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Spatial behavioural response of coastal bottlenose dolphins to habitat disturbance in southern Brazil

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Abstract

1. A small population of coastal bottlenose dolphins (*Tursiops truncatus gephyreus*) inhabits the inland waters of Laguna, southern Brazil. A subset of this population interacts with artisanal fishermen. This specialized foraging tactic structures dolphin society into ‘cooperatives’ (participants of the interaction) and ‘non-cooperatives’ (non-participants).
2. Between 2012 and 2015, a bridge was constructed in Laguna over an important core area for dolphins. Photo-identification and georeferenced data collected on boat surveys, conducted both before and during bridge construction, were used to evaluate changes in both ‘cooperative’ and ‘non-cooperative’ dolphin distribution.
3. Changes in dolphin distribution were analysed with kernel densities and hurdle models. A grid of 120 cells of area 1 km^2 was used to model dolphin distribution, and the minimum distance from the grid cell centre to the bridge and to the area of gillnet use were defined as explanatory variables of human activities. Habitat descriptors (depth and distance) from the lagoon margin were also considered in the model procedure.
4. Dolphin distribution patterns shifted between periods. A core area used by ‘non-cooperative’ dolphins near the bridge construction works disappeared. The effects of habitat descriptor and anthropogenic activity on dolphin distribution also differed between periods. Before bridge construction, the abundance of ‘non-cooperative’ dolphin was higher close to the bridge area ($p < 0.05$). During bridge construction, the presence of ‘cooperative’ and ‘non-cooperative’ dolphins decreased significantly with the distance from gillnet fishing activity ($p < 0.01$ and $p < 0.001$ respectively).
5. This study highlights the importance of accounting for individual variations in response when assessing the effects of a habitat disturbance, or when implementing conservation plans.

KEYWORDS
anthropic impacts, bottlenose dolphin, conservation, distribution, habitat disturbance, hurdle models

1 | INTRODUCTION

The spatial behaviour and distribution of marine mammals are driven both by ecological and evolutionary factors, but also respond to anthropogenic activities; the extensive human use of coastal waters affects their behaviour and population dynamics (New et al., 2013). Although by-catch is one of the leading causes of unnatural mortality in a number of cetacean species (Reeves, Smith, Crespo, & de Sciara, 2003), there are concerns about multiple other anthropogenic interferences, such as recreation and tourism (Bejder et al., 2006; Constantine, Brunton, & Dennis, 2004), the transformation of estuaries into industrial ports (Cremer, Simões-Lopes, & Pires, 2009; Jefferson, Hung, & Würsig, 2009), drainage of mangroves for agriculture and aquaculture (Watson-Capps & Mann, 2005), modification by dredging, and civil construction works (Pirotta et al., 2013). Numerous short-term effects of these activities have been demonstrated, including changes in dive behaviour (Williams, Lusseau, & Hammond, 2009), behavioural state (Meissner et al., 2015), and vocalization rate (Pirotta et al., 2012). These behavioural responses can lead to decreases in individual fitness and population-level changes (Christiansen, Rasmussen, & Lusseau, 2013; Lusseau, Bain, Williams, & Smith, 2009). In this context, several researchers have evaluated spatial changes attributed to anthropogenic effects, such as home range reduction or area abandonment (Cremer, Hardt, Júnior, Simões-Lopes, & Pires, 2004; Hartel, Constantine, & Torres, 2014; Slooten, Rayment, & Dawson, 2006; Wedekin, Daura-Jorge, & Simões-Lopes, 2010). However, the animals in a population and human activities might both be heterogeneously distributed. These variations result in different exposure rates among individuals in a population, and therefore in different levels of behavioural response (Pirotta, New, Harwood, & Lusseau, 2014).

In southern Brazil, a small (55–60 individuals) resident population of bottlenose dolphins (*Tursiops truncatus gephyreus*) inhabits a coastal lagoon system next to Laguna town (Bezamat, Simões-Lopes, Castilho, & Daura-Jorge, 2018). Dolphins from Laguna are exposed to multiple and growing threats, such as boat traffic, gillnet by-catch, chemical and biological pollutants, and habitat change (Daura-Jorge, Ingram, & Simões-Lopes, 2013). Interestingly, a subset of this dolphin population employs a distinctive foraging tactic in cooperation with artisanal fishermen. Adult dolphins chase fish schools towards shallow waters where fishermen either stand in line or on moored canoes. The fishermen wait for stereotyped behavioural cues given by the dolphins, interpreted as indicating the right time to cast their nets (Simões-Lopes, Daura-Jorge, & Cantor, 2016). This foraging tactic structures the dolphin society into two categories: dolphins that routinely interact with fishermen but also forage independently (‘cooperative’), and dolphins that mostly forage independently and rarely or never interact with fishermen (‘non-cooperative’) (Daura-Jorge, Cantor, Ingram, Lusseau, & Simoes-Lopes, 2012). The ecological and socio-economic benefits derived from this dolphin–human tactic have generated emotional affinities in the local community, and motivated a municipal law (No. 521, 10 November 1997) recognizing dolphins as part of the cultural heritage of Laguna town (Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis, 2001).

Much of the current literature on Laguna's dolphin population has focused on estimating population parameters (Bezamat et al., 2018; Daura-Jorge et al., 2013), illuminating various different aspects of this dolphin–human interaction (Daura-Jorge et al., 2012; Romeu, Cantor, Bezamat, Simões-Lopes, & Daura-Jorge, 2017; Simões-Lopes et al., 2016) and analysing spatial requirements for individuals with different foraging tactics (Cantor, Simões-Lopes, & Daura-Jorge, 2018). Although the results of our long-term monitoring programme suggest that the apparent survival rate of adults has remained constant from 2007-2016, gillnet bycatch is a local threat (Bezamat et al., 2018). Moreover, habitat changes occurred as a result of the construction of a new bridge, between 2012 and 2015. This bridge, called the Anita Garibaldi Bridge, is the third largest in Brazil, and its construction required the dredging of 445,000 m^3 of material from the lagoon (RAPBA, 2014). Noise produced by pile drivers, the dredging itself, and the presence of vessel traffic—which is unusual in the area—are among the disturbances created by the bridge building work. We hypothesize that this disturbance had a more intensive effect on the subset of ‘non-cooperative’ dolphins, because they have larger home ranges and use areas closer to the bridge construction site and would therefore have greater exposure to the disturbance.

This study aims to assess the immediate ecological consequences of a major habitat disturbance on a small resident population of bottlenose dolphins. Specifically, changes in dolphin spatial behaviour in response to the new bridge built in the area were evaluated. These changes were compared between dolphins with different foraging tactics—the ‘cooperative’ and ‘non-cooperative’ dolphins—in order to investigate different responses depending on individual variations in behaviour. Understanding the different spatial behavioural responses of individuals in a population to a given impact is essential in assessing the conservation status of dolphins, and to informing future management decisions and licensing processes for cetaceans.

2 | METHODS

2.1 | Study area

The study area comprised coastal lagoons (28°29′S, 48°46′W) that form one of the largest lagoon systems in southern Brazil. Covering approximately 200 km^2, this system is divided into three subunits: St Antônio dos Anjos, Imaruí, and the Mirim lagoon (Figure 1). The Mirim lagoon, to the north, is dominated by nearby rice farms, and is the innermost and least urbanized of the subunits. The centrally located Imaruí lagoon is the largest subunit and is dominated by shrimp farms. The St Antônio dos Anjos lagoon is the outermost southern subunit, which is connected with the Atlantic Ocean by an inlet channel. Waters of the Tubarão River, the Imaruí lagoon, and the Mirim lagoon feed the St Antônio dos Anjos lagoon. The overall lagoon system is shallow, with an average depth of 2 m, except for

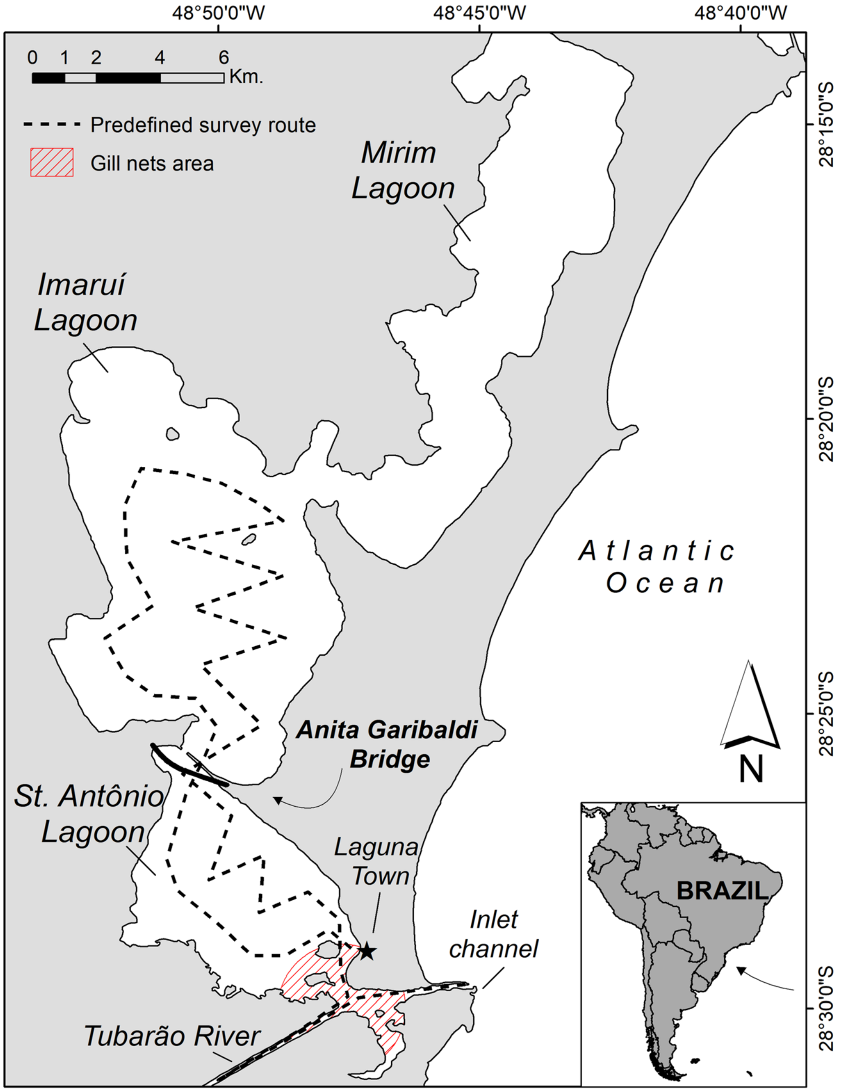

FIGURE 1 The St Antônio–Imaruí–Mirin costal lagoons next to Laguna town, in southern Brazil, and the new bridge location

some channels that can reach a maximum depth of 13 m. There is little information related to water quality in the area.

2.2 | Data collection

Systematic surveys were carried out in two periods: before (P1; from January 2008 to October 2009) and during (P2; from April 2013 to December 2014) bridge construction. The surveys were conducted from a small boat with a 15 hp engine, taking a predefined route of 30 km for nearly 5 hr of effort per day (see Bezamat et al., 2018; Daura-Jorge et al., 2013). Groups were defined as all individuals within a radius of 50 m that exhibited the same behavioural state (Lusseau et al., 2003). When a group was detected, the boat approached in order to register the geographical position using global positioning system coordinates. Individuals from each group were photographed in 20 min sessions. The photographic record was used to identify individuals based on natural long-term marks on the dorsal fin (Würsig & Jefferson, 1990); the proportion of marked individuals ranged from 0.721 in 2009 to 0.866 in 2014 (Bezamat et al., 2018). The relative frequency with which each photo-identified dolphin participated in interacting with fishermen was used to classify them as 'cooperative' or 'non-cooperative'. This relative frequency of participation (fp) was calculated as the number of independent events in which each photo-identified individual was observed actively foraging with fishermen—by performing the stereotyped behavioural cues described by Simões-Lopes et al. (2016)—divided by the total number of their foraging events. Kernel density estimation was used to fit a probability density function to this continuous distribution. The local minimum value of the kernel density estimation, $\min(x)$, was then used as the cut-off frequency of participation in order to classify individual dolphins as 'cooperative'—that is, $fp > \min(x)$—or 'non-cooperative'—that is, $fp < \min(x)$ (Cantor et al., 2018). Only good-quality photographs taken during favourable weather conditions (Beaufort scale ≤ 3) were included in the analysis (Williams, Dawson, & Slooten, 1993). Despite the population turnover between periods, abundance estimates fluctuated slightly between years, from 60 (95% confidence interval [CI] = 53–67) individuals in 2007 to 53 (95% CI = 47–60) in 2014, without significant trends (Bezamat et al., 2018).

2.3 | Identifying core and usage areas

The minimum convex polygon (MCP; Mohr, 1947) method was used to estimate the home range of both the whole population and identified individuals, and to compare the size of the area they used both before and during the bridge construction. The MCP method is a non-statistical measure, which calculates the smallest convex polygon enclosing all relocations. Only individuals that reached an asymptote in the MCP analysis were used in comparing periods with a non-parametric Mann–Whitney–Wilcoxon test.

The kernel density distribution (KUD; Worton, 1989) method was used to compare the distribution of 'cooperative' and 'non-cooperative' dolphins before and during the bridge works. This method employs a probabilistic approach, yielding both a density of use throughout the study area (UD; van Winkle, 1975) and the density of probabilities for locating individuals according to geographic coordinates. The KUD method is sensitive to spatial autocorrelation effects; therefore, only the first record of each individual within a sampling day was used. Because the aim of this study was to identify areas critical for dolphins, the smoothing parameter $h_{\text{reference}}$ was used (see Worton, 1989). Maps were produced of the usage areas (KUD 95%) and core areas (KUD 50%) for 'cooperative' and 'non-cooperative' dolphins for both periods and years. Home range was estimated excluding land areas.

2.4 | Modelling habitat use

The study area was divided into a grid of 120 cells of area 1 km^2. The number of 'cooperative' and 'non-cooperative' dolphin records within each cell were used as the response variables. Table 1 presents the four explanatory variables included in the model procedure: two were related to local physiographic features (depth and distance from the lagoon margin) and two to human activities (distance from the bridge and distance from the main gillnet area). Supporting Information Section S1 presents details of how each explanatory variable was measured.

TABLE 1 Explanatory variables selected to the model for bottlenose dolphin distribution in Laguna, southern Brazil. All distances were measured in metres

Variable	Calculation method	Abbreviation
Distance from margin	Minimum distance from the cell centre to the lagoon margin	Margin
Distance from bridge	Minimum distance from the cell centre to the bridge (Supporting Information Figure S1)	Bridge
Distance from gill net area	Minimum distance from the cell centre to the gill nets area (Supporting Information Figure S1)	Gill net
Depth	Depth data are derived from an inverse distance weighted interpolation performed from bathymetric data collected in the field	Depth

A data exploration analysis was performed following the protocol proposed by Zuur, Ieno, and Elphick (2010). The continuous explanatory variables (distance measures and depth) were standardized using a mean $M = 0$ and standard deviation $SD = 1$. Collinearity between variables was evaluated using the variance inflation factor (Zuur et al., 2010). The response variables showed a high percentage of zeros (P1 = 63%, P2 = 76%; Supporting Information Section S2). Therefore, a two-part model approach was applied to analyse spatial distribution (hurdle model; Cragg, 1971). In this model, the first part corresponds to a binary regression model (presence/absence), where the count data are considered as presence and the zeros as absence. In the second part of the model, only count data (greater than zero) are modelled, in either a truncated Poisson distribution (ZAP) or truncated negative binomial (ZANB) model. If the count data exhibit an extra overdispersion, ZANB is preferred to ZAP (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). The advantage of this kind of model is the possibility of identifying variables influencing dolphin presence and variables influencing count data.

Models were fitted for a period before and during the bridge construction work, and for both foraging tactics (for a total of four independent modelling procedures). The same set of variables (physiographic and human related) was included in the two parts of the model (presence/absence and count data). Saturated models were fitted using ZAP and ZANB with a 'logit' link function. For both period and foraging tactic, the ZANB model presented the lowest Akaike information criterion (AIC) value, indicating overdispersion in the count data (AIC differences between ZAP and ZANB were $\gg$10 for all fitted models). After selecting ZANB, a set of models was fitted, starting from the saturated model, dropping one by one the variables with the highest P value (backward selection). Model selection was performed using AIC (Burnham & Anderson, 2002). Average models were considered when AIC differences were <2. In addition, all the explanatory variables were transformed into 1 km^2 rasters, and a prediction map of dolphin distribution based on the selected models was constructed to validate the models. All data analysis was carried out using R software (R Core Team, 2015), and all maps were produced using geographical information system software (ArcGIS, V10; Esri).

3 | RESULTS

3.1 | Sample characteristics

A total of 100 boat-based surveys were carried out in P1 (2008–2009; 75 sampling days) and P2 (2013–2014; 25 sampling days) sampling periods. Twenty-five sampling days were randomly selected from P1 in order to homogenize sample size. Table 2 summarizes the sampling effort, and the number of dolphins and schools observed. Thirty-four individuals identified in P2 had previously been identified in P1, and 16 individuals were new records added to the catalogue. Twelve

TABLE 2 Sampling effort, number of dolphin schools and sightings, and number of identified dolphins categorized in 'cooperative' or 'non-cooperative' in a period before (period 1) and during (period 2) the bridge construction in Laguna, southern Brazil

	Period 1	Period 2
Year	2008–2009	2013–2014
Effort (hr)	114	92
No. dolphin schools	265	173
No. of sightings	622	455
No. identified dolphins	46	50
No. of 'cooperative' dolphins	19	22
No. of 'non-cooperative' dolphins	26	28

individuals identified in P1 were not encountered in P2, four of which were 'cooperative' dolphins and eight 'non-cooperative' dolphins. During both periods, 62 individuals were identified in total and classified according to foraging tactic.

3.2 | Comparison of home range size between periods

Dolphin home range estimated using MCP decreased by 57% between periods (P1 = 81.22 km^2, P2 = 35.31 km^2; Supporting Information Section S3). The mean of individual MPC home ranges decreased between periods. In P1, 'cooperative' individuals presented a small home range (6.73 ± 8.78 km^2) compared with 'non-cooperative' individuals (29.78 ± 5.33 km^2). In P2, there was a decrease in the home range of 'cooperative' and 'non-cooperative' individuals (5.08 ± 7.40 km^2 and 17.16 ± 7.12 km^2 respectively). This reduction between periods was significant for 'non-cooperative' individuals (W = 82, P = 0.0007; Figure 2).

Core (50% KUD) and usage (95% KUD) areas for 'cooperative' and 'non-cooperative' dolphins changed between periods (Figure 3). The core area of 'cooperative' dolphins increased by 40% from P1 (2.87 km^2) to P2 (4.02 km^2). Conversely, the core area for 'non-cooperative' dolphins decreased by 28% from P1 (12.21 km^2) to P2 (8.84 km^2), and a core area next to the bridge completely disappeared in 2014 (Supporting Information Section S4). The usage area of the 'cooperative' dolphin subset increased between periods (P1 = 33.38 km^2; P2 = 44.41 km^2), with a greater overlap with the decreased usage area of 'non-cooperative' dolphins (P1 = 60.41 km^2; P2 = 52.59 km^2).

3.3 | Modelling habitat use

Different environmental and anthropic variables explained dolphin spatial distribution with regard to the period and foraging tactic (Table 3; Supporting Information Section S5). The presence (binomial) and number of records (negative binomial)—hereafter termed abundance—of dolphins were both significantly higher in deeper areas, regardless of foraging tactic or period. However, the influence of the distance from bridge and gillnet areas on dolphin distribution changed between periods dependent on the foraging tactic employed. The presence of 'cooperative' dolphins in areas close to the bridge was significant only in P2, but in both periods for 'non-cooperatives'. The abundance of 'non-cooperative' dolphins was significantly higher close to the bridge in P1 but not in P2, when dolphins mainly reduced their use of this area. The distance from the gillnets was significant for presence of 'cooperative' and 'non-cooperative' dolphins, regardless of period, but was significant for the abundance of 'cooperative' and 'non-cooperative' dolphins only in P2 and P1 respectively. These results suggested that, in P2, 'cooperative' and 'non-cooperative' dolphins respectively increased and decreased their use of areas close to gillnets. The predictive map of dolphin distribution based on the selected models showed a similar spatial pattern to our observations (Figure 4, Supporting Information Section S3).

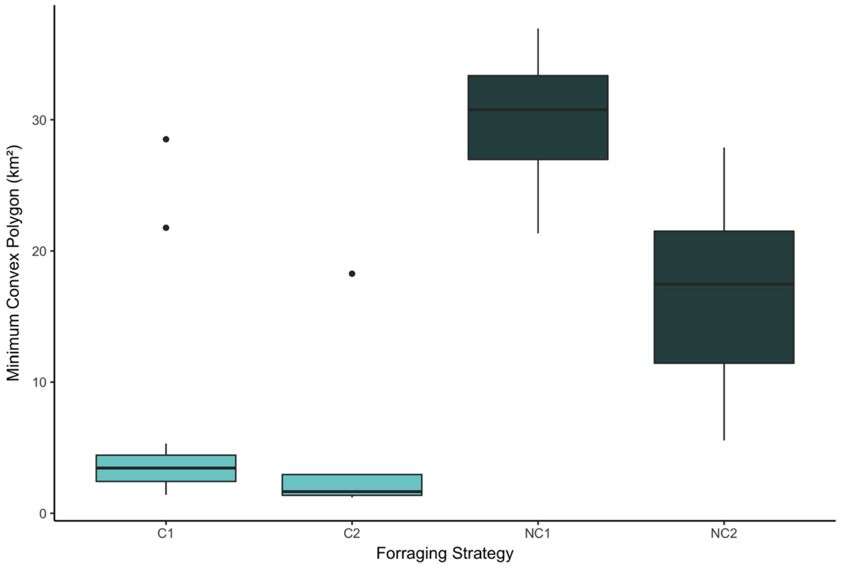

FIGURE 2 Minimum convex polygon for 'cooperative' dolphins in a period before and during the bridge works (C1, n = 12; C2, n = 5), and for 'non-cooperative' dolphins (NC1, n = 8; NC2, n = 11). Graphs represents the interquartile range (5th, 25th, 50th, 75th, 95th). Individual points indicate outliers

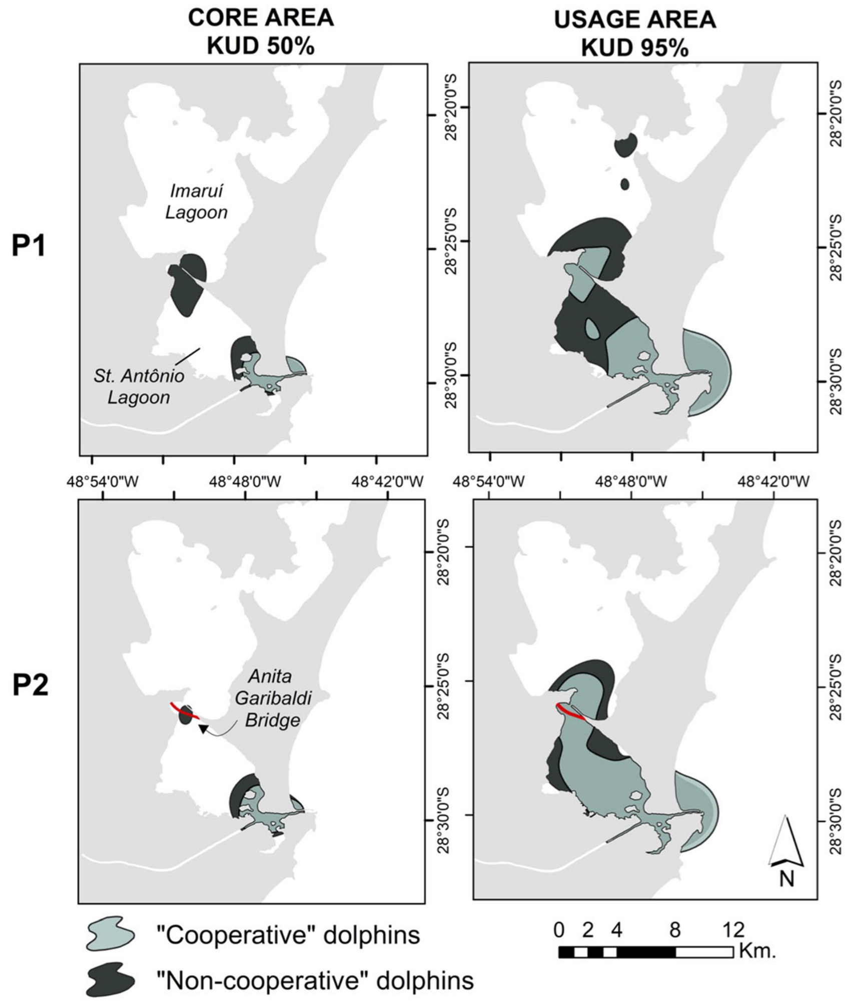

FIGURE 3 Core area (KUD 50%) and usage area (KUD 95%) of 'cooperative' and 'non-cooperative' dolphins in a period before (P1) and a period during the bridge construction (P2) in Laguna, southern Brazil

4 | DISCUSSION

A shift in bottlenose dolphin distribution was observed during the habitat disturbance associated with bridge construction activities. Individual home range sizes decreased, and locations of core and usage areas changed. Before the disturbance, the 'non-cooperative' dolphin subset was concentrated in two areas, one of which was close to the bridge construction area. During the disturbance, the core areas used by 'non-cooperative' dolphins reduced in size; this mainly affected the core area close to the bridge, which disappeared completely in 2014. Interestingly, though the individual home ranges of 'cooperative' dolphins also decreased, there was an increase in the area used by the 'cooperative' dolphin subset, possibly because the few individuals that interacted with fishermen tended to use different areas during the bridge construction, without increasing their home ranges. During the period of bridge disturbance (P2), 'non-cooperative' dolphins reduced their home ranges to coincide with areas more often used by 'cooperative dolphins', whereas a few 'cooperatives' moved to areas more often used by 'non-cooperatives'. These results indicated that an apparent behavioural response (spatial changes) to an anthropogenic disturbance may not be homogeneous throughout a population and depends on how individuals used the area before the disturbance.

As a major consequence of the spatial changes between the two periods, the environmental and human-related explanatory variables in our habitat-use models had different effects on dolphin distribution. In P1, the habitat models for 'non-cooperative' dolphins showed a negative and significant relationship between the number of records and distance from the bridge, suggesting the use of areas closer to the bridge declined when construction was underway. This change can be attributed to a strategy of avoiding disturbances during the bridge construction works. The effects of bridge construction included underwater acoustic disturbance, dredging, high levels of vessel traffic, and a lack of available prey. During dredging and bridge construction, several types of acoustic disturbance elicited a similar response to risk of predation (Frid & Dill, 2002). This behaviour can be interpreted as an acute reaction to a rare stimulus. Thus, it is possible that dolphins would abandon the area temporarily, until vessel traffic and the noise from dredging decreased. This is supported by studies that reported cetacean populations leaving the area temporarily for several weeks or even years during dredging activities, but then returning when the dredging intensity was lower (Bryant, Lafferty, & Lafferty, 1984;

TABLE 3 Negative binomial hurdle models for 'cooperative' and 'non-cooperative' dolphins a period before (P1) and during the bridge works (P2) in Laguna, southern Brazil. Coefficient estimates and standard errors (in parentheses) of four independent models (see Supporting Information Section S5 for model selection). Model average for each period and foraging strategy

	'Cooperative' dolphins		'Non-cooperative' dolphins	
	P1	P2	P1	P2
Negative binomial part				
Intercept	−3.121 (1.710)	−1.938 (1.306)	0.385 (0.352)	0.219 (0.635)
Margin	−0.047 (0.328)	−0.407 (0.298)	−0.409* (0.195)	−0.092 (0.275)
Gill net	−2.654 (1.361)	−2.24* (0.916)	−0.716** (0.252)	−0.849 (0.463)
Bridge	−0.334 (0.680)	−0.176 (0.440)	−0.366* (0.181)	−0.177 (0.559)
Depth	1.372** (0.436)	0.691** (0.264)	0.79*** (0.217)	0.825** (0.291)
Binomial part				
Intercept	−3.773*** (1.098)	−4.43*** (1.274)	−1.110 *** (0.293)	−3.136*** (0.734)
Margin	−1.196* (0.480)	−0.946* (0.464)	−0.54 (0.318)	−0.092 (0.274)
Gill net	−2.192** (0.827)	−2.381** (0.909)	−0.723* (0.307)	−2.052*** (0.572)
Bridge	−0.634 (0.525)	−1.244* (0.586)	−0.906** (0.315)	−1.243** (0.430)
Depth	2.083*** (0.603)	2.619*** (0.752)	1.507*** (0.391)	1.389** (0.426)

***$P < 0.001$. **$P < 0.01$. *$P < 0.05$.

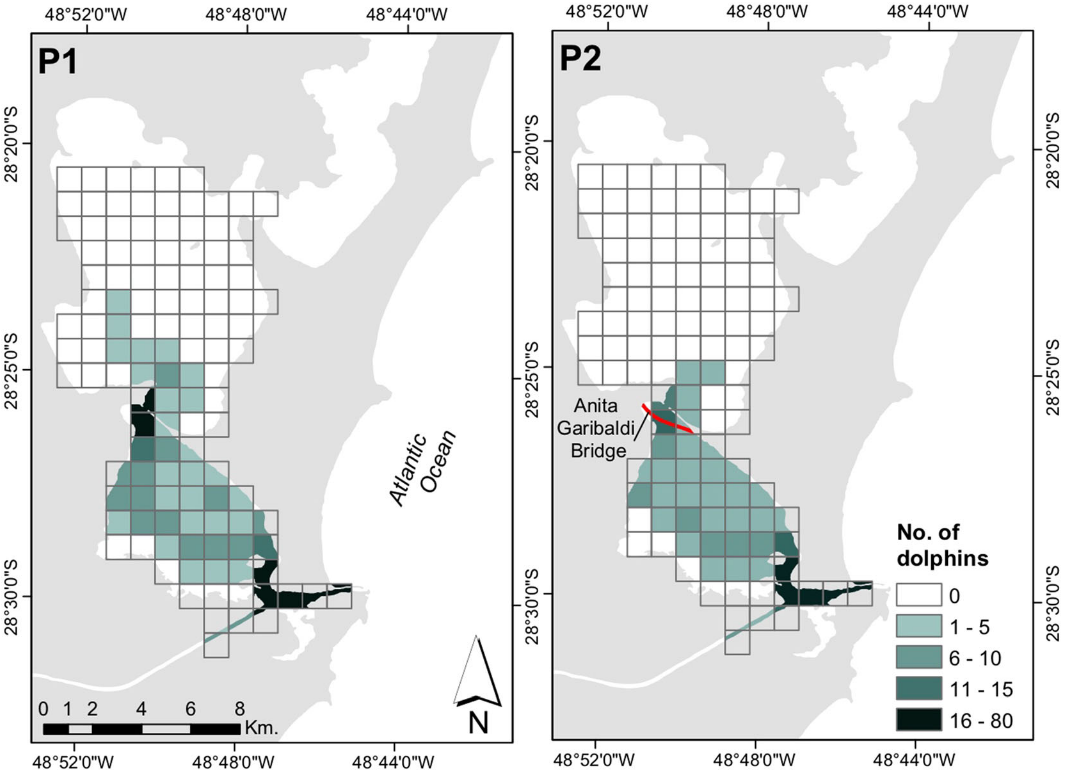

FIGURE 4 Dolphins' predicted distribution by means of hurdle models before (P1) and during the bridge works (P2) in Laguna, southern Brazil

Pirotta et al., 2013). Evidence suggests that the effects of dredging on marine mammals are most likely to be short-term alterations, mainly due to changes in prey availability (Todd et al., 2015).

In the present study, 'cooperative' dolphin presence was only significant in areas closer to the bridge construction during P2, and the number of 'cooperative' dolphin records was also significant in areas close to gillnet activity. Therefore, changes in spatial distribution during bridge construction may have increased the exposure of 'cooperative' dolphins to by-catch risk. We speculate that these distribution changes in 'cooperative' dolphins were a response to the distribution changes observed in 'non-cooperative' dolphins. When 'non-cooperative' dolphins reduced their home ranges, the areas they used also showed a greater overlap with those routinely used by 'cooperative' dolphins, pushing a few 'cooperative' individuals to use different areas. Indeed, competition for foraging patches seems to play a role in the spatial and foraging behaviour of this dolphin population (Cantor et al., 2018).

A broader outcome of all these distribution changes for 'cooperative' dolphins, however, is their use of areas closer to illegal gillnet activity. This may increase the risk of by-catch, a leading cause of mortality in aquatic mammals (Adimey et al., 2014; Brown, Reid, & Rogan, 2013; Fruet et al., 2010; Fruet, Laporta, & Flores, 2016). It is crucial that further studies are undertaken to verify if these spatial changes are permanent and, if so, determine the consequences for survival probability in dolphins that interact with fishermen. Since the core area for dolphins is superimposed on the main areas of gillnet use, it is critical to restrict and police this fishing activity if the risk of by-catch, mainly of 'cooperative' dolphins, is increased. Additionally, our study highlights that the dolphin core area is focused around the areas of dolphin–human cooperative fishing, an unusual foraging tactic that emerged hundreds of years ago and is now part of the behavioural repertoire of this dolphin population. Boat traffic and other anthropogenic activities should also be restricted in this area if this rare dolphin–human cooperative specialization is to be protected effectively.

Several researchers have appraised changes in the distribution of small cetaceans through time, attributing shifts to changes in foraging patch quality and to behaviours related to avoiding anthropogenic disturbances (Cremer et al., 2004; Hartel et al., 2014; Slooten et al., 2006; Wedekin et al., 2010). These spatial shifts may present a challenge in conservation planning. For instance, marine protected areas (MPAs) were created to protect resident populations of Hector's dolphin, *Cephalorhynchus hectori*, and bottlenose dolphin in New Zealand, and the Guiana dolphin, *Sotalia guianensis*, in southern Brazil. The effectiveness of these MPAs was evaluated a few years after their creation; it was found that modifications to dolphin distribution meant it was no longer contained within MPA boundaries (Hartel et al., 2014; Slooten, 2007; Wedekin et al., 2010). We agree that the development of a more flexible management scheme is needed to account for temporal changes in the distribution of mobile and wide-ranging species. This recommendation should be considered in the Laguna area, with reference to the implementation of management plans that limit fishing activities. Recently, fishing activities were banned in the core dolphin area (Laguna municipal law 1998/2018), but the effectiveness of this regulation must be assessed over time and adjusted accordingly with potential changes in the spatial distribution of the dolphin population. In addition, conservation plans should always consider variations in how individuals use the area, since individuals might be exposed unequally to a specific impact, and therefore respond differently. This seems to be the case in Laguna, as dolphins have different spatial distributions dependent on their main foraging tactic.

This research revealed changes in Laguna dolphin distribution patterns between two periods separated by a habitat disturbance. Core areas and spatial distribution were identified for two foraging tactics; we determined different spatial responses to the disturbance when comparing dolphins that cooperate with fishermen and those that do not. Although this research was based on the Laguna dolphin population, the field techniques and the distribution analysis approach employed can be applied to evaluate the effects of anthropogenic activity on other cetacean populations. A modelling protocol for analysing habitat use by small cetaceans was used for the first time, with promising results. We highlight the importance of considering differences in individual spatial requirements when assessing the effects of a disturbance, or when implementing conservation plans. Individuals might react to a disturbance in different ways, according to their foraging tactics, gender, life stage, or social interactions (Constantine, 2001; Lusseau, 2003; Pirotta et al., 2014). Finally, we found a potential side effect of the dolphin–fishermen interaction that might generate non-adaptive consequences: a potential increase (for 'cooperative' dolphins) in by-catch risk during disturbances caused by the bridge construction. Further studies could model the effect on the vital rates of the behavioural responses (i.e. spatial changes) observed in this study, and thus account for individual heterogeneity in exposition and response to human activity.

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