

# 1 **Whale distribution in a breeding area: spatial models of habitat use and abundance of** 2 **western South Atlantic humpback whales**

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12 **ABSTRACT:** The western South Atlantic humpback whale population was severely depleted by  
13 commercial whaling in the late 19<sup>th</sup> and 20<sup>th</sup> centuries, and today inhabits a human-impacted  
14 environment in its wintering grounds off the Brazilian coast. Here, we identify distribution patterns  
15 related to environmental features and provide new estimates of population size, which can inform  
16 future management actions. We fitted spatial models to line transect data from two research cruises  
17 conducted in 2008 and 2012 to investigate (1) habitat use and (2) abundance of humpback whales  
18 wintering in the Brazilian continental shelf. Potential explanatory variables were year, depth, seabed  
19 slope, sea-surface temperature (SST), northing and easting, current speed, wind speed, distance to  
20 coastline and to the continental shelf break, and shelter (a combination of wind speed and SST  
21 categories). Whale density was higher in slower currents, at shorter distances to both the coastline  
22 and shelf break, and at SSTs between 24 and 25°C. The distribution of whales was also strongly  
23 related to shelter. For abundance estimation, easting and northing were included in the model instead  
24 of SST; estimates were 14,264 whales (CV = 0.084) for 2008 and 20,389 (CV = 0.071) for 2012.  
25 Environmental variables explained well the variation in whale density; higher density was found to  
26 the south of the Abrolhos Archipelago, and shelter seems to be important for these animals in their  
27 breeding area. Estimated distribution patterns presented here can be used to mitigate potential human-  
28 related impacts, such as supporting protection in the population's core habitat near the Abrolhos  
29 Archipelago.

30 **Keywords:** shelter, conservation, density surface model, cetacean, line transect, reproduction

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32 **INTRODUCTION**

33 The Brazilian coast is inhabited every winter and spring by the western South Atlantic (WSA)  
34 humpback whale (*Megaptera novaeangliae*) population (also referred to as breeding stock A by the  
35 International Whaling Commission). Whales aggregate in coastal waters along the central and  
36 northeastern coasts of Brazil to mate and give birth before migrating to feeding areas (Martins et al.  
37 2001, Zerbini et al. 2006). This population was severely exploited by whaling between the late  
38 nineteenth and mid-twentieth centuries (Zerbini et al. 2011; Morais et al. 2017), to the point of near  
39 extinction in the 1950s, but has since been recovering (Andriolo et al. 2010, Zerbini et al. 2011,  
40 Bortolotto et al. 2016a). The Red List of the International Union for Conservation of Nature and  
41 Natural Resources (IUCN) lists the conservation status of this species as “Least Concern” (Reilly et  
42 al. 2008). Recent abundance estimates from ship-based line transect surveys suggest that the WSA  
43 population size was near 20,000 animals in 2012 (Bortolotto et al. 2016a). However, that estimate  
44 was not computed for the entire area currently recognized as the typical distribution range of these  
45 animals during the breeding season. This increasing population faces today an environment modified  
46 by human activities such as marine traffic (Bezamat et al. 2015), fishing (Rocha-Campos et al. 2011,  
47 Moura et al. 2013, Ott et al. 2016), coastal water pollution (Moura et al. 2013, Ott et al. 2016), noise  
48 pollution (Rossi-Santos 2015), and activities related to the oil industry (Iversen et al. 2009, Martins  
49 et al. 2013, Ronconi et al. 2015, Rossi-Santos 2015, Brasil 2017a). Specifically, there is an increasing  
50 interest for oil and gas production activities in the area; according to the Brazilian National Agency  
51 of Petroleum, Natural Gas and Biofuels (Agência Nacional do Petróleo, Gás Natural e  
52 Biocombustíveis, ANP) the majority of the Brazilian petroleum reserves is found in the marine  
53 environment (Brasil 2017a).

54 Human-related activities in the area are expected to increase and negative interactions with  
55 humpback whales are likely to become more frequent (Andriolo et al. 2010, Martins et al. 2013).  
56 Existing marine protected areas (MPAs) alone provide very limited effective protection in the  
57 breeding grounds for this population, because they only cover a small fraction of the range of these  
58 whales (Castro et al. 2014). Therefore, a broad understanding of their distribution patterns and habitat  
59 use is fundamental to inform management actions. Area-based management, with the objective of  
60 protecting this charismatic flagship species, may also enhance biodiversity protection, because  
61 populations occupy relatively large and biodiversity-rich marine habitats.

62 For seasonal migratory animals such as many baleen whale species, the environmental factors  
63 expected to be important in habitat selection differ between feeding areas, where prey distribution is  
64 the primary driver (e.g., MacLeod et al. 2004, Friedlaender et al. 2006), and breeding areas (Corkeron  
65 & Connor 1999). During the breeding season, large whales select habitat according to their breeding  
66 status (Rayment et al. 2015), presence of calves in groups (Cartwright et al. 2012) and other

67 reproduction-related characteristics (Ersts & Rosenbaum 2003, Craig et al. 2014, Lindsay et al. 2016).  
68 In this context, sheltered waters, bathymetric features, distance to the shore and sea-surface  
69 temperature (SST) are important factors for habitat usage of humpback whales in breeding areas (e.g.,  
70 Taber & Thomas 1982, Smultea 1994, Rasmussen et al. 2007, Felix & Botero-Acosta 2011,  
71 Cartwright et al. 2012, Trudelle et al. 2016). Understanding and explaining key features of the ecology  
72 of migratory whale populations, such as habitat use, distribution and abundance, may provide  
73 important information to evaluate the impacts of human use of the environment inhabited by them.

74 WSA humpback whales are found in their breeding area, the Brazilian continental shelf  
75 between Natal (5°S) and Cabo Frio (23°S) (Fig. 1), during winter and spring every year, and animals  
76 concentrate on the Abrolhos Bank (~18°S) (Zerbini et al. 2006, Andriolo et al. 2010). The few  
77 previous studies that formally investigated their distribution relative to environmental variables  
78 (Wedekin 2011, Pavanato et al. 2017), or how they use the available habitat (Martins et al. 2001),  
79 indicate that bathymetric features (i.e., depth) may play an important role in how WSA whale groups  
80 are distributed.

81 Here we provide new insights into the distribution and density of WSA humpback whales in  
82 relation to environmental features in their breeding grounds, and present new abundance estimates  
83 for this population. We applied density surface models (DSMs) to line transect data (Miller et al.  
84 2013) from ship-based surveys conducted in 2008 and 2012 (Bortolotto et al. 2016a) and fitted spatial  
85 models focusing on two main objectives: (1) to investigate habitat use and (2) to calculate model-  
86 based abundance estimates.

87 The new information should inform management actions to conserve humpback whales on their  
88 Brazilian breeding grounds. More specifically, new abundance estimates may be used to update this  
89 population's conservation status, and the distribution results to evaluate areas where this population  
90 may be at higher risk of being affected by human-related activities, such as oil and gas exploration  
91 and production activities.

## 92 **METHODS**

93 Shipboard visual line transect surveys were conducted in 2008 and 2012 during research cruises  
94 aboard the R/V Atlântico Sul (Universidade Federal do Rio Grande, FURG). Cruises were part of the  
95 Monitoring Whales by Satellite Project (Projeto Monitoramento de Baleias por Satélite, PMBS).  
96 PMBS main objectives were to deploy satellite-link tags on humpback whales to track their  
97 movements, to understand their space-use patterns in breeding and feeding grounds and characterize  
98 their migratory routes (Zerbini et al. 2006).

99 The survey area corresponded to the Brazilian continental shelf, between the shore and the shelf  
100 break (defined here as up to the 500 m isobath) from Cabo de São Roque (5°S), in Rio Grande do

101 Norte State, to Cabo Frio (23°S), in Rio de Janeiro State (Fig. 1). Surveys were conducted from 25  
102 August to 23 September in 2008 and from 7 August to 3 September in 2012, during the expected  
103 annual peak of occurrence of humpback whales in the area (August–September; Martins et al. 2001,  
104 Morete et al. 2003). Lines were designed to survey the full extent of this population’s breeding area  
105 and data collection followed the distance sampling methodology (Buckland et al. 2001). Trackline  
106 design, observation effort and data collection details are described in previous work (Bortolotto et al.  
107 2016a, Bortolotto et al. 2016b).

### 108 ***Correcting for imperfect detection: detection function modelling***

109 We used a detection function to correct for whales that were not detected when lines were surveyed  
110 (Buckland et al. 2001). Because other large whale species were rarely seen during the survey,  
111 sightings that were attributed to “unidentified large whales” were pooled with those of confirmed  
112 humpback whales. It is very unlikely that unidentified whale sightings were not of humpback whales,  
113 as discussed in Bortolotto et al. (2016a).

114 Detection functions were fitted to perpendicular distance data using R (version 3.2.1; R Core  
115 Team 2015) and “Distance” package (version 0.9.6; Miller 2016). Factor covariates sea conditions  
116 (“calm” for Beaufort 0–3 and “moderate” for Beaufort 4–6), detection cue (splash, body, blow or  
117 “other”), detection method (binoculars or naked eye) and year (2008 or 2012), and the continuous  
118 covariate group size (from 1 to 7) were considered. Variance in the detection function parameters was  
119 estimated using Fisher’s information matrix (Buckland et al. 2001, p. 61–68).

### 120 ***Data for spatial modelling***

121 Survey tracklines were divided into 8 km segments using QGIS software (version 2.8.3; QGIS  
122 Development Team 2015). Standard segment length was chosen to be twice the truncation distance  
123 (= 4 km), resulting in 8 by 8 km squares for most segments. During line segmentation, some segments  
124 at the end of lines were shorter than 8 km. In those cases, segments less than 4 km long were merged  
125 with the previous one and those longer than 4 km were considered as an independent new segment.  
126 A few segments (5 out of 516) that were less than 4 km long, and that could not be merged with  
127 another line, were excluded from the analysis. The response variable used to model whale distribution  
128 was the whale counts in each segment, which were corrected using the detection function described  
129 above.

130 Based on previous studies on the distribution of cetaceans in breeding areas and environmental  
131 data availability, covariates considered as potential explanatory variables were: current speed close  
132 to the surface, depth, distance to coast, distance to the shelf break, SST, seabed slope, wind speed at  
133 the surface, geographic position (northing and easting) and year (Table 1). Additionally, to represent  
134 a combination of environmental conditions that may be related to energy saving for the calf, six

135 categories for shelter (Table 1) were created by combining three categories of wind speeds at the  
136 surface (“light” for values between 0.94 and 5.15 m s<sup>-1</sup>; “moderate” for values between 5.15 and  
137 6.67 m s<sup>-1</sup>; “strong” for values between 6.67 and 9.16 m s<sup>-1</sup>) and two categories of SST (“cold” for  
138 values between the minimum of 20.2° and 24.7°C; “warm” for values between 24.7° and the  
139 maximum 26.9°C). The wind and SST categories were delimited by quantiles of wind speed (33<sup>rd</sup>  
140 percentile = 5.15 m s<sup>-1</sup> and 66<sup>th</sup> percentile = 6.67 m s<sup>-1</sup>) and SST (median = 24.7°C).

141 Values for depth were extracted from the global model of land topography and ocean  
142 bathymetry ETOPO1 (Amante & Eakins 2009). Circular buffers (radius = 4 km) were created around  
143 segment midpoints in QGIS and the average of depth values within the buffer zone was computed for  
144 each segment. This procedure was adopted because the resolution of ETOPO1 was much finer than  
145 the size of segments and buffers (between 13 and 16 ETOPO1 cells were included in the 50 km<sup>2</sup>  
146 buffers and used to compute mean depth values). After mean depth values extraction, 25 out of 511  
147 segments gave values greater than 500 m and were excluded from the analysis because the study area  
148 was previously defined as the continental shelf, from the shore up to the 500 m isobath. Slope values  
149 were derived from ETOPO1 data and were obtained in the same way, i.e., extracting mean values  
150 using the same circular buffers.

151 Distances to physical features (distance to coast and distance to shelf break) were calculated in  
152 QGIS or R as the shortest distance between the segment midpoint and the feature. For the distance to  
153 coast variable, the Brazilian coastline was obtained from a shapefile provided by SisCom (IBAMA  
154 2011). To represent the continental shelf break, the 500 m isobath was generated from ETOPO1 in  
155 ArcGIS software using the “contour tool” function (Esri 2011).

156 SST was extracted from “MUR Global Foundation Sea Surface Temperature Analysis” dataset  
157 (JPL MUR MEaSURES Project 2010) and ocean currents from “OSCAR” dataset (ESR 2009), both  
158 available from PO.DAAC/NASA website. Wind speed data were extracted from “ERA-Interim”  
159 dataset (ECMWF; Dee et al. 2011). With the exception of SST, the resolution of these datasets was  
160 too coarse when compared to the size of the circular buffers, so segment midpoints were used to  
161 extract covariate values in R software (“raster” package; Hijmans 2016). For SST, the circular buffers  
162 previously described were used to obtain mean values (around 40 SST values per buffer).

### 163 *Spatial models and model selection*

164 An initial investigation was performed to assess correlation among explanatory variables, and those  
165 that were highly correlated (i.e., a pair of variables that presented Pearson’s correlation coefficient  
166 greater than 0.7, or clear correlation identified via pair plots) were not included in the same model at  
167 the same time. Interaction terms, combining year and other covariates, were not tested because part  
168 of the study area was not surveyed in 2012, which would make the comparison severely unbalanced.

169 The quasi-Poisson distribution with logarithmic link function was assumed for the response  
170 variable (negative binomial and Tweedie distributions were also tested). An offset of  $\ln(\text{segment}$   
171  $\text{length})$  was included in all models. Generalized Additive Models (GAMs) were fitted using the “dsm”  
172 R package (version 2.2.14; Miller et al. 2017). Smooth functions were fitted to covariates, with a  
173 bivariate smooth for geographic position, since this included easting and northing. The basis  
174 dimension parameter  $k$  for the geographic position smooth term was set to 20, and for the univariate  
175 smooth terms it was set to 8 (see Wood 2006, p. 161, for an explanation on setting the dimension  
176 parameter). Model selection was conducted using a forward approach (i.e., adding one variable at a  
177 time), starting with a set of models, each with only one candidate explanatory variable. The model  
178 selected at each step was chosen by looking for an improvement in the Restricted Maximum  
179 Likelihood (REML) (Harville 1977) score. This score was used to minimize problems with parameter  
180 estimation that other potential scores (e.g., UBRE and GCV) may present when applying DSMs,  
181 following the recommendation in Miller et al. (2013). The auto-correlation in the residuals (ordered  
182 by the time of data collection) of spatial models was checked using the “acf” function (“stats” R  
183 package; R Core Team 2015). Model performance was assessed with model diagnostic plots (function  
184 “gam.check”, “dsm” R package) and 10-fold cross validation (Refaeilzadeh, Tang & Liu 2009).

185 Two modelling exercises were undertaken, each considering a different set of covariates and  
186 having different objectives:

- 187 1. Habitat Use Model (HUM): to explain habitat use in a way that could be interpreted  
188 biologically. All variables, except geographic position (northing/easting), were considered;
- 189 2. Abundance Estimation Model (AEM): to compute abundance estimates from the spatial  
190 model and all available variables were considered.

191 The HUM was designed to investigate which environmental variables were more related to  
192 distribution, while the AEM was designed to obtain the best density surface prediction, possibly  
193 including northing/easting, which could explain variability that was not explained by the  
194 environmental covariates.

### 195 ***Predictions***

196 A prediction grid formed by 8 by 8 km cells was created over the entire study area using QGIS. The  
197 size of the prediction grid cells was chosen to match that of the segments used in the models.  
198 Covariate values for each grid cell were obtained in a similar way of that described for segments,  
199 using cell midpoints or 4 km buffers around midpoints. For covariates that varied in time within each  
200 survey (e.g., SST), the mean of values for the survey period was used for predictions.

201 The model-based abundance estimates for 2008 and 2012 were obtained from the sums across  
202 all grid cells of predicted values from the AEM, for each year. Maps showing patterns of distribution

203 (density surface) were created using the AEM predictions in QGIS. Variances were obtained with the  
204 delta method, combining the variance from the detection function and the spatial models, using the  
205 “dsm.var” function of the “dsm” R package. Maps of uncertainty in model predictions (standard  
206 deviation surface) were also created with the variance calculated for each grid cell (Fig. S6).  
207 Predictions in 2012 were extrapolated to the area to the north of Salvador (~13°S), which was not  
208 surveyed in 2012 (Fig. 1) because of poor weather conditions (Bortolotto et al. 2016a).

## 209 **RESULTS**

210 Survey effort used in the analysis totaled 2,350 km in 2008 and 1,700 km in 2012. The number of  
211 whale groups (including mother-calf pairs and solitary animals) in the data was 493 (416 humpbacks  
212 and 77 unidentified large whales) and 737 (557 humpbacks and 180 unidentified large whales) in  
213 2008 and 2012, respectively.

### 214 *Detection function*

215 Perpendicular distances were truncated at 4 km, resulting in 81 (out of 1230) detections being  
216 excluded from the detection function analysis. The best-fitting detection function was a hazard rate  
217 model with covariates cue, year and sea conditions (Fig. 2; Table S1). The average probability of  
218 detection  $p$  was estimated as 0.482 (CV = 0.044) and the goodness of fit tests showed a good fit  
219 (Kolmogorov-Smirnov test statistic = 0.016, p-value = 0.930; Cramer-von Mises test (unweighted)  
220 statistic = 0.036, p-value = 0.952).

### 221 *Spatial models*

222 Model diagnostics (Fig. S1 and S2) indicated the quasi-Poisson distribution to be adequate and to  
223 provide a better fit than the other distributions that were considered. Cross-validation yielded root-  
224 mean-square errors of 6.932 (SD = 1.116) for 2008 and 7.981 (SD = 0.967) for 2012 (Table S7). SST  
225 was found to be highly correlated with geographic position. Depth, slope and distance to the shelf  
226 break were also correlated to each other. Therefore, if one of the above variables was selected at a  
227 model selection step, those correlated were not considered in subsequent steps of model selection.

228 The selected HUM included variables distance to the coast, distance to the shelf break, SST,  
229 current speed and shelter, and presented 54.1% of deviance explained. The variable with the most  
230 pronounced effect was SST, with a peak around 24–25°C (Fig. 3). Whale density was positively  
231 related to distance to the coast and distance to the shelf break, but negatively related to current speed,  
232 apparent from around 0.2 m s<sup>-1</sup> and greater. Shelter coefficients indicated differences in whale  
233 densities between shelter categories, with significantly (at  $\alpha = 0.05$ ) higher densities in relatively cold  
234 waters with light winds (Table 2; Tables S2 and S3).

235 The selected AEM included variables distance to the coast, distance to the shelf break, current  
236 speed, shelter and geographic position, and had an explained deviance of 66.8%. This model was  
237 used for plotting purposes here, because this model presented a larger portion of explained deviance  
238 and the distribution patterns are likely better represented. Very weak signs of auto-correlation were  
239 found in the residuals of HUM and no signs of auto-correlation were present in the residuals of AEM  
240 (ACF plots; Fig. S1 and S2).

#### 241 *Abundance estimates*

242 Estimated abundances for prediction grid cells ranged from 0.139 to 53.0 animals (mean = 7.47,  
243 SD = 8.90) in 2008 and from 0.144 to 60.9 animals (mean = 10.7, SD = 12.7) in 2012. Model-based  
244 abundance estimates were 14,264 whales (CV = 0.084) for 2008 and 20,389 (CV = 0.071) for 2012  
245 (Table S6). Surface maps for predicted density showed higher numbers in the Abrolhos Bank region,  
246 with a concentration area to the south of the Abrolhos Archipelago, which was more pronounced for  
247 2012 (Fig. 4). Other areas also showed relatively high densities, such as the coast of Alagoas and  
248 Sergipe States (Fig. S4), and near the city of Salvador, Bahia State (Fig. S5).

#### 249 **DISCUSSION**

250 Systematically collected sightings data were used to model the distribution and abundance of  
251 humpback whales in their wintering areas off the coast of Brazil. The suite of environmental  
252 covariates tested included powerful predictors of whale density across the study area, with SST and  
253 geographic position being the most powerful explanatory terms. The effect of year was not selected  
254 in the spatial models, suggesting that differences in the distribution patterns from 2008 to 2012 were  
255 better explained by the variation in the spatial covariates than by temporal changes between survey  
256 years.

257 These sighting data were previously used to estimate abundance of humpback whales off the  
258 coast of Brazil in 2008 and 2012 using design-based methods (Bortolotto et al. 2016a). However, the  
259 realized effort in that study did not conform exactly to the designed lines. For example, because of  
260 unfavorable weather conditions in 2012, there were no data available for areas to the north of  
261 Salvador, Bahia State (Fig. 1). Consequently, the abundance estimate previously presented for that  
262 year was computed for only part of what is currently known to be the typical breeding area for WSA  
263 humpback whales. Because of logistical restrictions, our results likely represent WSA humpback  
264 distribution during the annual peak of their occurrence in the area (August–September) and it is not  
265 possible to infer intra-season variations.

266 Migratory whales show marked differences in habitat preferences according to different age  
267 classes, sexes, reproductive-related individual characteristics and/or group composition (Best 1990,  
268 Craig & Herman 2000, Martins et al. 2001, Ersts & Rosenbaum 2003, Elwen & Best 2004a, Oviedo



269 & Solis 2008, Cartwright et al. 2012, Craig et al. 2014, Rayment et al. 2015, Lindsay et al. 2016), and  
270 for specific group types (Elwen & Best 2004b, Felix & Botero-Acosta 2011) when in breeding areas.  
271 However, the passing mode data collection procedure adopted here prevented obtaining more specific  
272 data on individual whales, such as sex, age class or accurate group composition. Because of this,  
273 results presented here are representative of the population as a whole, not of any particular sex, age  
274 or group. Although some of the results may be consistent with what could be expected for habitat  
275 preferences of breeding or/and calving animals in the area, such as the importance of shelter as a  
276 predictor of density, it is not possible to make robust inferences for specific reproductive stages. A  
277 study to investigate the distribution and habitat use of WSA humpback whales based on data from  
278 satellite tagging of individual whales (Zerbini et al. 2006) is underway, which is expected to provide  
279 information on predictors of distribution and habitat use in relation to sex and group composition.  
280 Because the procedure of attaching tags requires close proximity to the animals, collection of  
281 individual and group information is possible at the moment of tagging.

### 282 *Spatial modelling*

283 The covariates retained in the models explained a high portion of the variation in whale density across  
284 the surveyed area (deviance explained = 54.1% for HUM; 66.8% for AEM). In addition to this  
285 increase in explained deviance, in the AEM the residual auto-correlation in the HUM (“ACF” plots;  
286 Fig. S1 and S2) was no longer apparent (although the auto-correlation in the residuals of the HUM  
287 was not high and required no further action; see Wood 2006 for concerns about residual auto-  
288 correlation of GAMs). It is likely, therefore, that the bivariate smooth for easting/northing included  
289 in the AEM is acting as a proxy for unmodelled environmental or social characteristics. For example,  
290 because it was highly correlated with SST, which was not included in the AEM, easting/northing may  
291 be representing not only SST but also some other environmental feature(s). This may explain the  
292 increase in percentage of explained deviance when SST is substituted by easting/northing in the  
293 AEM.

294 Shelter (a combination of SST and wind speed) was created as an environmental feature that  
295 could be important to whales that are calving, for example to represent conditions that may be related  
296 to energy saving for the calf (Corkeron & Connor 1999). Because the effects of wind speed on  
297 detectability have been accounted for in the estimation of detection probability, no confounding with  
298 the effects of wind in the shelter variable is expected. The response variables in the detection function  
299 model and the habitat use/abundance estimation spatial models are completely different; in the  
300 detection process it is the perpendicular distance (in relation to the trackline) and in the spatial models  
301 the response variable is abundance (corrected count per segment). Furthermore, wind speed may  
302 influence both the detectability of animals and how animals use their habitat, which is supported by

303 the present results. Indeed, a major advantage of density surface modelling using data from distance  
304 sampling surveys is that the effects of variables on detectability and on abundance can be teased apart.

305 The density surface modelling approach permitted inference and extrapolation from the AEM  
306 to the area not surveyed in 2012 by Bortolotto et al. (2016a), resulting in a 2012 abundance estimate  
307 for a larger part of the breeding ground distribution than would otherwise be available. The lack of  
308 data to the north of Salvador in 2012 implies that the effect of the bivariate smooth for  
309 easting/northing on the predictions for that area is largely influenced by data from 2008. However,  
310 the other variables retained in the model were responsible for the large majority of the explained  
311 deviance, as illustrated by the percentage of explained deviance of the HUM (54.1%), so this is not  
312 considered to be an important limitation for our inferences about abundance.

313 Model-based abundances for humpback whales breeding off the coast of Brazil (14,264,  
314 CV = 0.084 for 2008; 20,389, CV = 0.071 for 2012) were estimated to be close to those computed by  
315 design-based methods (16,410, CV = 0.228 for 2008; 19,429, CV = 0.101 for 2012; Bortolotto et al.  
316 2016a). This similarity could be expected because both estimates are derived from the same data. The  
317 higher precision in the model-based abundance estimates (CV = 0.084 vs 0.228 for 2008; CV = 0.071  
318 vs 0.101 for 2012) is mainly because the covariates explained some of the variability in the data,  
319 demonstrating the value of the analysis.

### 320 *Habitat use*

321 The main reasons for SST to be considered an important factor in explaining the distribution of  
322 migratory whales in their breeding grounds are likely related to presence of calves, which are not as  
323 efficient in conserving their body temperature as older animals (Corkeron & Connor 1999). SST was  
324 the most important variable selected in the HUM and it was highly correlated with geographic  
325 position (northing/easting). The overall relation between whale density and SST was positive,  
326 peaking at 24 to 25°C. This result for SST may reflect habitat selection of calving females for the  
327 reason stated above. The habitat use of North Atlantic right whales in their calving grounds off south-  
328 eastern United States was also observed to be strongly related to SST (Keller et al. 2006), however  
329 differences in species characteristics (e.g., latitudinal range) should be taken into account in any  
330 comparison. Trudelle et al. (2016) did not find a relationship between SST and humpback whale  
331 movements in their Madagascar coastal breeding area, possibly because of the relatively low variation  
332 in SST in the area. Although a temporal change in distribution was not supported by our models, long  
333 term monitoring should provide important insights on this, as the effects of climate change (Walther  
334 et al. 2002), for example, may impact the distribution of marine animals.

335 Shelter, which incorporated SST, was consistently retained in our spatial models and therefore  
336 can be considered an important factor to explain this population's distribution in the breeding area.

337 The fitted relationship for this covariate suggests that relatively slow and moderate surface winds had  
338 a significant positive effect on density, when the water was relatively colder. Because wind speed  
339 was not selected in the spatial models, our results suggest that wind may be an important habitat  
340 feature for WSA humpback whales only when the water temperature is relatively cool. A possibility  
341 is that, because temperature is one of the most important features for these animals in the area, they  
342 tolerate a range of wind speeds that is not their preferred, when the SST is relatively warmer. As  
343 mentioned above, because calves may benefit from an environment where they can save body energy  
344 reserves, calm conditions at the water surface are likely preferable for calves to swim and to surface  
345 to breathe (Taber & Thomas 1982, Cartwright et al. 2012). At a daily scale study of habitat use, Felix  
346 & Botero-Acosta (2011) found that mother-calf humpback whale pairs in Ecuador preferred  
347 shallower waters during the afternoon hours, when wind speeds in the area tended to increase and the  
348 sea to become rougher. The combination of water temperature and wind at the surface seems to be an  
349 important factor for WSA humpback whale habitat selection in breeding grounds. Rayment et al.  
350 (2015), to the best of our knowledge, was the only study that incorporated a variable to explicitly  
351 represent shelter in habitat use models for breeding migratory whales. These authors investigated the  
352 influence of shelter in breeding right whales distribution and found that wave exposure and distance  
353 to shelter (defined as areas with lower wind exposure) influenced habitat selection of right whale  
354 groups with calves.

355 It is still unclear which environmental features really represent shelter for breeding whales and  
356 how this may vary among different species. Martins et al. (2001) showed that the occurrence of WSA  
357 humpback whales groups containing calves increased with the proximity to the Abrolhos  
358 Archipelago, which may represent shelter for these animals, with the archipelago presence perhaps  
359 creating a calmer environment. Also, Zerbini et al. (2004) observed that WSA mothers-calf groups  
360 were more frequently found closer to the shore than other group types off the north-eastern coast of  
361 Brazil. Our results add to this discussion of which environmental variables may combine to create a  
362 sheltered environment that benefits migratory whale species in their breeding grounds. While several  
363 other covariates could have been included or combined to create a spatial covariate to represent shelter  
364 (e.g., speed and direction of ocean currents), the simple combination that we present here for shelter  
365 permits easy interpretation of model results. A complicated combination of several covariates would  
366 likely produce results that would be difficult to interpret biologically.

367 The relationships between whale density and environmental covariates revealed by our models  
368 are consistent with what could be expected for mothers, which may prefer a secure environment for  
369 the development of their calves in sheltered waters. However, Trudelle et al. (2016) noted that while  
370 the movements of female humpback whales in a breeding area off the Madagascar coast are  
371 influenced by environmental features such as depth and distance to the shore, male movements are

372 probably more influenced by social factors, such as female occurrence. Despite the fact that their  
373 distribution may also be influenced by the presence of other males (Herman 2017), adult males are  
374 indeed likely to seek receptive females, not those that are about to or have just given birth. Calving  
375 females may prefer shallow waters where the chances of being harassed by males are lower; their  
376 habitat selection may be driven primarily by avoidance of males (Craig et al. 2014). Humpback whale  
377 groups containing calves have been found significantly more frequently in shallower waters than  
378 groups without calves in Brazilian breeding grounds (Martins et al. 2001, Zerbini et al. 2004). Thus,  
379 bathymetric features may also be related to what may represent shelter for the whales.

380 Overall, this discussion highlights the importance of having data on the sex and reproductive  
381 status of individuals and not only on environmental features to understand the distribution of large  
382 whales in breeding areas. For example, we did not consider bathymetry as part of shelter to facilitate  
383 interpretation of results, but if such individual data were available it could be informative to  
384 investigate a wider range of covariate combinations representing shelter in models of habitat use.  
385 Future studies could also investigate in detail the conditions of the marine environment in areas  
386 surrounding the Abrolhos Archipelago. For example, the presence of coral reefs may be related to (or  
387 contribute to) shelter from rough water (Lindsay et al. 2016).

388 The positive relationship between whale density and distance to both the coast and the  
389 continental shelf break could mean that humpback whales off the coast of Brazil prefer to be in the  
390 middle part of the shelf, or that they prefer to avoid the shelf boundaries. Trudelle et al. (2016)  
391 suggested that the distance to the coast was one of the most important factors affecting the movement  
392 patterns of female humpback whales off the Madagascar breeding grounds and other studies have  
393 shown that calving humpback whales are associated with areas close to the shore (Martins et al. 2001,  
394 Zerbini et al. 2004, Felix & Botero-Acosta 2011). Avoidance of the shelf edge could be in response  
395 to the risk of predation by large predators in offshore waters, such as large shark species (Smultea  
396 1994). Areas too close to the shore could be avoided because they are too shallow for swimming  
397 (Oviedo & Solis 2008) or because of disturbances that were not considered here, such as noise from  
398 human activities.

399 The estimated negative effect on predicted whale numbers of current speeds greater than 0.2 m  
400  $s^{-1}$  is not very well supported by the data (95% confidence interval widens with increasing current  
401 speed). In a study that supports the importance of the current for large whales in breeding areas,  
402 Trudelle et al. (2016) found that differences in current speed between shelf and oceanic waters  
403 influenced the movement patterns of humpback whales in their Madagascar breeding area. Whales  
404 of both sexes swam faster in slower currents and the authors suggest that when animals are engaged  
405 in mate-searching-related movements close to the coast, the current speed probably did not have an  
406 important effect. Therefore, it is likely that data on the behavioral status and/or movements of

407 individual animals are needed to better understand the effects of current speed on habitat use of  
408 humpback whales off Brazil. In addition, the resolution of this covariate (5-day bins and  $0.33 \times 0.33^\circ$   
409 of latitude/longitude; Table 1) was likely unable to capture fine scale variability, particularly around  
410 complex coastlines.

#### 411 ***Implications for conservation and management***

412 The predicted distributions support previous work showing that WSA humpback whales have a strong  
413 preference for the Abrolhos Bank region during their breeding season in coastal waters of Brazil  
414 (Siciliano 1997, Andriolo et al. 2010, Wedekin 2011, Martins et al. 2013, Pavanato et al. 2017).  
415 However, other areas also had relatively high predicted densities, such as near Salvador and off the  
416 coasts of Sergipe and Alagoas States (Figs. S4 and S5). Little is known about their distribution or  
417 habitat use in these areas (Zerbini et al. 2004, Baracho-Neto et al. 2012), but relatively recent  
418 observations indicate that the distribution of WSA humpback whales in Brazil may be broader than  
419 currently recognized (e.g., Wedekin et al. 2014, Bortolotto et al. 2016c, Pavanato et al. 2017).

420 The Abrolhos Archipelago is included in the Abrolhos Marine National Park, which is a  
421 national “Conservation Unit” (abbreviated as UC in Portuguese) area of 880 km<sup>2</sup> (ICMBio 2017).  
422 According to the Brazilian Ministry of Environment (Brasil 2017b) this is a federal UC of “integral  
423 protection” where only scientific research and educational, recreational and small-scale ecotourism  
424 activities are permitted. All of these activities are regulated by the Chico Mendes Institute for  
425 Biodiversity Conservation (ICMBio), the federal body responsible for protected areas in Brazil.  
426 Commercial activities are therefore mostly limited to those related to small-scale ecotourism. The  
427 nearby Environmental Protection Area of Ponta da Baleia is regulated by the Bahia State and is in the  
428 category of “sustainable use area” (INEMA 2017). These protected areas cover a very small portion  
429 of the area predicted to have the highest concentration of animals (Fig. 5). Our results support the  
430 conclusions of Castro et al. (2014) who used satellite tracked movement data to show that MPAs only  
431 cover a very small portion of the areas most used by WSA humpback whales in their breeding  
432 grounds.

433 The Abrolhos Bank is a region of high biodiversity (Werner et al. 2000) and expanding the area  
434 under protection could benefit not only cetaceans but also other marine organisms, such as the unique  
435 coral reefs in the area (Francini-Filho & Moura 2008). Because most humpback whale births are  
436 expected to occur on or near Abrolhos Bank (Martins et al. 2001), expanding the protected area during  
437 the period when whales are present consistently (winter–spring), could reduce the risk of  
438 anthropogenic impact especially for calves that are known to be more vulnerable to disturbance  
439 (Schaffar et al. 2013). To conserve marine species in the area, past management actions have included  
440 the cancellation of seismic activity on the Bank during humpback breeding season and other oil and

441 gas exploitation activities (Engel et al. 2004, Marchioro et al. 2005). However, there is increasing  
442 interest from the oil and gas industry to explore for oil on the Bank (Brasil 2017a). Because young  
443 animals are more vulnerable to stressors (Schaffar et al. 2013, Ott et al. 2016, Dunlop et al. 2017) and  
444 we did not include group composition in this study, future studies aiming to provide information for  
445 conservation should investigate the distribution of different group types at a finer scale and include  
446 potentially stressors and displacement factors associated with human presence in the marine  
447 environment, with special attention to the Abrolhos Bank region.

448 Abundance estimates presented here (14,264, CV = 0.084 for 2008 and 20,389, CV = 0.071  
449 for 2012) provide additional confirmation that the WSA humpback whale population is growing  
450 (Zerbini et al. 2011). A new population status assessment in the framework of Zerbini et al. (2011) is  
451 currently underway, which will take the present results and new catch history data (Morais et al.  
452 2017) into account to provide an updated understanding of this population's recovery, more than four  
453 decades after whaling ceased in 1973 in this area.

454 Going forward, it is important that efforts to monitor potential threats are intensified, because  
455 our current knowledge on this is very limited (Bezamat et al. 2015, Bortolotto et al. 2016c, Ott et al.  
456 2016). To evaluate adequately the need for improvement or adjustment of current conservation  
457 strategies and management actions, such as enhancing protection in the area (Castro et al. 2014), it is  
458 essential to assess the conservation status of WSA humpback whales and to take into account the  
459 current and future potential impacts on the population. The distribution results presented here may  
460 also be used in evaluating areas of higher risk for this population by investigating sources of impact  
461 by human-related activities in the areas predicted to be most used by the animals.

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476 **LITERATURE CITED**

- 477 Amante C, Eakins BW (2009) ETOPO1 1 Arc-Minute Global Relief Model: procedures, data sources  
478 and analysis. NOAA Technical Memorandum NESDIS NGDC-24. National Geophysical Data  
479 Center, NOAA
- 480 Andriolo A, Kinas PG, Engel MH, Martins CCA, Rufino AM (2010) Humpback whales within the  
481 Brazilian breeding ground: distribution and population size estimate. *Endanger Species Res*  
482 11:233–243
- 483 Baracho-Neto CG, Santos Neto E, Rossi-Santos MR, Wedekin LL, Neves MC, Lima F, Faria D  
484 (2012) Site fidelity and residence times of humpback whales (*Megaptera novaeangliae*) on the  
485 Brazilian coast. *J Mar Biol Assoc United Kingdom*, 92:1783–91
- 486 Best PB (1990) Trends in the inshore right whale population off South Africa, 1969–1987. *Mar*  
487 *Mammal Sci* 6:93–108
- 488 Bezamat C, Wedekin LL, Simões-Lopes PC (2015) Potential ship strikes and density of humpback  
489 whales in the Abrolhos Bank breeding ground, Brazil. *Aquat Conserv Mar Freshw Ecosyst*  
490 25:712–725
- 491 Bortolotto GA, Danilewicz D, Andriolo A, Secchi ER, Zerbini AN (2016a) Whale, whale,  
492 everywhere: increasing abundance of western South Atlantic humpback whales (*Megaptera*  
493 *novaeangliae*) in their wintering grounds. *PLoS One* 11:e0164596
- 494 Bortolotto GA, Danilewicz D, Andriolo A, Zerbini AN (2016b) Humpback whale *Megaptera*  
495 *novaeangliae* (Cetartiodactyla: Balaenopteridae) group sizes in line transect ship surveys: an  
496 evaluation of observer errors. *Zool* 33:1–5
- 497 Bortolotto GA, Kolesnikovas CKM, Freire AS, Simões-Lopes PC (2016c) Young humpback whale  
498 *Megaptera novaeangliae* feeding off Santa Catarina coastal waters, Southern Brazil, and a ship  
499 strike report. *Mar Biodivers Rec* 9:1–6
- 500 Brasil (2017a) BDEP Webmaps. <http://app.anp.gov.br/webmaps/> (accessed in 14 Feb 2017).
- 501 Brasil (2017b) Ministério do Meio Ambiente. [www.mma.gov.br](http://www.mma.gov.br) (accessed in 16 Jul 2017).
- 502 Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L (2001) Introduction  
503 to distance sampling. Oxford University Press, Oxford
- 504 Cartwright R, Gillespie B, LaBonte K, Mangold T, Venema A, Eden K, Sullivan M (2012) Between  
505 a rock and a hard place: habitat selection in female-calf humpback whale (*Megaptera*  
506 *novaeangliae*) pairs on the Hawaiian breeding grounds. *PLoS One* 7:e38004
- 507 Castro FR, Mamede N, Danilewicz D, Geyer Y, Pizzorno JLA, Zerbini AN, Andriolo A (2014) Are  
508 marine protected areas and priority areas for conservation representative of humpback whale  
509 breeding habitats in the western South Atlantic? *Biol Conserv* 179:106–114
- 510 Corkeron PJ, Connor RC (1999) Why do baleen whales migrate? *Mar Mammal Sci* 15:1228–1245

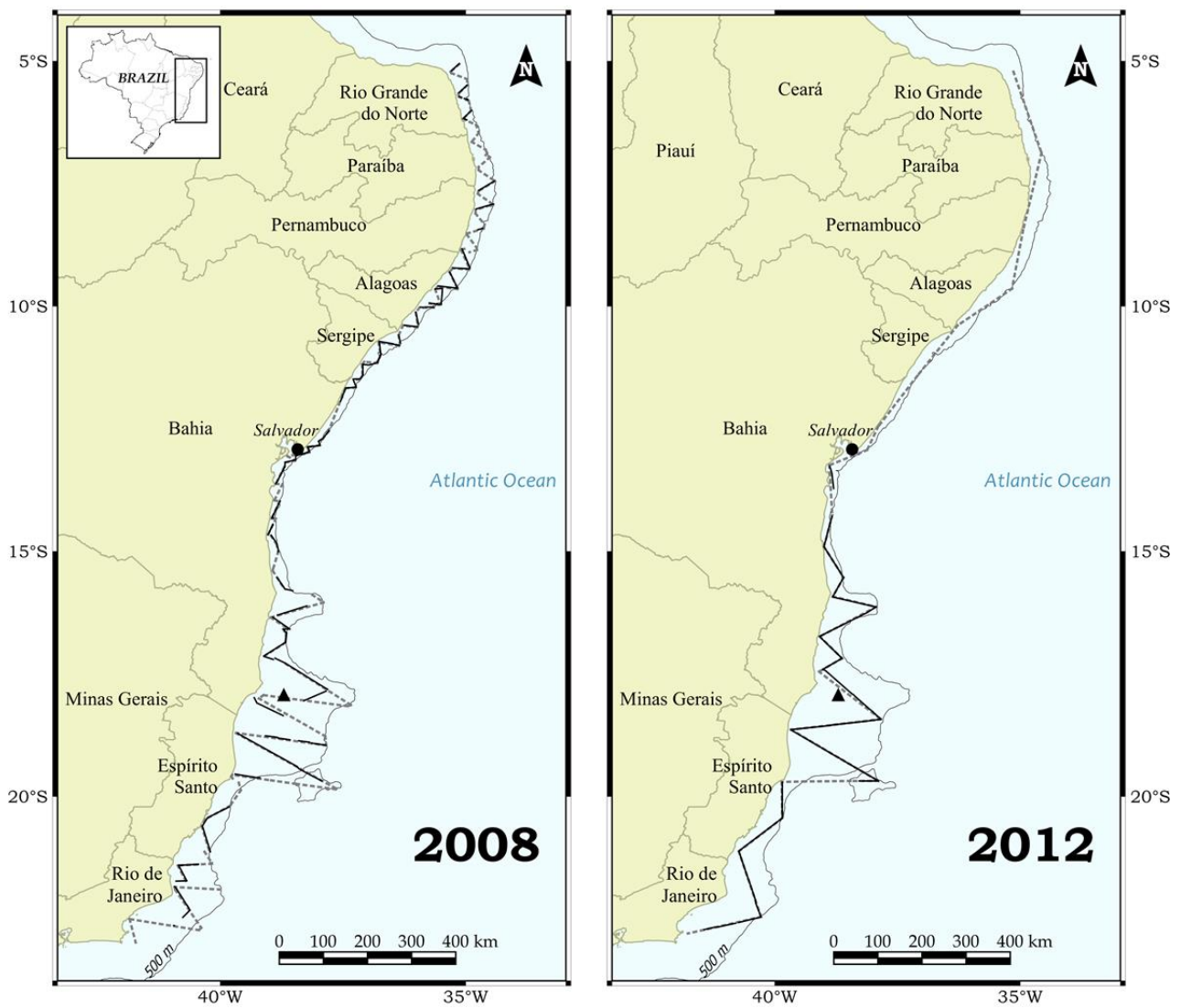
- 511 Craig AS, Herman LM (2000) Habitat preferences of female humpback whales *Megaptera*  
512 *novaeangliae* in the Hawaiian Islands are associated with reproductive status. *Mar Ecol Prog Ser*  
513 193:209–216
- 514 Craig AS, Herman LM, Pack AA, Waterman JO (2014) Habitat segregation by female humpback  
515 whales in Hawaiian waters: avoidance of males? *Behaviour* 151:613–631
- 516 Dee DP, Uppala SM, Simmons AJ, Berrisford P, Poli P, Kobayashi S, Andrae U, Balmaseda MA,  
517 Balsamo G, Bauer P, Bechtold P, Beljaars ACM, Berg L van de, Bidlot J, Bormann N, Delsol C,  
518 Dragani R, Fuentes M, Geer AJ, Haimberger L, Healy SB, Hersbach H, Hólm E, Isaksen L,  
519 Kållberg P, Köhler M, Matricardi M, McNally AP, Monge-Sanz BM, Morcrette JJ, Park BK,  
520 Peubey C, Rosnay P de, Tavolato C, Thépaut JN, Vitart F (2011) The ERA-Interim reanalysis:  
521 configuration and performance of the data assimilation system. *Q J R Meteorol Soc* 137:553–  
522 597
- 523 Dunlop RA, Noad MJ, McCauley RD, Scott-Hayward L, Kniest E, Slade R, Paton D, Cato DH (2017)  
524 Determining the behavioural dose-response relationship of marine mammals to air gun noise and  
525 source proximity. *J Exp Biol* 220:2878–2886
- 526 Elwen SH, Best PB (2004a) Environmental factors influencing the distribution of southern right  
527 whales (*Eubalaena australis*) on the south coast of South Africa I: broad scale patterns. *Mar*  
528 *Mammal Sci* 20:567–582
- 529 Elwen SH, Best PB (2004b) Female southern right whales *Eubalanena australis*: are there  
530 reproductive benefits associated with their coastal distribution off South Africa? *Mar Ecol Prog*  
531 *Ser* 269:289–295
- 532 Engel MH, Marcondes MCC, Martins CCA, Luna FO (2004) Are seismic surveys responsible for  
533 cetacean strandings? An unusual mortality of adult humpback whales in Abrolhos Bank,  
534 Northeastern coast of Brazil. Work SC/56/E28 presented to the International Whaling  
535 Commission Scientific Committee, Sorrento, Italy.
- 536 Ersts PJ, Rosenbaum HC (2003) Habitat preference reflects social organization of humpback whales  
537 (*Megaptera novaeangliae*) on a wintering ground. *J Zool* 260:337–345
- 538 ESR (2009) OSCAR third degree resolution ocean surface currents, PO.DAAC., Ver. 1.  
539 [podaac.jpl.nasa.gov/dataset/OSCAR\\_L4\\_OC\\_third-deg](http://podaac.jpl.nasa.gov/dataset/OSCAR_L4_OC_third-deg) (accessed in 04 Apr 2016).
- 540 Esri (2011) ArcGIS Desktop: release 10. Environmental Systems Research Institute, Redlands, CA.
- 541 Félix F, Botero-Acosta N (2011) Distribution and behaviour of humpback whale mother-calf pairs  
542 during the breeding season off Ecuador. *Mar Ecol Prog Ser* 426:277–287
- 543 Francini-Filho RB, Moura RL de (2008) Dynamics of fish assemblages on coral reefs subjected to  
544 different management regimes in the Abrolhos Bank, eastern Brazil. *Aquat Conserv Mar Freshw*  
545 *Ecosyst* 18:1166–1179
- 546 Friedlaender AS, Halpin PN, Qian SS, Lawson GL, Wiebe PH, Thiele D, Read AJ (2006) Whale  
547 distribution in relation to prey abundance and oceanographic processes in shelf waters of the  
548 Western Antarctic Peninsula. 317:297–310
- 549 Harville DA (1977) Maximum Likelihood approaches to variance component estimation and to  
550 related problems. *J Am Stat Assoc* 72:320–338



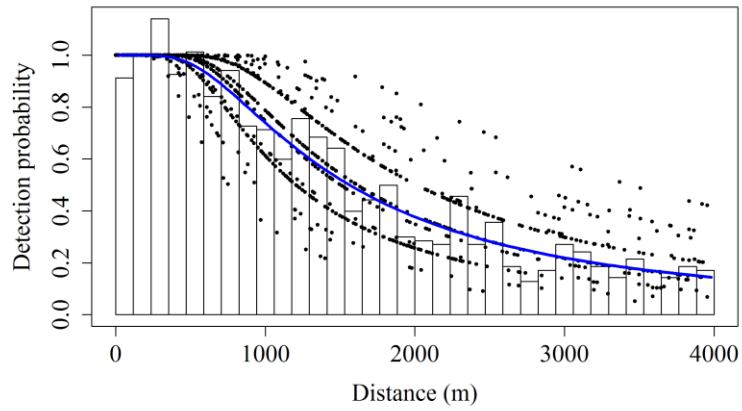
- 551 Herman, LM (2017) The multiple functions of male song within the humpback whale (*Megaptera*  
552 *novaeangliae*) mating system: review, evaluation, and synthesis. *Biol Rev Camb Philos Soc*  
553 92:1795–1818
- 554 Hijmans RJ (2016) Raster: geographic data analysis and modeling. R package version 2.5-8.
- 555 IBAMA (2011) SisCom: sistema compartilhado de informações ambientais. [siscom.ibama.gov.br/](http://siscom.ibama.gov.br/)  
556 (accessed in 12 Jul 17).
- 557 ICMBio (2017) PARNA Marinho dos Abrolhos.  
558 [www.icmbio.gov.br/portal/component/content/article?id=2267:parna-marinho-dos-abrolhos](http://www.icmbio.gov.br/portal/component/content/article?id=2267:parna-marinho-dos-abrolhos)  
559 (accessed 7 Feb 2017).
- 560 INEMA-BAHIA (2017) APA Ponta da Baleia/Abrolhos. [www.inema.ba.gov.br/gestao-2/unidades-de-conservacao/apa/apa-ponta-da-baleia-abrolhos/](http://www.inema.ba.gov.br/gestao-2/unidades-de-conservacao/apa/apa-ponta-da-baleia-abrolhos/) (accessed 29 Mar 2017).
- 562 Iversen PE, Stokke R, Bloor P, Unger S, Nilsen H-G, Jarrah J (2009) Assessment of impacts of  
563 offshore oil and gas activities in the North-East Atlantic. Report of the OSPAR Commission,  
564 Offshore Industry Service.
- 565 JPL MUR MEaSURES Project (2010) GHRSSST level 4 MUR global foundation sea surface  
566 temperature analysis, PO.DAAC, Ver. 2. [podaac.jpl.nasa.gov/dataset/JPL-L4UHFnd-GLOB-](http://podaac.jpl.nasa.gov/dataset/JPL-L4UHFnd-GLOB-MUR)  
567 MUR (accessed in 14 Jun 2016).
- 568 Keller CA, Ward-Geiger LI, Brooks WB, Slay CK, Taylor CR, Zoodsma BJ (2006) North Atlantic  
569 right whale distribution in relation to sea-surface temperature in the southeastern United States  
570 calving grounds. *Mar Mammal Sci* 22:426–445
- 571 Refaeilzadeh P, Tang L, Liu H (2009) Cross-validation. In: Liu L, Özsu MT *Encyclopedia of database*  
572 *systems* vol. 6. Springer, New York
- 573 Lindsay RE, Constantine R, Robbins J, Mattila DK, Tagarino A, Dennis TE (2016) Characterising  
574 essential breeding habitat for whales informs the development of large-scale Marine Protected  
575 Areas in the South Pacific. *Mar Ecol Prog Ser* 548:263–275
- 576 Macleod K, Fairbairns R, Gill A, Fairbairns B, Gordon J, Blair-Myers C, Parsons ECM (2004)  
577 Seasonal distribution of minke whales *Balaenoptera acutorostrata* in relation to physiography  
578 and prey off the Isle of Mull, Scotland. *Mar Ecol Prog Ser* 277:263–274
- 579 Marchioro GB, Nunes MA, Dutra GF, Moura RL, Pereira PGP (2005) Avaliação dos impactos da  
580 exploração e produção de hidrocarbonetos no Banco dos Abrolhos e adjacências.  
581 *Megadiversidade* 1:225–310
- 582 Martins CCA, Andriolo A, Engel MH, Kinas PG, Saito CH (2013) Identifying priority areas for  
583 humpback whale conservation at Eastern Brazilian Coast. *Ocean Coast Manag* 75:63–71
- 584 Martins CCA, Morete ME, Engel MH, Freitas AC, Secchi ER, Kinas PG (2001) Aspects of habitat  
585 use patterns of humpback whales in the Abrolhos Bank, Brazil, breeding ground. *Mem Queensl*  
586 *Museum* 47:563–570
- 587 Morete, ME, Pace RM, Martins CCA, Freitas AC, Engel MH (2003) Indexing seasonal abundance  
588 of humpback whales around Abrolhos Archipelago, Bahia, Brazil. *Lat Am J Aquat Mamm* 2:21–  
589 28

- 590 Miller DL (2016) Distance: distance sampling detection function and abundance estimation. R  
591 package version 0.9.6.
- 592 Miller DL, Burt ML, Rexstad EA, Thomas L (2013) Spatial models for distance sampling data: recent  
593 developments and future directions. *Methods Ecol Evol* 4:1001–1010
- 594 Miller DL, Rexstad E, Burt L, Bravington M V., Hedley SL (2017) dsm: density surface modelling  
595 of distance sampling data. R package version 2.2.14.
- 596 Morais IOB, Danilewicz D, Zerbini AN, Edmundson W, Hart IB, Bortolotto GA (2017) From the  
597 southern right whale hunting decline to the humpback whaling expansion: a review of whale  
598 catch records in the tropical western South Atlantic Ocean. *Mamm Rev* 47:11–23
- 599 Moura JF, Rodrigues DP, Roges EM, Souza RL, Ott PH, Tavares M, Lemos LS, Tavares DC,  
600 Siciliano S (2013) Humpback whales washed ashore in southeastern Brazil from 1981 to 2011:  
601 stranding patterns and microbial pathogens survey. *Biologia* 68:992–999
- 602 Ott PH, Milmann L, Santos MC de O, Rogers EM, Prazeres D (2016) Humpback whale breeding  
603 stock “A”: increasing threats to a recently down-listed species off Brazilian fauna. Work  
604 SC/66b/SH/04 presented to the International Whaling Commission. Scientific Committee, Bled,  
605 Slovenia.
- 606 Oviedo L, Solís M (2008) Underwater topography determines critical breeding habitat for humpback  
607 whales near Osa Peninsula, Costa Rica: implications for Marine Protected Areas. *Rev Biol Trop*  
608 56:591–602
- 609 Pavanato HJ, Wedekin LL, Guilherme-Silveira FR, Engel MH, Kinas PG (2017) Estimating  
610 humpback whale abundance using hierarchical distance sampling. *Ecol Modell* 358:10–18
- 611 QGIS Development Team (2015) QGIS Geographic Information System. Open source Geospatial  
612 Foundation Project: <http://www.qgis.org/>.
- 613 R Core Team (2015) R: a language and environment for statistical computing. R Foundation for  
614 Statistical Computing, Vienna, Austria
- 615 Rasmussen K, Palacios DM, Rosa LD, Secchi ER, Steiger GH, Allen JM, Stone GS (2007) Southern  
616 Hemisphere humpback whales wintering off Central America: insights from water temperature  
617 into the longest mammalian migration. *Biol Lett* 3:302–305
- 618 Rayment W, Dawson S, Webster T (2015) Breeding status affects fine-scale habitat selection of  
619 southern right whales on their wintering grounds. *J Biogeogr* 42:463–474
- 620 Reilly SB, Bannister JL, Best PB, Brown M, Brownell Jr. RL, Butterworth DS, Clapham PJ, Cooke  
621 J, Donovan GP, Urbán J, Zerbini AN (2008) *Megaptera novaeangliae*. The IUCN Red List of  
622 Threatened Species 2008: e.T13006A3405371 (accessed in 9 Oct 2017)
- 623 Rocha-Campos CC, Moreno IB, Rocha JM, Palazzo Jr JT, Groch KR, Oliveira LR, Gonçalves L,  
624 Engel MH, Marcondes MCC, Muelbert MMC, Ott PH, Silva VMF (2011) Plano de ação nacional  
625 para conservação dos mamíferos aquáticos: grandes cetáceos e pinípedes. In: Rocha-Campos  
626 CC, Câmara IG (eds) Série espécies ameaçadas no 14. Instituto Chico Mendes de Conservação  
627 da Biodiversidade, ICMBio, Brasília
- 628 Ronconi RA, Allard KA, Taylor PD (2015) Bird interactions with offshore oil and gas platforms:  
629 review of impacts and monitoring techniques. *J Environ Manage* 147:34–45

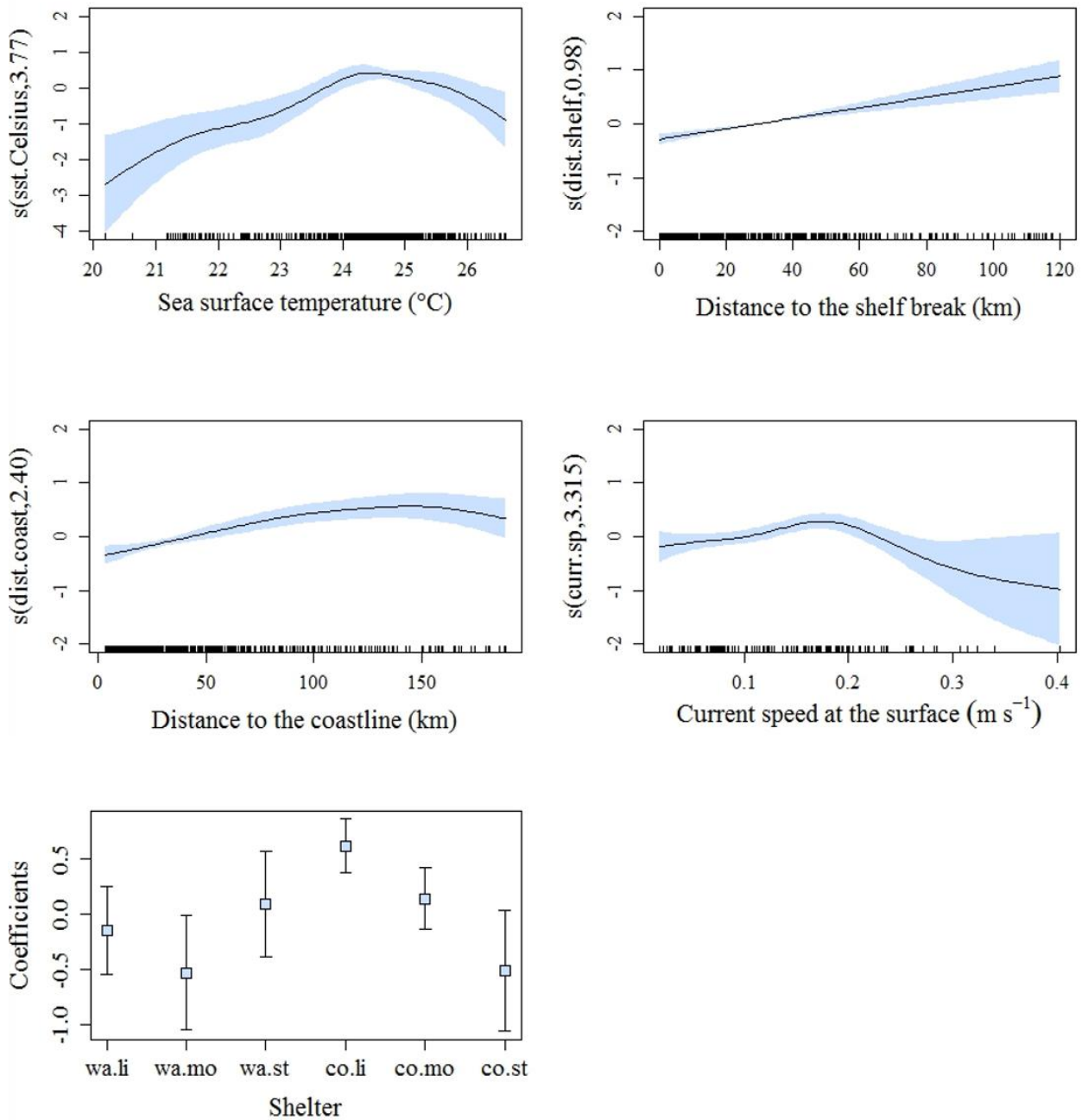
- 630 Rossi-Santos MR (2015) Oil industry and noise pollution in the humpback whale (*Megaptera*  
631 *novaeangliae*) soundscape ecology of the Southwestern Atlantic breeding ground. *J Coast Res*  
632 31:184–195
- 633 Schaffar A, Madon B, Garrigue C, Constantine R (2013) Behavioural effects of whale-watching  
634 activities on an Endangered population of humpback whales wintering in New Caledonia.  
635 *Endanger Species Res* 19:245–254
- 636 Siciliano S (1997) Características da população de baleias-jubarte (*Megaptera novaeangliae*) da costa  
637 Brasileira, com especial referência aos Bancos de Abrolhos. Masters dissertation, Universidade  
638 Federal Rural do Rio de Janeiro, Rio de Janeiro, RJ.
- 639 Smultea MA (1994) Segregation by humpback whale (*Megaptera novaeangliae*) cows with a calf in  
640 coastal habitat near the island of Hawaii. *Can J Zool* 72:805–811
- 641 Taber S, Thomas P (1982) Calf development and mother-calf spatial relationships in southern right  
642 whales. *Anim Behav* 30:1072–1083
- 643 Trudelle L, Cerchio S, Zerbini AN, Geyer Y, Mayer F-X, Jung J, Hervé MR, Pous S, Adam O,  
644 Charrassin J-B, Sallée J-B, Rosenbaum HC, Adam O, Charrassin J-B (2016) Influence of  
645 environmental parameters on movements and habitat utilization of humpback whales  
646 (*Megaptera novaeangliae*) in the Madagascar breeding ground. *R Soc Open Sci* 3:160616
- 647 Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin JM, Hoegh-Guldberg  
648 O, Bairlein F (2002) Ecological responses to recent climate change. *Nature* 416:389–395
- 649 Wedekin LL (2011) Ecologia populacional da baleia-jubarte (*Megaptera novaeangliae* Borowski,  
650 1871) em sua área reprodutiva na costa do Brasil, Oceano Atlântico Sul. PhD dissertation,  
651 Universidade Federal do Paraná, Curitiba, PR.
- 652 Wedekin LL, Rossi-Santos MR, Baracho C, Cypriano-Souza AL, Simões-Lopes PC (2014) Cetacean  
653 records along a coastal-offshore gradient in the Vitória-Trindade Chain, western South Atlantic  
654 Ocean. *Brazilian J Biol* 74:137–144
- 655 Werner T, Pinto LP, Dutra GF, Pereira PGP (2000) Abrolhos 2000: conserving the Southern  
656 Atlantic's richest coastal biodiversity into the next century. *Coast Manag* 28:99–108
- 657 Wood SN (2006) Generalized additive models: an introduction with R. Chapman & Hall/CRC, Boca  
658 Raton, Florida
- 659 Zerbini AN, Andriolo A, Heide-Jørgensen MP, Pizzorno JL, Maia YG, VanBlaricom GR, Demaster  
660 DP, Simões-Lopes PC, Moreira S, Bethlem C (2006) Satellite-monitored movements of  
661 humpback whales *Megaptera novaeangliae* in the Southwest Atlantic Ocean. *Mar Ecol Prog Ser*  
662 313:295–304
- 663 Zerbini AN, Andriolo A, Rocha JM, Simões-Lopes PC, Siciliano S, Pizzorno JL, Waite JM, Demaster  
664 DP, VanBlaricom GR (2004) Winter distribution and abundance of humpback whales  
665 (*Megaptera novaeangliae*) off Northeastern Brazil. *J Cetacean Res Manag* 6:101–107
- 666 Zerbini AN, Ward EJ, Kinas PG, Engel MH, Andriolo A (2011) A Bayesian assessment of the  
667 conservation status of humpback whales (*Megaptera novaeangliae*) in the western South Atlantic  
668 Ocean. *J Cetacean Res Manag* (special issue 3):131–144



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 670 Fig. 1. Survey lines in 2008 and 2012. Planned (dashed grey lines) and completed effort (black thick lines) are  
 671 shown. A black triangle indicates the location of the Abrolhos Archipelago.



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673 Fig. 2. Detection function curve (red line) from a hazard rate model fitted to the perpendicular distances (in  
674 meters) of humpback whale groups detected. Different dotted curves represent different combinations of  
675 covariates sea conditions, cue and year. Each point represents the predicted value for observation.



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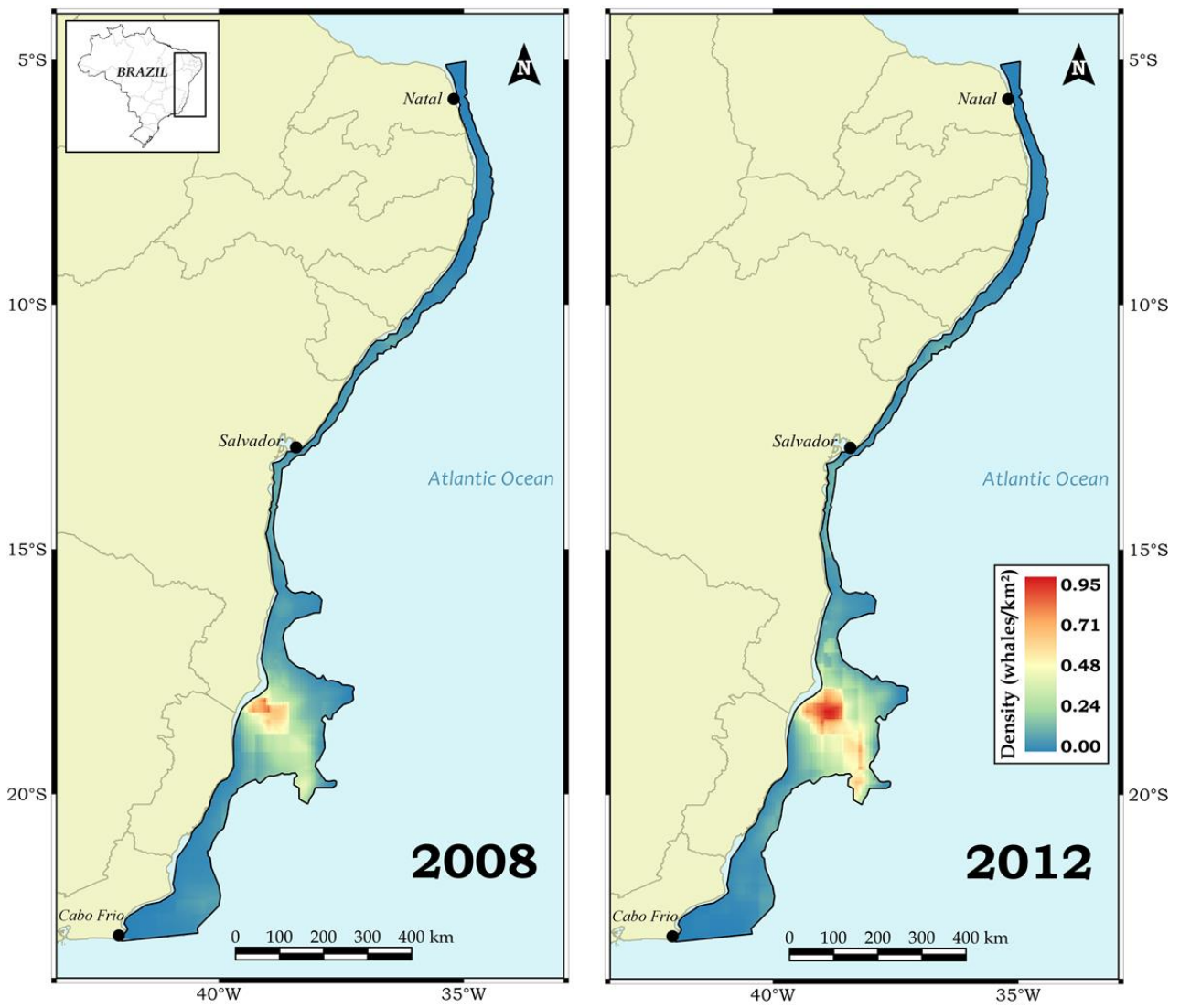
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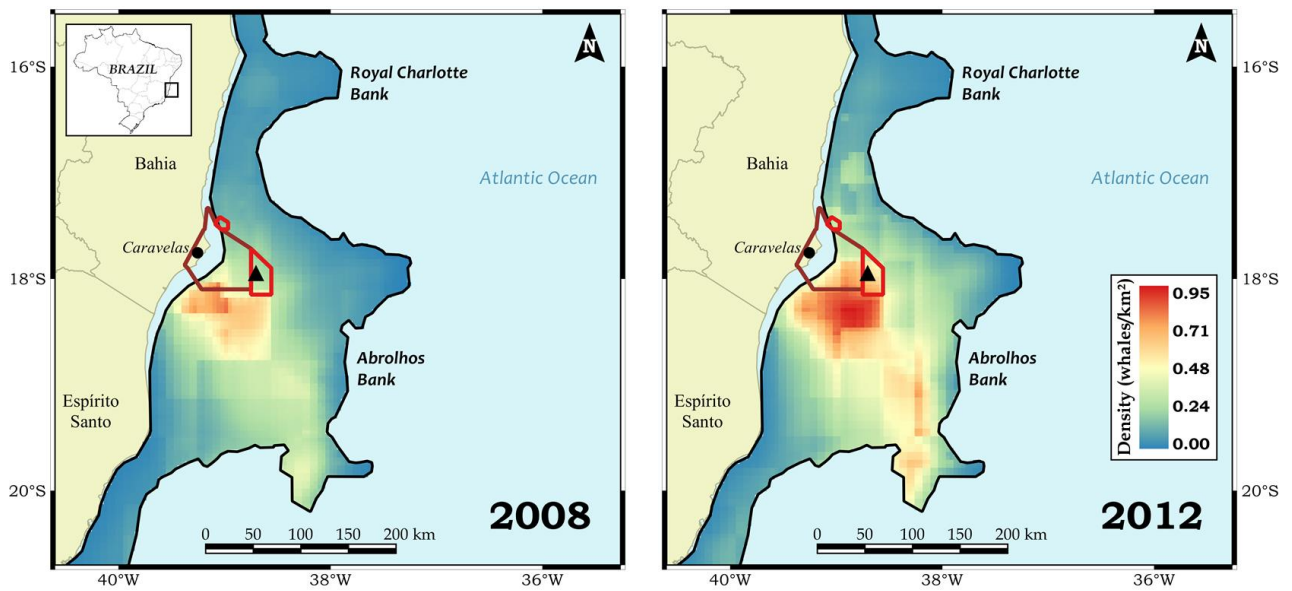
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Fig. 3. Model terms for the Habitat Use Model (HUM) of humpback whales off the coast of Brazil. Smooth terms' effective degrees of freedom are shown inside brackets in the vertical axis. The shelter coefficients are presented relative to the intercept. (wa = warm SST, co = cold SST, li = light wind, mo = moderate wind, st = strong wind).



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Fig. 4. Density surface maps for 2008 and 2012. Predictions were made with the Abundance Estimation Model (AEM)..



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 686 Fig. 5. Density surface maps for 2008 and 2012 for the Abrolhos Bank region. Predictions were made with the  
 687 Abundance Estimation Model (AEM). A black triangle shows the location of the Abrolhos archipelago. Red  
 688 polygons represent the Abrolhos Marine National Park and the brown polygon represents the Ponta da Baleia  
 689 MPA.



690 Table 1. Explanatory variables tested in Generalized Additive Models to model the density of humpback  
 691 whales off the coast of Brazil.

<b>Variables</b>	<b>Description</b>	<b>Resolution*</b>	<b>Unit</b>	<b>Reference/Data source</b>
curr.sp	Speed of the water current close to the surface	5-day; 0.33 x 0.33° (latitude x longitude)	m s <sup>-1</sup>	OSCAR dataset (ESR 2009)
depth	Depth	0.1 x 0.1° (latitude x longitude)	m	ETOPO1 (Amante & Eakins 2009)
dist.coast	Distance to the coastline	–	m	SisCom (IBAMA 2011)
dist.shelf	Distance to the 500 meter isobath	–	m	500 meter isobath created from ETOPO1 in GIS software
shelter	Category according to values of wind.sp and sst	–	–	–
slope	Seabed slope: percentage of elevation over distance	0.1 x 0.1° (latitude x longitude)		Derived from ETOPO1
sst	Temperature at the surface of the sea	1-day; 0.011 x 0.011° (latitude x longitude)	°C	JPL-L4UHfnd-GLOB-MUR dataset (JPL MUR MEaSURES Project 2010)
wind.sp	Speed of wind at the surface	6-hour (the daily mean was used); 80 x 80 km	m s <sup>-1</sup>	ERA-Interim dataset (Dee et al. 2011)
x	Easting	–	m	Survey GPS
y	Northing	–	m	Survey GPS
year	Year of survey	–	year	Survey data

\*Spatial and/or temporal resolution, depending on covariate nature.

693 Table 2. Generalized Additive Model results for the HUM (Habitat Use Model) and AEM (Abundance  
 694 Estimation Model). Variables are described in Table 1. Effective degrees of freedom for smooth terms are  
 695 presented inside brackets. Blank spaces represent variables not selected and a dash represents a covariate not  
 696 considered in the model selection. (*S* = smooth term, *F* = factor)

<b>Variable</b>	<b>HUM</b>	<b>AEM</b>
curr.sp	<i>S</i> (3.315)	<i>S</i> (3.294)
Depth		
dist.coast	<i>S</i> (2.401)	<i>S</i> (5.528)
dist.shelf	<i>S</i> (0.975)	<i>S</i> (0.940)
Shelter	<i>F</i>	<i>F</i>
Slope		
Sst	<i>S</i> (3.766)	
wind.sp		
x, y	—	<i>S</i> (15.865)
year		
% Deviance explained	54.1	66.8
-REML score	718.5	678.0

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*The following supplement accompanies the article*

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**Whale distribution in a breeding area: spatial models of habitat use and abundance of western South Atlantic humpback whales**

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**Guilherme A. Bortolotto\*, Daniel Danilewicz, Philip S. Hammond, Len Thomas, Alexandre N.**

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**Zerbini**

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\*Corresponding author: bortolotto.ga@gmail.com

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**Detection function model results**

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Table S1. Detection function parameters from a hazard-rate key-model fitted to 1149 perpendicular distance values for humpback whale sightings (data were truncated at 4000 m). Coefficient values are on the scale of the log link function. The intercept includes terms “cue blow”, “year 2008” and “sea state calm”.

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<b>Scale Coefficients</b>	<b>Estimate</b>	<b>Standard error</b>
Intercept	7.097	0.125
Cue splash	0.535	0.162
Cue body	-0.470	0.164
Cue “other”	0.363	0.310
Year 2012	0.291	0.107
Sea state moderate	-0.220	0.107

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711 **Habitat Use Model (HUM) results**

712 Table S2. Parametric coefficients in the Habitat Use Model (HUM). (t = t distribution value)

<b>Coefficients</b>	<b>Estimate</b>	<b>Standard error</b>	<b>t</b>	<b>p-value</b>
Intercept	-15.704	0.116	-134.819	< 0.001*
shelter.cold.moderate	-0.473	0.111	-4.272	< 0.001*
shelter.cold.strong	-1.122	0.271	-4.138	< 0.001*
shelter.warm.light	-0.760	0.193	-3.942	< 0.001*
shelter.warm.moderate	-1.140	0.261	-4.364	< 0.001*
shelter.warm.strong	-0.524	0.242	-2.164	0.031
*Significant at $\alpha = 0.05$				

713

714 Table S3. Smooth terms in the Habitat Use Model (HUM). (edf = effective degrees of

715 freedom, df = degrees of freedom, F = F distribution value)

<b>Smooth terms</b>	<b>edf</b>	<b>Reference df</b>	<b>F</b>	<b>p-value</b>
s(sst)	3.766	7	6.347	< 0.001*
s(dist.shelf)	0.975	7	5.041	< 0.001*
s(coast)	2.401	7	4.918	< 0.001*
s(curr.sp)	3.315	7	2.535	< 0.001*
*Significant at $\alpha = 0.05$				

716

717 **Abundance Estimation Model (AEM) results**

718 Table S4. Parametric coefficients in the Abundance Estimation Model (AEM). (t = t distribution  
719 value)

<b>Coefficients</b>	<b>Estimate</b>	<b>Standard error</b>	<b>t</b>	<b>p-value</b>
Intercept	-16.007	0.105	-153.078	< 0.001*
shelter.cold.moderate	-0.279	0.109	-2.559	0.011*
shelter.cold.strong	-0.830	0.247	-3.364	< 0.001*
shelter.warm.light	-0.484	0.148	-3.268	0.001*
shelter.warm.moderate	-0.532	0.221	-2.402	0.012*
shelter.warm.strong	-0.470	0.207	-2.272	0.024*
*Significant at $\alpha = 0.05$ .				

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721 Table S5. Smooth terms in the Abundance Estimation Model (AEM). (edf = effective degrees  
722 of freedom, df = degrees of freedom, F = F distribution value)

<b>Smooth terms</b>	<b>Edf</b>	<b>Reference df</b>	<b>F</b>	<b>p-value</b>
s(x,y)	15.865	19	9.911	< 0.001*
s(curr.sp)	3.294	7	4.009	< 0.001*
s(coast)	5.528	7	4.283	< 0.001*
s(dist.shelf)	0.940	7	2.155	< 0.001*
*Significant at $\alpha = 0.05$				

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724 **Abundance estimates results**

725 Table S6. Summaries of uncertainty in a density surface model (Abundance Estimation Model,  
 726 AEM) calculated analytically for GAM, with delta method, for 2008 and 2012.

<b>2008</b>		
Approximate asymptotic confidence interval		
2.5%	Mean	97.5%
12,108	14,264	16,805
Abundance		
Point estimate		14,264
CV of detection function		0.044
CV from GAM		0.071
Total standard error		1,195
Total coefficient of variation		0.084
<b>2012</b>		
Approximate asymptotic confidence interval		
2.5%	Mean	97.5%
17,746	20,389	23,426
Abundance		
Point estimate		20,389
CV of detection function		0.044
CV from GAM		0.056
Total standard error		1,446
Total coefficient of variation		0.071

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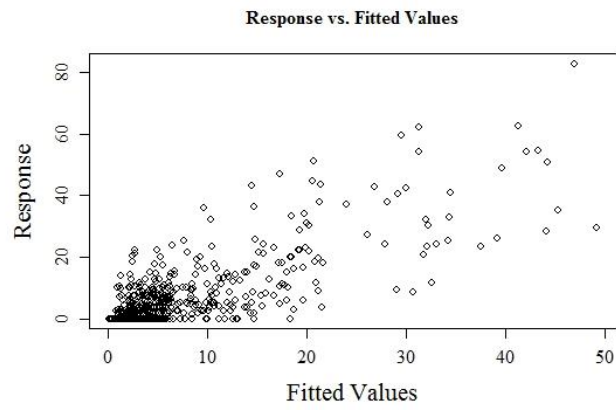
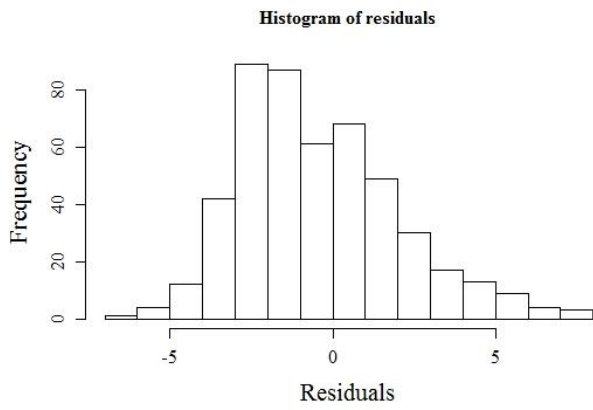
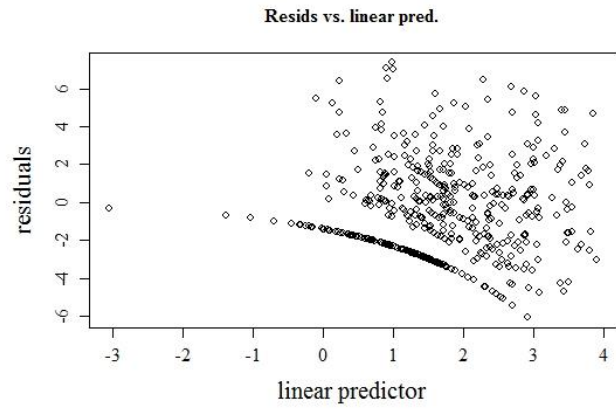
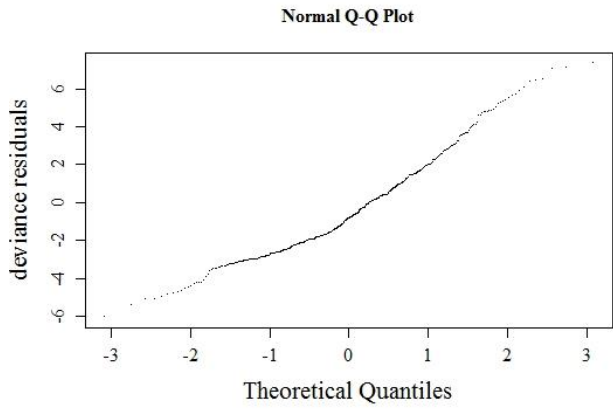
728 **Cross-validation results**

729 Table S7. Root-Mean-Squared-Errors (RMSEs) for 10-fold cross-validation of Abundance

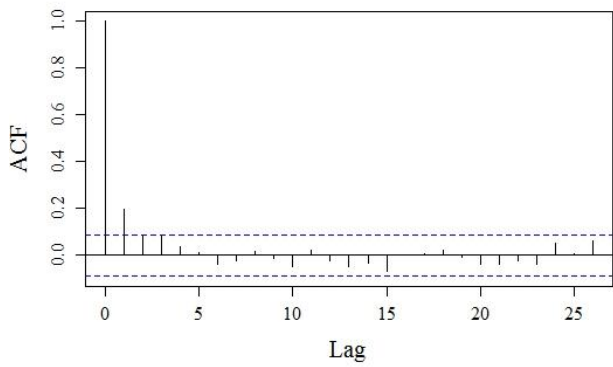
730 Estimates Model (AEM) and Habitat Use Model (HUM).

	Model	
Cross-validation fold	AEM	HUM
1	7.429	8.413
2	7.295	7.185
3	8.855	8.875
4	5.517	6.998
5	6.696	8.046
6	6.813	7.422
7	8.271	9.705
8	6.852	8.563
9	5.213	6.500
10	6.382	8.097
Mean	6.932	7.981
Standard deviation	1.116	0.967

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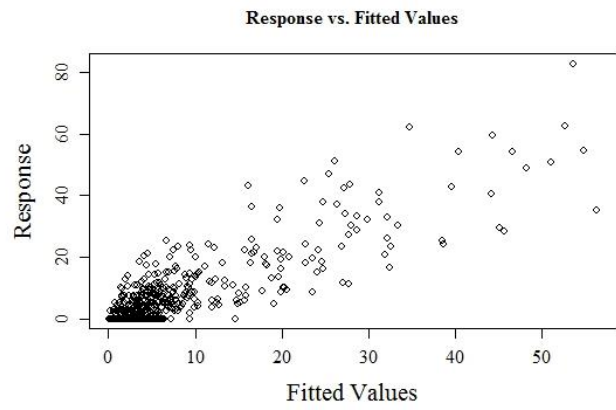
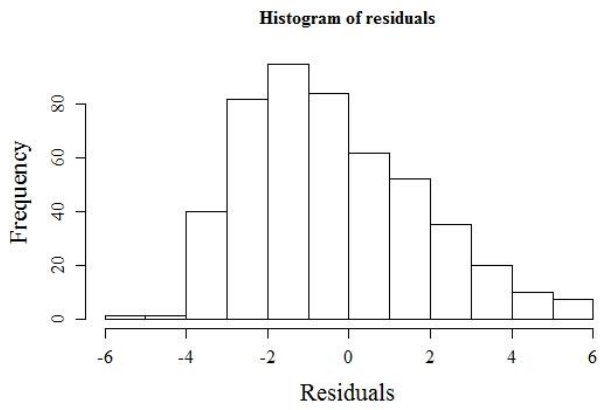
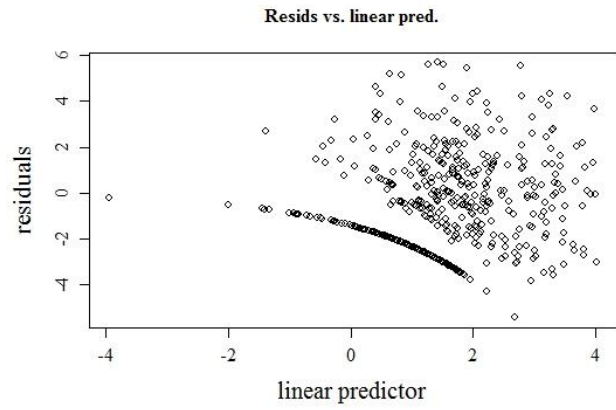
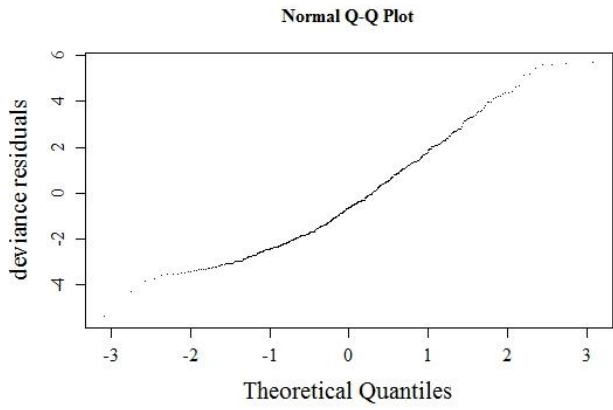
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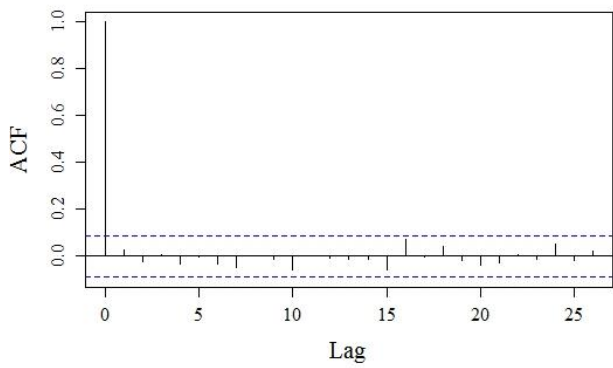
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734 Fig. S1. Habitat Use Model (HUM) diagnostic plots from “gam.check” R function and auto-  
 735 correlation regression plot from “acf” function.





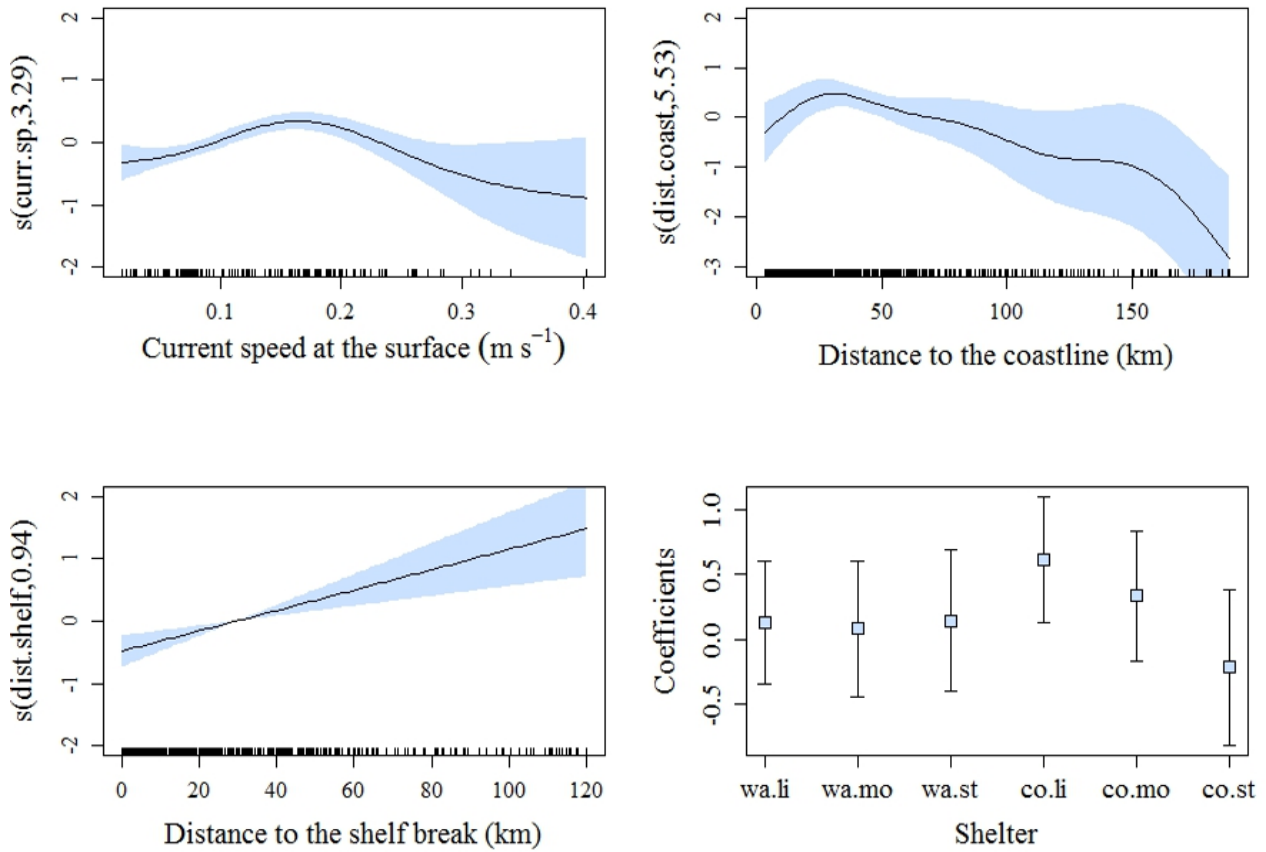
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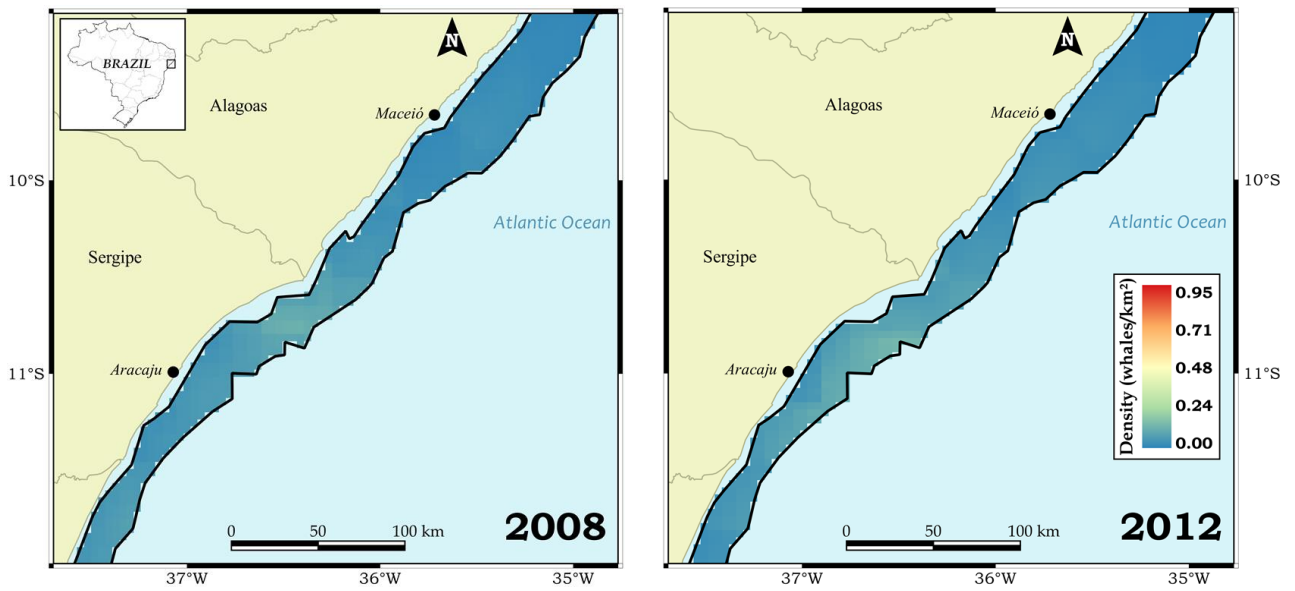
738 Fig. S2. Abundance Estimation Model (AEM) diagnostic plots from “gam.check” R function and

739 auto-correlation regression plot from “acf” function.



740

741 Fig. S3. Model terms for the Abundance Estimation Model (AEM) of humpback whales off the  
 742 coast of Brazil. Smooth terms' effective degrees of freedom are shown inside brackets in the  
 743 vertical axis. The plot for  $s(x,y)$  is not included here. The shelter coefficients are presented relative  
 744 to the intercept. (wa = warm SST, co = cold SST, li = light wind, mo = moderate wind, st = strong  
 745 wind).

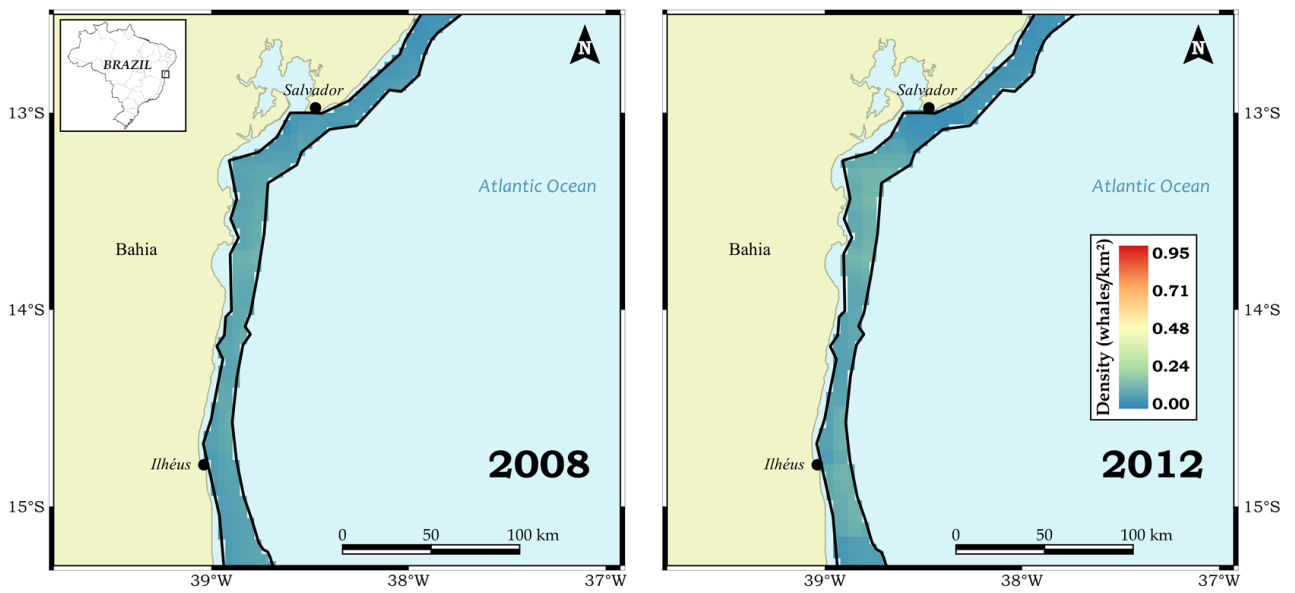


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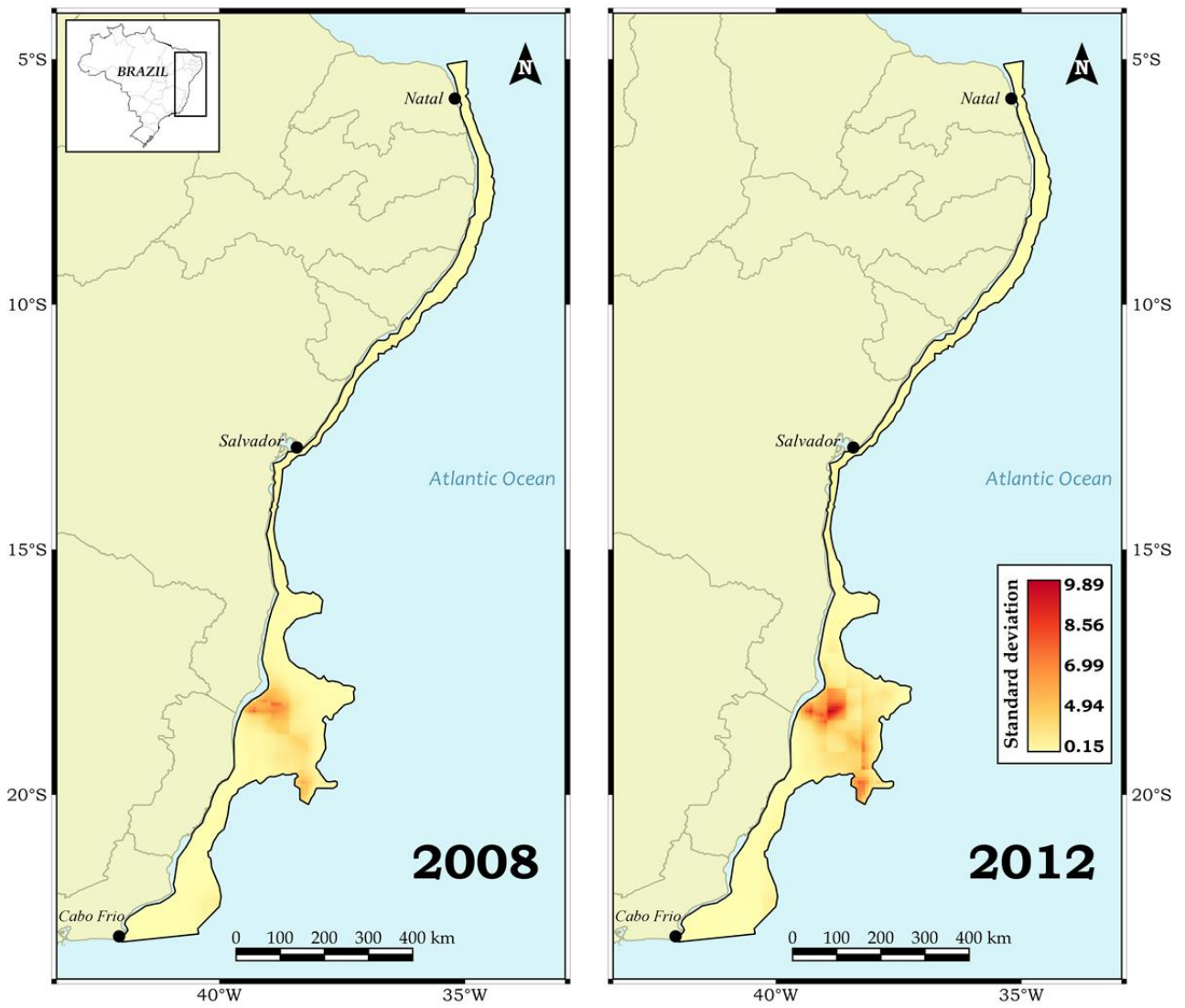
748 Fig. S4. Density surface maps for 2008 and 2012 for the region of Sergipe and Alagoas coasts.

749 Predictions were made with the Abundance Estimation Model (AEM).



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752 Fig. S5. Density surface maps for 2008 and 2012 for part of the coast of Bahia State. Predictions  
753 were made with the Abundance Estimation Model (AEM).



754  
 755 Fig. S6. Standard deviation surface maps for 2008 and 2012. Standard deviations from the  
 756 Abundance Estimation Model (AEM).