

Modeling habitat use by Bryde's whale *Balaenoptera edeni* off southeastern Brazil

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ABSTRACT: Habitat-use models are a powerful tool for improving our understanding of the relationships between animals and their environment. With the development of GIS, these models have been used increasingly for the analysis of ecological data. However, they often suffer from inappropriate model specifications, particularly the assumption of independence, which is essential in conventional statistical models, and may often be violated during the collection of spatial data. Spatial autocorrelation occurs when the values of variables sampled close to each other are not independent, representing a major problem that must be accounted for systematically. We used a spatial eigenvector (SEV) generalized linear model framework to investigate the distribution of *Balaenoptera edeni* off Cabo Frio, in southeastern Brazil, an upwelling area impacted by human activities (tourism and fisheries). Sighting data were collected during 94 boat trips conducted between December 2010 and November 2014. A quasi-Poisson model using SEV indicated that the use of habitat by the whales varied with depth and the distance from the coast, and predicted that whales would be found most frequently around Cabo Frio Island and along the coastline, apparently overlapping with their prey. We found that habitat use was better predicted with the inclusion of SEV and that it is also possible to produce predictions of habitat use by correcting for spatial autocorrelation without the use of expensive surveys conducted by specialized research ships. This study provides useful insights into the habitat use of *B. edeni* in the southwestern Atlantic Ocean, and represents an important contribution to the conservation of this data-deficient species.

KEY WORDS: Spatial autocorrelation · Spatial eigenvector filtering · Habitat use · Distribution model · Balaenopteridae · Arraial do Cabo municipality · Cetacean

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INTRODUCTION

Understanding the processes that affect the distribution of organisms is an important component of conservation and management planning (Redfern et al. 2006). Habitat use is a product of the interaction of multiple factors that influence a given space simultaneously. Animals may select their habitats by adjusting their behavior to a set of conditions that allows them to survive, feed, and reproduce (Powell 2000).

Recent advances in computing techniques, such as Geographical Information Systems (GIS), led to the rapid development of habitat-use models (Redfern et al. 2006). These models are commonly used to investigate the relationships between animals and their environment (Marubini et al. 2009, Corkeron et al. 2011, Garaffo et al. 2011, Gill et al. 2011, Pirota et al. 2011, Anderwald et al. 2012, Weir et al. 2012, Tardin et al. 2013), and their products are often used for the development of management plans and actions, such

as the designation of protected areas (Corkeron et al. 2011). Austin (2002) recommends prioritizing the selection of the relevant resource variables (e.g. fish or prey abundance) when modeling the distribution of a species. However, as reliable information on these variables is usually difficult to obtain, these data may be substituted by direct (e.g. oceanographic) or indirect (e.g. physiographic) proxies to represent the complex relationships between a species and its environment (Austin 2002). Physiographic variables may influence cetacean habitat use either directly or indirectly and may be associated with biotic factors, such as the availability of prey or the presence of predators (Blasi & Boitani 2012). A number of studies have demonstrated the influence of physiographic variables on cetacean habitat use (e.g. Pirotta et al. 2011, Keller et al. 2012, Weir et al. 2012, Arcangeli et al. 2013). Oceanographic variables, in turn, such as sea surface temperature (SST), chlorophyll *a* (chl *a*) concentration, and salinity, provide a more detailed picture of the dynamics of a study area, and a growing number of studies of cetacean habitat use are based on the analysis of these variables, facilitated by recent advances in remote sensing technology (e.g. Gill et al. 2011, Anderwald et al. 2012, Dalla-Rosa et al. 2012, Forney et al. 2012).

The most commonly used approach to studying habitat use in cetaceans is to conduct systematic line transect surveys by vessels or aircraft, with the principal objective of determining the abundance and distribution of a species in the surveyed area (Panigada et al. 2008, Marubini et al. 2009, Andriolo et al. 2010, Gill et al. 2011, Dalla-Rosa et al. 2012, Forney et al. 2012, Keller et al. 2012). In developing countries, however, there are limited resources for the funding of large research vessels, specialized equipment, and scientists, which may limit the collection of data to study cetacean habitat use and, consequently, the potential for conservation actions (but see Dick & Hines 2010). Under these circumstances, a common solution is to employ field surveys to collect a wide range of ecological and behavioral data, for which a non-standardized or haphazard sampling schedule is adopted, to optimize the cost–benefit ratio. As with line transect surveys, the haphazard sampling may lead to spatial autocorrelation (SAC) in the data collected because spatially proximate observations tend to have similar values (Fortin & Dale 2009), reflecting a strong association (Dormann 2007).

SAC occurs when the values of variables sampled close to each other are not independent (Dormann et al. 2007). While SAC might be a goal of some ecological studies, most often it is a problem, leading to

biased standard errors and estimates of parameters (Lichstein et al. 2002). SAC may be derived from a number of different biological or physical sources (Griffith & Peres-Neto 2006). Geographically contiguous biotic processes include population growth, dispersal, reproduction, survival, social organization, movement, and competition (Griffith & Peres-Neto 2006, Dormann 2007). Physical drivers include barriers to movement, travel corridors that may facilitate movement, and spatially structured habitat characteristics. While SAC affects ecological models, including those used to analyze habitat use (Dormann et al. 2007, Bailey et al. 2013), it is often overlooked in the modeling of cetacean distributions (e.g. Cañadas et al. 2005).

Eigenvector spatial filtering (or the Moran eigenvector) is a powerful approach that compensates explicitly for SAC. Griffith & Peres-Neto (2006) provide a detailed and succinct introduction to eigenfunction spatial analyses. Briefly, this approach involves the identification of spatial patterns represented by maps of eigenvectors as covariates in a regression model to account for unexplained (latent) spatial dependency. Habitat variables may be included as non-spatial explanatory variables. Model selection allows identification of which environmental factors influence habitat use after spatial dependence is removed. This approach can be extended easily to a generalized linear model (GLM). While the use of eigenvectors in ecological modeling is computationally intensive (Dormann et al. 2007), the earliest studies showed some advantages in including eigenvectors (Diniz-Filho & Bini 2005, Dormann et al. 2007, Corkeron et al. 2011, Diniz-Filho et al. 2013, Thayn & Simanis 2013). They tend to reduce errors of spatial misspecification, which increases the strength of the model fit, and the normality and homoscedasticity of the residuals (Corkeron et al. 2011, Thayn & Simanis 2013). In addition, spatial eigenvectors may stabilize and accentuate the relative importance of the variables that may actually influence habitat use by the species (Diniz-Filho & Bini 2005, Corkeron et al. 2011, Diniz-Filho et al. 2013).

When the sampling design includes a haphazard component and non-independent location data, the use of eigenvector spatial filtering allows for the use of the dataset, in contrast with other commonly used modeling techniques, such as GLMs and generalized additive models (GAMs) (Legendre 1993). This approach may thus ensure the development of a model based on sequential GPS locations for a species or individual. One alternative analytical method

is to construct an autoregressive model, but those are computationally intensive and may be impractical for large datasets (Griffith & Peres-Neto 2006). Another potential solution is to exclude large numbers of data points to create an independent dataset for analysis (Dormann et al. 2007). However, for poorly known species, the exclusion of repeated measures of the spatial location of individuals may entail the loss of valuable information on which to base reliable management decisions (Harris et al. 2008). In fact, Corkeron et al. (2011) presented a case study on how sparse occurrence data from humpback whales *Megaptera novaeangliae* and Bryde's whales *Balaenoptera edeni* collected from non-systematized surveys can be used to inform cetacean conservation planning.

The Bryde's whale is one of the least known baleen whales (Kato & Perrin 2008). The species ranges from 40° N to 40° S, in tropical and temperate waters, including the Indian, North and South Pacific, and Atlantic Oceans (Kato & Perrin 2008). There have been relatively few systematic surveys of *B. edeni* (e.g. Zerbini et al. 1997, Best 2001, De Boer 2010, Wiseman et al. 2011, Weir et al. 2012, Figueiredo et al. 2015, Lodi et al. 2015, Pastene et al. 2015, L. A. Pastene & S. Ohsumi unpubl.). The species is not observed frequently in Brazilian waters, which may be due to intensive whaling in the early to mid-20th century (Andriolo et al. 2010).

The Brazilian Marine Mammal Survey Support System (Sistema de Apoio ao Monitoramento de Mamíferos Marinhos – SIMMAM) reports a paucity of data for *B. edeni* off the Brazilian coast (SIMMAM 2014). Only 88 records were obtained between 1990 and 2014 along the entire Brazilian coast, which extends for more than 8000 km. Most (73.9%) of these records were of stranded animals, with only 26.1% derived from visual sightings (SIMMAM 2014). Previous studies indicate that *B. edeni* occurs in deep water far off the Brazilian coast (Andriolo et al. 2010). While coastal sightings are rare, this species is found in relatively close proximity to the coast in some parts of Brazil, such as Laje de Santos (Gonçalves & Andriolo 2006), Cabo Frio (Figueiredo et al. 2015), and near the city of Rio de Janeiro (Lodi et al. 2015). The occurrence of *B. edeni* near the coast provides an unparalleled opportunity to gather more data on this species in Brazilian waters. The International Union for Conservation of Nature considers this species to be Data Deficient (IUCN 2013), while the Brazilian National Plan for Large Cetaceans emphasizes the need to investigate distribution patterns for the designation of strict conservation areas

for *B. edeni* off the Brazilian coast (Rocha-Campos & Câmara 2011).

Recent research has shown that *B. edeni* occurs at different depths, often far from the coast, and at relatively high densities in upwelling areas (Wiseman et al. 2011, Forney et al. 2012, Weir et al. 2012). However, few studies have modeled the influence of dynamic oceanographic variables, such as SST and chl *a* concentration, on the distribution of the species (Corkeron et al. 2011, Forney et al. 2012, Weir et al. 2012). The present study investigates the influence of physiographic and oceanographic variables on *B. edeni* habitat use in the waters off Cabo Frio in the state of Rio de Janeiro, southeastern Brazil, using a GLM with spatial eigenvector filters. We hypothesized that the individuals found off the coast of Cabo Frio would be associated with physiographic and oceanographic variables and that these whales would be found more frequently in deep, cold waters far from the coast.

MATERIALS AND METHODS

Study area and data collection

The study area (500 km²) is located off the coast of Cabo Frio, in northeastern Rio de Janeiro state, Brazil, and includes the municipalities of Arraial do Cabo, Cabo Frio, and Buzios (Fig. 1). These 3 municipalities play a prominent role in the state's coastal tourism industry, which depends on the region's clear blue waters and white sandy beaches. Coastal development is unregulated and dynamic, and the total population of the 3 municipalities exceeds 250 000 inhabitants. The gross domestic product exceeds 4 billion USD (Instituto Brasileiro de Geografia e Estatística. www.ibge.gov.br/ [accessed 1 may 2016]). The Cabo Frio coast (22° 50' 21" S, 41° 54' 37" W–23° 00' 18" S, 42° 05' 53" W) is steeply sloped and characterized by a change in the orientation of the shoreline from north-south to southwest-northeast (De Leo & Pires-Vanin 2006) (Fig. 1). During the austral spring and summer, the more intense north-northeasterly winds, combined with the meanders and eddies in the Brazil Current, result in the mixing of 2 water masses (the Brazil Current and the South Atlantic Central Water [SACW]) and the formation of upwelling (Carbonel 1998, Coelho-Souza et al. 2012). Upwelling events typically result in increased primary productivity and high fish density and abundance, creating favorable foraging conditions for many cetacean species (Keiper et al. 2005, Costa 2008).

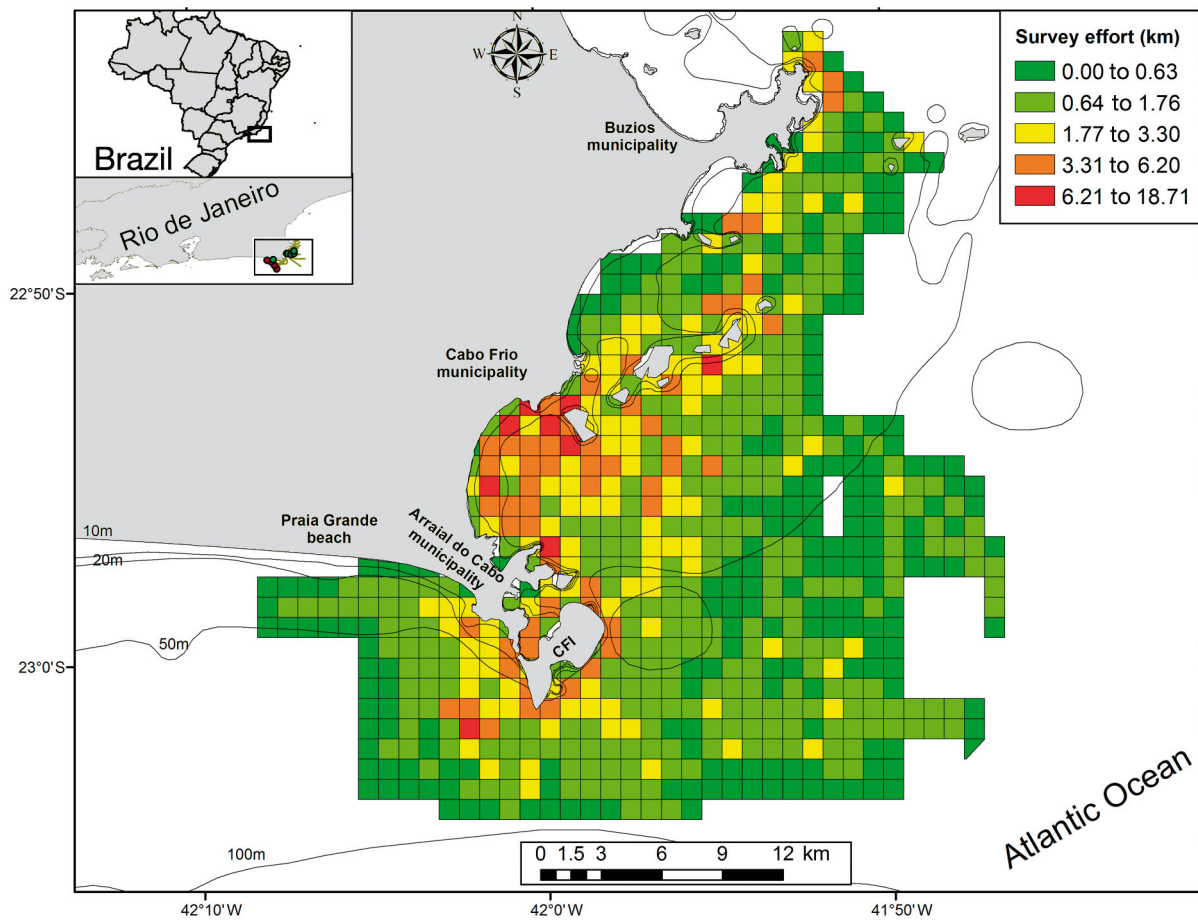


Fig. 1. Study area located in southeastern Brazil, Rio de Janeiro, showing isobaths. Grid cell colors represent kilometers of survey effort during which *Balaenoptera edeni* search and focal follow occurred. CFI: Cabo Frio Island

We conducted surveys with a mean duration of 5.7 h (range: 3.25–8.00 h) from December 2010 to November 2012 and from January to August 2014 in a 6.5 m inflatable boat equipped with a 150 hp outboard motor. The surveys followed a haphazard route at approximately 20 km h⁻¹ to maximize study area coverage (Fig. 1). When there were 2 or more individuals, we conducted focal group follows. We defined a group as individuals that swam no further than 50 m from one another and engaged in the same behavior (including coordinated breathing and swimming) simultaneously (Tershy 1992). When there was only one individual, we conducted focal individual follows (Lehner 1992). When a whale or a group of whales was spotted, it was followed at a reduced speed (mean of approximately 10 km h⁻¹) at a minimum distance of 50 m. The geographic coordinates of the whale's or group's location were recorded using a GARMIN VISTA CX GPS device after every 500 m that the focal follow moved (Lehner 1992). This resulted in multiple GPS locations for a

given individual during a single day. On 5 May 2011, for example, we monitored one *Balaenoptera edeni* for 3.5 h, during which time, 7 GPS locations were obtained in distinct portions of the study area.

Environmental data

Because prey distribution data were unavailable, we used direct (oceanographic) and indirect (physiographic) variables as proxies for prey distribution to estimate *B. edeni* habitat use. We plotted all variables in a grid composed of 718 1-km² cells using the ArcGIS-compatible Marine Geospatial Ecology Tools 0.8a64 (Roberts et al. 2010). To characterize the study area, we estimated oceanographic and physiographic parameters for every grid cell, as explained below.

We used SST and chl *a* concentration to estimate the influence of oceanographic parameters on *B. edeni* habitat use. We obtained near-real-time

SST measurements from the Advanced Very High Resolution Radiometer (AVHRR) provided by the Group for High Resolution Sea Surface Temperature (GHRSSST), which are available from the NASA Physical Oceanography Distributed Archive Center, PO.DAAC (http://podaac.jpl.nasa.gov/dataset/JPL_OUROCEAN-L4UHfnd-GLOB-G1SST). These data have a spatial resolution of 1 km. We obtained measurements of chl *a* from MODIS (Moderate Resolution Imaging Spectroradiometer), which is also available at NASA's PO.DAAC (http://podaac.jpl.nasa.gov/dataset/MODIS_Aqua_L3_CHLA_Daily_4km_R). The spatial resolution of the MODIS data was 4 km. To best capture the variability of oceanographic parameters within the study area, we obtained daily SST and chl *a* measurements for the center of each grid cell. The measurements were obtained for the same days as the surveys, regardless of whether whales were sighted. On a cell-by-cell basis we then calculated the mean, minimum, maximum, and standard deviation of the SST and chl *a* values for the 94 survey days, as in previous studies (e.g. Azzellino et al. 2008).

Similarly, we obtained physiographic parameter values (depth and distance to the coast) for the center point of every grid cell surveyed. We created a depth raster from nautical charts 1505 and 1508 obtained from the Hydrography and Navigation Department of the Brazilian Navy (<https://www1.mar.mil.br/dhn/>). We defined the distance from the coast as the distance from the center point of the grid cell to the nearest point of any type of land, e.g. continent, island, rocky coast, etc., which we measured using the 'Near' tool in the ArcGIS 10.3.1® Spatial Analyst toolbox. The distances were calculated in meters based on Albers Equal Area Conic projection. We plotted all GIS data in the SIRGAS 2000 geodesic system.

Data analysis

For modeling purposes and to avoid problems of pseudoreplication, we only used sighting and re-sighting data on individual whales that could be recognized reliably through natural marks and nicks on their dorsal fins, following the protocol applied in previous studies (Mazzoil et al. 2004, Espécie et al. 2010, Figueiredo et al. 2015, Lodi et al. 2015).

We built a standard GLM specification with a log link function to investigate the influence of the explanatory variables on the total number of *B. edeni* individual sightings (including re-sightings) per grid.

If a single individual was sighted more than once in a cell, the individual was only recounted if the sightings occurred on different days. Since few ecological studies are truly Poisson distributed (Ver Hoef & Boveng 2007), we used a quasi-Poisson distribution to account for overdispersion using the function 'dispersiontest' from AER package v.1.2-5 (Kleiber & Zeileis 2008). To balance the uneven survey effort, we summed the log length of boat tracks travelled per grid cell (in kilometers) and used this (rather than calculated probabilities) as an offset in the quasi-Poisson model to account for sampling intensity.

To test for SAC on residuals, we used Moran's *I* using the *spdep* package (v.0.5-56) in R (Bivand et al. 2013, Corkeron et al. 2011), which tests whether a given set of features is clustered with an associated attribute, dispersed, or randomly distributed. In general, values of Moran's *I* close to +1.0 indicate clustering, whereas values near -1.0 indicate dispersion, although it is necessary to verify the statistical significance of the values to determine whether they are in fact different from a random distribution (Griffith 1987).

Since our GLMs displayed SAC on the residuals ($I = 0.35$, $p < 0.001$), we used an eigenvector spatial filtering method to account for SAC using the 'ME' function in the *spdep* package of the R environment (Bivand et al. 2013). First, we generated the spatial eigenvectors from a binary spatial neighborhood matrix based on grid pixel adjacency, in which the value is 1 when 2 pixels share a common boundary and 0 when they have no common boundary (Dormann et al. 2007). Then, we added the spatial eigenvectors in the GLMs, now called spatial eigenvector generalized linear models (SEV-GLM). The SEV-GLMs were also estimated with the 'ME' function in the *spdep* package of the R environment (Bivand et al. 2013).

After a visual inspection of the response variable against each explanatory variable (see Supplement 1 at www.int-res.com/articles/suppl/m576p089_supp1.pdf), we noticed some relationships were curvilinear. Therefore, we fitted a polynomial term (quadratic) to depth, standard deviation SST, minimum SST and maximum SST.

To avoid algorithm errors in model selection, biased parameter estimation, and inappropriate confidence for a single model, we did not use the backward stepwise selection procedure that has been applied in some studies (Wittingham et al. 2006). Rather, we used a set of 3 pre-defined models to investigate habitat use (see Supplement 2 at

www.int-res.com/articles/suppl/m576p089_supp2.txt for more details about the modeling procedure):

(1) Physiographic model:

total number of whale sightings \approx depth + (depth²) + distance from the coast + offset (log (km))

(2) Oceanographic model:

total number of whale sightings \approx mean SST + maximum SST + maximum SST² + minimum SST + minimum SST² + SD SST + SD SST² + mean chl *a* + maximum chl *a* + minimum chl *a* + SD chl *a* + offset(log(km))

(3) Full model:

total number of whale sightings \approx depth + depth² + distance from the coast + mean SST + maximum SST + maximum SST² + minimum SST + minimum SST² + SD SST + SD SST² + mean chl *a* + maximum chl *a* + minimum chl *a* + SD chl *a* + offset(log(km))

Multicollinearity was also evaluated using a generalized variance inflation factor (GVIF) applied to the explanatory variables of the models using the *car* package 2.0-19 (Fox & Weisberg 2011). Variables with GVIF values of 10 or higher were removed from the analyses, as was the case for maximum chl *a* concentration and respective standard deviation (Table 1). As in previous studies, we used a hierarchical partitioning analysis to estimate the contribution of each variable (Quinn & Keough 2002, Gill et al. 2011) using the *hier.part* package 1.0-4 (Walsh & MacNally 2013).

Table 1. Summary of *Balaenoptera edeni* occurrence on the Cabo Frio coast, Rio de Janeiro, Brazil, for December 2010 to November 2012 and February–August 2014. Monthly encounter rate = number of sightings in a given month/number of boat trips undertaken in the same month. *Numbers in parentheses within the monthly encounter rate column use individuals as a sampling unit

Month	No. of sightings	No. of ind.	No. of trips	Monthly encounter rate
January	1	1	4	0.25 (0.25)
February	4	6	10	0.25 (0.6)
March	2	5	10	0.2 (0.5)
April	2	6	7	0.29 (0.86)
May	6	10	10	0.6 (1.0)
June	2	2	10	0.2 (0.2)
July	1	1	8	0.12 (0.12)
August	0	0	8	0
September	0	0	4	0
October	0	0	8	0
November	4	6	10	0.4 (0.6)
December	5	9	5	1.0 (1.8)

Since models were overdispersed, a quasi Akaike's information criterion (QAIC) was used for model selection using the 'MuMIn' v1.15.6 package in R (Barton 2016). \hat{c} is the dispersion parameter estimated from the global model and can be calculated by dividing the model's deviance by the number of residual degrees of freedom. In the calculation of QAIC, the number of model parameters is increased by 1 to account for estimating the overdispersion parameter. Without overdispersion, $\hat{c} = 1$ and QAIC is equal to AIC (Supplement 2). We used QAIC to determine the best GLM model and, separately, we used QAIC to determine the best SEV-GLM model. Then, we used a likelihood ratio test to determine whether the best SEV-GLM was better than the correspondent GLM. The QAIC value reflects the explanatory power of the independent variables, taking the degrees of freedom into account (Akaike 1973). As QAIC evaluates model fit by penalizing the number of parameters, models with more parameters than necessary will have higher QAIC values (Burnham & Anderson 2004). The models can be ranked according to their AIC values, with smaller values representing a more parsimonious and, consequently, more plausible model.

The prediction of our best model was calculated from the means of the predictors during the surveyed periods using *glm.predict* in the R stats package v. 3.4.0. We imported the predicted probabilities of habitat use by the whales to ArcGIS 10.3.1. As in Corkeron et al. (2011), we also mapped residuals using the *residuals.glm* function in R stats package v. 3.4.0. We imported the residuals from both GLM and SEV-GLM to ArcGIS 10.3.1.

RESULTS

A total of 94 boat surveys were conducted, covering 4970 km over 454.5 h. *Balaenoptera edeni* were observed during 46.4 h (10.1% of total survey time), with no sightings recorded between August and October of any year (Table 1). In general, we sighted at least 1 individual on 23 surveys (24.4%). On 16 surveys (69.6%), we photo-identified 10 individuals, of which 3 (33.3%) were seen on at least 4 different surveys (Table 2). Individuals with no apparent marks on the dorsal fin were sighted alone on 7 surveys (30.4%). We photographed 5 individuals once and another 5 individuals multiple times. The maximum individual re-sighting interval was 1113 d. We sighted individuals alone on 12 d and in pairs and trios on 6 d each.

Table 2. Summary of *Balaenoptera edeni* individual sighting and re-sighting history on Cabo Frio coast, Rio de Janeiro, Brazil. ID: identity code. Asterisks indicate individuals seen with calf

ID	1st sighting	2nd sighting	3rd sighting	4th sighting	5th sighting	6th sighting
001	11 Dec 2010	–	–	–	–	–
002*	19 Jan 2011	25 Mar 2012	–	–	–	–
003	21 Feb 2011	–	–	–	–	–
004*	20 Apr 2011	21 Apr 2011	25 Mar 2012	8 May 2012	20 Feb 2014	8 May 2014
005	20 Apr 2011	21 Apr 2011	5 May 2011	7 May 2012	–	–
006	18 Nov 2011	19 Feb 2014	30 Mar 2014	7 May 2014	8 May 2014	–
007	25 Mar 2012	7 May 2014	–	–	–	–
008	07 May 2012	–	–	–	–	–
009	07 Nov 2011	–	–	–	–	–
010	20 Feb 2014	–	–	–	–	–

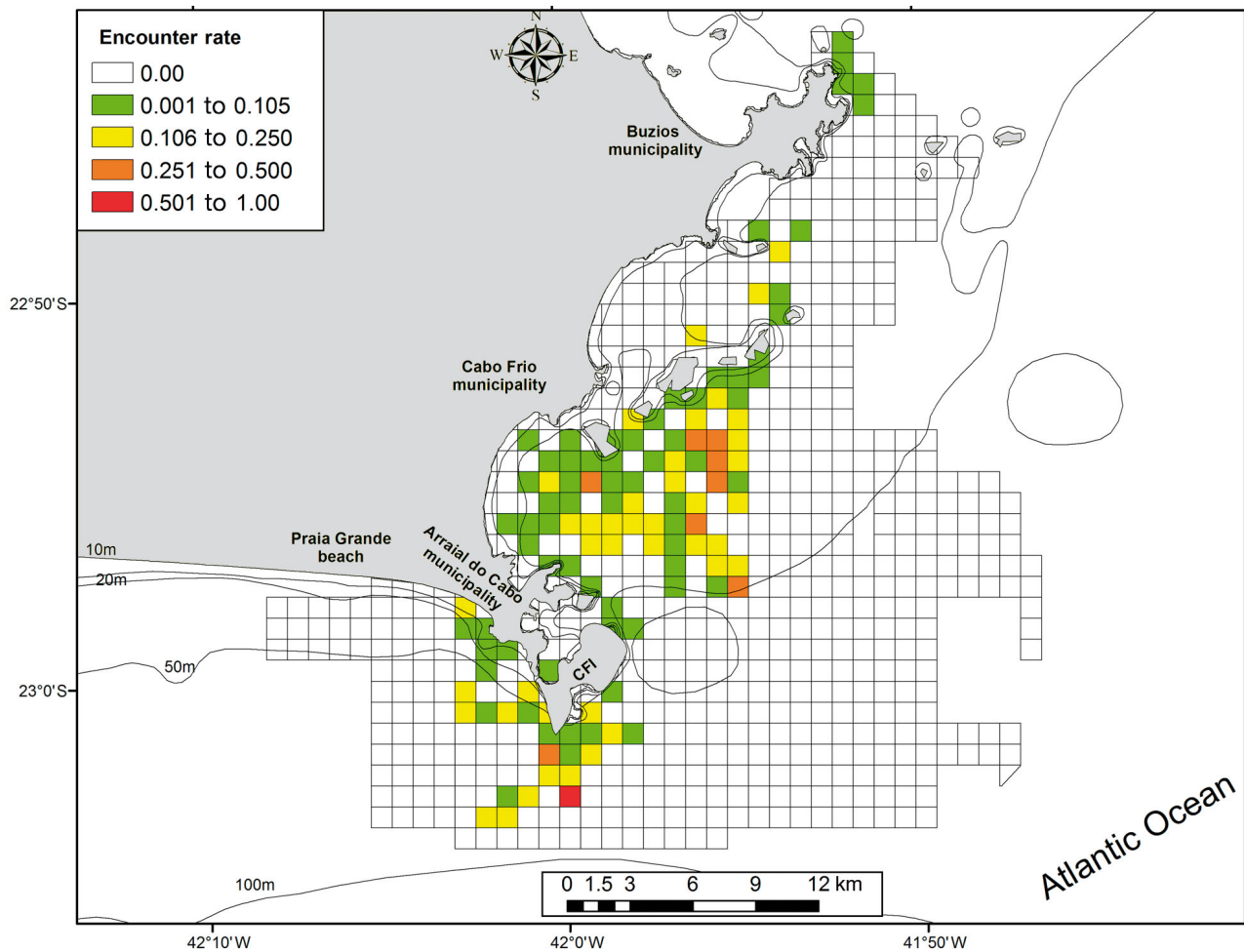


Fig. 2. Encounter rates of *Balaenoptera edeni* on the Cabo Frio coast, Rio de Janeiro, Brazil, within 1 km² grid cells. Encounter rate was calculated as the number of sighted whales in a given cell per kilometer surveyed in that cell. CFI: Cabo Frio Island

The overall sighting rate for the entire sampling period was 0.38 sightings per kilometer, with whales being encountered most frequently at 2 locations—near Cabo Frio Island and off the coast

of Cabo Frio (Fig. 2). Individuals were observed in areas where the water depth ranged from 17 to 100 m (mean = 44.8 m) and the distance from the coast was between 0.2 and 7.1 km (mean = 1.9 km),

with SSTs of 19.3–26.8°C (mean = 22.7°C) and chl *a* of 0.2–39.8 mg m⁻³ km⁻¹ (mean = 2.9 mg m⁻³ km⁻¹). An overview of the oceanographic and physiographic values for the study area is provided in Table 3.

Moran's *I* (0.49, *p* < 0.001) found the residuals had significant SAC. The best fitting SEV-GLM was the physiographic model (Table 4). When we compared the best SEV-GLM directly with the corresponding GLM (Table 5), the addition of the eigenvectors improved the model (likelihood ratio test, *p* < 0.001), with differences between both the coefficients and the significance of the variables (Table 5). Our best SEV-GLM indicated that *B. edeni* habitat use is influenced by depth and distance from the coast, retaining 5 eigenvectors (Table 5). The hierarchical partitioning analysis indicated that distance from the coast contributed most to the explanation of the model (Table 6).

The best SEV-GLM model predicted that the whales would be found more frequently around Cabo Frio Island and along the open coast (Fig. 3a), whereas the corresponding GLM predicted that the whales would be found more frequently in areas far from the coastline beyond the 100 m isobath (Fig. 3b). Our analysis of deviance showed that the fitted values explained the observed values (null residual deviance: 549.6; fitted model residual deviance: 374.2; *p* < 0.001). Fig. 4 shows

a map of residuals from the GLM and SEV-GLM, and Fig. 5 displays the linear combination of the eigenvectors with their estimated coefficients and shows the SAC pattern that is not explained by the SEV-GLM. The pseudo-R² estimated for the best SEV-GLM was 0.36.

Table 3. Summary statistics of study area environmental characterization in relation to 4 explanatory variables in Cabo Frio, Rio de Janeiro, southeastern Brazil

Explanatory variable	N	Mean	Median	SD
Depth (m)	718	44.8	39.5	19.9
Distance to coast (km)	718	1.9	1.4	1.9
Sea surface temperature (°C)	718	22.7	22.2	2.4
Chlorophyll (mg m ⁻³ km ⁻¹)	718	2.9	1.4	4.3

Table 4. Standard generalized linear models (GLM) and spatial eigenvector generalized linear models (SEV-GLM) used to test for *Balaenoptera edeni* habitat use in Cabo Frio, Rio de Janeiro, southeastern Brazil. Lowest quasi Akaike's information criterion (QAIC) indicated the best model (see 'Materials and methods' for details). The SEV-GLM in **bold** is the most parsimonious (presented in detail in Table 5). SST: sea surface temperature. Polynomial terms were included for depth, SD SST, minimum SST and maximum SST

Model	Coefficients	AIC	
		GLM	SEV-GLM
Physiographic	Depth + Depth ² + Distance to coast	560.9	506.3
Oceanographic	Mean SST + SD SST + SD SST ² + Minimum SST + Minimum SST ² + Maximum SST + Maximum SST ² + Mean chlorophyll + Minimum chlorophyll	563.9	521.0
Full	Depth + Depth ² + Distance to coast + Mean SST + SD SST + SD SST ² + Minimum SST + Minimum SST ² + Maximum SST + Maximum SST ² + Mean chlorophyll + Minimum chlorophyll	548.4	513.9

Table 5. Comparison among estimates for the best spatial eigenvector generalized linear model (SEV-GLM) and its correspondent standard GLM for *Balaenoptera edeni* in the Cabo Frio region, Brazil. Eigenvector values correspond only to SEV-GLM

SEV-GLM					GLM				
Coefficient	Estimate	SE	<i>t</i>	<i>p</i>	Coefficient	Estimate	SE	<i>t</i>	<i>p</i>
Intercept	-3.22	0.05	-6.7	<0.001	Intercept	-3.13	0.48	-7.7	<0.001
Depth	0.04	0.019	2.23	0.02	Depth	0.064	0.02	3.55	<0.001
Depth ²	-3.04 × 10 ⁻⁴	1.77 × 10 ⁻⁴	-1.72	0.08	Depth ²	-3.04 × 10 ⁻⁴	1.77 × 10 ⁻⁴	-2.9	<0.001
Distance to coast	-2.02 × 10 ⁻⁴	3.78 × 10 ⁻⁵	-5.31	<0.001	Distance to coast	-2.02 × 10 ⁻⁴	3.8 × 10 ⁻⁵	-4.2	<0.001
Eigenvec43	10.1	2.57	4.35	<0.001					
Eigenvec16	1.71	3.11	5.50	<0.001					
Eigenvec121	6.09	1.88	3.23	<0.001					
Eigenvec40	8.20	2.63	3.11	0.001					
Eigenvec125	1.20	2.82	2.82	<0.001					

Table 6. Relative importance of each statistically significant variable from the best spatial eigenvector generalized linear model for *Balaenoptera edeni* in Cabo Frio, Rio de Janeiro, Brazil. *I*: percentage likelihood, ascertained by hierarchical partitioning, that each habitat variable contributes to variation in the presence of Bryde's whale

Variable	Importance rank	<i>I</i> (%)
Distance to coast	1	90.2
Depth	2	9.8

DISCUSSION

This is the first study to model *Balaenoptera edeni* habitat use and the first to take into account SAC in the Atlantic Ocean off the Brazilian coast (Cabo Frio). In this study, we quantified the differences in the estimates of coefficients and the predictions provided by alternative models with and without the addition of spatial eigenvectors. By correcting for SAC, our predictions suggested a preference for patchy areas close to Cabo Frio Island around Arraial do Cabo municipality and other small islands around Cabo Frio municipality (Fig. 3), instead of a less distinct large, widespread area. Also, as found in Corkeron et al. (2011), our mapped residuals from SEV-GLM were substantially smaller and less clumped than GLM, suggesting that SEV-GLM predicts Bryde's whale sightings better than GLM.

Inspection of our mapped predictions showed the whales are found more frequently at depths between 30 and 90 m and in the proximity of islands with a rocky coastline. We hypothesize their presence at these depths may reflect the distribution of their prey. Previous data from the study area (Figueiredo et al. 2015, Maciel et al. in press) indicated that *B. edeni* use this area to feed and reproduce, suggesting a degree of site fidelity. In the proximity of rocky coastlines, *B. edeni* would be able to herd and trap fish shoals to facilitate their capture, as observed in other cetaceans (Heithaus & Dill 2006). Small schooling fish, such as Brazilian sardine *Sardinella brasiliensis* and Atlantic thread herring *Opisthonema oglinum*, and asscombrids, such as the chub mackerel *Scomber japonicus*, are known prey items for *B. edeni* (Tershy 1992, Siciliano et al. 2004, De Boer 2010). The presence of large shoals of these fish may influence the distribution of *B. edeni*, particularly because such large predators have high energetic requirements and must forage constantly (Costa 2008).

The range of depths at which *B. edeni* were most frequently observed are consistent with the behavior of *S. brasiliensis* (reported at depths of up to 80 m, with the largest shoals being found between 31 and 60 m; Paiva & Motta 2000), *O. oglinum* (found at depths up to 50 m; Murdy & Musick 2013), and *S. japonicas* (reported between 50 and 200 m; Castro-Hernández & Santana-Ortega 2000). Data from the Rio de Janeiro State Fisheries Federation (Fundação Instituto de Pesca do Estado do Rio de Janeiro [FIPERJ]) from 2011 to 2014 suggest that these species were the most common fish in the study area during our study period (FIPERJ 2011, 2012, 2014). In addition, the Cabo Frio region represents an important breeding ground for *S. brasiliensis* in Brazilian waters (Saccardo & Rossi-Wongtschowski 1991), and both *O. oglinum* and *S. japonicus* form mixed-species shoals with *S. brasiliensis* off Rio de Janeiro (Paiva & Motta 2000). The occurrence of *S. brasiliensis* is influenced by cold, nutrient-rich waters, such as those of the SACW (Paiva & Motta 2000), which are common off Cabo Frio (Carbonel 1998). One of locations used most commonly by the whales was near Cabo Frio Island, an area of marked upwelling dynamics, with depths of 70–90 m, which coincide with the environments in which *S. brasiliensis* and *S. japonicas* are found (Paiva & Motta 2000). In *B. edeni*'s preferred habitat around the islands closer to Cabo Frio, depths ranged from 20 to 40 m, which is also consistent with the distribution of *S. brasiliensis* and *O. oglinum*.

Monthly sighting rates indicate that *B. edeni* is found in the study area primarily in April and May (Table 1), when *S. brasiliensis* are in their post-reproductive period and occur in large shoals (Paiva & Motta 2000). The timing of the peak *B. edeni* occurrence with the high abundance of *S. brasiliensis* may have additional biological relevance given that during this period, we sighted pregnant and lactating females, who may take advantage of improved feeding opportunities to meet their high energetic requirements. This reinforces the conclusion that the coast of Cabo Frio is an important area for *B. edeni* (Figueiredo et al. 2015).

Seasonal fluctuations in the occurrence of these whales have also been observed in other regions. In Gabonese waters, for example, *B. edeni* is the most frequently sighted balaenopterid in May and July, when they feed on *Sardinella* species (De Boer 2010). In another upwelling area in the Gulf of California, Mexico, these whales were sighted most frequently while feeding on Pacific sardine *Sardinops sagax* (Tershy 1992). On the South African coast, Plettenberg Bay is an important feeding area for Bryde's

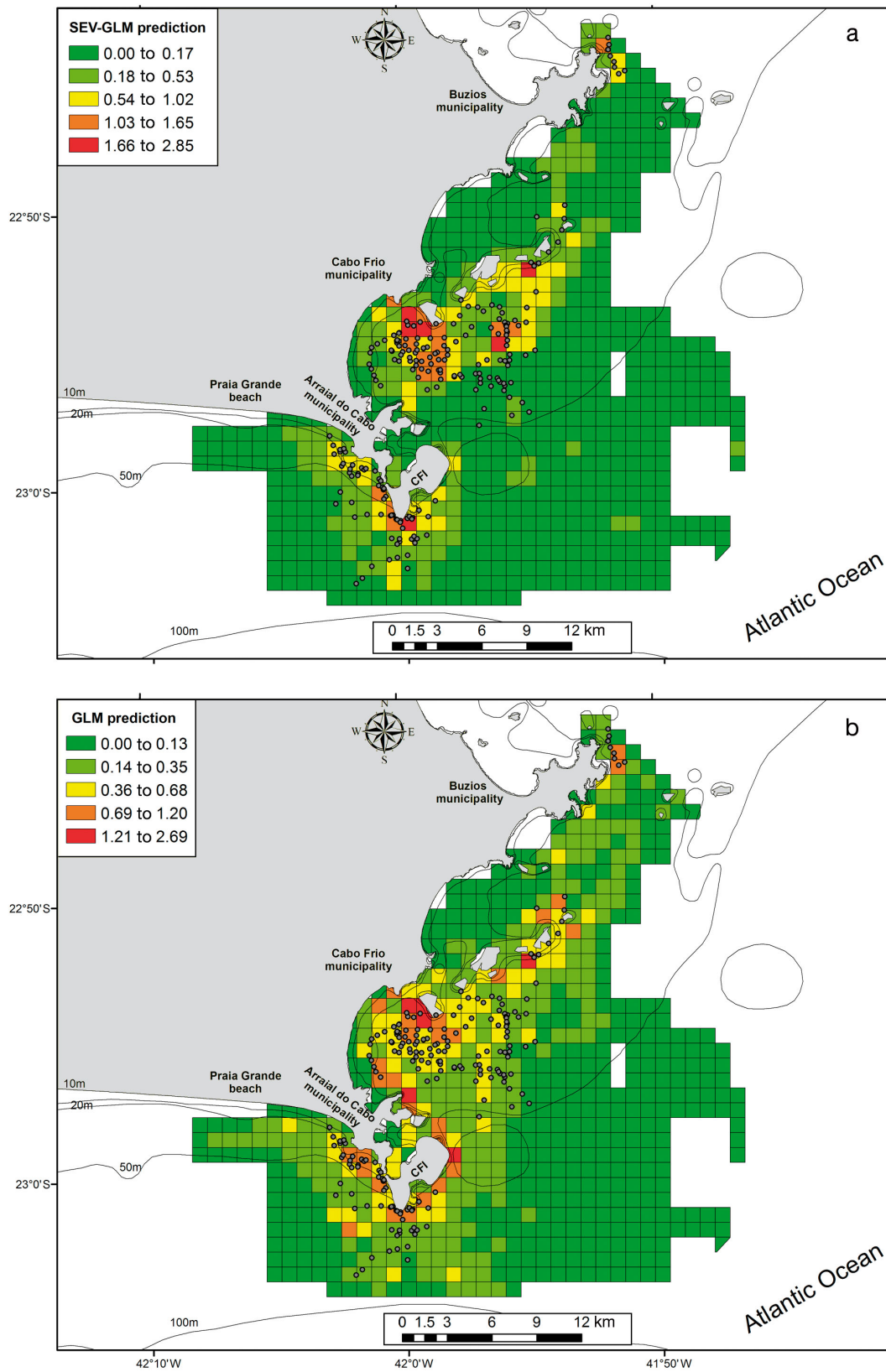


Fig. 3. Predicted habitat use for *Balaenoptera edeni* along the Cabo Frio Coast, Rio de Janeiro, Brazil, using quasi-Poisson generalized linear models with (a) and (b) without spatial eigenvectors. Grey circles indicate sighting locations. CFI: Cabo Frio Island

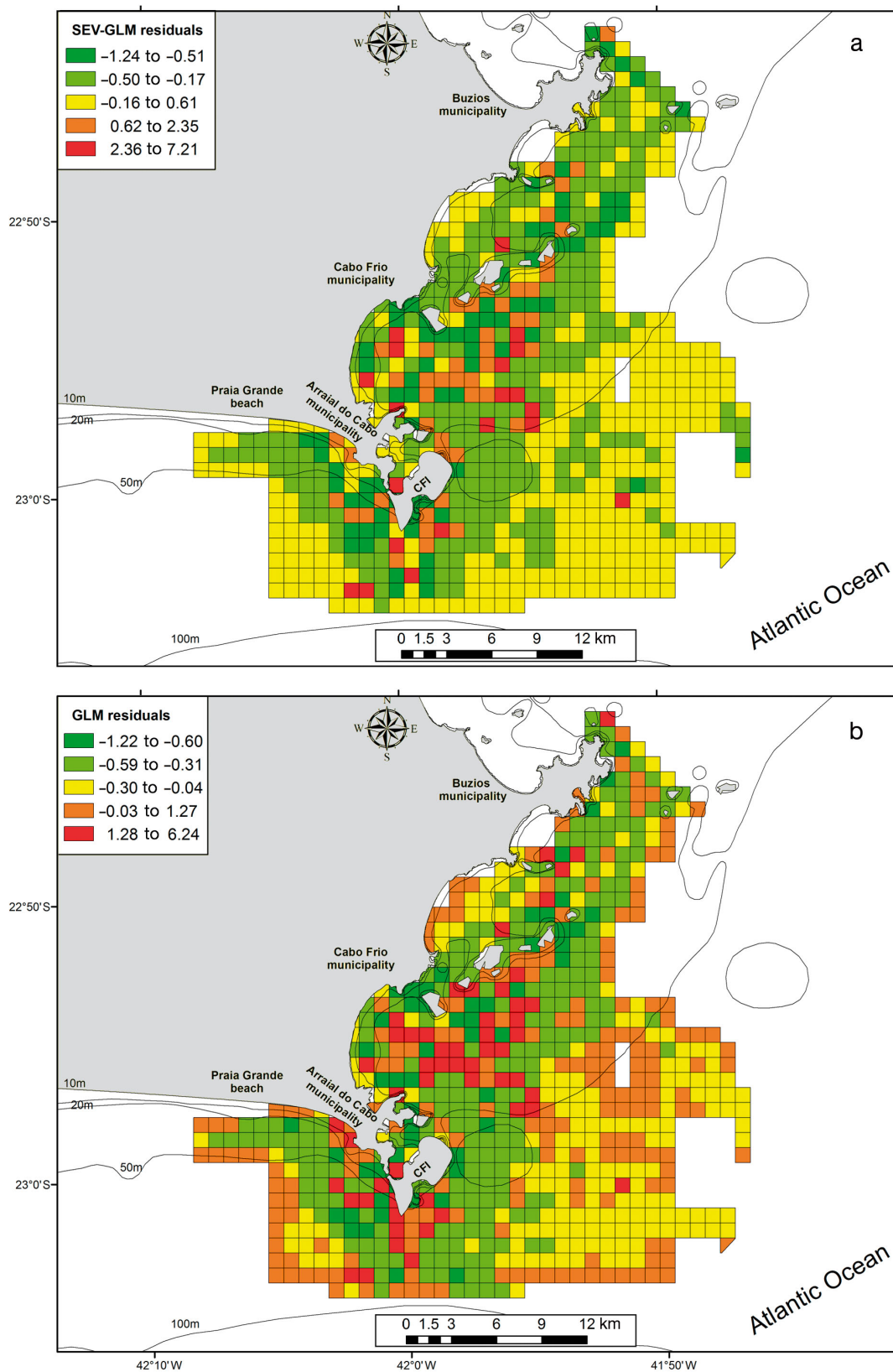


Fig. 4. *Balaenoptera edeni* model residuals for each grid cell along the Cabo Frio Coast, Rio de Janeiro, Brazil, from quasi-Poisson generalized linear models (a) with and (b) without spatial eigenvectors. CFI: Cabo Frio Island

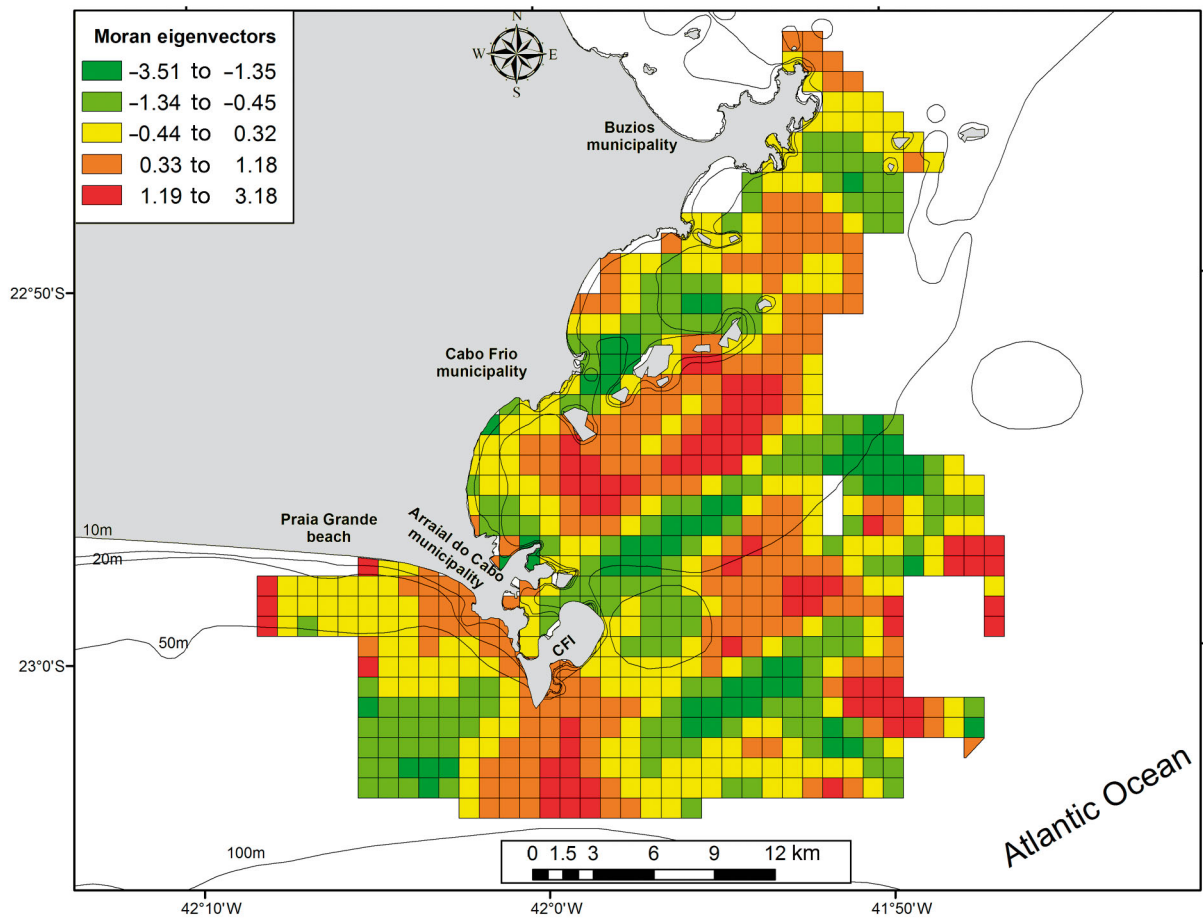


Fig. 5. Map of the linear combination for the 4 Moran's *I* eigenvectors with estimated coefficient values retained of the best spatial eigenvector generalized linear models for *Balaenoptera edeni* in Cabo Frio, Rio de Janeiro, Brazil. CFI: Cabo Frio Island

whale, with a peak of sighting in the austral autumn, associated with the annual northeastward migration of sardines into KwaZulu-Natal waters (Penry et al. 2011).

A number of studies have shown that the distribution of *B. edeni* species may be influenced by a range of physiographic and/or oceanographic variables. Corkeron et al. (2011), for example, used 15 *B. edeni* sightings off the Oman coast and SEV-GLM models to study the influence of physiographic variables on the distribution of *B. edeni*. They found that distance to the coast and slope had the greatest influence on whale distribution, which partly corroborates our findings. Conversely, on the eastern African coast between Gabon and Angola, Weir et al. (2012) found that the occurrence of *B. edeni* was correlated strongly with SSTs cooler than 20.6°C, but not any physiographic variables, which contrasts with our model.

While 23 d of sightings may seem like a small sample for the development of a reliable habitat-use

model when compared with other, better-studied cetacean species, no models are available for the understanding and prediction of habitat use by Bryde's whale in the Atlantic Ocean. The results of our study, which focused on the waters off Cabo Frio, provide important new insights into how *B. edeni* use the area, and which environmental variables may shape its distribution off the Brazilian coast. This is especially important because sightings of *B. edeni* near the Brazilian coast are rare, and the waters off Cabo Frio offer an excellent opportunity to survey the species without the need for expensive ocean-going vessels. One advantage of using distribution models is that they can be updated and improved as new sightings and environmental data become available (Cañadas et al. 2005), refining our understanding of the use of the environment by the animals. Despite being computationally intensive, the SEV-GLM used here is a powerful approach to remove the SAC from residuals and improve model predictions.

Cabo Frio is the second most important tourist destination in the state of Rio de Janeiro, attracting more than one million tourists every year (Prefeitura Municipal de Cabo Frio. www.cabofrio.rj.gov.br/ [accessed in 1 May 2016]). As the region has scenic beaches and transparent waters, it is popular for marine tourism, and it is used intensively for diving, fishing, and other recreational activities by vessels of all sizes. This traffic poses a serious threat to the *B. edeni* population that visits the study area. Whales may collide with vessels, for example, or avoid some areas due to the intensity of the traffic or increase their energy expenditure due to the penetrating underwater noise caused by the concentration of vessels. Although part of the study area is located within a marine protected area (MPA), there is still no management plan which could be used to regulate the different human uses or the number of vessels that may travel within the reserve. For conservation managers who must balance the interests of the people and wildlife that use an MPA, this difference may be fundamentally important. While the MPAs in our study area were not originally designed to protect cetaceans, our results indicate that the study area may be important for *B. edeni* and emphasize the need for government decision makers to include this species in future conservation plans.

Our study may contribute to these efforts in 3 ways. First, on a local scale, our map predicts areas of high *B. edeni* habitat use that can help to define the priority areas for protection. The protection of these areas would also potentially safeguard local fishery resources, and biodiversity in general, given that whales may act as top predators, and keystone or sentinel species (Zacharias & Roff 2001, Roberge & Angelstam 2004). On a national scale, our results contribute to the understanding the distribution of *B. edeni* along the entire Brazilian coast, especially because this species does not engage in long latitudinal migrations (Kato & Perrin 2008) and may be under constant pressure from anthropogenic impacts, particularly from oil and gas exploration, which are common in offshore waters in the Cabo Frio area. Second, from a conservation perspective, the study provides valuable data on the occurrence and distribution of a species listed as Data Deficient by the IUCN. While recent efforts have encouraged the prioritization of Data-Deficient species in conservation programs, these species tend to be under-represented when threats are evaluated, which may increase their risk of extinction (Bland et al. 2015, Jetz & Freckleton 2015). And third, our study was relatively inexpensive in comparison with surveys that depend

on large, ocean-going vessels, and provides a model that can be applied to other species and regions where this type of information is needed, but resources are scarce.

Acknowledgements. We thank Stephen Ferrari for the English review, Sergio S. Moreira for ArcGIS support, Luciana D. Figueiredo, Israel S. Maciel, Liliane Lodi and Marco Aurelio Crespo for their valuable support in the field, and Daniel Passos for valuable comments on the manuscript. We also thank the 2 anonymous reviewers for valuable comments on the manuscript. The authors gratefully acknowledge research grants from Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) (No. 479348/2010-3 and Grupo Fundação Boticario de Proteção a Natureza Grant Bo. 0997/2013-2). We also thank Fundação de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ) for a scholarship to R.H.T. (processes E-26/100.866/2011 and E-26/202.803/2016) and a grant to M.A.S.A. (E-26/102.837/2012 and E-26/201.724/2015), and Conselho Nacional de Pesquisa e Desenvolvimento for a productivity grant to M.A.S.A. (processes 308792/2009-2 and 305798/2014-6).

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