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Critically endangered franciscana dolphins in an estuarine area: fine-scale habitat use and distribution from acoustic monitoring in Babitonga Bay, southern Brazil

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ABSTRACT: Franciscana dolphins in Babitonga Bay represent the only fully estuarine population of this critically endangered species, but this location is also home to a population of Guiana dolphins. Surrounded by large cities and harbors, Babitonga Bay presents intense human activities and potential impacts that may threaten the dolphins. Understanding their habitat use and distribution can inform the implementation of conservation actions and mitigation of such impacts. Here, we used acoustic data from 60 fixed passive acoustic monitoring stations, implemented between June and December 2018. The relationship between the occurrence of franciscanas and environmental variables was investigated with generalized additive mixed models. The selected model presented 51% of explained deviance and included time of day, intensity of presence of Guiana dolphins, maximum slope, and bottom sediment, among other less statistically significant variables. A daily distribution pattern was identified, with franciscanas remaining in the areas of greatest occurrence especially in the morning and seeming to prefer sandy bottom and flatter areas. Areas intensively used by Guiana dolphins were avoided. Additionally, we mapped their distribution using empirical Bayesian kriging to identify the main areas of occurrence and for foraging. Franciscanas are consistently predominant in the innermost region of the estuary, without expressive use of the entrance channel, but with a wider range in winter than in spring. The area around the islands, between the north and south banks, represents an important foraging area, a behavior more frequent during dawn and night. This study provides important insights into critical habitats and behavioral patterns of critically endangered franciscanas in Babitonga Bay.

KEY WORDS: Passive acoustic monitoring · Critical habitat · Diel distribution · *Pontoporia blainvillei* · Threatened species · Conservation · Sympatry · *Sotalia guianensis*

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1. INTRODUCTION

Information on the habitat use and distribution of wild animal populations can guide management of conflicting human activities, allowing promotion of conservation strategies (Hastie et al. 2003, Cañadas et al. 2005). Because designating the entire distribution ranges of highly mobile species, such as marine mammals, as protected areas can be practically impossible, identifying priority areas which are essential to their survival, such as those used for foraging and breeding, is of great importance (Hoyt 2012).

The franciscana dolphin *Pontoporia blainvillei* is endemic to the southwestern Atlantic Ocean and oc-

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curs from Espírito Santo in Brazil (18° 25′ S) to Argentinian Patagonia (42° 35′ S; Crespo 2009). With high risk of extinction mainly due to high accidental mortality from entanglement in fishing nets (Pinheiro & Cremer 2003), the species is listed as Vulnerable globally by the IUCN (Zerbini et al. 2017) and is considered critically endangered by the Government of Brazil (MMA 2014). Their habitat use is poorly known, with information limited to how that relates to bathymetry at a relatively coarse spatial resolution. Fine-scale habitat use and temporal movement dynamics have not yet been well studied (e.g. Danilewicz et al. 2009, do Amaral et al. 2018, Sucunza et al. 2019). The species is mainly found in coastal habitats on the continental shelf, between the surf zone and 50 m depth, predominantly up to 30 m depth (Danilewicz et al. 2009). Some individuals are occasionally seen visiting bays and river deltas (Bordino et al. 1999, Di Beneditto et al. 2001, Azevedo et al. 2002, Failla et al. 2004, Santos et al. 2009, Zappes et al. 2018).

The only known distinct franciscana population residing exclusively in an estuarine habitat is found in Babitonga Bay, southern Brazil (Cremer & Simões-Lopes 2008, Cremer et al. 2018). With only 50 individuals, there is evidence of a high degree of isolation, corroborated by satellite telemetry data, photo-identification, and genetic analyses (Sartori et al. 2017, Cremer et al. 2018, Nara et al. 2022, Wells et al. 2022). This population is considered as a demographically independent management unit for conservation purposes (Nara et al. 2022). In addition to accidental catches in gillnets (Pinheiro & Cremer 2003), habitat degradation by chemical pollution (Alonso et al. 2012) and the construction and expansion of ports, including underwater blasting work and dredging, likely compromise the health of the bay's ecosystem and, consequently, the survival of this dolphin population (Cremer et al. 2018, Paitach et al. 2019).

Visual surveys have indicated a heterogeneous distribution of franciscanas in Babitonga Bay, with dolphins typically occurring in the innermost regions of the estuary and concentrating around the islands in its central portion (Cremer & Simões-Lopes 2008, Paitach et al. 2017, Cremer et al. 2018). Factors already recognized to influence their habitat use include variations in tidal cycles, which probably reflect prey availability fluctuation, and the presence of sympatric Guiana dolphins *Sotalia guianensis* (Paitach et al. 2017, Cremer et al. 2018). The Guiana dolphin population has 150 individuals and is also considered resident, although unlike franciscanas, they commonly move out of the bay (Cremer et al. 2018). There is a high distribution overlap between these 2 cetacean populations, although their core areas do not overlap (Cremer et al. 2018).

Understanding the ecological requirements of small cryptic cetaceans is a major challenge, and standard visual surveys are not always a viable option (Mellinger et al. 2007). Franciscanas are one of the smallest dolphin species; they form small groups, rarely display aerial behaviors, and only expose a small part of their body during relatively short surfacings (Wells et al. 2013, Cremer et al. 2018). Furthermore, visual observations, whether from vessels or aircrafts, are restricted to daylight periods and require very good weather conditions. Like most cetaceans, they produce sounds when diving, which allows acoustic sampling (Tyack & Clark 2000).

Passive acoustic monitoring (PAM) allows the autonomous logging of underwater sounds generated by cetaceans and can be an efficient alternative to visual surveys for detecting their presence (Van Parijs et al. 2009). PAM can be used to investigate various ecological and behavioral aspects of cetaceans, can sample habitat during poor weather conditions or at night, and may have relatively low associated costs (Mellinger et al. 2007). Cetacean echolocation click trains detected in PAM stations distributed in an area of interest, for example, illustrate how PAM can be used to identify potential foraging areas and periods (e.g. Pirotta et al. 2014, Tubbs et al. 2020, Paitach et al. 2021). PAM has been widely used worldwide for studies on cetacean distribution, migrations, behavior, habitat use, and identification of impacts and threats (e.g. Mellinger et al. 2007, Verfuß et al. 2007, Van Parijs et al. 2009, Jaramillo-Legorreta et al. 2017, Carlén et al. 2018). For franciscanas, PAM has only been used to describe their acoustic repertoire and sound production characteristics (Tellechea et al. 2017, Barcellos & de Oliveira Santos 2021, Paitach et al. 2021).

For our study, we used an array of PAM devices for sampling franciscana sounds during winter and spring in Babitonga Bay. Our objectives were to identify the main environmental variables related to how that population uses the habitat in the bay, including in the presence of Guiana dolphins, and to map franciscana distribution and foraging areas that could inform conservation strategies and management of human activities. We hypothesized that franciscanas vary their seasonal and diel distribution and that the distribution patterns are linked to environmental features and niche partitioning with Guiana dolphins.

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2. MATERIALS AND METHODS

2.1. Study area

Babitonga Bay (26° 02′–26° 28′ S, 48° 28′–48° 50′ W; Fig. 1), Santa Catarina State, southern Brazil, is approximately 160 km^2 wide, with 6 m average water depth and some extremely shallow areas, which become exposed at low tide (Vieira et al. 2008). The bay is supplied by waters from several rivers, but its physical–chemical characteristics are spatially homogenous (IBAMA 1998). It has a semi-diurnal regime of microtides, meaning 2 well-defined daily cycles of floods and ebbs during spring tides, reaching a maximum amplitude of less than 2 m (Vieira et al. 2008). Bathymetric and morphosedimentary maps of Babitonga Bay can be viewed in Vieira et al. (2008). Since the closure of the narrow southern channel by the construction of a causeway to the São Francisco do Sul island in 1937 (thick black line in Fig. 1), the only connection to the open ocean is through a 28 m deep channel to the north.

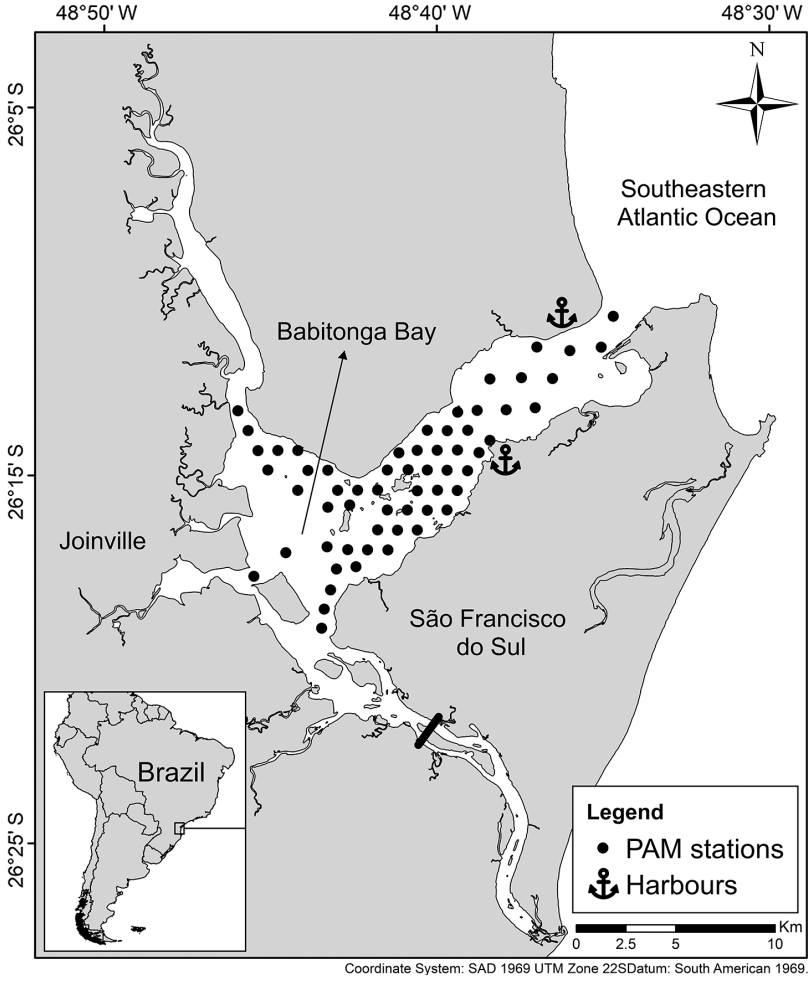

Fig. 1. Distribution of 60 passive acoustic monitoring (PAM) stations deployed in Babitonga Bay, southern Brazil, for recording franciscana dolphins. The thick black line indicates the location where the historical southern channel was closed in 1937 for construction of an access road to the São Francisco do Sul island

2.2. Sampling design and methods

Acoustic monitoring was done using C-PODs (Chelonia), i.e. autonomous acoustic loggers designed to log trains of tone-like pulses between 20 and 160 kHz. Such devices have an omnidirectional hydrophone (i.e. records in all directions) and are ideal to record narrowband high-frequency (NBHF; i.e. peak frequency at 130 kHz and no essential energy below 100 kHz) sonar click trains of franciscanas but also the broadband clicks of Guiana dolphins (Paitach et al. 2021). C-PODs were fitted into custom-made cages, designed to protect them from net entanglement, with no or negligible interference in the acoustic recordings (Paitach et al. 2021).

A systematic grid was designed for deploying 60 PAM stations. Deployment sites were determined at semi-random within the survey area, constrained to locations with an average depth of 4 m or deeper (maximum depth sampled 22.3 m), and were at least 1600 m apart in the access channel and 800 m in other areas (Fig. 1) to proportionally address the expected distribution of franciscanas in those areas (cf. Cremer et al. 2018) (i.e. in areas where a higher density of franciscanas is expected, the distance adopted was the lesser possible — without the risk of a franciscana being detected in more than 1 PAM station simultaneously — for a fine-scale coverage).

It is virtually impossible that a franciscana was detected by more than 1 C-POD of the grid at the same time, and the difference in detection rate between PAM stations basically depends on the density of individuals in the area. For the transmission loss of NBHF sounds with a source level of 190 dB (i.e. similar to harbor porpoises; Villadsgaard et al. 2007) and a C-POD

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detection threshold of 120 dB, the theoretical detection range of a franciscana should be around 400 m on-axis of the sonar beam; off-axis, this distance drops to a few meters (N. Tregenza, Chelonia, pers. comm. 2017). In practice, however, this distance should be considerably less, as it is an estuarine environment with high turbidity and topographical complexity, which greatly reduce NBHF sound propagation.

Acoustic samples were collected from June 26 to December 24, 2018, with a varying number of days monitored at each station. In total, 35 C-PODs were used, with a maximum of 20 C-PODs operating simultaneously. A subset of C-PODs (usually 20) was replaced every ~30 d by others with fresh batteries and secure digital cards, always using a new PAM station. To minimize systematic bias from possible differences in C-POD detection potential due to temporal degradation (Dähne et al. 2013), devices were randomly placed at each deployment, as recommended by Carlén et al. (2018). The design aimed at sampling each position for 30 d in the winter and 30 d in the spring, on average. Ten C-POD subsets were defined with 3 station positions each, considering the closest possible positions for each group, and each of these positions was sampled at each exchange, ensuring that the distribution of the monitored points remained as homogeneous as possible in the area over the study period.

2.3. Data analysis

Franciscana sonar click trains were identified using the KERNO click train classifier in CPOD.exe (Chelonia). That software identifies NBHF-type sounds with higher robustness and lower levels of false positives than classifiers based on individual clicks (Dähne et al. 2013, Roberts & Read 2015). Only click trains classified by KERNO as having a high or moderate probability of being generated by franciscanas were analyzed. The detection positive minutes (DPM) per hour (number of minutes with at least 1 franciscana click train within an hour) were extracted and were used here as a proxy for the intensity of franciscana presence.

The C-POD has a limited number of logged pulses per minute (4095) to avoid data overload and, consequently, saturation of the memory card and battery consumption. After that limit, the logging is interrupted and only resumed in the following minute. Ambient noise, such as the sound of rain or moving bottom sand or the sound produced by living organisms such as shrimp and fish, may generate pulsed sounds that can be logged by the C-PODs. Excessive noise data were evaluated with the Detections and Environment tool in CPOD.exe — corresponding to 2.4% of the collected data — and disregarded to ensure sampling homogeneity.

2.4. Habitat use

For modelling the habitat use of franciscanas on a fine scale, the intensity of their presence around PAM stations, expressed as DPM h^{-1}, was modelled as a function of environmental variables. Generalized additive models (GAMs; Hastie & Tibshirani 1990) were applied using R software v.4.0.3 (R Core Team 2020) to accommodate the possibly complex relationships between franciscana presence and variables. Because the data set to be modelled was large (n = 64 745), models were fitted using the function bam (mgcv R package; Wood 2017), which allows relatively fast model fitting. Preliminary inspection was conducted to ensure that the data contained information useful for inference on habitat use. Maps and graphics illustrating sampling distribution balance over space and time confirmed the adequacy of the data (Fig. S1 in Supplement 1 at www.int-res.com/articles/suppl/m707p131_supp1.pdf).

Environmental variables (Table 1) were obtained for each PAM station using ArcGIS Pro 2.3 (https://www.esri.com), with input data from morphosedimentary and topographic databases (provided by Vieira et al. 2008). Tidal conditions for each monitoring hour were attributed to PAM stations using tide tables published by the Directorate of Hydrography and Navigation of the Brazilian Navy for the port of São Francisco do Sul. The DPM h^{-1} of the Guiana dolphin was also included as a variable. The classification procedure for this species was like that for franciscanas, with virtually zero risk of miss-specification (see Paitach et al. 2021).

Linear correlation and concurvity, a measure of the non-linear relationship between smooth terms within a GAM, were verified for a preliminary model that includes all available variables. Pearson coefficients equal or stronger than 0.5 (positive or negative) were used for identifying correlated variables. All measures of depth (Table 1) were linearly correlated to each other, to slope measures, and to geographic location (UTMX and UTMY). Aspect and topographic complexity index were linearly correlated to each other. Correlated variables were not included in the same model.

Preliminary models indicated that residual autocorrelation could be a problem. Correlation structures presented a cyclic pattern with an apparent

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Table 1. Variables used for modelling habitat use of franciscana dolphins in Babitonga Bay

Variable	Range of values	Explanation and categories
UTMX	723237–741747	Longitude in UTM
UTMY	7086720–7101381	Latitude in UTM
Hour.of.day	Cyclic	24 h circadian cycle
Month	Categorical	Months of the year, from Jun to Dec
Tide.state	Categorical	Tidal cycles: flood, high, ebb, low
Tide.type	Categorical	Type of tidal amplitude as a function of the sun–moon gravitational conjunction: syzygy = full and new moons; quadrature = first quarter and third quarter moons
Sg.DPM	0–60	Detection positive minutes of *Sotalia guianensis* per hour
Season	Categorical	Austral seasons: winter = Jun 20 to Sep 21; spring = Sep 22 to Dec 20
Carbonate	Categorical	Percentage of inorganic salts in the sediment within a radius of 400 m: 0–10%, 10–20%, 20–30%, 30–40%
Organic.matter	Categorical	Percentage of organic matter in the sediment within a radius of 400 m: 0–2%, 2–4%, 4–6%, 6–8%, 8–10%
Sediment	Categorical	Predominant texture of the bottom sediment within a radius of 400 m: sand, sand with mud, mud with sand, mud
Deep.max	2–22.3	Maximum depth in meters within a radius of 400 m
Deep.min	0.1–6.9	Minimum depth in meters within a radius of 400 m
Deep.mean	1.8–10.7	Average depth in meters within a radius of 400 m
Deep.range	1.5–18.1	Range between minimum and maximum depth within a radius of 400 m
Slop.mean	0.179–3.364	Average slope in degrees within a radius of 400 m
Slope.max	1.519–51.388	Maximum slope in degrees within a radius of 400 m
Aspect	59.096–258.092	Average direction of the slope in degrees from north within a radius of 400 m
TCI	0.0001–0.6613	Topographic complexity index calculated by multiplying scaled values for slope and aspect (Bouchet et al. 2015) averaged within a radius of 400 m
Margin.distance	146.5–1952.5	Distance in meters from the nearest margin
Margin.feature	categorical	Feature of the nearest margin: continent or island

peak every 24 units apart. Therefore, a 2-dimensional (2-D) smoother (Wood 2017) for easting (i.e. UTMX) and northing (i.e. UTMY) combined, with a different tensor for each hour of the day, was added to all models to account for autocorrelation. This approach allowed the spatial heterogeneity in the data to be explicitly modelled as a function of time and space. Also, a first-order autoregressive (AR1) error structure function was added in the models. For each model, the AR1 correlation parameter ρ was calculated by fitting models without correlation structure and measuring the first lag in the autocorrelation function (acf) in R. In the present modelling framework, the autoregressive correlation structure corresponded to a generalized estimating equation (Ziegler 2011) approximation which, in practice, increased the uncertainty in the estimated smoothers. That means that p-values for smooth terms became larger when compared to corresponding models without AR1 structure. Since the data set was formed by time series, with observations representing repeated measurements for each location, a smooth term for each sampled PAM station as a random variable was used in all models.

Smooth functions were used to model the relationship between continuous variables and the response value. Except for the 2-D smoother for easting and northing combined with a tensor for each hour of the day and a cyclic spline for hour of day (Hour.of.day), thin plate regression splines were used (R package mgcv; Wood 2017). The dimension basis (i.e. parameter *k* on smooth functions, mgcv R package) was set to a maximum of 7 for all tested smoothers of variables, to both avoid overfitting and prevent smooth functions impossible to interpret biologically. For variables Aspect and Maximum Slope, that parameter was further decreased to 5, because preliminary modelling showed fitted smoothers of hard biological interpretation, i.e. with several peaks.

Model variables were selected in a forward step approach, based on the minimum Akaike's information criterion (AIC; Akaike 1974): the initial model presented a 2-D smooth function for UTMX and UTMY with a different tensor for each hour of the day, a smooth function for Point as a random variable, and a cyclic smooth term for Hour.of.day. In the first round of variable selection, models with only 1 additional variable were fitted, and the one presenting the smallest AIC score was considered as the initial model in the following step. In each step, only 1 additional variable was separately added to the model selected in the previous step. Those steps

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were repeated until the AIC could not be improved by the addition variables, so the resulting model was retained as the most efficient to describe the variation in the presence of franciscanas.

2.5. Distribution

The distributions of franciscanas and their foraging activity were investigated through interpolation of spatial data (i.e. kriging) using software ArcGIS Pro 2.3 (Geostatistical Analyst; Geostatistical Wizard; https://www.esri.com). Kriging is a geostatistical interpolation method that assumes that the distance or direction between the points in the sample reflects a spatial correlation that can be used to explain the variation in the surface (Oliver & Webster 1990). Without imposing *a priori* environmental variables, the spatial autocorrelation of a specified number of points is modeled in semi-variograms which are used to estimate density at each location (Oliver & Webster 1990). More specifically, empirical Bayesian kriging (EBK) was used. While other kriging methods require several projection parameters to be manually adjusted, EBK automatically calculates these parameters at each predicted location using a subset process and data simulations. The method also differs from other kriging methods by taking the SE introduced by the estimate of the underlying semivariogram into account, propagating that uncertainty when generating predictions in locations not surveyed (Oliver & Webster 1990, Krivoruchko 2012). Semi-variogram parameters were estimated using restricted maximum likelihood, which is indicated for small data sets to avoid overestimating densities at restricted areas (Krivoruchko 2012).

Two variables were separately used to generate distribution maps: (1) detection positive hours (DPH) were used to identify the main areas of franciscana occurrence, and (2) adjusted feeding buzz ratio (FBR) was used to identify foraging areas. The DPH was obtained using the KERNO classifier and a similar selection criteria as the DPM used in the analysis of habitat use but with hours as the period of interest (i.e. coarser temporal resolution). All click trains recorded throughout the study were exported and classified as feeding buzzes, based on an inter-click interval (ICI) of less than 10 ms (Carlström 2005, Paitach et al. 2021). FBR values were then calculated as the ratio between the number of buzzes and the number of non-buzz click trains (with ICI > 10 ms). A weighted metric of the importance of the foraging areas was obtained by adjusting FBRs by the intensity of franciscana occurrence (i.e. multiplying the FBR by the DPH).

Seasonal (winter and spring) and diel (dawn = 00:00–05:59 h, morning = 06:00–11:59 h, afternoon = 12:00–17:59 h, and night = 18:00–23:59 h) maps were produced. The midday and midnight cut-off limits were chosen to allow some understanding for distribution patterns within the light and dark periods. Those periods can be more easily used for illustrating management strategies related to the time of the day. Average values of DPH and adjusted FBR were calculated separately for each day (for season maps) and for each period of the day (for diel period maps), and then averages for all sampled days were calculated for each PAM station. Days with less than 24 h of data collected or periods of the day with less than 6 h collected were not considered in this analysis. Since the FBR values are adjusted, biological interpretation can be difficult. Therefore, maps for FBR values were grouped into classes of importance. Outliers were removed, and the resulting scale of values was divided into 4 equally sized classes. The lowest class was disregarded (low importance), and the others were moderate, high, and very high importance for foraging.

3. RESULTS

Of the 60 monitoring stations planned throughout the study area, only 6 were not sampled in winter and 11 in spring, due to loss of equipment. PAM stations were monitored for an average of 28 d (minimum of 3 and maximum of 57 d) in winter and 24 (minimum of 2 and maximum of 91) in spring. A total of 66 350 h of acoustic recordings were collected in 182 d, both seasons considered. After data filtering (i.e. removing data with excess noise), 64 745 h were analyzed, including 7432 (11.5%) with franciscana recordings.

3.1. Habitat use

The final selected habitat use model had 51% of explained deviance and fitted the data well, except for high values of the response variable (Table S1 in Supplement 2 at www.int-res.com/articles/suppl/m707p131_supp2.xlsx). Despite the assumption of residual constant variance not being fully met, the negative binomial distribution ($\theta = 0.092$) showed the most supported fit to the residuals and was adopted for modelling. Residual autocorrelation was greatly

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reduced by the inclusion of an autoregressive function in the model yet was still mildly present (Supp. material). For that reason, the inclusion of variables in the final model must be interpreted carefully, especially for variables with lower significance (i.e. large p-values). Coefficients for factor variables and smooth functions included in the final model can be evaluated in Table 2.

The forward step variable selection resulted in the inclusion of smooth functions for intensity of presence of Guiana dolphins (SG.DPM) and maximum slope (Slope.max), in addition to the compulsory smoother in the initial model (i.e. Point as a random variable; a 2-D smoother for UTMX and UTMY, with a tensor for each hour of the day; and a cyclic smoother for Hour.day) (Fig. 2). There was a clear cyclic pattern in the occurrence of franciscanas across the study area, indicating that in the areas where their presence was more intense, they were more likely to occur during the early hours of the day. Areas with very high values of intensity of presence of Guiana dolphins were avoided by the franciscanas, but to a lesser extent, they seemed to be tolerated. Franciscanas seem to avoid steeper areas within the range of slopes in Babitonga Bay.

The final model also included factor variables Month, Sediment, Tide.type, and Tide.state. Because of multiple factor variables, partial effects for each combination of factor levels would require several plots. Boxplots of values adjusted for the intensity of the presence of franciscana (Pb.DPM) for each selected factor variable are shown individually (Fig. 3). The presence of franciscanas seems to vary slightly over the months of study, but a clear seasonal pattern was not observed. The presence of franciscanas in Babitonga was associated with the granulometry of the bottom sediments, with a greater presence over sandy bottoms and less presence over mud bottoms. Despite contributing to improving the model AIC, it is not clear how tide variables were related to the variations of presence of franciscanas, since the levels were not precisely estimated, as indicated by large p-values (Table S2).

Table 2. Parametric coefficients for factor variables and smooth terms included in the final model of habitat use of franciscana dolphins in Babitonga Bay (Akaike's information criterion = 71430.59, deviance explained = 51%). edf: effective degrees of freedom; DPM: detection positive minutes. **Bold**: significant at 0.05

Parametric coefficient	Estimate	p (*t*-distribution)
Intercept	−3.253	**<0.001**
Month–Jul	0.428	**0.012**
Month–Aug	0.685	**<0.001**
Month–Sep	0.591	**0.002**
Month–Oct	0.119	0.516
Month–Nov	−0.006	0.974
Month–Dec	−0.404	0.123
Sediment–mud + sand	1.830	**<0.001**
Sediment–sand	0.679	0.124
Sediment–sand + mud	1.776	**<0.001**
Tide type–syzygy	0.103	0.060
Tide state–flood	−0.007	0.880
Tide state–high	0.021	0.673
Tide state–low	−0.073	0.147
Smooth terms	**edf**	**p (*F*-statistic)**
s(point)[a]	50.843	**<0.001**
s(UTMX, UTMY, hour of day)[b]	[b]	[b]
s(hour of day)	3.281	**<0.001**
s(Guiana dolphin DPM)	5.861	**<0.001**
s(maximum slope)	3.695	**<0.001**

[a]Random effect term for sampling point; [b]Coefficients for compulsory model term representing the interaction between eastings (UTMX), northings (UTMY), and of hour of day as a factor are omitted because of large number of levels (i.e. 24) but are presented in Table S2

3.2. Distribution

Predictive maps of occurrence and foraging areas were generated for each season (Fig. 4). The distribution of franciscanas was predominant in the innermost region of the estuary, close to the community of Vila da Glória, without a marked use of the open sea access channel. In the winter, their distribution expanded, extending to the mouth of the Palmital River (northwest axis), the entrance to Saguaçú Lagoon (western margin), and the Linguado Channel (south axis) and further along the northeastern margin of the bay. In the spring, the distribution was predominantly in the central region of the bay, between the northern and southern margins. The area with the highest density in winter was located slightly towards the west compared to that in spring, which remained closer to the north-central margin. The area between the northern margin and the islands represents important franciscana foraging areas, both in winter and spring, but in winter, the area between the islands and the southern margin were also important for foraging. In winter, the northeastern margin and the area close to the mouth of the Palmital River (northwest axis) also appear to be areas used for foraging, which was not seen in the spring.

Areas of occurrence and importance for foraging for franciscanas varied slightly throughout the diel

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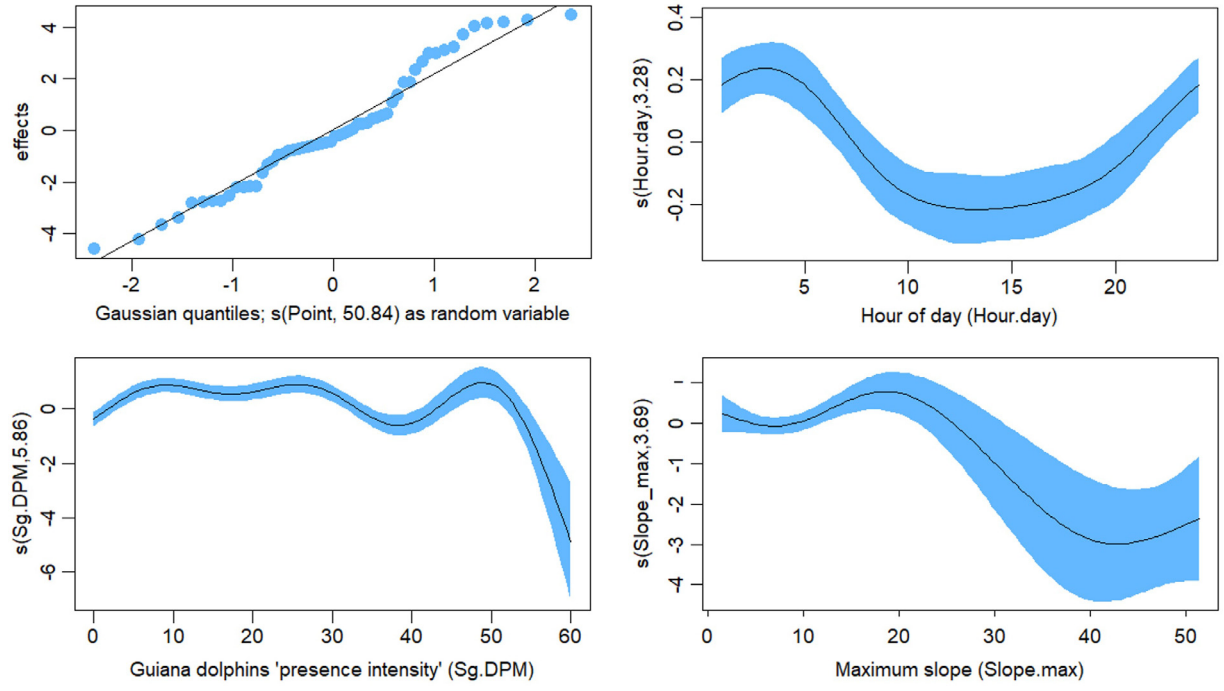

Fig. 2. Smooth functions for variables hour of day, Guiana dolphin presence intensity, and slope, included in the final model for habitat use of franciscana dolphins in Babitonga Bay (numbers in *y*-axis labels indicate df)

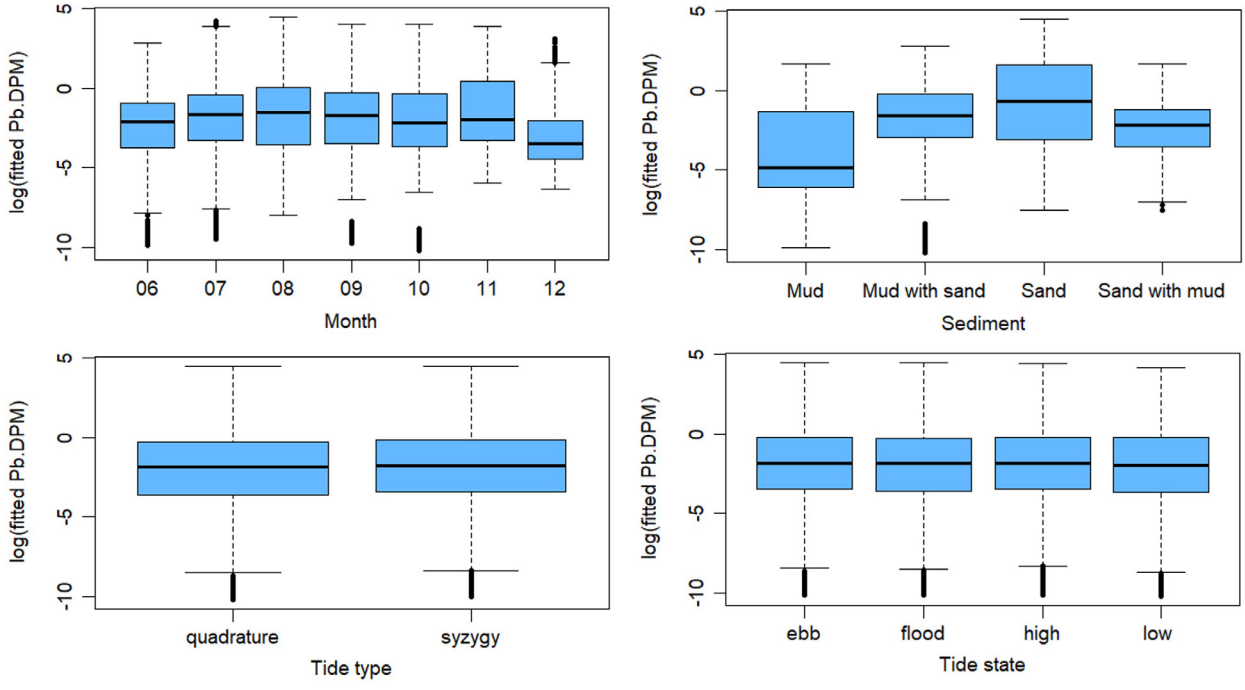

Fig. 3. Boxplots for fitted values for different levels of the factor variables months, sediment, tide type and tide state, included in the final model for habitat use of franciscana dolphins in Babitonga Bay. Bar: median; box: interquartile range (IQR); whiskers: max./min. values within 1.5 × IQR above/below box; dots: outliers

periods in both seasons (winter: Fig. 5; spring: Fig. 6). The central area of the bay, between the islands and the northern margin, remained as the core area of franciscanas throughout the day, in both seasons, while areas with less intensity of use varied throughout the day in each season. In winter, forag-

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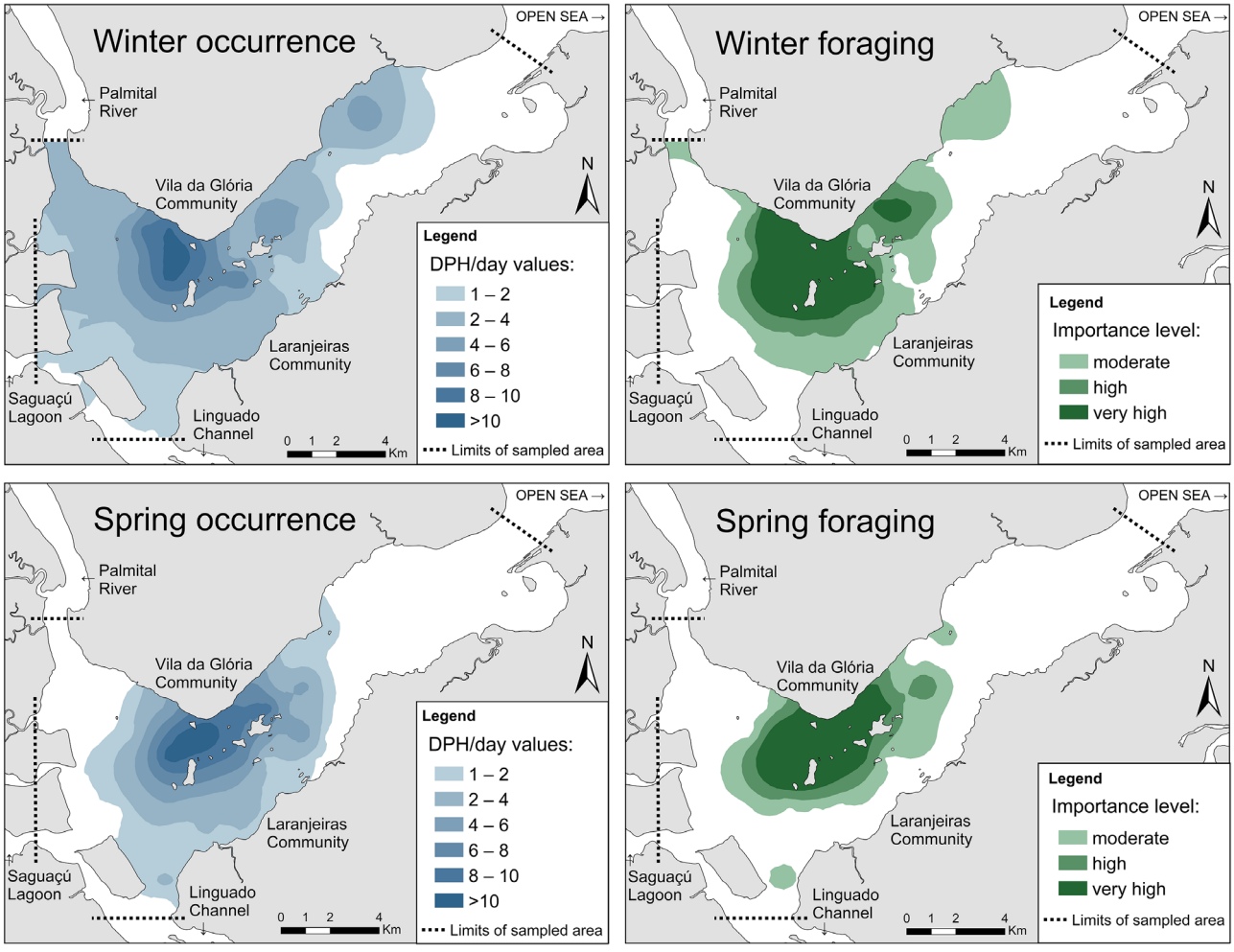

Fig. 4. Occurrence of franciscana dolphins in Babitonga Bay during winter and spring as well as foraging areas in each of those seasons. Foraging importance level estimated by multiplying detection positive hours (DPH) per day by the feeding buzz ratio (see Section 2.5 for details)

ing was more concentrated near the core area during the morning and afternoon, and at night, it expanded southwards, to a region close to the community of Laranjeiras, and was intensified at dawn (Fig. 5). In spring, the foraging areas were more restricted, with some oscillation in the east–west direction (Fig. 6). During the night, they expanded eastwards, occupying the entire surroundings of the islands. During the afternoon, the pattern was towards the opposite direction, with foraging in the innermost portion of the bay up to its western margin, in an extensive area of shallow water and muddy banks (Fig. 6). In both seasons, the dawn period showed the biggest patches of very high importance for foraging, indicating that the feeding behavior is more intense in that period, followed by the night in winter and the afternoon in spring (Figs. 5 & 6).

4. DISCUSSION

4.1. Cyclic patterns of habitat use

There was a clear diel cyclic pattern in the presence of franciscanas across the study area. In the areas where their occurrence was more intense, they were more likely to occur during the early hours of the day (Fig. 3). This means that in the main area of occurrence of franciscanas, the highest densities of calls were in the early hours of the day and late afternoon (individuals are more clustered), and in the rest of the day, the density of calls decreased in this area and increased in other areas, that is, reducing the difference in the density of calls between the different areas of occurrence (individuals are more dispersed). This is possibly a reaction to environmental cycles, which modify the abiotic conditions of ecosystems,

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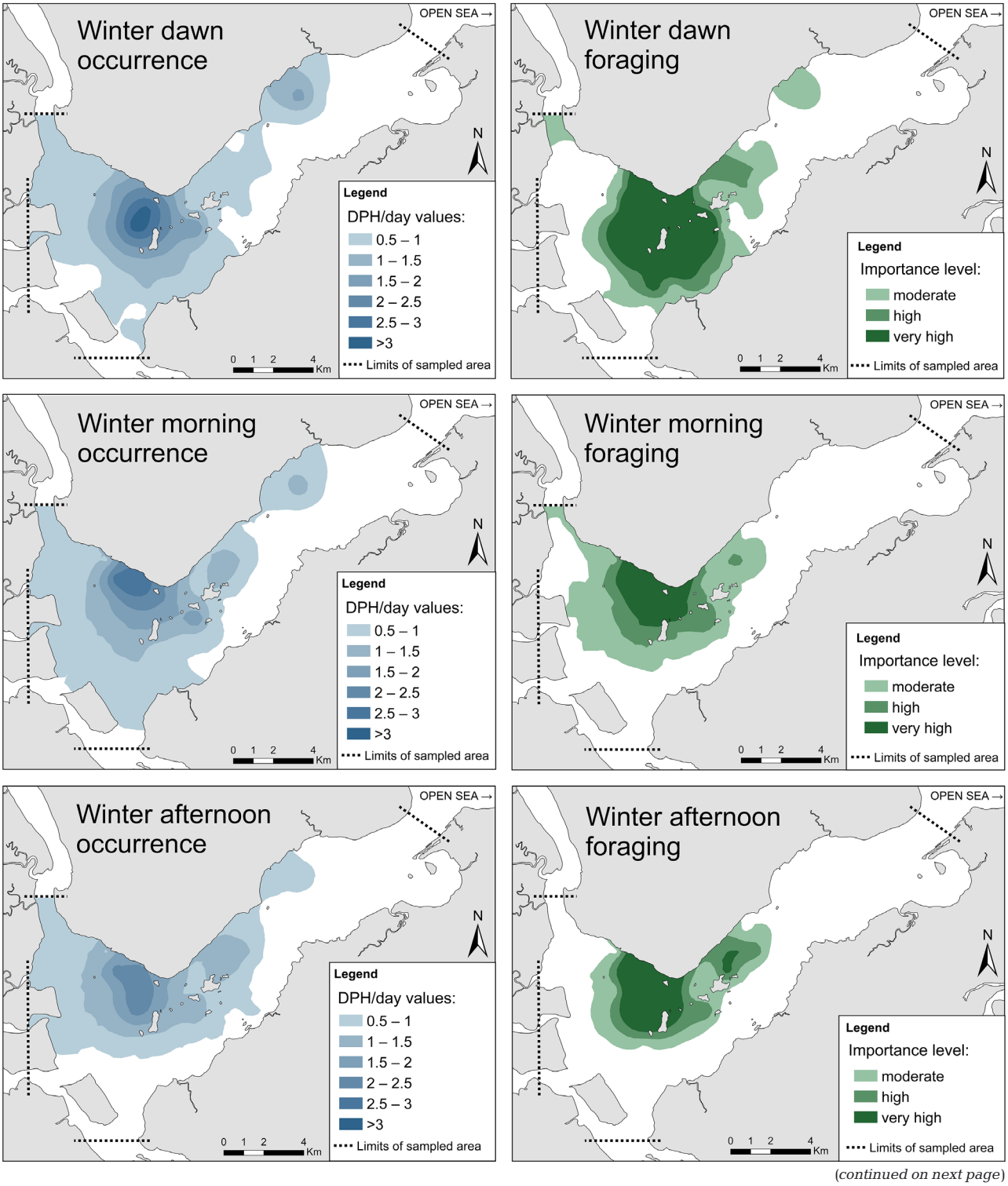

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Fig. 5. Occurrence of franciscana dolphins in Babitonga Bay during winter as well as when foraging only in each period of the day (dawn = 00:00–05:59 h, morning = 06:00–11:59 h, afternoon = 12:00–17:59 h, and night = 18:00–23:59 h). DPH: detection positive hours

with biological organisms corresponding, like fishes and squids that are preys of dolphins (Aschoff 2013). Behavior patterns in response to diel cycles can be diurnal, nocturnal, or twilight (Fernandez-Betelu et al. 2019). In coastal environments, tidal cycles can also cause environmental changes that can result in

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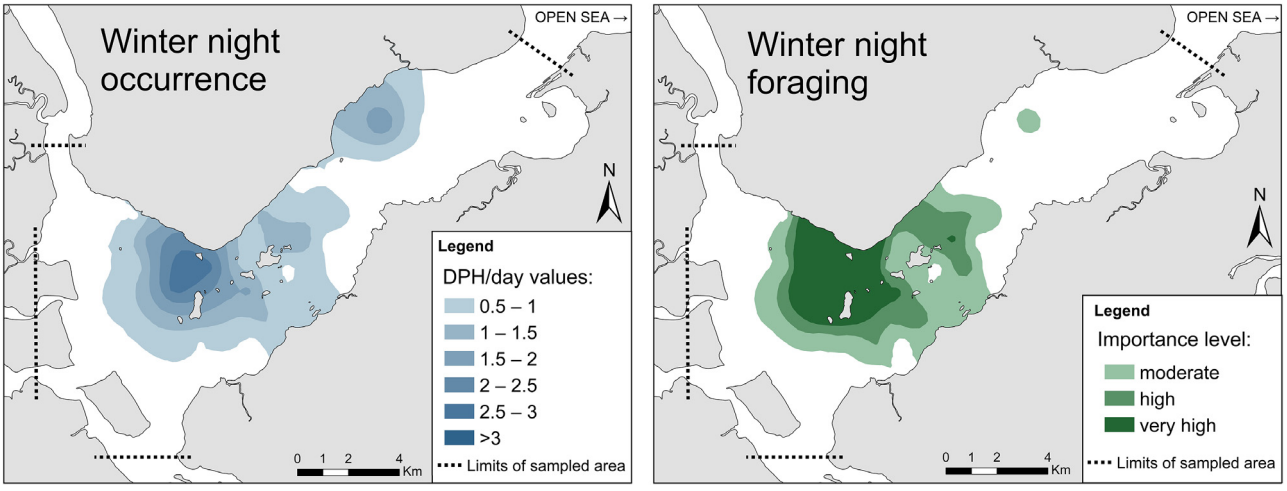

Fig. 5 (continued)

periodic movements of many species, including cetaceans (Gibson 2003). Similarly to what happens in Anegada Bay, Argentina (Bordino et al. 1999), the franciscanas in Babitonga Bay were found to present movement patterns related to the tides, moving towards the mouth of the bay during ebb and in the opposite direction during the flood, following the current flow (Paitach et al. 2017). In the present study, although the tide was selected as an important factor for habitat use, it was not possible to clearly identify a pattern. In fact, the effects of tidal cycles on dolphin habitat use patterns can vary seasonally, and cetaceans appear to be less influenced by tides in open areas than in narrow channels (Pierpoint 2008, Fernandez-Betelu et al. 2019).

Franciscanas seem to avoid steeper areas within the range of bottom slopes in Babitonga Bay. This may be linked to bathymetry also, since depth variables were not included because of their correlation with geographic location (i.e. UTMX, UTMY). Holz (2014) observed the influence of the average depth on the distribution of this same population of franciscanas, with a preference for deeper areas, although non-linear influences were not explored in this study; therefore, conclusions should be cautious. Do Amaral et al. (2018) also identified depth as limiting the distribution of the species, without detecting slope effects. However, their study assesses the topographic slope of studied environments in a much wider spatial scale, which may have weakened the power of analysis of this variable. In 2 gulfs in southern Australia, the bottlenose dolphin *Tursiops truncatus* also prefers habitats associated with a flat bottom topography (Bilgmann et al. 2019).

The heterogeneous distribution of franciscanas within Babitonga Bay was found to be associated with sand in the bottom sediment. The species occurs mainly in coastal regions, outside bays and estuaries, where sandy bottoms predominate, and although the Babitonga population is resident in an estuarine environment (Cremer & Simões-Lopes 2008), the main prey observed in its diet (*Stelifer rastrifer*, frequency of occurrence of 62%) are small fish typical of the coastal environment and that have habits associated with sandy bottoms (Paitach 2015), demonstrating that the population may still maintain preferences related to the usual distribution of the species. The preference of sandy bottom areas by franciscanas has already been noted, especially in spring, with an increase in the use of muddy areas in winter (Paitach et al. 2017). These findings were based on visual sightings, but they are now corroborated and expanded by the present study. When we look at the foraging areas at dawn and night, there was an increase in the use of muddy bottom areas, demonstrating that these areas are also important for the population in the spring. A very similar result was observed for the harbour porpoise in the Moray Firth, Scotland, where only sandy banks were identified as important foraging areas without including time variables (Brookes et al. 2013), but when the diel cycles were investigated, adjacent muddy areas were also found to be important habitats for them at night (Williamson et al. 2017).

Studies on the habitat use of franciscanas throughout their distribution are rare, partly explained by the difficulty of studying this species in the wild. Based on bycatch data, Danilewicz et al. (2009) observed that the distribution of franciscanas in Rio Grande do Sul reaches predominantly up to 30 m depth, although they occur up to 50 m depth. That study, however, did not investigate whether water depth is an

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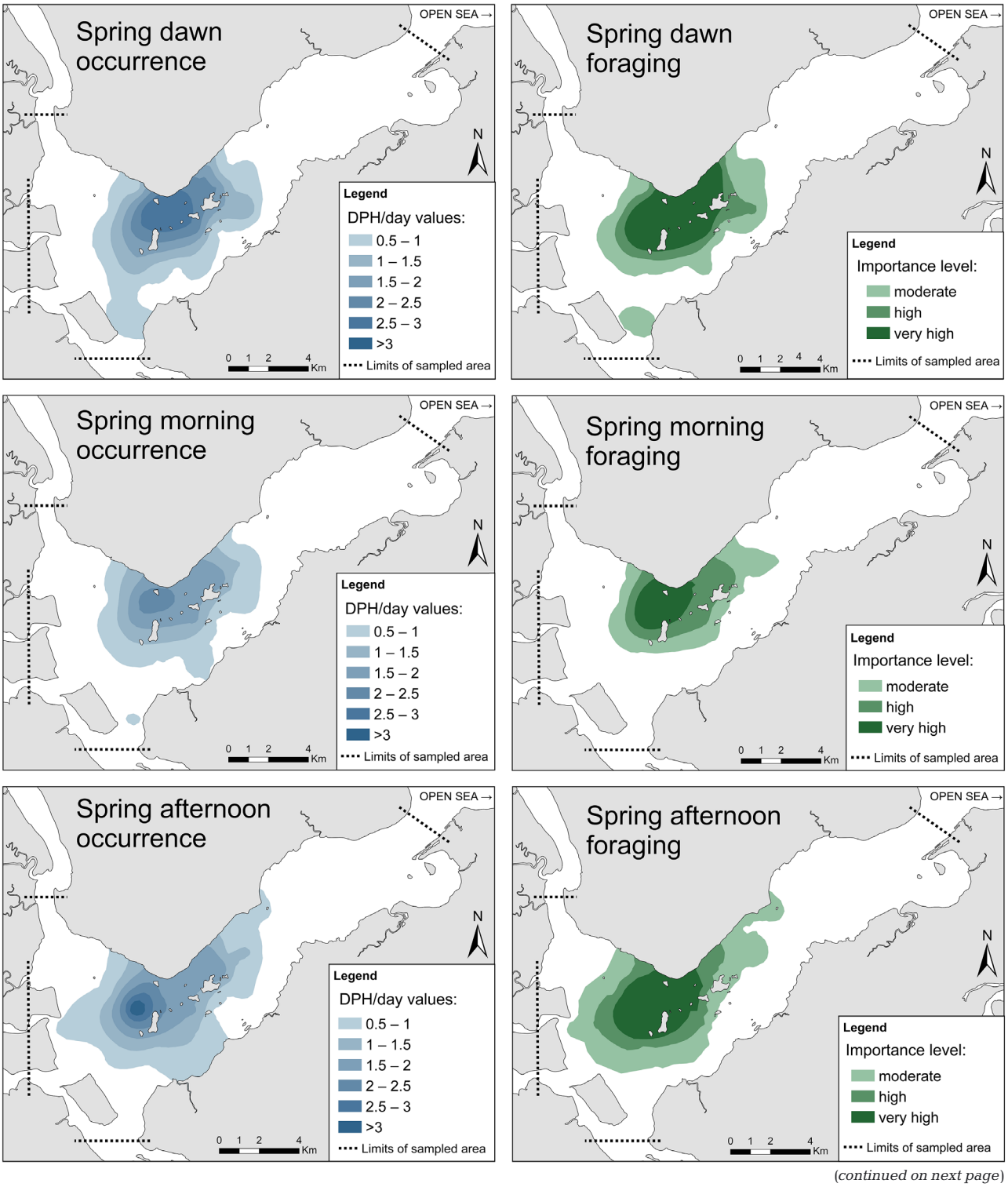

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Fig. 6. Same as Fig. 5, except during spring

important factor related to the distribution of the species. More recently, Amaral et al. (2018) analyzed the influence of environmental variables to predict the spatial niche of franciscanas on a wide scale, verifying that depth and salinity can influence the presence of franciscanas. Using aerial surveys of distribution over a wide area in southeastern and southern Brazil, Sucunza et al. (2019) observed 54 groups of

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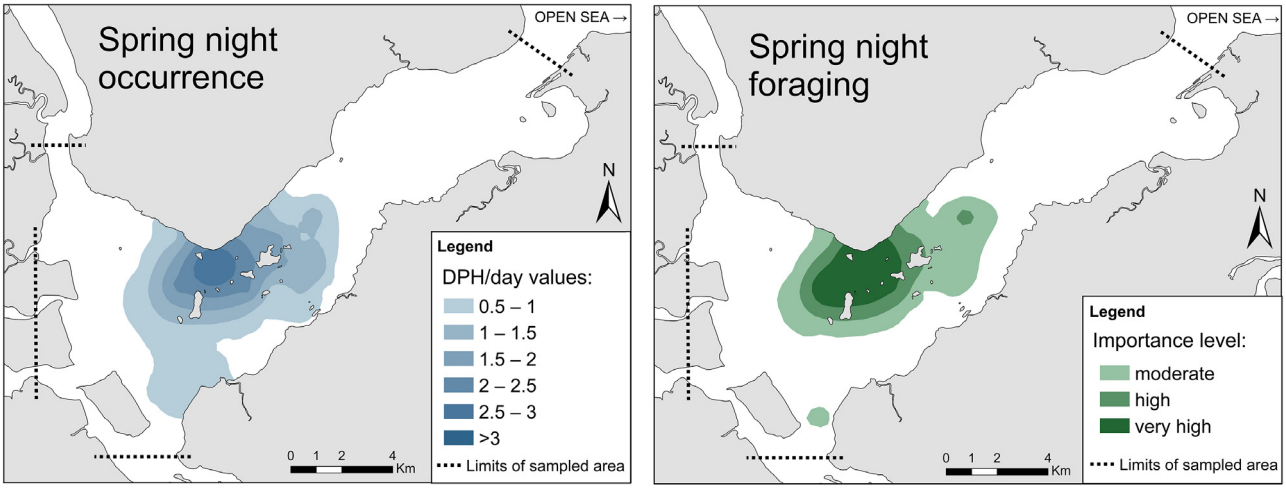

Fig. 6 (continued)

franciscanas in waters with an average depth of 7.15 m. Although focused on a typical estuarine population, the novel habitat use investigation presented here allows insights into important environmental features to the species in general. The main insights are that franciscana behavior can be variable throughout the day, with movement patterns between specific areas; bottom topography is important for the presence of franciscanas, which prefer areas with some bottom irregularity; the bottom substrate is also important, probably due to the types of prey available in each habitat; and the presence of other dolphins strongly influences the distribution of franciscanas.

Environmental cycles typically affect the food chain from lower trophic levels to higher. Therefore, these cycles are expected to affect the prey and, consequently, the dolphins (Hastie et al. 2004). Predators must be able to take advantage of these temporal changes in the aquatic environment to optimize feeding success (Lin et al. 2013). However, the distribution dynamics between predators and prey are bidirectional — both sides in this relationship affect each other — so predators seek to optimize prey capture and prey correspondingly to reduce risk of predation (Trites 2009, Becker & Suthers 2014). Thus, the trade-off between foraging success and predator avoidance is decisive in the habitat use of a species (Trites 2009). The franciscanas have no frequent predators in Babitonga Bay, such as large sharks and orcas (Cremer 2015, Gerhardinger et al. 2020). Therefore, the availability of prey is the main factor affecting their distribution. Franciscanas in Babitonga Bay are considered a generalist and opportunistic species, preying on the most abundant small fish species in the environment (Cremer et al. 2012, Paitach 2015). However, considering the bidirectionality of the predator–prey relationship mentioned above, it is expected that competing predators will affect each other (discussed in Section 4.2).

Despite contributing to improving the model's AIC, it is not clear how many of the factor variables are related to the presence of franciscanas. Many levels were not precisely estimated, as indicated by large p-values (Table S2). The modelling approach adopted here was adequate to provide insights into the environmental variables related to the presence of franciscanas within Babitonga Bay. However, model fit was not perfect, although optimal with the selected variables; therefore, this ecological investigation could greatly benefit from further modelling exploration, such as inclusion of additional variables (e.g. prey availability), exploring more complex interactions between variables, modelling habitat use for specific periods (e.g. additional seasons), exploring models that accommodate more complex autoregressive structures, and others as well.

4.2. Sympatry with the Guiana dolphin

The intensity of presence of Guiana dolphins was identified in the models as the main variable related to habitat use of franciscanas in Babitonga Bay. Cremer (2007) observed a high overlap in the spatial niche of these populations but with no competition for interference between them, which has been reaffirmed over the years (Cremer et al. 2018). The Guiana dolphins also have larger areas of distribution in seasons with less prey availability elsewhere (Wedekin et al. 2010) and in Babitonga Bay (Cremer

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et al. 2011). Analysis of stomach content points to a high degree of prey sharing between the species (Cremer et al. 2012, Paitach 2015). It is interesting to note that although both species have wider amplitudes of the trophic niche in cold months, when the prey availability is lower (Cremer 2007), there is a decrease in the trophic overlap between them, attenuating the effects of competition (Paitach 2015). This may be the reason why our models showed some overlap between the 2 species, with franciscanas apparently indifferent to the presence of Guiana dolphins up to an extreme extent (Fig. 3).

It is not possible to disregard the hypothesis that the franciscanas are silent when Guiana dolphins are present, but according to visual observations made over the years, it is evident that franciscanas leave the area as soon as the *Sotalia* approach (Cremer et al. 2018), which leads to the belief that acoustic data actually indicate an evasion of franciscanas from the area with the increase of Guiana dolphin density, but this should be better investigated and validated in the future.

Different ecological processes may be involved in the niche partition between ecologically similar species living in direct sympatry, such as differences in behavior patterns and diet, differences in habitat use, and temporal segregation in the use of resources (Parra 2006, Méndez-Fernandez et al. 2013, Nichol et al. 2013). Considering the high overlap of the trophic and spatial niches and the absence of agonistic interactions between franciscanas and Guiana dolphins in Babitonga Bay (Cremer et al. 2018), we suggest that the main factors that make possible the coexistence of these 2 species are fine-scale differences in habitat use with temporal segregation in the foraging behavior. A fine-scale study of Guiana dolphin habitat use and other analytical approaches that integrate different spheres of the realized niche of both species would assist in elucidating that question. Joint conservation strategies for sympatric species, ecologically similar and that share limited resources, can benefit from the understanding of how such species affect or influence each other (Bearzi 2005).

4.3. Spatio-temporal patterns of occurrence and foraging

The distribution of the franciscanas was predominant in the central region of the bay, with greater dispersal in winter than in spring, with little to no detections in the connection channel with the open sea in either season. This corroborates conclusions from previous studies derived from visual observations (Cremer & Simões-Lopes 2008, Cremer et al. 2018). However, we observed a much more acute use of the south-central portion of the bay in relation to what was observed in previous studies. In fact, franciscana preys are known to concentrate in the region of the bay (Cremer 2007, Paitach 2015). In the present study, the south-central portion of the distribution area was most frequented at night and at dawn, mainly for foraging purposes. The innermost muddy banks in the western part of the estuary are also used for foraging, especially on spring afternoons. Since foraging is expected to intensify when/where individuals can maximize their food intake (Pirotta et al. 2014), cyclic use of such areas can be related to the distribution of the Guiana dolphin. Not surprisingly, the south-central portion of the bay is considered the core area of Guiana dolphin distribution (Cremer et al. 2011, 2018).

The present study is the first to analyze the distribution of franciscanas throughout the day and to preliminarily identify the main foraging areas in Babitonga Bay, on seasonal and diel scales. Multiscale approaches have been shown to be very useful in studies of distribution of highly mobile species that explore dynamic habitats (González-García et al. 2018), such as the characteristics of the environment and species dealt with here. In particular, the association of foraging with specific environmental characteristics must be considered in the management of anthropic disorders (New et al. 2013, Pirotta et al. 2014). In the present work, the distribution analyses were descriptive and did not aim to associate foraging behavior with environmental characteristics; however, such an approach would be desirable in future studies.

4.4. Potential and limitations of passive acoustic monitoring

The PAM approach and especially the use of C-PODs showed promising signs of a very valuable tool for investigating spatio-temporal patterns of habitat use and distribution of franciscanas. This is the first systematic effort of this nature for the species. The processing of the large data volume obtained (more than 66 000 h of recordings) was facilitated through the C-POD system automated procedure, which saves time and also reduces the potential subjectivity bias of the researcher due to differences in human perception when evaluating acoustic signals and the exhaustion that would result from a manual analysis of a dataset of this proportion (Rayment et al. 2009).

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A key assumption in the present study is that the heterogeneity observed in the franciscana acoustic detections would reflect the density of these animals in the bay. Failure to meet that could rise from when animals are present but not detected, but comparative studies using visual and acoustic detections indicate that acoustic detections are extremely robust to reflect the density of individuals; therefore, depending on the species, dolphin silence periods may not be an issue (Verfuss et al. 2007). Similarly to harbour porpoises *Phocoena phocoena* in the wild, that click almost continuously and with maximum silent intervals of less than 15 s (Akamatsu et al. 2005), it is very likely that franciscanas also continuously echolocate in the estuarine waters of Babitonga Bay, which presents a complex topography and very high water turbidity with virtually no visibility (Oliveira et al. 2006, Vieira et al. 2008), but it is interesting that this assumption be validated when possible. Furthermore, and because this is an isolated population (Cremer et al. 2018, Nara et al. 2022), numbers of acoustic detections in the study area are not expected to be influenced by emigration/immigration of individuals. Finally, since areas with an average depth of less than 4 m, potentially dry at low tides, were undersampled, it is possible that in periods when lower detection numbers were recorded within the sampled area (i.e. where the water was continuously deeper than 4 m), animals might have been in those shallower areas.

We assumed a homogeneous probability of detection of franciscanas by C-PODs over space and time. It is known, however, that sound propagation may be influenced by spatial and temporal variations in the behavior of the dolphins (Verfuss et al. 2009, Leeney et al. 2011) and by environmental conditions, such as water temperature and salinity (Richardson et al. 1995). There is a trade-off between the range and directionality of the sounds produced by dolphins during traveling and foraging behaviors (Tyack & Clark 2000). Understanding how different behaviors can affect detection probability of franciscanas by PAM can assist the accuracy of future studies. Temperature and salinity affect the speed and absorption of sound in water (Richardson et al. 1995, Ainslie & McColm 1998), but considering a low variation of these parameters in the study area, we hypothesize that this bias is negligible.

Despite the protective cages, entanglement in nets became a problem throughout the study, causing the loss of some equipment units, a problem that was intensified during the spring and forced an early ending of survey after 6 mo of start. The loss of equipment occurred randomly, without any consistent damage to any region sampled. In some cases, after the loss of a C-POD, a new deployment was carried out onsite to complement the data collection. We recommend that future studies employ more extensive effort into clearly communicating with fishing communities, so that such incidents can be avoided or the PAM devices can be returned in the case of undesired misplacement.

The 2 seasons sampled in the present study, winter and spring, were strategically selected to identify priority habitats for the franciscanas. Winter is the season of least availability of food (Cremer 2007), so franciscana distribution reflects its most critical places for foraging during a period of food scarcity. The protection of foraging areas is essential for small cetaceans, which are particularly vulnerable to environmental impacts that can reduce prey availability, due to their high food requirements and apex position in the marine food webs (Ross et al. 2011, Wisniewska et al. 2016). In turn, spring represents the main birthing period for the franciscana population of Babitonga Bay (Cremer et al. 2013), so the area of distribution of the population in this season is of great importance for the protection of newborns. The protection of important breeding areas is essential for the conservation of small cetaceans, since the stages of young life are particularly vulnerable to species threats (Ross et al. 2011).

4.5. Implications for management and conservation

The endangered nature of the franciscana population of Babitonga Bay is evident, with a restricted habitat, small population size, and isolation and genetic distinction from other populations (Cremer et al. 2018). Some anthropogenic activities in Babitonga Bay constitute direct or indirect threats to the survival of this population of franciscanas, such as overfishing, chemical pollution, intense vessel traffic, and port construction and maintenance activities (Cremer 2007, Paitach et al. 2019). Above all, the cumulative and potentially synergetic effects of these different sources of anthropogenic impact on coastal environments put the dolphins under strong pressure and are often neglected by environmental authorities (Cremer 2007, Azevedo et al. 2017, Herbst et al. 2020). The establishment and operation of big ports represent a major threat to marine biodiversity, causing acute disturbances and a chronic decrease in environmental quality (Domit et al. 2009). Underwater blasting work, periodic dredging of the seabed,

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and intensification of sea traffic result in suspension of sediments and thereby increase the bioavailability of contaminants, oil slicks on the surface, increased underwater noise, and the risk of collision between cetaceans and vessels, among other impacts that disrupt the natural communities, reduce the availability of prey, and compromise the entire health of the ecosystem (Domit et al. 2009, Jefferson et al. 2009, Herbst et al. 2020). It is known that franciscanas avoid areas with known higher levels of underwater noise in Babitonga, areas which are close to the existing ports (Holz 2014). It has also been observed that after activities requiring the use of dredges, pile drivers, and other heavy machinery, the Guiana dolphins abandoned the São Francisco do Sul port inlet for years (Cremer et al. 2018).

Several new ports are planned within Babitonga Bay, at least 3 of which are in the areas identified as critical habitats for the franciscanas. In light of the results presented here, some key aspects must be considered in environmental impact studies, such as (1) the importance of franciscana foraging areas as critical habitats for their survival; (2) impacts caused to the population of Guiana dolphins that can also result in fundamental consequences for the franciscanas, since the core area of Guiana dolphins is strongly threatened by port expansion, and if such impacts materialize, it is likely that there will be a shift in the distribution of this population to other areas, probably increasing the pressure of competition on franciscanas; (3) the exclusion of artisanal fishing areas, due to the delimitation of vessel maneuvering areas in ports, which may displace the fishing fleet in areas of the bay that are important to the franciscana, resulting in an increased risk of bycatch of this species; and (4) the cumulative and potentially synergetic impacts caused by the new ports and those already operating in the territory.

In Babitonga, dredging for the extraction of sand from the bottom occurs throughout the year (Herbst et al. 2020), and the uncontrolled removal of this substrate can also be an indirect threat to the franciscanas, as indicated by the association between the species' habitat and this type of substrate found in our study. The operation of dredgers also generates substantial noise, which can be impactful for franciscanas (Holz 2014). The licensing of new sand extraction areas needs to take this potential negative impact into account and adopt the necessary mitigation measures, such as avoiding critical franciscana habitats.

The franciscana bycatch in artisanal fisheries, although not as frequent in Babitonga Bay as in other areas within the range of the species, still represents an important threat considering that the removal of any individual from this small population can be critical to its sustainability (Pinheiro & Cremer 2003, Cremer et al. 2018). Distribution and foraging maps presented here can guide the participatory development and implementation of exclusion zones in areas and periods of greater use by the franciscana. Unfortunately, there is no efficient mechanism for fisheries management in Babitonga Bay, making it difficult to implement strategies to prevent accidental captures, including fishing exclusion zones or the use of acoustic deterrent devices on nets (FAO 2021).

In recent years, many marine protected areas (MPAs) have been designated with the aim of managing human activities for the protection of marine mammals (Hoyt 2012). Dynamic approaches with flexible spatial and temporal limits of protection areas have been recommended for mobile species such as dolphins (de Castro et al. 2014, Santos et al. 2017, Hazen et al. 2018, Tardin et al. 2020). However, there are many difficulties for the creation or effective implementation and maintenance of MPAs in Brazil (e.g. lack of staff and funding for monitoring and enforcement, deficient or absent interinstitutional governance, excessive bureaucracy, and lack of political incentives for any significant change) (Gerhardinger et al. 2011). A proposal to create an MPA in Babitonga Bay has been underway in the national environmental agency (i.e. Chico Mendes Institute for Biodiversity Conservation, Brazilian Ministry of the Environment) for more than 10 yr (Herbst et al. 2020). We suggest that this study be considered for the establishment of an MPA in Babitonga Bay and for the elaboration of the management plan or other similar instruments.

4.6. Final considerations

PAM with C-PODs has provided a useful method to get important information for the management of low-density and threatened cetacean populations worldwide, such as the vaquita *P. sinus* (Jaramillo-Legorreta et al. 2017), the Maui dolphin *Cephalorhynchus hectori maui* (Rayment et al. 2011), the Baltic harbour porpoise (Carlén et al. 2018), and now the franciscanas of Babitonga Bay. Unfortunately for vaquitas, that information came too late, and the species is on the brink of extinction (Jaramillo-Legorreta et al. 2019). Effective conservation actions need to be implemented while the franciscana population in Babitonga Bay is still viable, or this unique and critically endangered population may also be subject to

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premature decline and extinction. This study provides new insights into their habitat use and distribution that should fundamentally be used to design conservation actions. The challenge ahead is to identify effective ways to integrate information on the ecological needs of the franciscana into relevant public policies for the management of human activities.

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