lower  
18  
19 333 probabilities of extinction (Models 4, 5 and 6, Table 2) over the baseline model. Although  
20  
21 334 avoiding the bycatch of one juvenile or one adult every year (Models 4 and 5,  
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23 335 respectively) led to a considerable improvement over baseline, the 'zero bycatch' (Model  
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25 336 6) was the only model that resulted in a positive growth rate and zero risk of extinction  
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27 337 within 100 years.  
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35 339 *Add table 2 here*

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39 341 *Add figure 2 here*

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43 343 *Sensitivity Analyses*

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45 344 Population growth rate ( $r$ ) was most sensitive to proportional changes in adult  
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47 345 female and juvenile survival rates (Table 3). Proportional changes in reproductive rates,  
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49 346 calf (irrespective of whether it was a male or female) and male adult survival rates had  
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51 347 relatively little effect on population growth rate (Table 3). In terms of relative sensitivity,  
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53 348 female adult survival rate (relative sensitivity = 1.22) followed by female juvenile  
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55 349 survival rate (relative sensitivity = 0.74) were most influential on the population  
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3 350 dynamics. Conversely, in the observed-variation scenarios, the low-to-high range of  
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5 351 population growth rates was greater for reproductive rates ( $\Delta \lambda\% = 5.3$ ) than other  
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8 352 parameters (Table 3). Because there is more natural variation in birth rates, its impact on  
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10 353 population dynamics is greater, in absolute terms. Inbreeding had a negligible effect  
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12 354 (Table 3).

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17 356 *Add table 3 here*

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21 358 *Assessing impacts and evaluating management options*

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24 359 The effects of a hypothetical gradual increase in bycatch and the potential impact  
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26 360 of intense boat traffic and pile driving (i.e. reduced first-year calf survival) on growth rate  
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28 361 are presented on Figure 3. These sensitivity analyses confirmed that growth rate was most  
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30 362 sensitive to a gradual increase in adult female bycatch. The addition of one female  
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32 363 removal annually resulted in a rate of decline ( $r = -0.0963$ ) more than double that resulting  
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34 364 from the addition of one adult male bycatch every year ( $r = -0.0432$ ), and similar to a  
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36 365 reduction in 90% in calf survival rate ( $r = -0.1049$ ; Figure 3). The impact on population  
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38 366 dynamics caused by the addition of one adult male bycatch every year ( $r = -0.0432$ ) was  
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40 367 equivalent to a 30% reduction in calf survival ( $r = -0.0417$ ; Figure 3), and the addition of  
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42 368 two adult male bycatches annually ( $r = -0.0493$ ) was equivalent to a 40% reduction in  
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44 369 calf survival ( $r = -0.0488$ ; Figure 3). Thus, the influence on population growth rate of  
45  
46 370 reduction in adult survival rates (especially of females) due to increased bycatch was  
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48 371 greater than the reduction in first-year calf survival rate that could result from the  
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50 372 disturbance effects of underwater noise.

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54 374 *Add figure 3 here*

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5 376 Discussion

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7 377 The viability of the small Lahille's bottlenose dolphin population in Laguna was  
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9 378 evaluated using the best demographic parameters estimates available. Population size has  
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11 379 remained apparently stable from 2007 to 2016 (Bezamat et al., 2019), but bycatch has  
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13 380 been increasing since 2016. Under current conditions of two bycatches every year on  
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15 381 average (one juvenile and one adult male), the baseline scenario forecasts a declining  
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17 382 population ( $r = -0.014$ ), with a chance of extinction in the next 30 years (PE = 0.058), and  
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19 383 a high probability of extinction in the next 100 years (PE = 0.714). If bycatch increases,  
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21 384 the population is doomed to extinction. Conversely, avoiding bycatch would increase  
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23 385 population growth and lower probabilities of extinction. As expected, population growth  
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25 386 rate was most sensitive to proportional changes in adult female and juvenile survival.  
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27 387 However, population dynamics were more influenced by observed absolute variation in  
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29 388 birth rate than in survival. When comparing the relative effects of human impacts (i.e.  
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31 389 additional bycatches leading to increased adult mortality vs reduced calf survival) on  
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33 390 population dynamics, the population growth rate was more sensitive to changes in adult  
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35 391 bycatch (especially females) than to a reduction in calf survival. Combined, our results  
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37 392 indicate that only a zero-bycatch management strategy can lead to the persistence of this  
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39 393 dolphin population in the long term.

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41 394 Population viability was greatly affected by incidental bycatch. Projections  
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43 395 indicated that the current level of bycatch mortality in Laguna is unsustainable. Several  
44  
45 396 recovered carcasses have shown evidence of entanglement in fishing gear (Bezamat et  
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47 397 al., 2019). Many individuals have been photographed with scars or nets and lines around  
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49 398 their bodies, including a young calf in early December 2017 (Bezamat et al., 2020) and  
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51 399 two adults that died that same year, 20 and 27 months after being entangled. For small  
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3 400 populations like this, it is well-known that the removal of even a single individual each  
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5 401 year, especially females, may have a great impact on the population viability (see  
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7 402 Burgman, Ferson & Akçakaya, 1993, for the classic example of white rhinoceros  
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9 403 *Ceratotherium simum simum*). For another cetacean species—the humpback dolphin  
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11 404 *Sousa chinensis*, for instance, a single non-natural death in the critically endangered  
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13 405 population in the eastern Taiwan Strait exceeds the potential biological removal (PBR)  
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15 406 level, which was estimated as one individual every 7 years (Slooten et al., 2013). Only  
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17 407 the most optimistic mitigation of bycatch—a zero bycatch scenario—would make the  
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19 408 difference between a declining and an increasing population, greatly improving the  
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21 409 chances of long-term persistence of Lahille’s bottlenose dolphins in Laguna. The largest  
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23 410 population of Lahille’s bottlenose dolphins, in the Patos Lagoon estuary, shows great  
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25 411 chances of persistence under current levels of bycatch, but a slight increase of bycatches,  
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27 412 particularly of adult females, would have also severe consequences for the population  
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29 413 dynamics and chance of persistence (Fruet, Möller & Secchi, 2021).

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35 414 Population growth rates for dolphins in Laguna were more sensitive to  
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37 415 proportional changes in adult and juvenile survival but long-term observed variations in  
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39 416 reproductive rates—estimated from 2007 to 2017 (Bezamat et al., 2020)—had a greater  
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41 417 impact on growth rates and population size ( $N_{100}$ ) forecasts in absolute terms. This finding  
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43 418 is similar to Indo-Pacific common dolphin *Tursiops aduncus* populations off Australia  
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45 419 (Manlik et al., 2016) and a killer whale *Orcinus orca* population of the north-eastern  
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47 420 Pacific Ocean (Lacy et al., 2017). These two previous studies, with different cetacean  
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49 421 species, highlight the importance of natural variation in reproduction on population  
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51 422 viability, warning that management actions to reverse or prevent population declines  
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53 423 should address both survival and reproduction. While fixed-proportion sensitivity  
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55 424 analyses have been commonly used to evaluate the importance of vital rates for  
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3 425 population viability, the observed-variation analyses reflect variability likely to occur in  
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5 426 wild populations, offering insight into feasibility and effectiveness of management  
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7 427 options (Manlik et al., 2016).  
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10 428 In Laguna, adult survival rates were relatively constant from 2007 to 2016  
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12 429 (Bezamat et al., 2019), whereas reproductive rates showed a large temporal variation  
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14 430 (Bezamat et al., 2020). Birth rates in small populations are naturally variable, but it is  
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16 431 more challenging to identify management options that directly influence reproduction to  
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18 432 improve population viability. Therefore, a management focused on improving survival  
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20 433 by reducing bycatch seems to be an effective option. However, identifying which non-  
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22 434 natural factors, if any, influence reproduction and thus population viability is key. For  
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24 435 instance, increased boat traffic seems to affect dolphins' reproductive behaviours  
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26 436 (Lusseau et al. 2006). Particularly in Laguna, boat traffic affects dolphin's acoustic  
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28 437 behaviour during the interaction with artisanal fishers (Pellegrini et al., 2021). Further  
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30 438 studies should investigate the potential impact of boat traffic on reproduction in this  
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32 439 population, and managing boat traffic should be considered in management actions.  
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37 440 Evaluation based on the sensitivity analyses of the potential impact of additional  
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39 441 bycatches and decreased calf survival showed that bycatch of adult females had the  
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41 442 greatest influence on population growth rate and should be immediately eliminated—as  
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43 443 expected for mammals with a polygynous mating system in which a single male can mate  
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45 444 with multiple receptive females in a given year (Breed & Moore, 2015). The influence of  
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47 445 bycatch on probability of extinction is also biased towards females in the population of  
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49 446 Indo-Pacific humpback dolphins in the eastern Taiwan Strait (Araújo et al., 2014). In that  
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51 447 case, PVA showed that the probability of population decline within 100 years was 91.7%  
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53 448 when removing one additional female from the population every year, and 78.4% when  
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55 449 removing one additional male every year (Araújo et al., 2014). As also reported for Indo-  
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3 450 Pacific humpback dolphins, sensitivity analysis showed that breeding females are  
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5 451 extremely important in the Laguna population, suggesting that a higher recruitment rate  
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7 452 is needed to increase population growth rate. The influence of additional male mortality  
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9 453 on population growth rate, was lower than female mortality. However, neither of these  
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11 454 studies, the Indo-Pacific humpback dolphins in the Taiwan Strait and Lahille's bottlenose  
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13 455 dolphins in Laguna, considered the genetics effect and the contribution of males for gene  
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15 456 distribution. This could be an important component for dolphins in Laguna and it should  
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17 457 be included in further assessments, since this population has the lowest genetic variability  
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19 458 among the small discrete populations of Lahille's bottlenose dolphins (Fruet et al., 2014).

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23 459 Although the influence of reduced calf survival as a potential impact of planned  
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25 460 developments in the lagoon system was lower than an increase in adult female bycatch,  
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27 461 it was not negligible. A dredging operation associated with the maintenance of the Laguna  
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29 462 harbour is expected to take place shortly to increase the channel depth, and consequently  
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31 463 increase boat traffic, in a transit and core area for the dolphins, where most of the  
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33 464 cooperative sites are located. An increase in boat traffic would increase the risk of  
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35 465 dolphins being killed or injured by boat collisions, especially calves. Besides that, an  
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37 466 increase in underwater noise could also potentially decrease calf survival due to  
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39 467 communication masking between mothers and their calves (Parsons & Dolman, 2004),  
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41 468 but we have no information to quantify the extent of such an effect, nor whether there  
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43 469 may be other impacts on population dynamics.

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47 470 Effects of dredging on marine mammals varies with species, location and dredging  
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49 471 equipment type (Todd et al., 2014). Overall, more likely effects include acoustic masking,  
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51 472 avoidance and short-term changes to behaviour, and prey availability (Todd et al., 2014).  
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53 473 High intensities of dredging caused bottlenose dolphins to spend less time in a foraging  
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55 474 patch in Aberdeen harbour, Scotland, and ultimately leave the harbour completely for  
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3 475 approximately five weeks (Pirootta et al., 2013). In Laguna, the dredging events and the  
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5 476 associated increase in boat traffic must be considered in management actions, since it can  
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7 477 impact calf survival and affect behavioural patterns such as foraging, but also  
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9 478 reproduction (Lusseau et al., 2006), which seems key for population viability. Another  
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11 479 potential development in Laguna in the near future is the construction of a wind farm,  
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13 480 which is still being discussed, but which may also compromise habitat quality for the  
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15 481 dolphins. Should this development go forward, mitigation measures such as those that  
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17 482 have been used elsewhere should be considered in Laguna, such as reducing underwater  
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19 483 noise of pile driving using air bubble curtains (e.g. Jefferson, Hung & Wu, 2009; Dähne  
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21 484 et al., 2017).

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26 485         Nevertheless, increased underwater noise—from intense boat traffic and regular  
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28 486 dredging operations and constructions—is not the only factor that could contribute to a  
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30 487 reduction in calf survival. Increased levels of persistent organic pollutants, especially  
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32 488 PCBs, and decreased resource availability could add in reducing calf survival as well  
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34 489 (Reddy et al., 2001; Wells et al., 2005). Dolphins in Laguna are exposed to contaminants  
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36 490 and some biopsied individuals have shown high blubber PCB levels (Righetti et al.,  
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38 491 2019). Females transfer PCBs to their calves through the placenta and during lactation,  
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40 492 which may increase the chances of fetal and first-year calf mortality (Reddy et al., 2001;  
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42 493 Wells et al., 2005), and potentially depress population growth rates (Hall et al., 2006).  
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44 494 Moreover, since lactation is the most energetically demanding time of reproduction,  
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46 495 females need a great abundance of food at this stage (Kastelein et al., 2002; Rechsteiner  
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48 496 et al., 2013). Thus, a decrease in resource availability could compromise calf nutrition  
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50 497 and reduce its chances of survival; calves born just after the peak of the mullet season  
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52 498 have been shown to have higher chances of survival (Bezamat et al., 2020).  
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3 499 Management actions to reduce the current anthropogenic pressures to this small  
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5 500 Lahille's bottlenose dolphin population are needed immediately. The present level of  
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7 501 bycatch in Laguna is unsustainable and thus a reduction in associated mortality is an  
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9 502 urgent priority. To achieve this, a Municipal Law (N° 222 033/2018) has recently banned  
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11 503 the trammel net fishery in the dolphins' core area. This restriction is essential and new  
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13 504 management actions should consider the need and possibilities to expand this area in the  
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15 505 near future, to include not only the dolphins' core area, but their entire distribution area  
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17 506 in the lagoon system. However, even after the implementation of this restricted fishing  
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19 507 area, systematic beach monitoring during 2018 and 2019 reported four non-natural  
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21 508 deaths, three likely by bycatch and one likely by boat collision (P.V. Castilho,  
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23 509 unpublished data), which suggests that enforcement was insufficient, compromising the  
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25 510 effectiveness of the fishing ban in the early years. In 2019, the Santa Catarina Institute of  
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27 511 Environment (IMA) defined a State Action Plan (SAP) in which the main aims are to  
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29 512 reduce the trammel net bycatch and regulate boat traffic and noise pollution, and  
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31 513 guarantee the habitat quality. As the first action and results motivated by the  
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33 514 implementation of the SAP, continued enforcement operations were articulated and then  
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35 515 no bycatch events were reported throughout 2020—although ~20 gillnets illegally  
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37 516 distributed in the area were removed, suggesting that illegal fisheries continue despite the  
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39 517 recent restrictions.

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46 518 Therefore, besides a permanent and strict enforcement, the local fishing  
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48 519 community needs to be better involved in conservation actions. Interestingly, fishers who  
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50 520 cooperate with dolphins perceive multiple values from their occurrence in Laguna and  
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52 521 their interaction with them. This close relationship between dolphins and fishers is an  
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54 522 opportunity to better engage fishers in an alternative co-management strategy to help  
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56 523 monitor the banned fishery or even change how some fishers behave (Machado et al.,  
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3 524 2019). Engaging these fishers would be facilitated if they clearly understood the need for  
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5 525 zero bycatch to increase the probability that this dolphin population and the dolphin-fisher  
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7 526 interaction will persist in the long-term. Our results can be used by managers to highlight  
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9 527 how essential the elimination of bycatch is to population viability, as well as  
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11 528 complementary measures to regulate increasing boat traffic and other habitat  
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13 529 perturbations that can affect dolphin reproduction. Finally, our results reinforce how  
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15 530 vulnerable the Lahille's bottlenose dolphin subspecies is, since its largest population—in  
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17 531 the Patos Lagoon estuary—is likely to decline with any increase in bycatches (Fruet,  
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19 532 Möller & Secchi, 2021), and the second largest population—in Laguna—have a great  
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21 533 chance of being extinguished with the current bycatch rates.  
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#### 52 53 546 Conflict of interest

54  
55 547 The authors declare that they have no conflict of interests.

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3 549 CRediT authorship contribution statement  
4  
5 550 C.B.: Conceptualization, formal analysis, fieldwork, writing - original draft, writing -  
6  
7 551 review & editing; F.G.D.J.: Conceptualization, coordination, supervision, formal  
8  
9 552 analysis, writing - review & editing, funding acquisition; P.S.H.: Supervision, formal  
10  
11 553 analysis, writing - review & editing. P.V.C.: Fieldwork, funding acquisition, writing -  
12  
13 554 review & editing; P.C.S.L.: Funding acquisition, writing - review & editing. All authors  
14  
15 555 read and approved the final manuscript.  
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3 917 Tables:  
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6 918 Table 1: Summary of demographic parameters used as input data in the modeling of the  
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8 919 viability of the bottlenose dolphin population in Laguna, Brazil. Standard deviations due  
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10 920 to environmental variation are shown in parenthesis.  
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Parameter	Value	Reference
Percent of females breeding yr <sup>-1</sup>	32.8 (± 10.0)	Bezamat et al., 2020
1 <sup>st</sup> year calf survival (%)	78.0 (± 7.0)	Bezamat et al., 2020
2 <sup>nd</sup> year calf survival (%)	83.0 (± 9.0)	Bezamat et al., 2020
Adult = Juvenile survival (%)		
Females	95.7 (± 1.3)	Bezamat et al., 2019
Males	93.6 (± 1.9)	Bezamat et al., 2019
Initial population size	60	Bezamat et al., 2019
Age at first offspring		Bezamat et al., 2020
(females/males)	10/11	
Maximum age of reproduction	45	Hohn et al., 1989,
Maximum observed age	50	Wells & Scott, 1999
Sex ratio at birth (% males)	50	Caughley, 1977
Carrying capacity	90	

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34 922 Table 2: Summary of the results of the Population Viability Analysis for six scenarios of  
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36 923 bycatch mortality of bottlenose dolphins in Laguna, Brazil. Shown are stochastic growth  
37  
38 924 rate (stoch-r) and its standard deviation (SD), population size after 30 years (N<sub>30</sub>) and 100  
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40 925 years (N<sub>100</sub>) and their SD, and probability of extinction after 30 years (PE<sub>30</sub>) and 100 years  
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42 926 (PE<sub>100</sub>). M: male, F: female.  
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Bycatch scenarios	stoch-r	SD (r)	N <sub>30</sub>	SD (N <sub>30</sub> )	PE <sub>30</sub>	N <sub>100</sub>	SD (N <sub>100</sub> )	PE <sub>100</sub>
(1) Baseline:								
1 Juvenile M/F + 1 Adult M yr <sup>-1</sup>	-0.0143	0.0782	48	22.1	0.058	20	32.0	0.714
(2) 1 Juvenile M/F + 2 Adults M yr <sup>-1</sup>	-0.0426	0.0763	16	7.2	0.861	0	0.0	1.000
(3) 1 Juvenile M/F + 1 Adult M/F yr <sup>-1</sup>	-0.0480	0.1172	31	16.4	0.018	1	7.5	0.959
(4) 1 Adult M yr <sup>-1</sup>	-0.0047	0.0666	66	21.4	0.023	57	38.0	0.291
(5) 1 Juvenile M/F yr <sup>-1</sup>	-0.0040	0.0646	68	15.5	0.000	68	21.7	0.006
(6) Zero bycatch	0.0139	0.0561	80	11.2	0.000	84	7.4	0.000

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929 Table 3: Effects of fixed-proportion ( $\pm 1\%$ ) and observed-variation changes ( $\pm 1 \text{ SD}_{\text{EV}}$ )  
 930 in the input parameters on stochastic growth rate ( $r$ ) for the bottlenose dolphins in Laguna,  
 931 Brazil. Relative sensitivity ( $S_X$ ) of population growth rates ( $\lambda$ ) is shown for the fixed-  
 932 proportion scenarios, and low-to-high range ( $\Delta \lambda\%$ ) is shown for the observed-variation  
 933 scenarios.

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	Growth rate ( $r$ )			$S_X$	$\Delta \lambda\%$
	Low	Base	High		
<b><i>Fixed-proportion</i></b>					
Reproduction	-0.0156	-0.0143	-0.0132	0.12	-
1st year calf survival	-0.0156	-0.0143	-0.0132	0.12	-
2nd year calf survival	-0.0155	-0.0143	-0.0140	0.07	-
<b><i>Juvenile survival</i></b>					
Females	-0.0218	-0.0143	-0.0069	0.74	-
Males	-0.0171	-0.0143	-0.0118	0.26	-
<b><i>Adult survival</i></b>					
Females	-0.0266	-0.0143	-0.0022	1.22	-
Males	-0.0151	-0.0143	-0.0138	0.06	-
Inbreeding	-0.0142	-0.0143	-0.0142	-	-
<b><i>Observed-variation</i></b>					
Reproduction	-0.0406	-0.0143	0.0131	-	5.30
1st year calf survival	-0.0243	-0.0143	-0.0047	-	1.93
2nd year calf survival	-0.0268	-0.0142	-0.0021	-	2.43
<b><i>Juvenile survival</i></b>					
Females	-0.0238	-0.0142	-0.0046	-	1.89
Males	-0.0207	-0.0143	-0.0099	-	1.06
<b><i>Adult survival</i></b>					
Females	-0.0306	-0.0142	0.0016	-	3.17
Males	-0.0159	-0.0143	-0.0131	-	0.28

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3 937 Figure legends:  
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8 939 Figure 1: Study area: the coastal lagoon system adjacent to Laguna, southern Brazil. The  
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10 940 red line shows the predefined sampling route for the long-term individual-based  
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12 941 monitoring. The blue circles are the main sites where dolphins and fishers interact. The  
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14 942 green line shows the dolphins' core area, and the yellow area shows where trammel net  
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16 943 fishing has been banned.  
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21 945 Figure 2: Predicted trajectories of mean population size for the six scenarios of annual  
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23 946 bycatch mortality of bottlenose dolphins in Laguna, southern Brazil. Numbers refer to  
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25 947 models in Table 2. Dashed vertical line highlights the population trajectory after 30 years.  
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30 949 Figure 3: Sensitivity analysis. Effect of additional adult (a) male and (b) female bycatches  
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32 950 and (c) different first year calf survival rates on stochastic growth rate ( $r$ ) forecasts.  
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3 1 Dolphin population specialized in foraging with artisanal fishers requires zero-bycatch  
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5 2 management to persist  
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10 4 Carolina Bezamat<sup>1</sup>, Philip S. Hammond<sup>2</sup>, Pedro V. Castilho<sup>3</sup>, Paulo C. Simões-Lopes<sup>1</sup>,  
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12 5 Fábio G. Daura-Jorge<sup>1</sup>  
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20 9 Andrews, UK  
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32  
33 14 Abstract  
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35 15 1. The small population paradigm assumes that populations with low numbers of  
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37 16 individuals intrinsically have a high probability of extinction. The small  
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39 17 population of Lahille's bottlenose dolphins *Tursiops truncatus gephyreus* that  
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41 18 specializes in foraging with artisanal fishers in Laguna, southern Brazil, faces  
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43 19 human pressures including bycatch in fishing gear. The viability of this population  
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45 20 was modelled over 30 and 100 years under different levels of bycatch, including  
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47 21 the current scenario of two bycatches every year, two scenarios with higher  
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49 22 incidence of bycatches, and three management scenarios. The sensitivity of  
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51 23 predicted growth rates to fixed-proportion and observed-variation changes in life  
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53 24 history parameters was explored.  
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3 25 2. The current scenario predicted a declining population ( $r=-0.014$ ;  $\lambda=0.986$ ) with a  
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5 26 high probability of extinction in the long term ( $PE=0.71$ ). A small increase in  
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7 27 bycatches, would result in a marked increase in the probability of extinction.  
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10 28 Management scenarios seem promising, but only the zero-bycatch management  
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12 29 would make the difference between a declining and an increasing population.  
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14 30 3. As expected for slow-growing species, population growth rate was most sensitive  
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16 31 to proportional changes in adult female and juvenile survival. However,  
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18 32 considering observed variation in vital rates, population dynamics were most  
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20 33 influenced by variation in reproductive rates.  
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23 34 4. To determine the highest priority for management action, another simulation was  
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25 35 made of how additional threat scenarios of recognized human activities (i.e.  
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27 36 bycatch influencing adult survival and increased underwater noise or pollution  
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29 37 influencing calf survival) would affect population dynamics. Population growth  
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31 38 rate was very sensitive to changes in adult bycatch (especially females), as  
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33 39 expected, and only subtly sensitive to a reduction in calf survival.  
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36 40 5. The current level of bycatch is unsustainable. Bycatch needs to be eliminated to  
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38 41 maximize the probability of long-term persistence of this dolphin population. Still,  
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40 42 this population's persistence could be threatened by natural variation in  
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42 43 reproductive rates.  
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45 Keywords: bottlenose dolphins, Population Viability Analysis, *Tursiops truncatus*  
46 *gephyreus*, bycatch, conservation, sensitivity analysis, wildlife management.

## 48 Introduction

49 In conservation biology, the small population paradigm focuses on population-  
50 level processes primarily to identify minimum viable population sizes and extinction risk

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3 51 (Shaffer, 1981; Gilpin & Soulé, 1986) in face of both demographic and environmental  
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5 52 stochasticity (May, 1973). The smaller the population, the more susceptible it is to  
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7 53 extinction from stochastic processes. Stochastic perturbations include natural variation in  
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9 54 reproductive and survival rates (demographic stochasticity), and reduction of genetic  
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11 55 variability and inbreeding depression (genetic stochasticity). Stochasticity can also be  
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13 56 generated by natural or anthropogenic fluctuations in environmental conditions  
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15 57 (environmental stochasticity) or, in extreme situations, by environmental catastrophes  
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17 58 (Shaffer, 1981; Caughley, 1994). By including stochasticity in population-level  
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19 59 processes, it is possible to better predict how current threats affect the viability of small  
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21 60 populations.  
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26 61 Population viability analysis (PVA) is a powerful modelling tool for examining  
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28 62 the risks posed by different threats to the persistence of small populations over time  
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30 63 (Boyce, 1992; Akçakaya & Sjögren-Gulve, 2000). PVA is helpful in evaluating the  
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32 64 effectiveness of management alternatives, which can assist conservation decision-making  
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34 65 (Drechsler & Burgman, 2004). PVA estimates a population's (or species') risk of  
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36 66 extinction through stochastic simulations of demographic and life-history parameters in  
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38 67 different scenarios (Beissinger & Westphal, 1998). With robust estimates of life history  
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40 68 parameters, a challenging task that requires long-term studies, PVA can reliably assess a  
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42 69 population's status (e.g. Kraus et al., 2001; Runge, Langtimm & Kendall, 2004; Currey  
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44 70 et al., 2011).  
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49 71 An additional valuable output of a PVA is the identification of the key life history  
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51 72 parameters that influence the dynamics of the population under study (e.g. Manlik et al.,  
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53 73 2016; Lacy et al., 2017). Traditionally, for slow-growing populations, including  
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55 74 cetaceans, several studies have shown that female survival tends to influence population  
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57 75 growth more significantly than reproduction (e.g. Caughley, 1966; Heppell et al., 2000;  
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3 76 Young & Edward, 2011). Therefore, conservation strategies should aim to increase adult  
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5 77 survival in order to be more effective (van de Kerk et al., 2013). However, a number of  
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7 78 studies has questioned this generalization (e.g. Mills, Doak & Wisdom, 1999; Morris &  
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9 79 Doak, 2002), suggesting that the importance of vital rates for conservation depends on  
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11 80 their observed variation and chance of being manipulated by management actions. In this  
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13 81 context, even for slow-growing population with long life expectancy, investigating the  
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15 82 influence of each vital parameter on population growth is then crucial for making wildlife  
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17 83 management decisions.

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21 84 PVA has been used to assess a number of marine mammal species, including  
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23 85 manatees *Trichechus manatus latirostris* (Marmontel, Humphrey & O'Shea, 1997),  
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25 86 southern elephant seals *Mirounga leonina* (McMahon et al., 2005), killer whales *Orcinus*  
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27 87 *orca* (Lacy et al., 2017), Indo-Pacific humpback dolphins *Sousa chinensis* (Araújo et al.,  
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29 88 2014), Hector's dolphins *Cephalorhynchus hectori* (Burkhart & Slooten, 2003), and  
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31 89 common bottlenose dolphins *Tursiops truncatus* (Thompson et al., 2000) and Indo-  
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33 90 Pacific common dolphins *Tursiops aduncus* (Manlik et al., 2016). Adult survival is,  
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35 91 indeed, as observed for many slow breeding and slow growing species, a key vital rate  
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37 92 for marine mammals, as shown in the modelling of the Florida manatee (Marmontel,  
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39 93 Humphrey & O'Shea, 1997). However, natural variability in birth rate can also influence  
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41 94 cetacean's population growth more than natural variability in mortality, as found in PVAs  
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43 95 of Indo-Pacific common dolphins off Australia and killer whales in the northeastern  
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45 96 Pacific Ocean (Manlik et al., 2016; Lacy et al., 2017).

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51 97 Several globally abundant species are exposed to human pressures that threaten  
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53 98 local populations. The common bottlenose dolphin *Tursiops truncatus* is one of these  
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55 99 species, with its global conservation status classified as Least Concern on the IUCN Red  
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57 100 List (Hammond et al., 2012). However, although some populations inhabiting coastal  
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3 101 waters are stable or increasing (e.g. Arso-Civil et al., 2019), others have declined (Currey  
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5 102 et al., 2009; Félix et al., 2017). Coastal populations are especially vulnerable because their  
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7 103 distributional ranges overlap with human activities (Reeves & Reijnders, 2002; Reeves et  
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9 104 al., 2003). PVA of the bottlenose dolphin population from eastern Scotland illustrates  
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11 105 how it can be informative to stakeholders in consideration of precautionary management  
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13 106 actions to deal with human pressures that threaten local populations (Thompson et al.,  
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15 107 2000).

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19 108 In the Southwestern Atlantic Ocean, morphological and genetic distinctions  
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21 109 between coastal and offshore bottlenose dolphins suggests adaptation to different habitats  
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23 110 (Costa et al., 2016; Wickert et al., 2016; Fruet et al., 2017; Costa et al., 2019).  
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25 111 Consequently, the Society for Marine Mammalogy has recognized the coastal bottlenose  
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27 112 dolphins as the subspecies *Tursiops truncatus gephyreus* (Lahille's bottlenose dolphin),  
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29 113 consisting of small discrete populations with high site fidelity to estuaries (Fruet et al.,  
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31 114 2014). Although robust data on these regional coastal populations are limited, the small  
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33 115 number of individuals (likely no more than 600 individuals in total), evidence of  
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35 116 declining, and the low genetic variability, motivated a recent regional assessment that  
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37 117 classified the subspecies as Vulnerable (Vermeulen et al., 2019). In fact, the first risk  
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39 118 assessment for Lahille's bottlenose dolphins confirms that its largest population in the  
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41 119 Patos Lagoon estuary, southern Brazil, ~~—and probably the other smaller populations of~~  
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43 120 ~~the subspecies—~~ is vulnerable to any increase in non-natural mortality (Fruet, Möller &  
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45 121 Secchi, 2021). The other smaller populations of this subspecies are probably in the same  
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47 122 situation.

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53 123 One of these coastal populations of this subspecies is found in Laguna, southern  
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55 124 Brazil. It is a resident population of about 60 animals (Bezamat et al., 2019)—one of the  
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57 125 largest populations among all population units (*sensu* Fruet et al. 2014) of the  
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3 126 subspecies—, in which some individuals specialize in interaction with artisanal net-  
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5 127 casting fishers in apparently cooperative foraging (Simões-Lopes, Fabián & Menegheti,  
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7 128 1998; Simões-Lopes, Daura-Jorge & Cantor, 2016). Cooperative dolphins drive the  
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9 129 schools of fish towards the fishers that are waiting in shallow waters; fishers recognize  
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11 130 dolphins' stereotyped behaviours as cues indicating when and where they should cast  
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13 131 their nets (Simões-Lopes, Daura-Jorge & Cantor, 2016). Fishers benefit from this  
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15 132 interaction by catching more fish and, apparently, dolphins accrue similar benefits  
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17 133 (Simões-Lopes, Fabián & Menegheti, 1998).

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21 134 This foraging tactic influences the dolphins in a number of ways at both individual  
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23 135 and population level, such as in population social structure (Daura-Jorge et al., 2012),  
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25 136 acoustic behaviour (Romeu et al., 2017) and spatial habitat use (Cantor, Simões-Lopes &  
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27 137 Daura-Jorge, 2018). The frequency of use of this foraging specialization varies among  
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29 138 individuals. However, all dolphins interact with each other and their home ranges overlap,  
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31 139 which may contribute to only a mild effect of cooperative foraging on survival and  
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33 140 reproduction (Bezamat et al., 2019; Bezamat et al., 2020). Calving is seasonal, with most  
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35 141 births occurring during late spring and summer, and calf survival seems to be affected by  
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37 142 the proximity of birth to the peak of the mullet fishing season, when resource availability  
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39 143 is high (Bezamat et al., 2020). Dolphin distribution in Laguna overlaps considerably with  
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41 144 human activities, which is a cause of concern for the viability of this small population.

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45 145 The dolphins in Laguna are subject to multiple anthropogenic pressures including  
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47 146 bycatch, the cumulative effect of pollutants, boat collisions, and anthropogenic noise  
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49 147 (Daura-Jorge, Ingram & Simões-Lopes, 2013; Bezamat et al., 2019; Righetti et al., 2019;  
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51 148 Bezamat et al., 2020). Dolphins are often accidentally entangled, injured, or killed in  
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53 149 trammel nets placed near the fishers-dolphin cooperation area overnight to catch catfish  
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57 150 *Genidens barbatus* (Simões-Lopes, 1991; Peterson, Hanazaki & Simões-Lopes, 2008;  
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3 151 Bezamat et al., 2019). Recently, this fishery was banned in the dolphins' core area  
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5 152 (Laguna, municipal law number 1.998/2018) but it continues to occur because  
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7 153 enforcement is insufficient due to lack of resources. Incidental bycatch is probably the  
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9 154 major conservation issue for small cetaceans worldwide (Reeves et al., 2003).  
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11 155 Unsustainable bycatch in local fisheries was probably the main cause of the extinction of  
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13 156 the baiji *Lipotes vexillifer* in the Yangtze River (Turvey et al., 2007). Other populations  
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15 157 and species are seriously threatened by entanglement mortality, such as the vaquita  
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17 158 *Phocoena sinus* (Taylor et al., 2017; Jaramillo-Legorreta et al., 2019), the Māui dolphin  
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19 159 subspecies *Cephalorhynchus hectori maui* (Slooten, 2007) and the Mahakam River  
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21 160 (Indonesia) population of Irrawaddy dolphins *Orcaella brevirostris* (Smith, Beasley &  
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23 161 Kreb, 2003).

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27  
28 162 Pollutants such as PCBs might also affect dolphins in Laguna; blubber PCB  
29  
30 163 concentrations in some biopsied dolphins exceeded toxicity thresholds (Righetti et al.,  
31  
32 164 2019). PCBs are known to reduce infant survival (Reddy et al., 2001; Wells et al., 2005)  
33  
34 165 and affect the immune system and consequently disease susceptibility (Desforges et al.,  
35  
36 166 2016). In fact, an increase in the number of dolphins with Lobomycosis-like disease, a  
37  
38 167 chronic dermal infection that affects small cetaceans, has been observed (Daura-Jorge &  
39  
40 168 Simões-Lopes, 2011). Susceptibility to Lobomycosis-like disease could be enhanced by  
41  
42 169 the very low genetic variability of this population (Fruet et al., 2014). Boat collision is  
43  
44 170 also a recognized threat. Recently, a one-month-old calf was found dead, and the necropsy  
45  
46 171 revealed a blunt trauma injury on its cervical spine, evidence that it was probably hit by  
47  
48 172 a boat (Bezamat et al., 2020). Anthropogenic noise from daily boat traffic and local  
49  
50 173 activities (e.g. pile driving) also have the potential to mask communication between  
51  
52 174 mothers and their calves, and consequently increase calf mortality (Bezamat et al., 2020).  
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3 175 Noise could affect foraging success because dolphins use echolocation to detect prey  
4  
5 176 (Papale et al., 2015).  
6

7  
8 177 In this study, a PVA modelling framework was applied to investigate the long-  
9  
10 178 term viability of the small [Lahille's](#) bottlenose dolphin population in Laguna, Brazil.  
11  
12 179 Based on estimates of demographic rates from long-term individual-based monitoring of  
13  
14 180 this population (Bezamat et al., 2019; Bezamat et al., 2020), PVA was used to: 1) model  
15  
16 181 the viability of this population over 30 and 100 years under different levels of annual  
17  
18 182 bycatch mortality, including the baseline (current conditions), two scenarios that assume  
19  
20 183 realistic higher incidence of bycatches (based on the bycatch records in recent years), and  
21  
22 184 a number of management scenarios to limit bycatch; 2) identify the life history parameters  
23  
24 185 to which the population dynamics were most sensitive; and 3) determine the highest  
25  
26 186 priority management action by simulating how additional threat scenarios of recognized  
27  
28 187 human activities (i.e. bycatch influencing adult survival and increased underwater noise  
29  
30 188 or pollution influencing calf survival) would affect population dynamics. Based on the  
31  
32 189 PVA results, recommendations are made on priorities for the management of human  
33  
34 190 activities and protection of this dolphin population that interacts with fishers from  
35  
36 191 extinction in the near future.  
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## 43 193 Methods

### 44 194 *Population Viability Analysis Inputs*

45  
46 195 Population viability analyses (PVAs) and sensitivity analyses of the year-round,  
47  
48 196 resident population of common bottlenose dolphins in Laguna (28°20'S, 48°50'W; Figure  
49  
50 197 1), southern Brazil, were conducted using software Vortex (version 10, available at  
51  
52 198 [www.vortex10.org/Vortex10.aspx](http://www.vortex10.org/Vortex10.aspx)) (Lacy, 1993; Lacy, 2000; Lacy & Pollak, 2018).  
53  
54 199 Vortex runs individual-based simulations to model the effects of deterministic factors and  
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1  
2  
3 200 demographic, environmental, and genetic stochasticity on population dynamics (Lacy,  
4  
5 201 1993). Essentially, Vortex creates a representation of each animal and follows the fate of  
6  
7  
8 202 the animal throughout its life. ~~The population dynamics are~~ then modelled as discrete,  
9  
10 203 ~~sequential events (e.g. births, deaths, catastrophes, etc.) that occur according to defined~~  
11  
12 204 ~~probabilities, which can be constants or random variables that follow specified theoretical~~  
13  
14 205 ~~distributions. These probabilities come from population parameters (survival~~  
15  
16 206 ~~probabilities, reproduction rate, migration rate, etc.), and their uncertainty (defined by~~  
17  
18 207 ~~their observed standard errors) defines the random effect, or the environmental~~  
19  
20 208 ~~stochasticity. Uncertainty in parameter estimates is implemented using Monte Carlo~~  
21  
22 209 ~~methods (Manly, 1997) when running multiple~~ several iterations. Each iteration randomly  
23  
24 210 ~~selects parameter values from a theoretical distribution (e.g. binomial, beta, normal)~~  
25  
26 211 ~~defined by the parameters standard errors of the parameters. The population dynamics is~~  
27  
28 212 ~~then modelled as discrete, sequential events (e.g. births, deaths, catastrophes, etc.) that~~  
29  
30 213 ~~occur according to defined probabilities, which can be constants or random variables that~~  
31  
32 214 ~~follow specified distributions. These probabilities come from input parameters (survival~~  
33  
34 215 ~~probabilities, reproduction rate, migration rate, etc), and uncertainty in these parameters~~  
35  
36 216 ~~(defined by their standard errors) defines the random effect, or the environmental~~  
37  
38 217 ~~stochasticity. Uncertainty in parameter estimates is implemented using Monte Carlo~~  
39  
40 218 ~~methods (Manly, 1997) when running several iterations. Each iteration randomly selects~~  
41  
42 219 ~~parameter values from probability distributions representing parameters uncertainty (the~~  
43  
44 220 ~~standard errors).~~

51 221 Vortex has been widely used to assess the viability of many threatened species  
52  
53 222 (Maehr et al., 2002; Carroll et al., 2013; Lacy et al., 2017; Fantle-Lepczyk et al., 2018).  
54  
55 223 To provide the most robust predictions, we used the best demographic parameters  
56  
57 224 estimates (i.e. population size, survival and reproductive rates) available for the [Lahille's](#)  
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3 225 bottlenose dolphin population in Laguna based on photo-identification surveys between  
4  
5 226 September 2007 and December 2017 (Daura-Jorge, Ingram & Simões-Lopes, 2013;  
6  
7 227 Bezamat et al., 2019; Bezamat et al., 2020).  
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12 229 *Add figure 1 here*  
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15  
16  
17 231 Estimates of first-, and second-year calf survival, sex-specific adult survival and  
18  
19 232 abundance were available for modelling (Bezamat et al., 2019; Bezamat et al., 2020;  
20  
21 233 Table 1). Since post-weaning survival could not be estimated, juvenile survival was  
22  
23 234 assumed to be the same as adult survival. Age at first offspring for females and males  
24  
25 235 were set at 10 and 11 years, respectively (Bezamat et al., 2020), and ~~reproductive lifespan~~  
26  
27 236 ~~maximum age of reproduction~~ and maximum ~~lifespan~~ ~~observed age (referred to as~~  
28  
29 237 ~~'maximum lifespan' in Vortex)~~ were set at 45 and 50 years, respectively, ~~which are the~~  
30  
31 238 ~~highest~~ values known for the species *Tursiops truncatus* (following Hohn et al., 1989  
32  
33 239 ~~and~~; Wells & Scott, 1999 ~~for Tursiops truncatus, since data from Lahille's bottlenose~~  
34  
35 240 ~~dolphins are not available~~). ~~Although there is some information on the maximum~~  
36  
37 241 ~~observed age of the Lahille's bottlenose dolphin (44 years - see Fruet et al., 2015a; Venuto~~  
38  
39 242 ~~et al., 2020), We chose to use these higher values older records for reproductive~~  
40  
41 243 ~~maximum age of reproduction and maximum observed age to be conservative. Although~~  
42  
43 244 ~~this~~ ~~This decision can make our model optimistic;~~ ~~however, the annual mortality rates likely~~  
44  
45 245 ~~prevent most that the individuals from reaching reach these maximum ages, and therefore,~~  
46  
47 246 ~~these variables should therefore may have little effect on the population dynamics.~~  
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53 247 Longitudinal photo-identification data were used to estimate the number of  
54  
55 248 females breeding (i.e. known to have given birth) in a given year as a percentage of all  
56  
57 249 adult females sighted during that period (see Bezamat et al., 2020 for more details), which  
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2  
3 250 we refer to as ‘reproductive rate’ from now on. Some births may have gone unnoticed,  
4  
5 251 particularly for females that have lost their calves very soon after birth, before we were  
6  
7  
8 252 able to observe them. We incorporated environmental stochasticity ( $SD_{EV}$ , environmental  
9  
10 253 variance in Vortex) in our simulations by randomly selecting, for each iteration, values  
11  
12 254 for mortality and reproduction rates from a beta distribution defined by the standard errors  
13  
14 255 of these parameters.

16  
17 256 ~~Uncertainty was accounted for using the standard errors of the estimated survival~~  
18  
19 257 ~~and reproductive rates as the standard deviations due to environmental variance ( $SD_{EV}$ ).~~

21 258 The population was assumed to be demographically isolated and the initial  
22  
23 259 population was assumed to have a stable age structure (i.e. since it was not possible to  
24  
25 260 specify the number of individuals within each age-sex class at the start of the simulation,  
26  
27 261 Vortex calculated the expected age distribution based on the input parameters and  
28  
29 262 allocated the initial population size accordingly). As we do not have data to sustain the  
30  
31 263 hypothesis of intraspecific competition, we set tThe carrying capacity ~~was set~~ at 90  
32  
33 264 dolphins, which is the size of the largest known population of the subspecies in the Patos  
34  
35 265 Lagoon estuary, ~400 km south of our study area (Fruet et al., 2015b). We set this value ~~—~~  
36  
37 266 about 30% higher than the maximum population size estimated for dolphins in Laguna—  
38  
39 267 not to restrict population growth by intraspecific competition. This decision can, which  
40  
41 268 makes our scenarios optimistic; thusthen, further studies should investigate the effects of  
42  
43 269 competition in this system to suggest more appropriate K values in future predictions. All  
44  
45 270 males were assumed to be in the breeding pool. Due to the lack of data on inbreeding in  
46  
47 271 Laguna, inbreeding depression was omitted from the standard models, but its potential  
48  
49 272 effect was evaluated with sensitivity analyses by varying the number of lethal equivalents,  
50  
51 273 a common measure of the severity of inbreeding depression (Lacy, Miller & Traylor-  
52  
53 274 Holzer, 2018). The inputs to the PVA are summarized in Table 1.

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5 276 *Add table 1 here*  
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10 278 *Modelled scenarios*  
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12 279 The baseline scenario (1) represented the current level of annual bycatch (based  
13  
14 280 on the annual average from 2016 to 2018 reported by a systematic carcass recovery  
15  
16  
17 281 programme in the study area), with no management of bycatch. An initial population size  
18  
19 282 of 60 individuals (Bezamat et al., 2019) was modelled and, since survival estimates used  
20  
21 283 as inputs were estimated for a previous period (2007-2016; Bezamat et al., 2019) with no  
22  
23  
24 284 bycatch records, two bycatches were included every year: one juvenile from 2 to 3 years  
25  
26 285 (alternating between a male and a female) and one adult male (only adult males were  
27  
28 286 bycaught from 2016 to 2018). To examine the impacts of additional bycatch or the  
29  
30 287 effectiveness of management actions, five other realistic scenarios were modelled based  
31  
32  
33 288 on the bycatch records in recent years: (2) baseline scenario plus one adult male killed  
34  
35 289 every year; (3) baseline scenario, but the annual adult bycatch alternated between a male  
36  
37 290 and a female; (4) one adult male bycatch every year; (5) one juvenile bycatch every year,  
38  
39 291 alternating between male and female; (6) zero bycatch. For each model, 1000 simulations  
40  
41  
42 292 were carried out in a 100-year projection. Model outputs are also presented for a shorter-  
43  
44 293 term (30 years).  
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47 294

48  
49 295 *Sensitivity Analyses*  
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51 296 Sensitivity analysis was conducted to evaluate which of the survival and  
52  
53 297 reproductive rate parameters most affected population dynamics (Akçakaya, 2000;  
54  
55 298 Akçakaya & Sjögren-Gulve, 2000). Based on the baseline scenario, fixed-proportion and  
56  
57 299 observed-variation sensitivity analyses (*sensu* Manlik et al., 2016) were conducted by  
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1  
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3 300 varying each vital rate by  $\pm 1\%$  or  $\pm 1 \text{ SD}_{\text{EV}}$ , respectively, while holding all other  
4  
5 301 parameters constant, to evaluate the effects of parameter variation on stochastic growth  
6  
7 302 rate ( $r$ ). Each parameter was sampled 1000 times.  
8  
9

10 303 For the  $\pm 1\%$  fixed-proportion scenarios, the relative sensitivity ( $S_X$ ) of population  
11  
12 304 growth rate ( $\lambda = e^r$ ) was calculated to changes in each vital rate, one at a time. Relative  
13  
14 305 sensitivity was calculated as:

$$S_X = \frac{(\lambda_+ - \lambda_-)}{(0.02 \times \lambda_0)}$$

16  
17 306  
18  
19 307  
20  
21 308 where  $\lambda_+$  and  $\lambda_-$  are the population growth rates from the adjusted parameter values,  $\lambda_0$   
22  
23 309 is the population growth rate of the baseline model, and 0.02 defines the total perturbation  
24  
25 310 of the parameter values ( $\pm 1\%$ ) (see Mortensen & Reed, 2016). For the  $\pm 1 \text{ SD}_{\text{EV}}$   
26  
27 311 observed-variation scenarios, the low-to-high range of population growth rate was  
28  
29 312 calculated to changes in each vital rate.  
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32

33 313 The number of lethal equivalents was also varied from 0 to 3.14 (the median value  
34  
35 314 reported for 38 mammalian species; Ralls, Ballou & Templeton, 1988) and 6.29 (the  
36  
37 315 combined mean effect of inbreeding on fecundity and first year survival; O'Grady et al.,  
38  
39 316 2006) to evaluate the potential effect of inbreeding depression.  
40  
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42

#### 43 317 44 45 318 *Assessing impacts and evaluating management options*

46  
47 319 Sensitivity analysis was also used to determine the highest priority management  
48  
49 320 action by simulating the impacts on population growth rate of decreased adult survival  
50  
51 321 caused by a hypothetical increase in adult bycatches, and decreased calf survival, which  
52  
53 322 could result from future construction in the lagoon system, if the increased underwater  
54  
55 323 noise (e.g. pile driving and intense boat traffic) acted to disturb mother-calf bonds  
56  
57 324 (Parsons & Dolman, 2004). The effects of an increase in bycatch on population dynamics  
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3 325 were simulated by gradually adding to the baseline scenario up to four adult male or  
4  
5 326 female removals every year. The potential impact of increased underwater noise was  
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7 327 simulated by reducing first-year calf survival rate by 10, 20, 30, 40, 50, 60, 70, 80 and  
8  
9 328 90%. Survival rate reduced by 50% was similar to the lowest calf survival rate recorded  
10  
11 329 for free-ranging bottlenose dolphins (0.375; Currey et al., 2009). We evaluated whether  
12  
13 330 these modelled effects on adult survival or first-year calf survival would have the greatest  
14  
15 331 influence on population growth rate and thus which vital rate should be a focus for future  
16  
17 332 management actions.  
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## 24 334 Results

### 25 335 *Population Viability Analysis Outputs*

26  
27  
28 336 The baseline model yielded a declining population ( $r = -0.014$ ; Model 1, Figure  
29  
30 337 2, Table 2). Probability of extinction within 30 years was low (0.058), but within 100  
31  
32 338 years was high (0.714), and the mean time to extinction was 52.9 years. Mean population  
33  
34 339 size was 48 dolphins within 30 years (20% reduction) and 20 dolphins within 100 years  
35  
36 340 (33.3% reduction). Compared to the baseline model, models with one additional male  
37  
38 341 adult bycatch every year or the replacement of one adult male bycatch with one adult  
39  
40 342 female bycatch every other year (Models 2 and 3, respectively), resulted in decreased  
41  
42 343 population growth rates and population sizes, and increased probabilities of extinction,  
43  
44 344 with all or nearly all populations going extinct within 100 years. Overall, the three  
45  
46 345 management models (avoiding either a juvenile or an adult bycatch, or both bycatches  
47  
48 346 every year) showed a marked improvement compared to the current conditions, resulting  
49  
50 347 in increases in population growth rate, population size and time to extinction, and lower  
51  
52 348 probabilities of extinction (Models 4, 5 and 6, Table 2) over the baseline model. Although  
53  
54 349 avoiding the bycatch of one juvenile or one adult every year (Models 4 and 5,  
55  
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1  
2  
3 350 respectively) led to a considerable improvement over baseline, the ‘zero bycatch’ (Model  
4  
5 351 6) was the only model that resulted in a positive growth rate and zero risk of extinction  
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7 352 within 100 years.  
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10 353

11  
12 354 *Add table 2 here*  
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14 355

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16 356 *Add figure 2 here*  
17  
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21 358 *Sensitivity Analyses*  
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23  
24 359 Population growth rate ( $r$ ) was most sensitive to proportional changes in adult  
25  
26 360 female and juvenile survival rates (Table 3). Proportional changes in reproductive rates,  
27  
28 361 calf (irrespective of whether it was a male or female) and male adult survival rates had  
29  
30 362 relatively little effect on population growth rate (Table 3). In terms of relative sensitivity,  
31  
32 363 female adult survival rate (relative sensitivity = 1.22) followed by female juvenile  
33  
34 364 survival rate (relative sensitivity = 0.74) were most influential on the population  
35  
36 365 dynamics. Conversely, in the observed-variation scenarios, the low-to-high range of  
37  
38 366 population growth rates was greater for reproductive rates ( $\Delta \lambda\% = 5.3$ ) than other  
39  
40 367 parameters (Table 3). Because there is more natural variation in birth rates, its impact on  
41  
42 368 population dynamics is greater, in absolute terms. Inbreeding had a negligible effect  
43  
44 369 (Table 3).  
45  
46

47 370

48  
49 371 *Add table 3 here*  
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53  
54 373 *Assessing impacts and evaluating management options*  
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3 374 The effects of a hypothetical gradual increase in bycatch and the potential impact  
4  
5 375 of intense boat traffic and pile driving (i.e. reduced first-year calf survival) on growth rate  
6  
7 376 are presented on Figure 3. These sensitivity analyses confirmed that growth rate was most  
8  
9 377 sensitive to a gradual increase in adult female bycatch. The addition of one female  
10  
11 378 removal annually resulted in a rate of decline ( $r = -0.0963$ ) more than double that resulting  
12  
13 379 from the addition of one adult male bycatch every year ( $r = -0.0432$ ), and similar to a  
14  
15 380 reduction in 90% in calf survival rate ( $r = -0.1049$ ; Figure 3). The impact on population  
16  
17 381 dynamics caused by the addition of one adult male bycatch every year ( $r = -0.0432$ ) was  
18  
19 382 equivalent to a 30% reduction in calf survival ( $r = -0.0417$ ; Figure 3), and the addition of  
20  
21 383 two adult male bycatches annually ( $r = -0.0493$ ) was equivalent to a 40% reduction in  
22  
23 384 calf survival ( $r = -0.0488$ ; Figure 3). Thus, the influence on population growth rate of  
24  
25 385 reduction in adult survival rates (especially of females) due to increased bycatch was  
26  
27 386 greater than the reduction in first-year calf survival rate that could result from the  
28  
29 387 disturbance effects of underwater noise.  
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37 389 *Add figure 3 here*

39 390

41 391 Discussion

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44 392 The viability of the small Lahille's bottlenose dolphin population in Laguna was  
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46 393 evaluated using the best demographic parameters estimates available. Population size has  
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48 394 remained apparently stable from 2007 to 2016 (Bezamat et al., 2019), but bycatch has  
49  
50 395 been increasing since 2016. Under current conditions of two bycatches every year on  
51  
52 396 average (one juvenile and one adult male), the baseline scenario forecasts a declining  
53  
54 397 population ( $r = -0.014$ ), with a chance of extinction in the next 30 years (PE = 0.058), and  
55  
56 398 a high probability of extinction in the next 100 years (PE = 0.714). If bycatch increases,  
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3 399 the population is doomed to extinction. Conversely, avoiding bycatch would increase  
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5 400 population growth and lower probabilities of extinction. As expected, population growth  
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7 401 rate was most sensitive to proportional changes in adult female and juvenile survival.  
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9  
10 402 However, population dynamics were more influenced by observed absolute variation in  
11  
12 403 birth rate than in survival. When comparing the relative effects of human impacts (i.e.  
13  
14 404 additional bycatches leading to increased adult mortality vs reduced calf survival) on  
15  
16  
17 405 population dynamics, the population growth rate was more sensitive to changes in adult  
18  
19 406 bycatch (especially females) than to a reduction in calf survival. Combined, our results  
20  
21 407 indicate that only a zero-bycatch management strategy can lead to the persistence of this  
22  
23  
24 408 dolphin population in the long term.

25  
26 409 Population viability was greatly affected by incidental bycatch. Projections  
27  
28 410 indicated that the current level of bycatch mortality in Laguna is unsustainable. Several  
29  
30 411 recovered carcasses have shown evidence of entanglement in fishing gear (Bezamat et  
31  
32 412 al., 2019). Many individuals have been photographed with scars or nets and lines around  
33  
34 413 their bodies, including a young calf in early December 2017 (Bezamat et al., 2020) and  
35  
36 414 two adults that died that same year, 20 and 27 months after being entangled. For small  
37  
38 415 populations like this, it is well-known that the removal of even a single individual each  
39  
40 416 year, especially females, may have a great impact on the population viability (see  
41  
42 417 Burgman, Ferson & Akçakaya, 1993, for the classic example of white rhinoceros  
43  
44 418 *Ceratotherium simum simum*). For another cetacean species—the humpback dolphin  
45  
46 419 *Sousa chinensis*, for instance, a single non-natural death in the critically endangered  
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48 420 population in the eastern Taiwan Strait exceeds the potential biological removal (PBR)  
49  
50 421 level, which was estimated as one individual every 7 years (Slooten et al., 2013). Only  
51  
52 422 the most optimistic mitigation of bycatch—a zero bycatch scenario—would make the  
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54 423 difference between a declining and an increasing population, greatly improving the  
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3 424 chances of long-term persistence of Lahille's bottlenose dolphins in Laguna. The largest  
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5 425 population of Lahille's bottlenose dolphins, in the Patos Lagoon estuary, shows great  
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7 426 chances of persistence under current levels of bycatch, but a slight increase of bycatches,  
8  
9 427 particularly of adult females, would have also severe consequences for the population  
10  
11 428 dynamics and chance of persistence (Fruet, Möller & Secchi, 2021).  
12  
13

14 429 Population growth rates for dolphins in Laguna were more sensitive to  
15  
16 430 proportional changes in adult and juvenile survival but long-term observed variations in  
17  
18 431 reproductive rates—estimated from 2007 to 2017 (Bezamat et al., 2020)—had a greater  
19  
20 432 impact on growth rates and population size ( $N_{100}$ ) forecasts in absolute terms. This finding  
21  
22 433 is similar to Indo-Pacific common dolphin *Tursiops aduncus* populations off Australia  
23  
24 434 (Manlik et al., 2016) and a killer whale *Orcinus orca* population of the north-eastern  
25  
26 435 Pacific Ocean (Lacy et al., 2017). These two previous studies, with different cetacean  
27  
28 436 species, highlight the importance of natural variation in reproduction on population  
29  
30 437 viability, warning that management actions to reverse or prevent population declines  
31  
32 438 should address both survival and reproduction. While fixed-proportion sensitivity  
33  
34 439 analyses have been commonly used to evaluate the importance of vital rates for  
35  
36 440 population viability, the observed-variation analyses reflect variability likely to occur in  
37  
38 441 wild populations, offering insight into feasibility and effectiveness of management  
39  
40 442 options (Manlik et al., 2016).  
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46 443 In Laguna, adult survival rates were relatively constant from 2007 to 2016  
47  
48 444 (Bezamat et al., 2019), whereas reproductive rates showed a large temporal variation  
49  
50 445 (Bezamat et al., 2020). Birth rates in small populations are naturally variable, but it is  
51  
52 446 more challenging to identify management options that directly influence reproduction to  
53  
54 447 improve population viability. Therefore, a management focused on improving survival  
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56 448 by reducing bycatch seems to be an effective option. However, identifying which non-  
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3 449 natural factors, if any, influence reproduction and thus population viability is key. For  
4  
5 450 instance, increased boat traffic seems to affect dolphins' reproductive behaviours  
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7 451 (Lusseau et al. 2006). Particularly in Laguna, boat traffic affects dolphin's acoustic  
8  
9 452 behaviour during the interaction with artisanal fishers (Pellegrini et al., 2021). Further  
10  
11 453 studies should investigate the potential impact of boat traffic on reproduction in this  
12  
13 454 population, and managing boat traffic should be considered in management actions.  
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16  
17 455 Evaluation based on the sensitivity analyses of the potential impact of additional  
18  
19 456 bycatches and decreased calf survival showed that bycatch of adult females had the  
20  
21 457 greatest influence on population growth rate and should be immediately eliminated—as  
22  
23 458 expected for mammals with a polygynous mating system in which a single male can mate  
24  
25 459 with multiple receptive females in a given year (Breed & Moore, 2015). The influence of  
26  
27 460 bycatch on probability of extinction is also biased towards females in the population of  
28  
29 461 Indo-Pacific humpback dolphins in the eastern Taiwan Strait (Araújo et al., 2014). In that  
30  
31 462 case, PVA showed that the probability of population decline within 100 years was 91.7%  
32  
33 463 when removing one additional female from the population every year, and 78.4% when  
34  
35 464 removing one additional male every year (Araújo et al., 2014). As also reported for Indo-  
36  
37 465 Pacific humpback dolphins, sensitivity analysis showed that breeding females are  
38  
39 466 extremely important in the Laguna population, suggesting that a higher recruitment rate  
40  
41 467 is needed to increase population growth rate. The influence of additional male mortality  
42  
43 468 on population growth rate, was lower than female mortality. However, neither of these  
44  
45 469 studies, the Indo-Pacific humpback dolphins in the Taiwan Strait and Lahille's bottlenose  
46  
47 470 dolphins in Laguna, considered the genetics effect and the contribution of males for gene  
48  
49 471 distribution. This could be an important component for dolphins in Laguna and it should  
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51 472 be included in further assessments, since this population has the lowest genetic variability  
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53 473 among the small discrete populations of Lahille's bottlenose dolphins (Fruet et al., 2014).  
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3 474 Although the influence of reduced calf survival as a potential impact of planned  
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5 475 developments in the lagoon system was lower than an increase in adult female bycatch,  
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7 476 it was not negligible. A dredging operation associated with the maintenance of the Laguna  
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9 477 harbour is expected to take place shortly to increase the channel depth, and consequently  
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11 478 increase boat traffic, in a transit and core area for the dolphins, where most of the  
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13 479 cooperative sites are located. An increase in boat traffic would increase the risk of  
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15 480 dolphins being killed or injured by boat collisions, especially calves. Besides that, an  
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17 481 increase in underwater noise could also potentially decrease calf survival due to  
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19 482 communication masking between mothers and their calves (Parsons & Dolman, 2004),  
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21 483 but we have no information to quantify the extent of such an effect, nor whether there  
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23 484 may be other impacts on population dynamics.

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28 485 Effects of dredging on marine mammals varies with species, location and dredging  
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30 486 equipment type (Todd et al., 2014). Overall, more likely effects include acoustic masking,  
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32 487 avoidance and short-term changes to behaviour, and prey availability (Todd et al., 2014).  
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34 488 High intensities of dredging caused bottlenose dolphins to spend less time in a foraging  
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36 489 patch in Aberdeen harbour, Scotland, and ultimately leave the harbour completely for  
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38 490 approximately five weeks (Pirotta et al., 2013). In Laguna, the dredging events and the  
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40 491 associated increase in boat traffic must be considered in management actions, since it  
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42 492 can impact calf survival and affect behavioural patterns such as foraging, but also  
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44 493 reproduction (Lusseau et al., 2006), which seems key for population viability. Another  
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46 494 potential development in Laguna in the near future is the construction of a wind farm,  
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48 495 which is still being discussed, but which may also compromise habitat quality for the  
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50 496 dolphins. Should this development go forward, mitigation measures such as those that  
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52 497 have been used elsewhere should be considered in Laguna, such as reducing underwater  
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3 498 noise of pile driving using air bubble curtains (e.g. Jefferson, Hung & Wu, 2009; Dähne  
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5 499 et al., 2017).

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7 500 Nevertheless, increased underwater noise—from intense boat traffic and regular  
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9 501 dredging operations and constructions—is not the only factor that could contribute to a  
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11 502 reduction in calf survival. Increased levels of persistent organic pollutants, especially  
12  
13 503 PCBs, and decreased resource availability could add in reducing calf survival as well  
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15 504 (Reddy et al., 2001; Wells et al., 2005). Dolphins in Laguna are exposed to contaminants  
16  
17 505 and some biopsied individuals have shown high blubber PCB levels (Righetti et al.,  
18  
19 506 2019). Females transfer PCBs to their calves through the placenta and during lactation,  
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21 507 which may increase the chances of fetal and first-year calf mortality (Reddy et al., 2001;  
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23 508 Wells et al., 2005), and potentially depress population growth rates (Hall et al., 2006).  
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25 509 Moreover, since lactation is the most energetically demanding time of reproduction,  
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27 510 females need a great abundance of food at this stage (Kastelein et al., 2002; Rechsteiner  
28  
29 511 et al., 2013). Thus, a decrease in resource availability could compromise calf nutrition  
30  
31 512 and reduce its chances of survival; calves born just after the peak of the mullet season  
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33 513 have been shown to have higher chances of survival (Bezamat et al., 2020).

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35 514 Management actions to reduce the current anthropogenic pressures to this small  
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37 515 [Lahille's](#) bottlenose dolphin population are needed immediately. The present level of  
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39 516 bycatch in Laguna is unsustainable and thus a reduction in associated mortality is an  
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41 517 urgent priority. To achieve this, a Municipal Law (N° 222 033/2018) has recently banned  
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43 518 the trammel net fishery in the dolphins' core area. This restriction is essential and new  
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45 519 management actions should consider the need and possibilities to expand this area in the  
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47 520 near future, to include not only the dolphins' core area, but their entire distribution area  
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49 521 in the lagoon system. However, even after the implementation of this restricted fishing  
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51 522 area, systematic beach monitoring during 2018 and 2019 reported four non-natural  
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3 523 deaths, three likely by bycatch and one likely by boat collision (P.V. Castilho,  
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5 524 unpublished data), which suggests that enforcement was insufficient, compromising the  
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7 525 effectiveness of the fishing ban in the early years. In 2019, the Santa Catarina Institute of  
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9 526 Environment (IMA) defined a State Action Plan (SAP) in which the main aims are to  
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11 527 reduce the trammel net bycatch and regulate boat traffic and noise pollution, and  
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13 528 guarantee the habitat quality. As the first action and results motivated by the  
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15 529 implementation of the SAP, continued enforcement operations were articulated and then  
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17 530 no bycatch events were reported throughout 2020—although ~20 gillnets illegally  
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19 531 distributed in the area were removed, suggesting that illegal fisheries continue despite the  
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21 532 recent restrictions.  
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26 533 Therefore, besides a permanent and strict enforcement, the local fishing  
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28 534 community needs to be better involved in conservation actions. Interestingly, fishers who  
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30 535 cooperate with dolphins perceive multiple values from their occurrence in Laguna and  
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32 536 their interaction with them. This close relationship between dolphins and fishers is an  
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34 537 opportunity to better engage fishers in an alternative co-management strategy to help  
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36 538 monitor the banned fishery or even change how some fishers behave (Machado et al.,  
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38 539 2019). Engaging these fishers would be facilitated if they clearly understood the need for  
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40 540 zero bycatch to increase the probability that this dolphin population and the dolphin-fisher  
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42 541 interaction will persist in the long-term. Our results can be used by managers to highlight  
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44 542 how essential the elimination of bycatch is to population viability, as well as  
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46 543 complementary measures to regulate increasing boat traffic and other habitat  
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48 544 perturbations that can affect dolphin reproduction. Finally, our results reinforce how  
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50 545 vulnerable the Lahille's bottlenose dolphin subspecies is, since its largest population—in  
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52 546 the Patos Lagoon estuary—is likely to decline with any increase in bycatches (Fruet,  
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3 547 Möller & Secchi, 2021), and the second largest population—in Laguna—have a great  
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5 548 chance of being extinguished with the current bycatch rates.  
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35 561 Conflict of interest

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37 562 The authors declare that they have no conflict of interests.  
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42 564 CRediT authorship contribution statement

43  
44 565 C.B.: Conceptualization, formal analysis, fieldwork, writing - original draft, writing -  
45  
46 566 review & editing; F.G.D.J.: Conceptualization, coordination, supervision, formal  
47  
48 567 analysis, writing - review & editing, funding acquisition; P.S.H.: Supervision, formal  
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50 568 analysis, writing - review & editing. P.V.C.: Fieldwork, funding acquisition, writing -  
51  
52 569 review & editing; P.C.S.L.: Funding acquisition, writing - review & editing. All authors  
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54 570 read and approved the final manuscript.  
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For Peer Review

935 Tables:

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

Parameter	Value	Reference
Percent of females breeding yr <sup>-1</sup>	32.8 (± 10.0)	Bezamat et al., 2020
1 <sup>st</sup> year calf survival (%)	78.0 (± 7.0)	Bezamat et al., 2020
2 <sup>nd</sup> year calf survival (%)	83.0 (± 9.0)	Bezamat et al., 2020
Adult = Juvenile survival (%)		
Females	95.7 (± 1.3)	Bezamat et al., 2019
Males	93.6 (± 1.9)	Bezamat et al., 2019
Initial population size	60	Bezamat et al., 2019
Age at first offspring		Bezamat et al., 2020
(females/males)	10/11	
Maximum age of reproduction	45	Hohn et al., 1989,
Maximum <del>lifespan</del> <u>observed age</u>	50	Wells & Scott, 1999
Sex ratio at birth (% males)	50	Caughley, 1977
Carrying capacity	90	

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940 Table 2: Summary of the results of the Population Viability Analysis for six scenarios of  
 941 bycatch mortality of bottlenose dolphins in Laguna, Brazil. Shown are stochastic growth  
 942 rate (stoch-r) and its standard deviation (SD), population size after 30 years (N<sub>30</sub>) and 100  
 943 years (N<sub>100</sub>) and their SD, and probability of extinction after 30 years (PE<sub>30</sub>) and 100 years  
 944 (PE<sub>100</sub>). M: male, F: female.

Bycatch scenarios	stoch-r	SD (r)	N <sub>30</sub>	SD (N <sub>30</sub> )	PE <sub>30</sub>	N <sub>100</sub>	SD (N <sub>100</sub> )	PE <sub>100</sub>
(1) Baseline:								
1 Juvenile M/F + 1 Adult M yr <sup>-1</sup>	-0.0143	0.0782	48	22.1	0.058	20	32.0	0.714
(2) 1 Juvenile M/F + 2 Adults M yr <sup>-1</sup>	-0.0426	0.0763	16	7.2	0.861	0	0.0	1.000
(3) 1 Juvenile M/F + 1 Adult M/F yr <sup>-1</sup>	-0.0480	0.1172	31	16.4	0.018	1	7.5	0.959
(4) 1 Adult M yr <sup>-1</sup>	-0.0047	0.0666	66	21.4	0.023	57	38.0	0.291
(5) 1 Juvenile M/F yr <sup>-1</sup>	-0.0040	0.0646	68	15.5	0.000	68	21.7	0.006
(6) Zero bycatch	0.0139	0.0561	80	11.2	0.000	84	7.4	0.000

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947 Table 3: Effects of fixed-proportion ( $\pm 1\%$ ) and observed-variation changes ( $\pm 1 \text{ SD}_{\text{EV}}$ )  
 948 in the input parameters on stochastic growth rate ( $r$ ) for the bottlenose dolphins in Laguna,  
 949 Brazil. Relative sensitivity ( $S_X$ ) of population growth rates ( $\lambda$ ) is shown for the fixed-  
 950 proportion scenarios, and low-to-high range ( $\Delta \lambda\%$ ) is shown for the observed-variation  
 951 scenarios.

	Growth rate ( $r$ )			$S_X$	$\Delta \lambda\%$
	Low	Base	High		
<b><i>Fixed-proportion</i></b>					
Reproduction	-0.0156	-0.0143	-0.0132	0.12	-
1st year calf survival	-0.0156	-0.0143	-0.0132	0.12	-
2nd year calf survival	-0.0155	-0.0143	-0.0140	0.07	-
<b><i>Juvenile survival</i></b>					
Females	-0.0218	-0.0143	-0.0069	0.74	-
Males	-0.0171	-0.0143	-0.0118	0.26	-
<b><i>Adult survival</i></b>					
Females	-0.0266	-0.0143	-0.0022	1.22	-
Males	-0.0151	-0.0143	-0.0138	0.06	-
Inbreeding	-0.0142	-0.0143	-0.0142	-	-
<b><i>Observed-variation</i></b>					
Reproduction	-0.0406	-0.0143	0.0131	-	5.30
1st year calf survival	-0.0243	-0.0143	-0.0047	-	1.93
2nd year calf survival	-0.0268	-0.0142	-0.0021	-	2.43
<b><i>Juvenile survival</i></b>					
Females	-0.0238	-0.0142	-0.0046	-	1.89
Males	-0.0207	-0.0143	-0.0099	-	1.06
<b><i>Adult survival</i></b>					
Females	-0.0306	-0.0142	0.0016	-	3.17
Males	-0.0159	-0.0143	-0.0131	-	0.28

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8 957 Figure 1: Study area: the coastal lagoon system adjacent to Laguna, southern Brazil. The  
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10 958 red line shows the predefined sampling route for the long-term individual-based  
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12 959 monitoring. The blue circles are the main sites where dolphins and fishers interact. The  
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14 960 green line shows the dolphins' core area, and the yellow area shows where trammel net  
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17 961 fishing has been banned.  
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21 963 Figure 2: Predicted trajectories of mean population size for the six scenarios of annual  
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23 964 bycatch mortality of bottlenose dolphins in Laguna, southern Brazil. Numbers refer to  
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25 965 models in Table 2. Dashed vertical line highlights the population trajectory after 30 years.  
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30 967 Figure 3: Sensitivity analysis. Effect of additional adult (a) male and (b) female bycatches  
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33 968 and (c) different first year calf survival rates on stochastic growth rate ( $r$ ) forecasts.  
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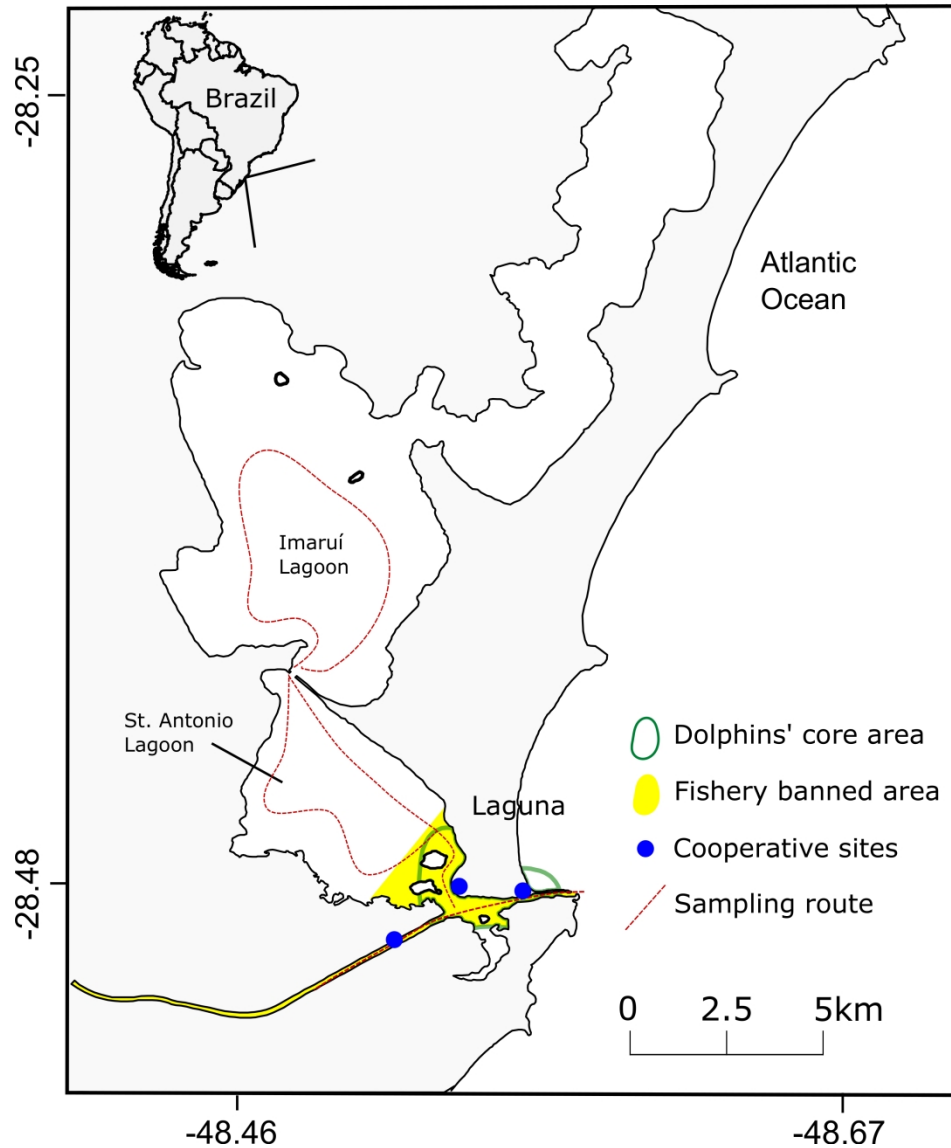


Figure 1: Study area: the coastal lagoon system adjacent to Laguna, southern Brazil. The red line shows the predefined sampling route for the long-term individual-based monitoring. The blue circles are the main sites where dolphins and fishers interact. The green line shows the dolphins' core area, and the yellow area shows where trammel net fishing has been banned.

102x130mm (800 x 800 DPI)

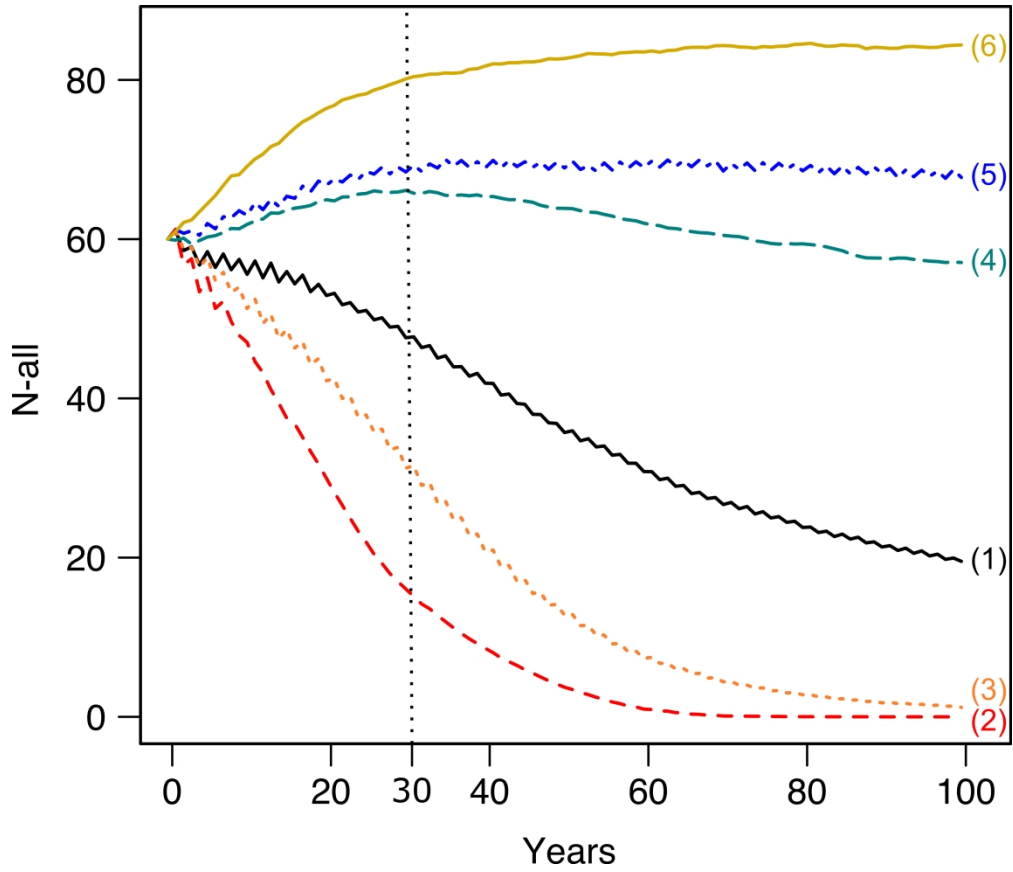


Figure 2: Predicted trajectories of mean population size for the six scenarios of annual bycatch mortality of bottlenose dolphins in Laguna, southern Brazil. Numbers refer to models in Table 2. Dashed vertical line highlights the population trajectory after 30 years.

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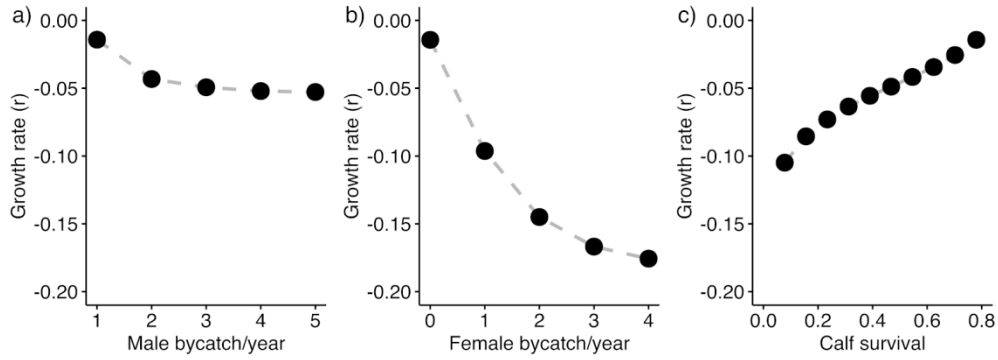


Figure 3: Sensitivity analysis. Effect of additional adult (a) male and (b) female bycatches and (c) different first year calf survival rates on stochastic growth rate (r) forecasts.

602x220mm (72 x 72 DPI)