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Modeling cetacean habitat use in an urban coastal area in southeastern Brazil

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ABSTRACT: Most studies of cetacean habitat use do not consider the influence of anthropogenic activities. We investigated the influence of environmental and anthropogenic variables on habitat use by humpback *Megaptera novaeangliae* and Bryde's whales *Balaenoptera brydei* off the coast of the Brazilian city of Rio de Janeiro. Although there are 2 marine protected areas (MPAs) in this area, few data are available on cetacean habitat use or on the overlap of different cetacean species within these MPAs. Our aim was to evaluate the effectiveness of the MPAs and propose a buffer zone to better protect the biodiversity of the study area. We conducted systematic surveys and developed spatial eigenvector generalized linear models to characterize habitat use by the species in the study area. Habitat use by humpback whales was influenced only by depth, whereas for Bryde's whales there was the additional influence of anthropogenic variables. For Bryde's whales, which use the area for feeding, sea surface temperature and the distance to anchorages had a major influence on habitat use. We also showed that neither of the MPAs in the study area adequately protects the hotspots of either whale species. Most of the humpback whale grid cells with high sighting predictions were located within 2 km of the MPAs, while areas of high sighting prediction of Bryde's whales were located up to 5 km from the MPAs, closer to beaches. Our findings provide important insights for the delimitation of protected areas and zoning of the MPAs.

KEY WORDS: Species distribution modeling · Whale · *Megaptera novaeangliae* · *Balaenoptera brydei* · Marine protected area · Spatial autocorrelation · Human impact · Rio de Janeiro

1. INTRODUCTION

Understanding where species occur and the factors that determine their occurrence at a given location has been a primary objective of ecology for decades. The study of the distribution of terrestrial organisms tends to receive more attention than for marine species, which are still widely overlooked (Redfern et al. 2006). For some long-lived species that have large home ranges, such as cetaceans, understanding distribution patterns can be a major challenge (Connor et al. 2000). Cetaceans are considered to be keystone species since their elimination from an ecosystem may lead to the disappearance of other species (Estes et al. 1998), and because many are top predators, often playing an important role in the structure of the community and patterns of coexistence (Estes et al. 2001). Cetaceans are also health sentinels of marine ecosystems, allowing the better identification and management of impacts that ultimately affect the health of animals and human populations associated with the oceans (Bossart 2011). Given all of these considerations, cetaceans are good candidate models for marine conservation.

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With the recent development of GIS techniques and remote-sensing satellites, our understanding of the factors that drive cetacean habitat use has been advancing considerably (Redfern et al. 2006). Dynamic and static environmental factors such as depth, sea surface temperature (SST), chlorophyll *a* (chl *a*) concentrations, seabed slope, bottom type, water transparency, and tidal currents have all been used as proxies for understanding cetacean habitat use (Cañadas et al. 2005, Garaffo et al. 2011, Tardin et al. 2019). Some studies have included prey availability as a variable influencing cetacean habitat use, and this can be a primary factor determining their distribution, although it can be difficult to obtain data on prey types and/or their biomass at sea (Torres et al. 2008, Herr et al. 2009, Doniol-Valcroze et al. 2012, Pirotta et al. 2014, Burrows et al. 2016, Giannoulaki et al. 2017). Despite recent advances, and increasing human pressures, to date few studies have investigated how human activities influence cetacean habitat use (Bonizzoni et al. 2014, Di Tullio et al. 2015, Carlucci et al. 2016, Díaz López & Methion 2017, Weinstein et al. 2017, Tardin et al. 2019). Due to the intense growth of human populations in coastal areas, pressure from fisheries, marine traffic, and pollution are increasingly threatening many cetacean species (Erbe 2002, Bearzi et al. 2006, Read et al. 2006, Dorneles et al. 2013, Marley et al. 2017).

A common tool for the mitigation of anthropogenic impacts on aquatic ecosystems is the creation and implementation of marine protected areas (MPAs) (e.g. Guisan et al. 2013, Notarbartolo di Sciara et al. 2016). As cetaceans are highly mobile animals that typically use extremely large areas over the course of their life span, most studies report only a partial overlap between their distribution and MPAs, which permits many human activities to continue to impact these animals (e.g. Pennino et al. 2017, Santos et al. 2017, Tardin et al. 2019, Passadore et al. 2018, Bonizzoni et al. 2019).

Two MPAs are located off the coast of the city of Rio de Janeiro, southeastern Brazil: the Itaipu Marine Extractive Reserve (RESEX Itaipu) and the Cagarras Archipelago Natural Monument (MoNaCa). Although previous studies have reported the occurrence of cetaceans within both MPAs (e.g. Lodi & Monteiro-Neto 2012, Lodi et al. 2014, Lodi & Tardin 2018), there has been no ecological modeling of their spatial overlap.

Considering this, we investigated the influence of environmental and anthropogenic factors on habitat use by humpback *Megaptera novaeangliae* and Bryde's whales *Balaenoptera brydei* in this biologically rich region that suffers profound human impacts. We hypothesized that the distribution of both species is influenced by environmental and anthropogenic variables, and we investigated the spatial overlap of the distribution of each species with the MPAs.

2. MATERIALS AND METHODS

2.1. Study area

Our study zone comprised an area of 394.5 km^2 off the coast of the city of Rio de Janeiro, which encompasses 2 MPAs (Fig. 1). The RESEX Itaipu was established on 30 September 2013 by Rio de Janeiro state law number 44417. This MPA, a category V protected area (Day et al. 2012), was created to protect the rights of local fishers, and to prevent overfishing. MoNaCa was created on 13 April 2010 by Brazilian Federal Law number 12229. The principal objective of this category III MPA (Day et al. 2012) is the protection of remnants of the insular ecosystem of the Atlantic Forest domain, its scenic beauty, and refuges and nesting areas for seabirds. The MoNaCa comprises 4 islands (Cagarra, Comprida, Palmas, and Redonda) and 2 islets (Filhote da Cagarra and Filhote da Redonda). Located 5 km off the coast of the city of Rio de Janeiro, this archipelago is exposed to pollution from the waters of Guanabara Bay and the Ipanema submarine sewage outfall (Van Weerelt et al. 2013). As the MoNaCa protects only the islands and islets themselves and the waters within a 10 m radius, most of the marine environment around the archipelago is unprotected, including the habitats used by cetaceans (e.g. Lodi & Monteiro-Neto 2012, Lodi et al. 2014, Lodi & Tardin 2018).

Guanabara Bay is the primary route of the maritime traffic of the port of Rio de Janeiro, and is surrounded by approximately 6 million inhabitants (IBGE 2018) and some 10 000 industrial installations, including 16 oil terminals and 12 shipyards, which all discharge domestic and industrial effluents into the bay (Perin et al. 1997). Anthropogenic influence in Guanabara Bay area began in the early 16^{th} century, although environmental impacts escalated after 1930, when this region underwent an intense process of industrialization (Fistarol et al. 2015). The coast adjacent to Guanabara Bay includes many beaches and islands with intrinsic natural beauty that attract millions of tourists every year.

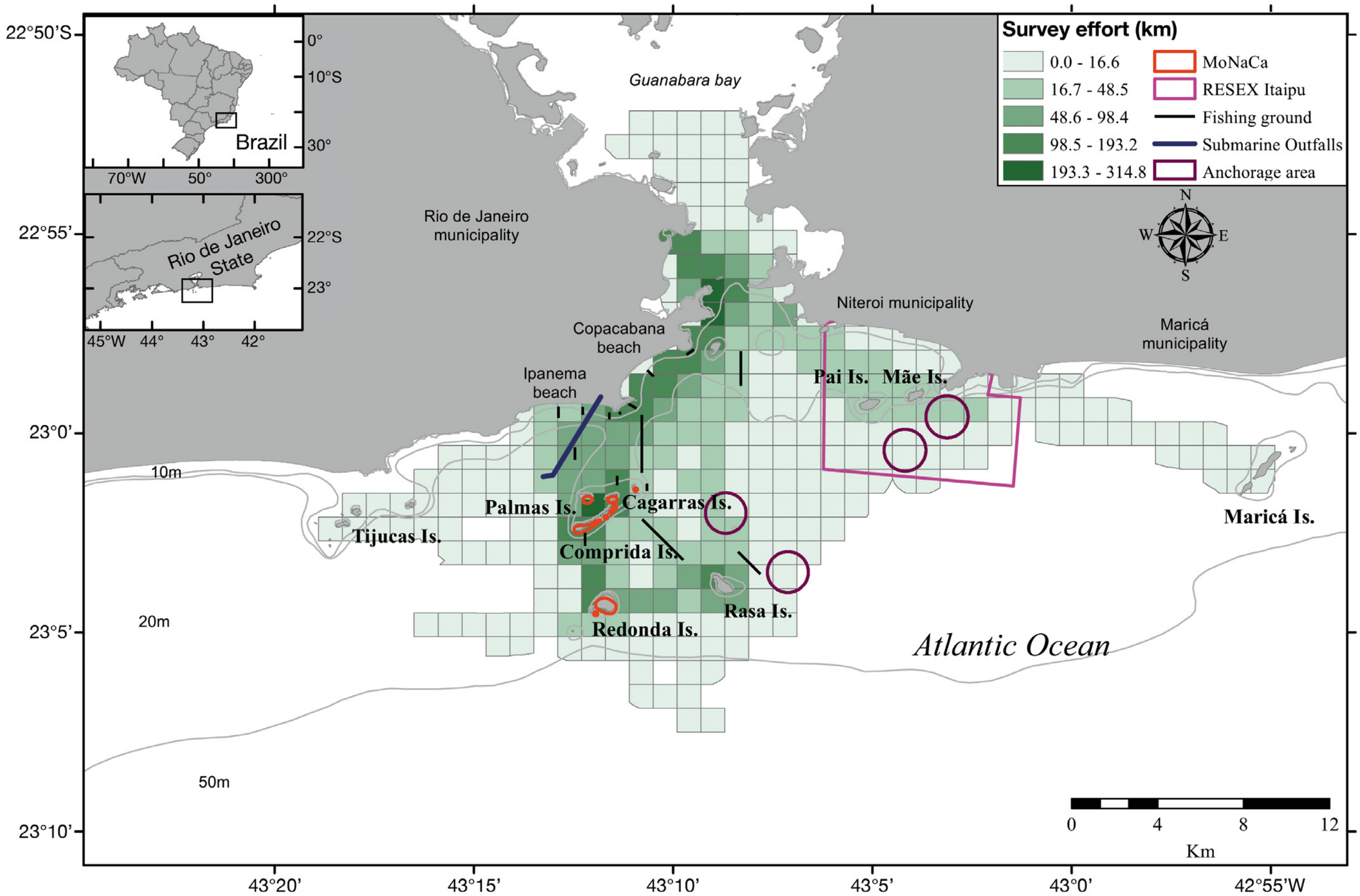

Fig. 1. Study area off the coast of the city of Rio de Janeiro, southeastern Brazil, showing the boat survey effort covered in a 1 km × 1 km grid, the 2 marine protected areas (MoNa Cagarras and RESEX Itaipu), and the distribution of the different human activities within the region. The MoNaCa comprises 4 islands (Cagarra, Comprida, Palmas, and Redonda) and 2 islets (Filhote da Cagarra and Filhote da Redonda). Isobaths are shown as continuous gray lines

2.2. Data collection

We conducted surveys onboard a 10 m scuba diving vessel, equipped with an inboard engine, between August and December in 2011 and 2012, and then throughout the year from 2014 to 2017. We followed 3 pre-established routes that were alternated randomly to survey the entire area whenever weather conditions were favorable (Beaufort scale ≤3). During surveys, we maintained boat speed at approximately 12 km h^{-1}. Whenever we sighted a cetacean, we initiated focal group or focal individual follows, at a slower speed of approximately 6 km h^{-1}.

We recorded the location of the cetaceans by GPS, following an established protocol (Tardin et al. 2017, 2019), with a new reading being taken whenever the focal animal or group had moved 500 m (Lehner 1998). This resulted in multiple GPS locations for a given individual or group during a single day. A group refers to all the cetaceans recorded in a single encounter when observed in a spatial aggregation with similar behavior, i.e. foraging, socializing, resting, or traveling (Shane et al. 1986).

2.3. Data processing

The study area was divided into a 1 km × 1 km grid with 318 cells using the ArcGIS-compatible Marine Geospatial Ecology Tools 0.8a64 software (Roberts et al. 2010). The environmental (mean depth, slope, distance to coast, distance to islands, mean SST, and mean chl *a* concentration) and anthropogenic variables (distance to fishing grounds, distance to anchorage areas, and distance to submarine outfalls) were determined for each grid cell. We calculated all distances from the center point of the cell, in meters, using the ArcGIS 10.3.1® 'near' tool from the Spatial Analyst toolbox. We produced 9 maps showing the environmental and anthropogenic features of the study area (see Supplement 1 at www.int-res.com/articles/suppl/m642p227_supp.pdf).

We obtained mean depth, distance to coast, distance to islands, and slope from nautical chart 1506 from the Hydrography and Navigation Department of the Brazilian Navy (https://www.marinha.mil.br/chm/dados-do-segnav/cartas-raster). We calculated the slope as the difference between the maximum and minimum depth values, recorded in each grid cell divided by the distance in meters between both depth values, as in previous studies (Clapham & Nicholson 2009).

We extracted chl *a* data from the Moderate Resolution Imaging Spectroradiometer (MODIS) using the finest resolution (4 km), which is available at NASA's Physical Oceanography Distributed Archive Center (PO.DAAC) website (http://podaac.jpl.nasa.gov/dataset/MODIS_Aqua_L3_CHLA_Daily_4km_R). The SST data, also at the lowest resolution possible (1 km), were obtained from the Advanced Very High Resolution Radiometer (AVHRR), which is provided by the Group for High Resolution Sea Surface Temperature (GHRSST), available at the PO.DAAC website (http://podaac.jpl.nasa.gov/dataset/JPL_OUROCEAN-L4UHfnd-GLOB-G1SST). For both SST and chl *a*, we obtained mean climatological parameters for the study period (2011 to 2017) using the ArcGIS-compatible Marine Geospatial Ecology Tools 0.8a64 (Roberts et al. 2010).

We obtained our measurements of anchorage areas and submarine outfalls from nautical chart 1506. Anchorage areas are the designated areas in which commercial ships anchor to await authorization for docking in the port of Rio de Janeiro port. The Ipanema submarine outfall is a pipeline used to discharge sanitary sewage into the sea (Van Weerelt et al. 2013). We obtained fishing grounds data from an earlier study of the area that interviewed fishers and mapped the fishing grounds they use most frequently (Moraes et al. 2013).

2.4. Modeling protocol

We ran all of the procedures described below separately for the 2 whale species (Supplement 2). As our data were autocorrelated spatially ($I_{humpback}$ = 0.46, $p < 0.001$; $I_{Bryde's}$ = 0.47, $p < 0.001$), we applied the Moran eigenvector filtering function to a generalized linear model to investigate the influence of the environmental and anthropogenic variables on cetacean habitat use (Corkeron et al. 2011, Tardin et al. 2017, 2019). The Moran eigenvector filtering function is a powerful method used to correct for spatial autocorrelation in the model residuals (Griffith & Peres-Neto 2006). This method involves the inclusion of spatial eigenvectors as covariates in the regression model to correct for spatial dependency (Griffith & Peres-Neto 2006). The removal of spatial dependency allows a more reliable assessment of the influence of environmental and anthropogenic variables. We created the spatial eigenvectors from a binary spatial neighborhood matrix based on grid pixel proximity. Within this matrix, when 2 pixels shared a common border, they were assigned a value of 1, and a value of 0 when no borders were shared (Dormann et al. 2007). We then generated the spatial eigenvector generalized linear models (SEV-GLMs) by including the spatial eigenvectors in the autocorrelated GLMs. We chose to use a binary spatial neighborhood, instead of a distance spatial neighborhood, because the observations used in this analysis were based on a regular square tessellation rather than point locations that are distributed irregularly (e.g. Griffith & Peres-Neto 2006). With a regular spatial tessellation, the distances between a pair of grid cells are standardized, unlike those between irregularly distributed points. Distances that are above a maximum threshold can usually be replaced with 0, which means that distant observations are not associated. The differences between these approaches have been discussed, and they appear to produce similar results (e.g. Griffith & Peres-Neto 2006, Diniz-Filho et al. 2009). The 'ME' function was used to create the Moran eigenvectors in the R package 'spdep' (v0.7-7) (Bivand & Piras 2015).

We ran a SEV-GLM considering the number of sightings per grid cell as the response variable and the Poisson distribution as the log-link function. As our sampling effort was heterogeneous, we used the log sum of the linear kilometers covered by the sampling boat in each grid as an offset. We tested for overdispersion using the 'dispersiontest' function in the 'AER' package, and determined that the data were not overdispersed (humpback whale: estimate = 0.89, $z = -3.4$, $p = 0.9$; Bryde's whale: estimate = 0.91, $z = -1.7$, $p = 0.9$; Kleiber & Zeileis 2008). We also conducted a visual examination of each explanatory variable to check for non-linear relationships (Supplement 3). In the case of the humpback whale model, we found that only depth was non-linear, whereas in the Bryde's whale model, depth, distance to the coast, and chl *a* were non-linear. For each of these variables, we fitted a quadratic mean term (see Supplements 2 and 3). We checked for multicollinearity using the generalized variance inflation factor (GVIF) in the 'car' package 2.0-19 (Fox & Weisberg 2011). If an explanatory variable had a GIVF value of 10 or higher, we removed it from the analysis (Guisan et al. 2017) (Supplement 3).

Wittingham et al. (2006) found that the stepwise procedure that initiates with the full model (containing both environmental and anthropogenic variables) and then lets the selection criteria identify the explanatory variables that contribute most to explain the variation in the data may have a number of potential problems, such as algorithm errors in the model selection, biased parameter estimates, and inappropriate confidence for a single model. This protocol identifies the best combination of variables that explains the most variation in the data (see Supplement 2 for more details on the modeling procedure). For this, the 'step' function was used in the 'stats' package v. 3.5.1 (R Core Team 2018). To minimize these biases, we used a stepwise multiple selection, with a backward elimination procedure within a set of 3 pre-defined models, through which we could evaluate how the natural environment and human activities explain habitat use in the 2 whales either separately or combined: (1) Environmental model: includes only depth, distance to coast, distance to island, slope, SST, and chl *a*; (2) Anthropogenic model: includes only distance to fishing grounds, the submarine outfall, and anchorage areas; and (3) Full model: includes all environmental and anthropogenic variables.

In the backward model selection, we began with the global model (containing all variables) and the global eigenvector spatial filtering function, with each set of models and variables being removed sequentially to optimize the model selection criterion based on Akaike's information criterion (AIC) values (Burnham & Anderson 2004). Models with smaller AIC values are more parsimonious, and when the difference between the values was less than 2, the models were considered to have similar power. In this case, we chose the more parsimonious models with the fewest variables and the highest pseudo-R value. To investigate the contribution of each variable to the final model, we conducted a hierarchical partitioning analysis in the 'hier.part' package v. 1.0-4 (Walsh & MacNally 2013). We used the pseudo-R to investigate the proportion of variance in the dependent variable associated with the independent variables.

We used 'glm.predict' in the R package 'stats' v. 3.4.0 to map the predictions of habitat use derived from our best models. We calculated the predictions from the means of the predictors during the study periods and then imported them into ArcGIS 10.3.1®. We mapped the residuals using the 'residuals.glm' function in the R package 'stats' v. 3.4.0 and imported them into ArcGIS.

We evaluated the degree of spatial overlap between both species of whale and the MPAs using the spatial predictions derived from the best models. All grid cells that had at least 1 predicted sighting were used to calculate the degree of protection provided by the MPAs. The percentage overlap with each MPA was then calculated by dividing the total number of grid cells with at least 1 predicted sighting by the total number of cells within each MPA.

3. RESULTS

We conducted a total of 170 boat surveys, with 1223.5 h of sampling effort, covering 9098.2 km (Table 1) in a heterogeneous fashion (Fig. 1). Sampling effort per day at sea ranged from 4.3 to 10.0 h (6.9 ± 0.75 [SD] h) over the study period. Humpback whales (n = 36) were sighted only during the winter, whereas Bryde's whales (n = 34) were sighted in the summer (44.1%), fall (32.3%), spring (17.7%), and winter (5.9%). Overall, 10 of the 1 km^2 grid cells occupied during the study were within the MoNaCa and 45 were within the RESEX Itaipu.

Table 1. Overall and yearly variation in cetacean sampling effort off the coast of the city of Rio de Janeiro. Sighting rate was calculated as the number of total groups sighted that year / number of effective survey days that year

Year	Months	Number of surveys	Daily mean effort (range) (h)	Overall effort (h)	Overall effort (km)	Sighting rate of humpback / Bryde's whales
2011	Aug–Dec	20	7.8 (4.3–9.0)	157.5	1010.9	– / –
2012	Aug–Dec	21	5.8 (4.3–9.4)	122.3	1039.6	– / 0.04
2014	Jan–Dec	35	7.3 (5.3 -10.0)	257.5	1868.4	0.05 / 0.51
2015	Jan–Dec	25	7.3 (5.1–9.1)	184.4	1456.8	0.08 / 0.16
2016	Jan–Dec	31	6.2 (5.1–8.5)	208.5	1714.9	0.84 / 0.19
2017	Jan–Dec	38	7.0 (5.4–8.3)	293.3	2007.6	0.05 / 0.13
Total		170		1223.5	9098.2	

3.1. Humpback whale models

We ran 12 different models to test the environmental, anthropogenic, and full models (Supplement 4). The environmental and full models both had similar fit to humpback whale habitat use data (Table 2). As the environmental model had fewer variables and a higher pseudo-R than the full model (pseudo-R_{env} = 0.38, pseudo-R_{full} = 0.35), we selected it as our best model for humpback whales.

This best model included 3 variables, and only depth was not statistically significant, retaining 2 eigenvectors (Table 3). The best model predicted that humpback whale sightings would increase linearly with distance from the coast and would decrease linearly with slope (Fig. 2). The hierarchical partitioning analysis indicated that distance to the coast was the most important variable, explaining 98.3 % of the distribution of humpback whales. The percentage of explained variability measured by the pseudo-R was 0.38. Our best model predicted that 40.0 % (n = 4) of the grid cells within the MPAs would have at least 1 sighting within the MoNaCa (max. = 1.81), although none of the cells (0 %) in the RESEX Itaipu had any predicted sightings (Fig. 3). Our predictions indicate that humpback whales would be found more commonly within the Cagarras archipelago (closer to Palmas and Comprida Islands), up to 2 km from the MoNaCa, and Rasa Island (Fig. 3).

Table 2. Spatial eigenvector generalized linear models (SEV-GLMs) used to assess habitat use by humpback and Bryde's whales off the coast of Rio de Janeiro. Only the 3 most parsimonious SEV-GLMs for each hypothesis are shown from a total of 32 candidate models. The full range of models with their respective coefficients and Akaike's information criterion (AIC) values are shown in Supplement 4. The SEV-GLMs in **bold** is the most parsimonious. The most parsimonious models for humpback and Bryde's whales are presented in detail in Tables 3 & 5, respectively

Model	Humpback whale AIC	Bryde's whale AIC
Environmental	**207.2**	335.9
Anthropogenic	211.8	349.9
Full	**208.1**	**331.2**

Table 3. Estimates of the best spatial eigenvector generalized linear model for habitat use by humpback whales off the coast of Rio de Janeiro. Significant variables are in **bold**

Coefficients	Estimate	SE	*z*	p
Intercept	**−8.7**	**0.79**	**−11.0**	**< 0.001**
Squared depth	1.3×10^{-3}	7.5×10^{-4}	1.7	0.08
Distance to coast	$\mathbf{5.9 \times 10^{-4}}$	$\mathbf{9.0 \times 10^{-5}}$	**6.5**	**< 0.001**
Slope	**−19.9**	**6.3**	**−3.1**	**0.001**
Eigenvector 39	**8.8**	**2.9**	**3.1**	**< 0.001**
Eigenvector 8	**23.8**	**8.0**	**3.0**	**< 0.001**

3.2. Bryde's whale models

We ran 15 different models to test the environmental, anthropogenic, and full model (Supplement 4), and the full model fitted better to the data (Table 2). Our best model included 5 environmental variables and retained 1 eigenvector (Table 4). In the environmental component, our best model predicted that Bryde's whales would be more likely to occur at depths of 20–30 m. Probability of occurrence in-

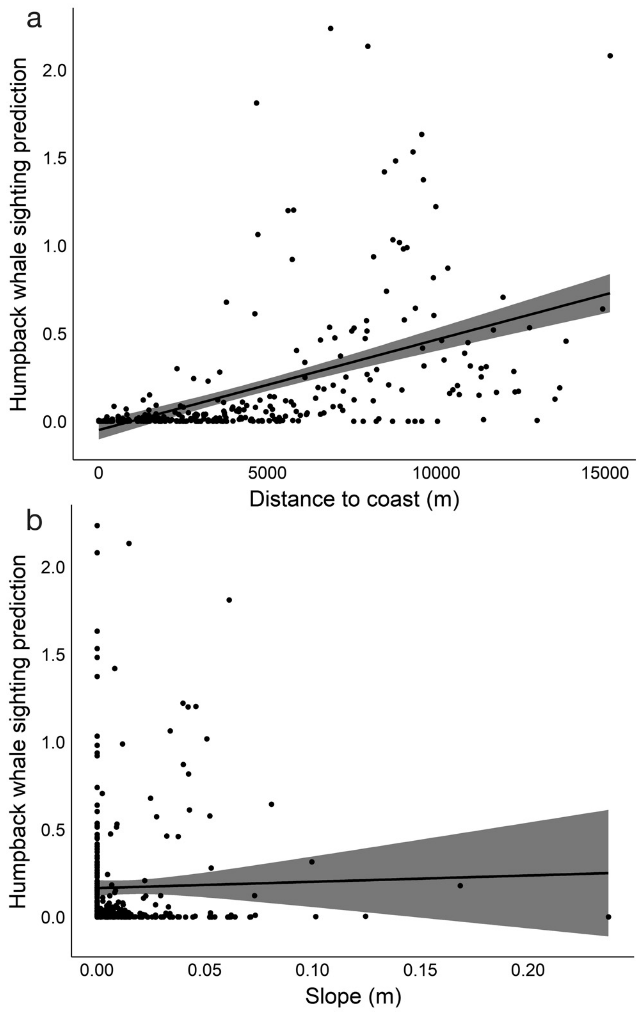

Fig. 2. Best-fit lines for the values fitted from the spatial eigenvector generalized linear model of the humpback whale sightings for (a) distance to coast and (b) slope. Shaded areas represent 95 % confidence interval

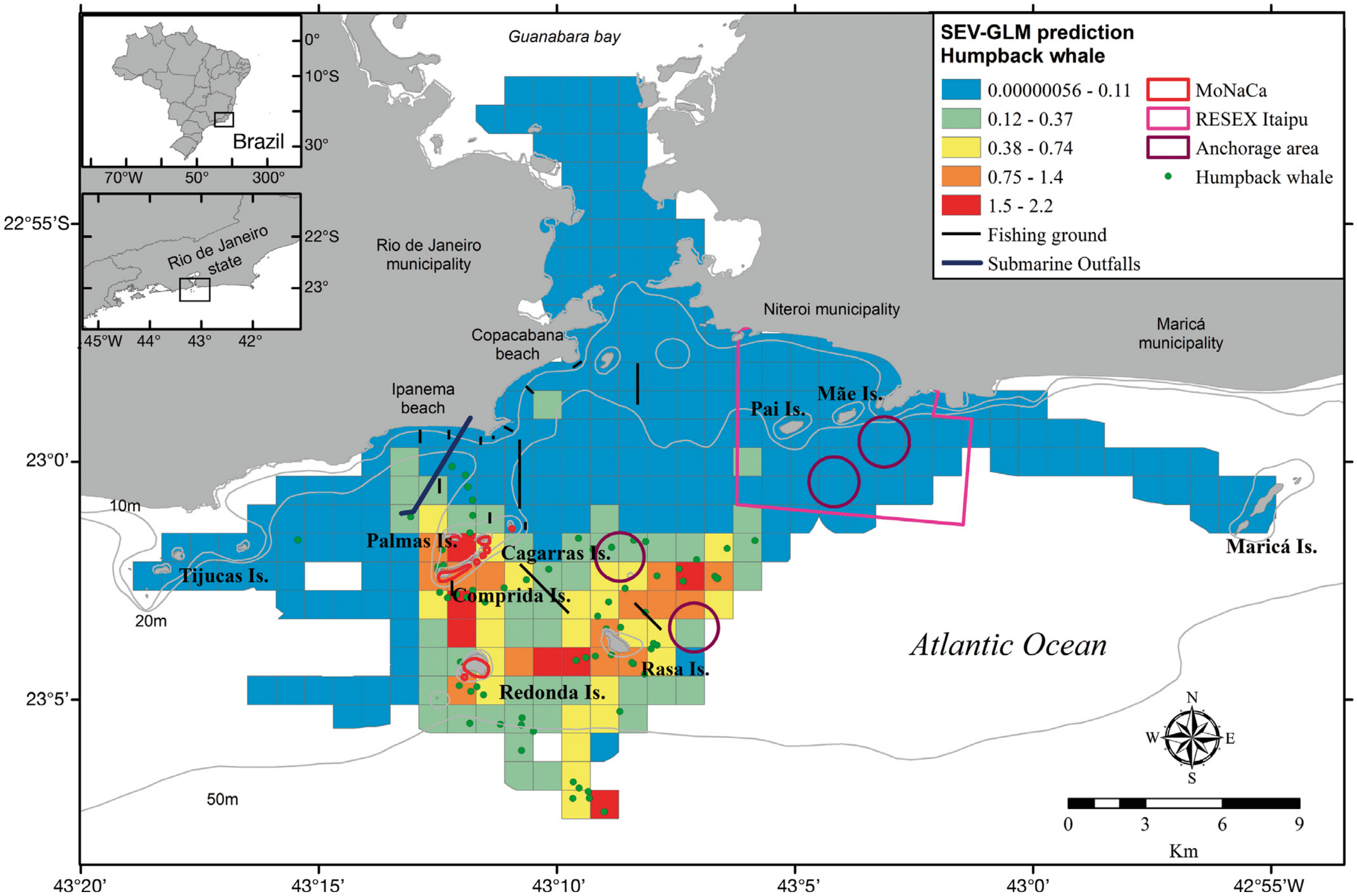

Fig. 3. Predicted habitat use by humpback whales off the coast of Rio de Janeiro, using Poisson spatial eigenvector generalized linear models to account for spatial autocorrelation. Marine protected areas are as marked in Fig. 1. Green dots mark humpback whale sightings. Predictions are sightings km^{-2}

Table 4. Relative importance of each statistically significant variable from the best generalized linear model of habitat use in the humpback and Bryde's whales, off the coast of Rio de Janeiro. *I*: % likelihood, ascertained by hierarchical partitioning, that each habitat variable contributes to the variation in the presence of the whales. SST: sea surface temperature

Variable	Importance rank	*I* (%)
Humpback whale		
Distance to coast	1	98.3
Slope	2	1.7
Bryde's whale		
Distance to anchorage area	1	48.4
Mean SST	2	26.4
Mean chl *a*	3	14.3
Depth	4	9.5
Distance to islands	5	1.4

creased linearly with chl *a* and distance to islands, and decreased with mean SST (Fig. 4). In the anthropogenic component, the whales would be more likely to occur up to 5 km from anchorage areas (Fig. 4). The hierarchical partitioning analysis indicated that the distance to anchorage areas and mean SST were the most important variables (Table 5). The percentage of the explained variability measured by the pseudo-R was 0.57.

Our predictions indicated that Bryde's whales would be found more commonly outside the Cagarras Archipelago, up to 5 km from the MoNaCa, closer to Ipanema and Copacabana beaches, and closest to Rasa Island (Fig. 5). None of the grid cells (0.0%) predicted by our best model to have at least 1 Bryde's whale sighting were within the MoNaCa and only 6.7% (n = 4) of the cells with at least 1 predicted sighting were within the RESEX Itaipu (max. = 1.92; Fig. 5).

Supplement 5 shows the spatial autocorrelation residuals mapped for each whale species and the linear combination of eigenvectors, which demonstrate that the spatial autocorrelation pattern was not explained by the SEV-GLM.

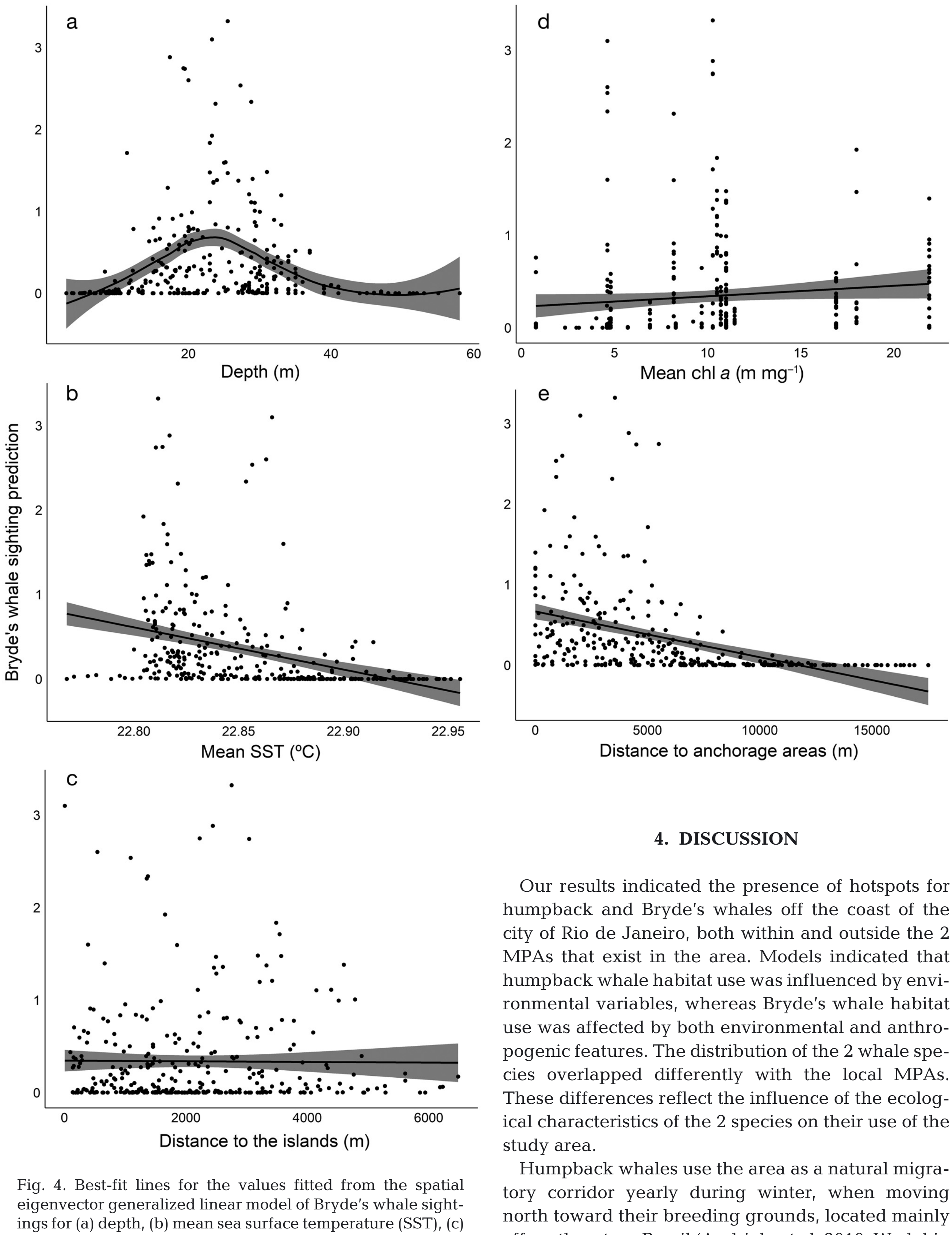

Fig. 4. Best-fit lines for the values fitted from the spatial eigenvector generalized linear model of Bryde's whale sightings for (a) depth, (b) mean sea surface temperature (SST), (c) distance to islands, (d) mean chl *a*, and (e) distance to anchorage areas. Shaded areas represent 95% confidence interval

4. DISCUSSION

Our results indicated the presence of hotspots for humpback and Bryde's whales off the coast of the city of Rio de Janeiro, both within and outside the 2 MPAs that exist in the area. Models indicated that humpback whale habitat use was influenced by environmental variables, whereas Bryde's whale habitat use was affected by both environmental and anthropogenic features. The distribution of the 2 whale species overlapped differently with the local MPAs. These differences reflect the influence of the ecological characteristics of the 2 species on their use of the study area.

Humpback whales use the area as a natural migratory corridor yearly during winter, when moving north toward their breeding grounds, located mainly off northeastern Brazil (Andriolo et al. 2010, Wedekin et al. 2017). The higher predicted occurrence proba-

Table 5. Estimates for the best generalized linear model for habitat use by Bryde's whale off the coast of Rio de Janeiro. All variables are significant. SST: sea surface temperature

Coefficients	Estimate	SE	*z*	p
Intercept	$5.7 \times 10^{+2}$	$1.7 \times 10^{+2}$	3.2	<0.001
Mean chl *a*	-1.5×10^{-1}	7.4×10^{-2}	−2.2	0.03
Squared mean chl *a*	4.1×10^{-2}	1.9×10^{-2}	2.0	0.04
Squared depth	-8.7×10^{-3}	2.2×10^{-3}	−3.9	<0.001
Distance to islands	3.3×10^{-4}	8.8×10^{-5}	3.7	<0.001
Mean SST	$-2.5 \times 10^{+1}$	7.7	−3.2	<0.001
Distance to anchorage areas	-2.6×10^{-5}	5.2×10^{-5}	−5.0	<0.001
Eigenvector	−4.5	1.6	−2.8	<0.001

bilities for areas farther from the coast are consistent with this migratory behavior, reinforced by the fact that in all of the humpback whale sightings, the animals were traveling (our pers. obs.). The humpback whale population of Brazil is recovering (Bortolotto et al. 2017, Wedekin et al. 2017), and sightings in southeastern Brazil appear to be increasing (our pers. obs.). Although humpback whale bycatch appears to be increasing in Brazilian waters (our pers. obs.), the movements of these whales tend to be more distant from the coast than those of Bryde's whales, which may decrease the likelihood of impacts from coastal sources of pollution, such as the submarine outfall, fishing grounds, and anchorage areas, as observed in the present study. This would also account for the fact that only environmental variables influenced humpback whale habitat use.

Few of the distribution modeling studies of humpback whales in the southwest Atlantic Ocean have investigated the influence of anthropogenic activities, but the available data indicate higher whale densities in more sheltered areas, 140 to 236 km from the coast, with SSTs of 24–25°C (Bortolotto et al. 2017, Pavanato et al. 2017). In the Cabo Frio region, approximately 150 km from the present study area, habitat use by humpback whales is influenced by both environmental and anthropogenic variables (Tardin et al. 2019).

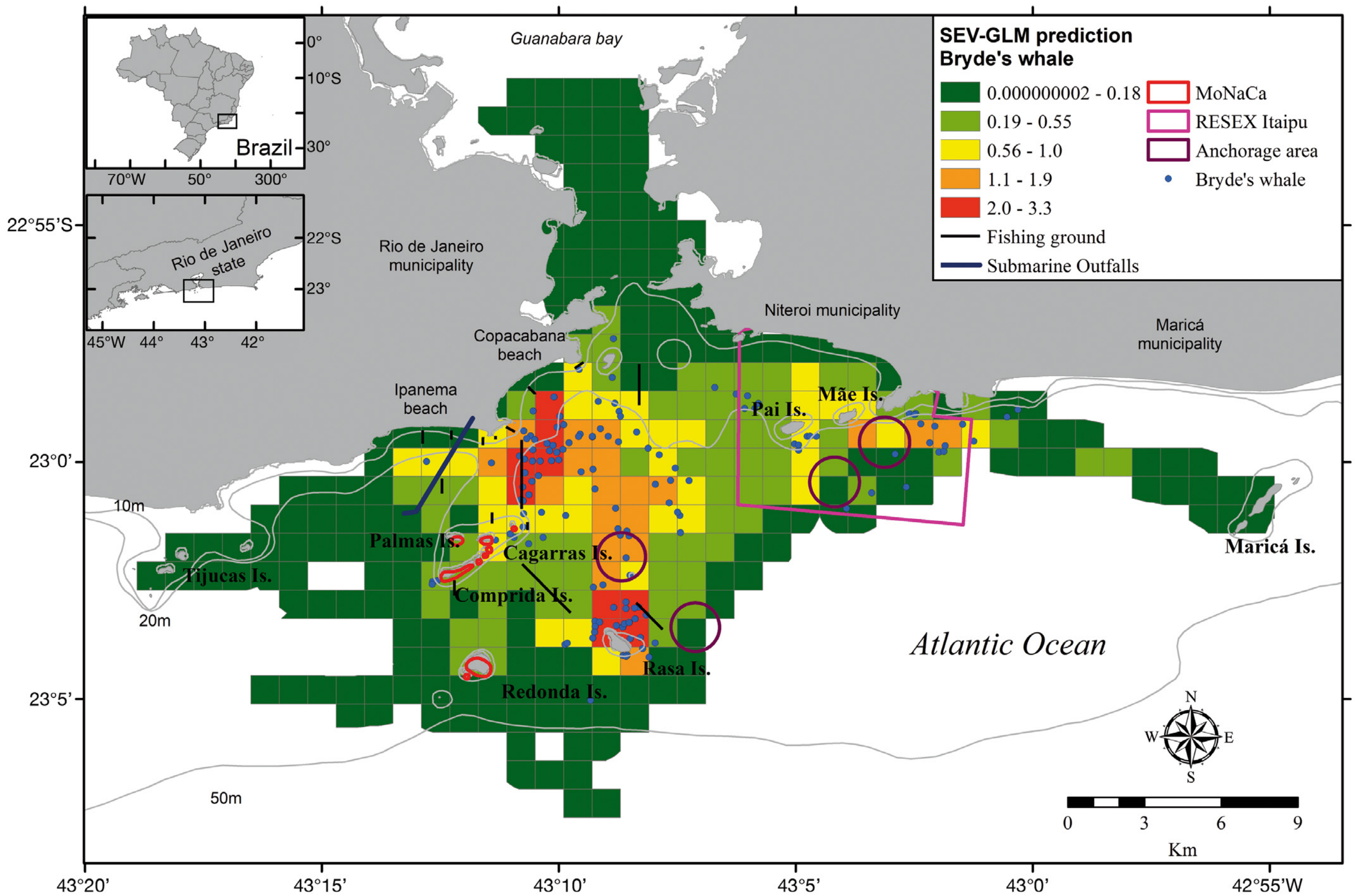

Fig. 5. Predicted habitat use by Bryde's whales off the coast of Rio de Janeiro, using Poisson generalized linear models to account for spatial autocorrelation. Marine protected areas are as marked in Fig. 1. Green dots mark Bryde's whale sightings. Predictions are sightings km^{-2}

At this locality, the number of whales increased linearly with distance from the coast, with minimum SSTs of 19.4–19.8°C, maximum SSTs of 25.5–26°C, and minimal variation in chl *a* concentrations. In the anthropogenic component, humpback whales were reported to occur within 10 km of diving areas, and to increase linearly with distance from fishing grounds (Tardin et al. 2019).

By contrast, Bryde's whales use the study area off Rio de Janeiro to feed in the summer and fall (Lodi et al. 2015), and are present in the area throughout the year. The areas off Ipanema and Copacabana beaches and around the MoNaCa were used preferentially by Bryde's whales. A diverse demersal and pelagic ichthyofauna, including the Brazilian sardine *Sardinella brasiliensis*, can be found at depths of 10–30 m up to 3 km off Ipanema and Copacabana beaches (FIPERJ 2012, Amorim & Monteiro-Neto 2016, Souza et al. 2018). These prey species are part of the diet of Bryde's whales (Siciliano et al. 2004, Lodi et al. 2015, Maciel et al. 2018). Prey abundance and availability affect the behavior, seasonality, and abundance of Bryde's whales in coastal waters (e.g. Tershy 1992, Penry et al. 2011). In southeastern Brazil, during the late spring, summer (Cergole & Rossi-Wongtschowski 2005), and fall (Paiva & Motta 2000), Brazilian sardines approach the coast to spawn in shallower waters. In our study, sightings of this species off Rio de Janeiro indicate that it is most common in coastal waters in the summer and fall. Other small schooling fish species that form large shoals are also observed at these times of year (our pers. obs.).

Anchorage areas also appear to have a considerable influence on Bryde's whale habitat use. These areas may impact the whales directly, e.g. by causing collisions (Waerebeek et al. 2007), or indirectly, by increasing noise levels that mask whale communication (e.g. Erbe 2002), alter their behavior (e.g. Marley et al. 2017), and/or affect their prey (e.g. Popper 2003). The port of Rio de Janeiro has intense shipping traffic, including commercial (export and import), industrial (oil and gas), and tourist (recreational diving and fishing) vessels.

Data on strandings and sightings indicate that Bryde's whales occur regularly in southeastern Brazil (Moura & Siciliano 2012, Lodi et al. 2015, Gonçalves et al. 2016, Maciel et al. 2018). Individuals identified off the coast of the city of Rio de Janeiro were also resighted off Cabo Frio (Lodi et al. 2015). Maciel et al. (2018) recorded Bryde's whales feeding from November to July from 2010 to 2012 off Cabo Frio, where its habitat use is influenced by depth and distance from the coast (Tardin et al. 2017).

Studies in other areas have identified different variables influencing habitat use by Bryde's whales, such as the distance from the coast and the slope of the bottom off the coast of Oman (Corkeron et al. 2011), and the SST off the eastern coast of Africa, between Gabon and Angola (Weir et al. 2012). However, none of these studies considered anthropogenic variables in their models. Differences are expected, given that animals will tend to adjust their behavior to local environmental conditions (Powell 2000). As habitat selection is an individual choice, individuals in different populations will be expected to use their sensory capabilities (including memory) to prefer some areas over others (Powell 2000). However, many similarities are also expected, based on the life history traits of the species. In all areas (Oman, Gabon, Angola, and Rio de Janeiro), Bryde's whale habitat use appears to be influenced primarily by the characteristics of their fish prey, in particular, sardines (Best 2001, Siciliano et al. 2004).

Although our models did not indicate a significant correlation with fishing grounds or the submarine outfall in either whale species, these results must be interpreted with caution. Fishing grounds are widely distributed within the study area, and some high prediction values, in particular for Bryde's whale, overlapped directly with some of these areas. In many cases, however, there was little overlap, which may have reduced the correlation in the final model.

While neither Bryde's nor the humpback whales avoided the area affected by the submarine outfall, previous studies in the study area have reported poor water quality (Van Weerelt et al. 2013) in the vicinity of this installation, which is reflected in low local fish diversity (Amorim & Monteiro-Neto 2016). Bryde's whales were predicted to occur in large numbers in relatively close proximity to the submarine outfall, which may result in the contamination of individual whales. However, no data are available on the presence of heavy metals or organochlorine compounds in either of the whale species in the study area.

The spatial patterns we report here for both humpback and Bryde's whales have some similarities with those reported by local citizen scientists, who have recorded Bryde's whales off Copacabana beach, and humpback whales near the MoNaCa. Sightings of humpback whales were recorded primarily during the winter, whereas Bryde's whales were observed mainly during the summer and fall (Lodi & Tardin 2018).

None of the MPAs in the study area overlapped to any considerable extent with the whale hotspots as predicted by our models for both species. The distribution of humpback whales overlapped primarily with the MoNaCa, which is the MPA farthest from the coast, whereas Bryde's whales were predicted to use areas outside both MPAs. This implies a series of risks for these individuals, given that activities such as shipping, fishing, and tourism are unregulated in areas outside the domain of the MPAs.

It is important to note, however, that neither of the MPAs was created specifically to protect cetaceans, and their limits were not designed to protect species with large home ranges. Despite the poor spatial overlap found in the present study, we cannot confirm that either MPA does not have some benefits for cetaceans, considering that they will contribute to the conservation of other species that interact directly or indirectly with these mammals, in particular, prey species (Notarbartolo di Sciara et al. 2016).

Brazilian studies have shown that MPAs provide at least partial protection for some species of whales, as is the case for Bryde's whales in southeastern Brazil (Santos et al. 2017, Tardin et al. 2019) and for humpback whales in northeastern-southeastern Brazil (Martins et al. 2013, Castro et al. 2014, Bortolotto et al. 2017). Southern right whales *Eubalaena australis* are also partially protected by MPAs in southern Brazil (Renault-Braga et al. 2018). Some MPAs, such as the Pelagos Sanctuary, a 90 000 km^2 area in the northwestern Mediterranean Sea, do provide full protection, however, by overlapping with the distribution of several cetacean species, including fin whales *Balaenoptera physalus* (Pennino et al. 2017).

In comparison with developed countries, the MPAs of Brazil are still in the early stages of development or implementation. There are many difficulties for the creation of an MPA, such as a lack of personnel or funds, poor inter-institutional governance, excessive bureaucracy, and a lack of political willingness to promote significant changes (Gerhardinger et al. 2011). Despite a recent increase in the protection of Brazilian coastal and marine waters by MPAs, which now cover 25% of the total area, their effectiveness is debatable (Magris & Pressey 2018).

We have presented our results at meetings of the MoNaCa Advisory Board to support conservation decisions and facilitate the link between scientists and decision makers (Guisan et al. 2013). Our results will help to evaluate the efficiency of this MPA and to propose a buffer zone to protect biodiversity, and will contribute directly to the definition of protected areas. Specifically, we propose that an area of up to 3 km around the MoNaCa including areas up to 2 km from Ipanema and Copacabana beaches should be incorporated within the buffer zone of this MPA to support conservation practices (Guisan et al. 2013). Based on our experience of monitoring cetaceans in the study area, it would also be important to consider seasonal restrictions of some activities, in particular fishing, within the proposed buffer zone, such as the period during which humpback whales migrate northward, and during the summer months when Bryde's whales are more common in the area. During the closed season for Brazilian sardine, fishery surveillance should be constant. Speed restrictions on the shipping lanes in Guanabara Bay would also be important to reduce the risk of collisions. We also demonstrated explicitly, in a modeling framework, that human activities can influence cetacean habitat use, and therefore must be included in any modeling approach to better understand the drivers of the distribution of these animals.

Our results complement existing knowledge on the distribution patterns and drivers of both whale species in the coastal waters of Rio de Janeiro state (Tardin et al. 2017, 2019). The continuation of data collection to include temporal variation in habitat use, as well as whale behavior, in these models will further enhance our understanding of cetacean habitat use off the coast of Rio de Janeiro and will contribute to the development of better management strategies for the area.

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