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

KEY WORDS: *Megaptera novaeangliae* · Shelter · Conservation · Density surface model · Cetacean · Line transect · Reproduction

INTRODUCTION

The Brazilian coast is inhabited every winter and spring by the western South Atlantic (WSA) humpback whale *Megaptera novaeangliae* population (also referred to as breeding stock A by the International Whaling Commission). Whales aggregate in coastal waters along the central and northeastern coasts of Brazil to mate and give birth before migrating to feeding areas (Martins et al. 2001, Zerbini et al. 2006). This population was severely exploited by whaling between the late 19th and mid-20th centuries (Zerbini et al. 2011, de Morais et al. 2017), to the point of near extinction in the 1950s, but has since

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been recovering (Zerbini et al. 2011, Wedekin et al. 2017). The Red List of the International Union for Conservation of Nature and Natural Resources (IUCN) lists the conservation status of this species as 'Least Concern' (Reilly et al. 2008). Recent abundance estimates from ship-based line transect surveys suggest that the WSA population size was near 20 000 individuals in 2012 (Bortolotto et al. 2016a). However, that estimate was not computed for the entire area currently recognized as the typical distribution range of these animals during the breeding season. This increasing population currently faces an environment modified by human activities such as marine traffic (Bezamat et al. 2015), fishing (Rocha-Campos et al. 2011, Moura et al. 2013, Ott et al. 2016), coastal water pollution (Moura et al. 2013, Ott et al. 2016), noise pollution (Rossi-Santos 2015) and activities related to the oil industry (Iversen et al. 2009, Martins et al. 2013, Ronconi et al. 2015, Rossi-Santos 2015). Specifically, there is an increasing interest for oil and gas production activities in the area; according to the Brazilian National Agency of Petroleum, Natural Gas and Biofuels (Agência Nacional do Petróleo, Gás Natural e Biocombustíveis, ANP), the majority of the Brazilian petroleum reserves is found in the marine environment (http://app.anp.gov.br).

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

For seasonal migratory animals such as many baleen whale species, the environmental factors expected to be important in habitat selection differ between feeding areas, where prey distribution is the primary driver (e.g. Macleod et al. 2004, Friedlaender et al. 2006), and breeding areas (Corkeron & Connor 1999). During the breeding season, large whales select habitat according to their breeding status (Rayment et al. 2015), presence of calves in groups (Cartwright et al. 2012) and other reproduction-related characteristics (Ersts & Rosenbaum 2003, Craig et al. 2014, Lindsay et al. 2016). In this context, sheltered waters, bathymetric features, distance to the shore and sea-surface temperature (SST) are important factors for habitat usage of humpback whales in breeding areas (e.g. Taber & Thomas 1982, Smultea 1994, Rasmussen et al. 2007, Félix & Botero-Acosta 2011, Cartwright et al. 2012, Trudelle et al. 2016). Understanding and explaining key features of the ecology of migratory whale populations, such as habitat use, distribution and abundance, may provide important information for evaluating the impacts of human use of the environment inhabited by them.

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

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

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

MATERIALS AND METHODS

Shipboard visual line transect surveys were conducted in 2008 and 2012 during research cruises aboard the RV 'Atlântico Sul' (Universidade Federal do Rio Grande, FURG). Cruises were part of the Monitoring Whales by Satellite Project (Projeto Moni-

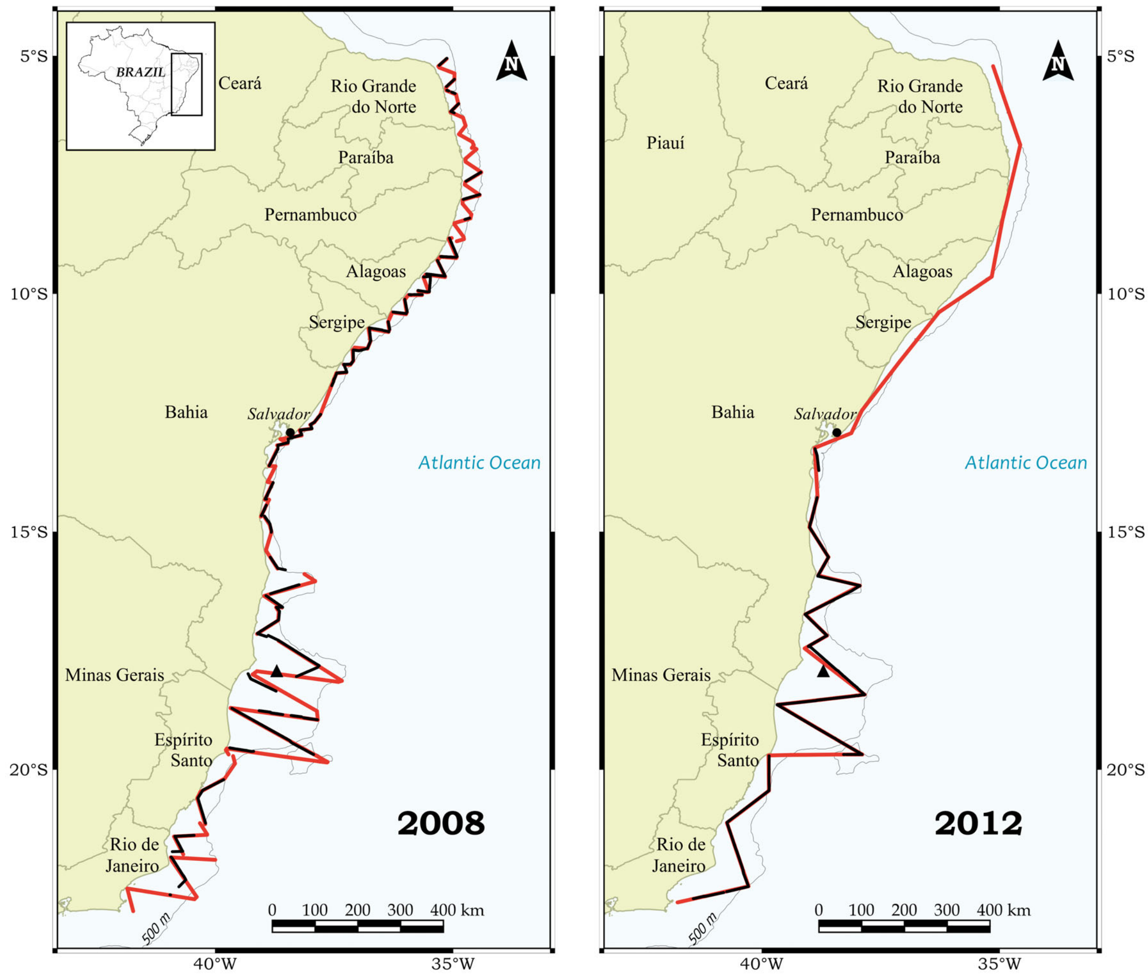

Fig. 1. Survey lines in 2008 and 2012. Planned (red lines) and completed effort (black thick lines) are shown. Black triangles indicate the location of the Abrolhos Archipelago

toramento de Baleias por Satélite, PMBS). The main objectives of PMBS were to deploy satellite-linked tags on humpback whales to track their movements, to understand their space-use patterns in breeding and feeding grounds and to characterize their migratory routes (Zerbini et al. 2006).

The survey area corresponded to the Brazilian continental shelf, between the shore and the shelf break (defined here as up to the 500 m isobath) from Cabo de São Roque (5° S), in Rio Grande do Norte State, to Cabo Frio (23° S), in Rio de Janeiro State (Fig. 1). Surveys were conducted from 25 August to 23 September in 2008 and from 7 August to 3 September in 2012, during the expected annual peak of occurrence of humpback whales in the area (August–September; Martins et al. 2001, Morete et al. 2003). Lines were designed to survey the full extent of this population's breeding area, and data collection followed the distance sampling methodology (Buckland et al. 2001). Trackline design, observation effort and data collection details are described in previous work (Bortolotto et al. 2016a,b).

Correcting for imperfect detection: detection function modelling

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

Detection functions were fitted to perpendicular distance data using R (version 3.2.1; R Core Team

2015) and the 'Distance' package (version 0.9.6; Miller 2016). The factor covariates sea condition ('calm' for Beaufort 0–3 and 'moderate' for Beaufort 4–6), detection cue (splash, body, blow or 'other'), detection method (binoculars or naked eye) and year (2008 or 2012), and the continuous covariate group size (from 1 to 7) were considered. Variance in the detection function parameters was estimated using Fisher's information matrix (Buckland et al. 2001).

Data for spatial modelling

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

Based on previous studies on the distribution of cetaceans in breeding areas, and also on environmental data availability, covariates considered as potential explanatory variables were: current speed close to the surface, depth, distance to coast, distance to shelf break, seabed slope, SST, wind speed at the surface, geographic position (northing and easting) and year (Table 1). Additionally, to represent a combination of environmental conditions that may be related to energy saving for calves, 6 categories for shelter (Table 1) were created by combining 3 categories of wind speeds at the surface ('light' for values between 0.94 and 5.15 m s^{-1}; 'moderate' for values between 5.15 and 6.67 m s^{-1}; 'strong' for values between 6.67 and 9.16 m s^{-1}) and 2 categories of SST ('cold' for values between the minimum of 20.2 and 24.7°C; 'warm' for values between 24.7°C and the maximum 26.9°C). The wind and SST categories were delimited by quantiles of wind speed (33rd percentile = 5.15 m s^{-1} and 66th percentile = 6.67 m s^{-1}) and SST (median = 24.7°C).

Values for depth were extracted from the global model of land topography and ocean bathymetry ETOPO1 (Amante & Eakins 2009). Circular buffers (radius = 4 km) were created around segment midpoints in QGIS, and the average of depth values within the buffer zone was computed for each segment. This procedure was adopted because the resolution of ETOPO1 was much finer than the size of segments and buffers (between 13 and 16 ETOPO1 cells were included in the 50 km^2 buffers and used to compute mean depth values). After extraction of mean depth values, 25 out of 511 segments gave values greater than 500 m and were excluded from the analysis because the study area was previously defined as the continental shelf, from the shore up to the 500 m isobath. Slope values were derived from

Table 1. Explanatory variables tested in generalized additive models to model the density of humpback whales *Megaptera novaeangliae* off the coast of Brazil. Resolution is given as spatial and/or temporal, depending on the covariate nature. SST: sea surface temperature

Variables	Description	Resolution	Unit	Reference/data source
Curr.sp	Speed of the water current close to the surface	5 d; 0.33 × 0.33° (latitude × longitude)	m s^{-1}	OSCAR dataset (ESR 2009)
Depth	Depth	0.1 × 0.1° (latitude × longitude)	m	ETOPO1 (Amante & Eakins 2009)
Dist.coast	Distance to the coastline	–	m	SisCom (IBAMA 2011)
Dist.shelf	Distance to the 500 m isobath	–	m	500 m 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 × 0.1° (latitude × longitude)		Derived from ETOPO1
SST	Temperature at the surface of the sea	1 d; 0.011 × 0.011° (latitude × longitude)	°C	JPL-L4UHfnd-GLOB-MUR dataset (JPL MUR MEaSUREs Project 2010)
Wind.sp	Speed of wind at the surface	6 h (the daily mean was used); 80 × 80 km	m s^{-1}	ERA-Interim dataset (Dee et al. 2011)
x	Easting	–	m	Survey GPS
y	Northing	–	m	Survey GPS
Year	Year of survey	–	yr	Survey data

ETOPO1 data and were obtained in the same way, i.e. extracting mean values using the same circular buffers.

Distances to physical features (distance to coast and distance to shelf break) were calculated in QGIS or R as the shortest distance between the segment midpoint and the feature. For the distance to coast variable, the Brazilian coastline was obtained from a shapefile provided by SisCom (IBAMA 2011). To represent the continental shelf break, the 500 m isobath was generated from ETOPO1 in ArcGIS software using the 'contour tool' function (ArcGIS Desktop: release 10, ESRI).

SST was extracted from the 'MUR Global Foundation Sea Surface Temperature Analysis' dataset (JPL MUR MEaSUREs Project 2010) and ocean currents from the 'OSCAR' dataset (ESR 2009). Wind speed data were extracted from the 'ERA-Interim' dataset (Dee et al. 2011). With the exception of SST, the resolution of these datasets was too coarse when compared to the size of the circular buffers, so segment midpoints were used to extract covariate values in R software ('raster' package; Hijmans 2016). For SST, the circular buffers previously described were used to obtain mean values (around 40 SST values buffer^{-1}).

Spatial models and model selection

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

The quasi-Poisson distribution with logarithmic link function was assumed for the response variable (negative binomial and Tweedie distributions were also tested). An offset of ln(segment length) was included in all models. Generalized additive models (GAMs) were fitted using the 'dsm' R package (version 2.2.14; Miller et al. 2017). Smooth functions were fitted to covariates, with a bivariate smooth for geographic position, since this included easting and northing. The basis dimension parameter k for the geographic position smooth term was set to 20, and for the univariate smooth terms it was set to 8 (see Wood 2006 for an explanation on setting the dimension parameter). Model selection was conducted using a forward approach (i.e. adding 1 variable at a time), starting with a set of models, each with only 1 candidate explanatory variable. The model selected at each step was chosen by looking for an improvement in the restricted maximum likelihood (REML) (Harville 1977) score. This score was used to minimize problems with parameter estimation that other potential scores (e.g. UBRE and GCV) may present when applying DSMs, following the recommendation of Miller et al. (2013). The auto-correlation in the residuals (ordered by the time of data collection) of spatial models was checked using the 'acf' function ('stats' R package; R Core Team 2015). Model performance was assessed with model diagnostic plots (function 'gam.check', 'dsm' R package) and 10-fold cross validation (Refaeilzadeh et al. 2009).

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

(1) Habitat use model (HUM): to explain habitat use in a way that could be interpreted biologically; all variables, except geographic position (northing/easting), were considered;

(2) Abundance estimation model (AEM): to compute abundance estimates from the spatial model; all available variables were considered.

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

Predictions

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

The model-based abundance estimates for 2008 and 2012 were obtained from the sums across all grid cells of predicted values from the AEM, for each year. Maps showing patterns of distribution (density surface) were created using the AEM predictions in QGIS. Variances were obtained with the delta method, combining the variance from the detection function and the spatial models, using the 'dsm.var' function of the 'dsm' R package. Maps of uncertainty in model predictions (standard deviation surface) were also created with the variance calculated for each grid cell (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m585p213_supp.pdf). Predictions in 2012 were extrapolated to the area to the north of Salvador (~13° S), which was not surveyed in that year (Fig. 1) because of poor weather conditions (Bortolotto et al. 2016a).

RESULTS

Survey effort used in the analysis totaled 2350 km in 2008 and 1700 km in 2012. The number of whale groups (including mother–calf pairs and solitary animals) in the data was 493 (416 humpbacks and 77 unidentified large whales) and 737 (557 humpbacks and 180 unidentified large whales) in 2008 and 2012, respectively.

Detection function

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

Spatial models

Model diagnostics (Figs. S2 & S3) indicated the quasi-Poisson distribution to be adequate and to provide a better fit than the other distributions that were considered. Cross-validation yielded root-mean-square errors of 6.932 (SD = 1.116) for 2008 and 7.981 (SD = 0.967) for 2012 (see Table S7). SST was highly correlated with geographic position. Depth, slope and distance to the shelf break were also correlated to each other. Therefore, if one of the above variables was selected at a model selection step, those correlated with it were not considered in subsequent steps of model selection.

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

The selected AEM included the variables distance to coast, distance to shelf break, current speed, shelter and geographic position (Fig. S4), and had an explained deviance of 66.8%. This model was used for plotting maps here, because it presented a larger portion of explained deviance and the distribution patterns are likely better represented. Very weak signs of auto-correlation were found in the residuals of HUM, and no signs of auto-correlation were present in the residuals of AEM (ACF plots; Figs. S2 & S3).

Abundance estimates

Estimated abundances for prediction grid cells ranged from 0.139 to 53.0 individuals (mean = 7.47, SD = 8.90) in 2008 and from 0.144 to 60.9 individuals

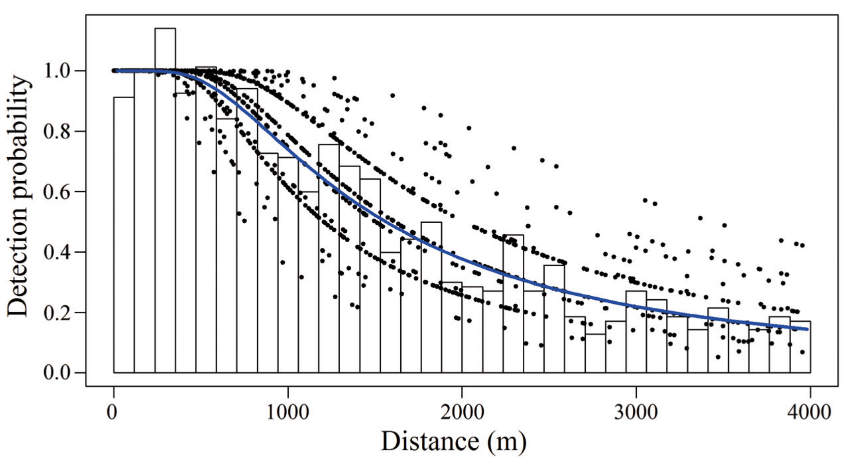

Fig. 2. Detection function curve (blue line) from a hazard rate model fitted to the perpendicular distances (in metres) of humpback whale *Megaptera novaeangliae* groups detected. Different dotted curves represent different combinations of the covariates sea condition, cue and year. Each point represents the predicted value for the observation

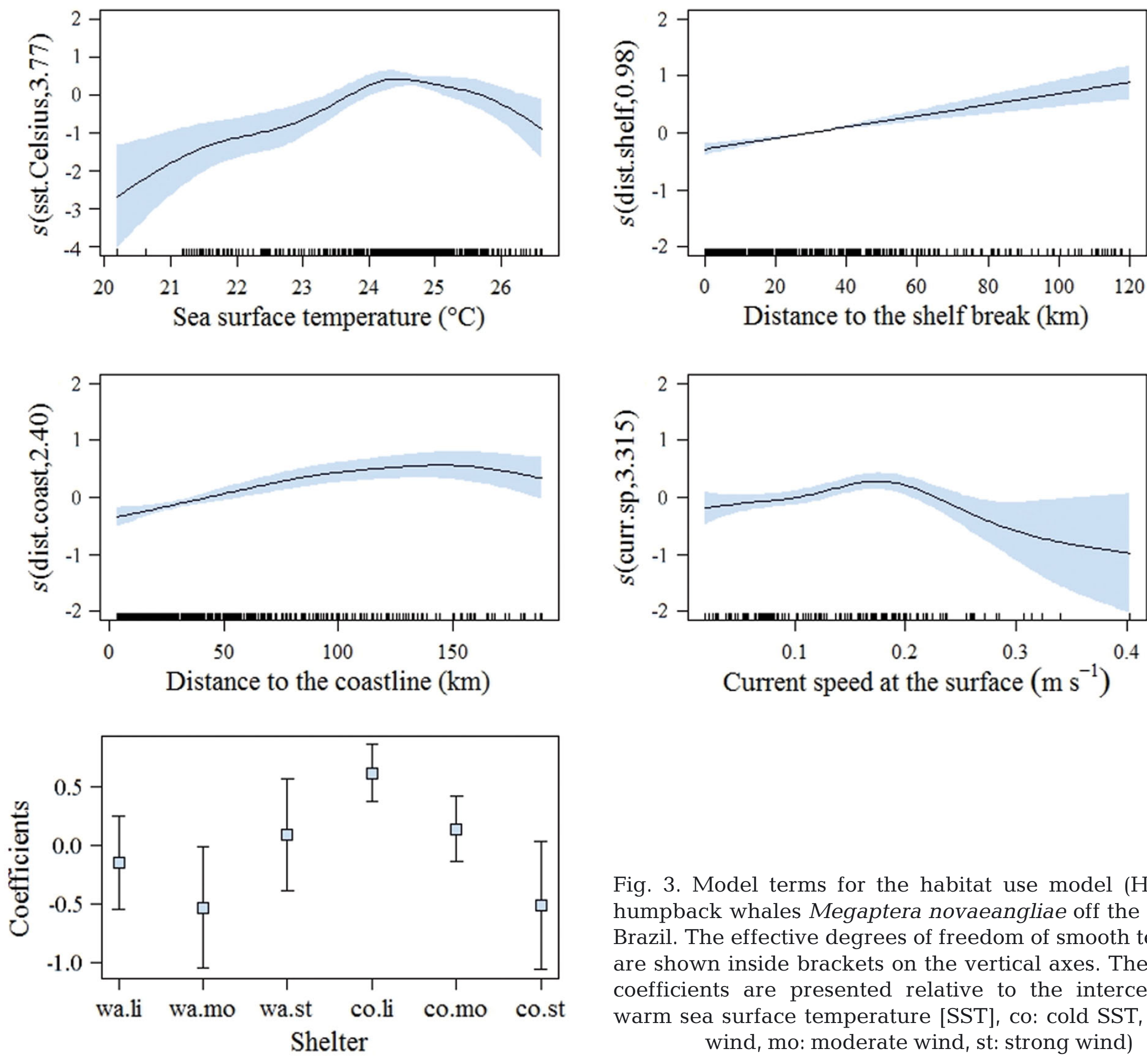

Fig. 3. Model terms for the habitat use model (HUM) of humpback whales *Megaptera novaeangliae* off the coast of Brazil. The effective degrees of freedom of smooth terms (*s*) are shown inside brackets on the vertical axes. The shelter coefficients are presented relative to the intercept (wa: warm sea surface temperature [SST], co: cold SST, li: light wind, mo: moderate wind, st: strong wind)

Table 2. Generalized additive model results for the habitat use model (HUM) and the abundance estimation model (AEM). Variables are described in Table 1. Effective degrees of freedom for smooth terms (*s*) are presented inside brackets. Blank spaces represent variables not selected, and a dash represents a covariate not considered in the model selection. REML: restricted maximum likelihood, *F*: factor

Variable	HUM	AEM
Curr.sp	*s*(3.315)	*s*(3.294)
Depth		
Dist.coast	*s*(2.401)	*s*(5.528)
Dist.shelf	*s*(0.975)	*s*(0.940)
Shelter	*F*	*F*
Slope		
SST	*s*(3.766)	
Wind.sp		
x, *y*	–	*s*(15.865)
Year		
% Deviance explained	54.1	66.8
REML score	718.5	678.00

(mean = 10.7, SD = 12.7) in 2012. Model-based abundance estimates were 14 264 whales (CV = 0.084) for 2008 and 20 389 (CV = 0.071) for 2012 (Table S6). Surface maps for predicted density showed higher numbers in the Abrolhos Bank region, with a concentration area to the south of the Abrolhos Archipelago, which was more pronounced for 2012 (Fig. 4). Other areas also showed relatively high densities, such as the coast of Alagoas and Sergipe States (Fig. S5), and near the city of Salvador, Bahia State (Fig. S6).

DISCUSSION

Systematically collected sightings data were used to model the distribution and abundance of humpback whales in their wintering areas off the coast of Brazil. The suite of environmental covariates tested included powerful predictors of whale density across

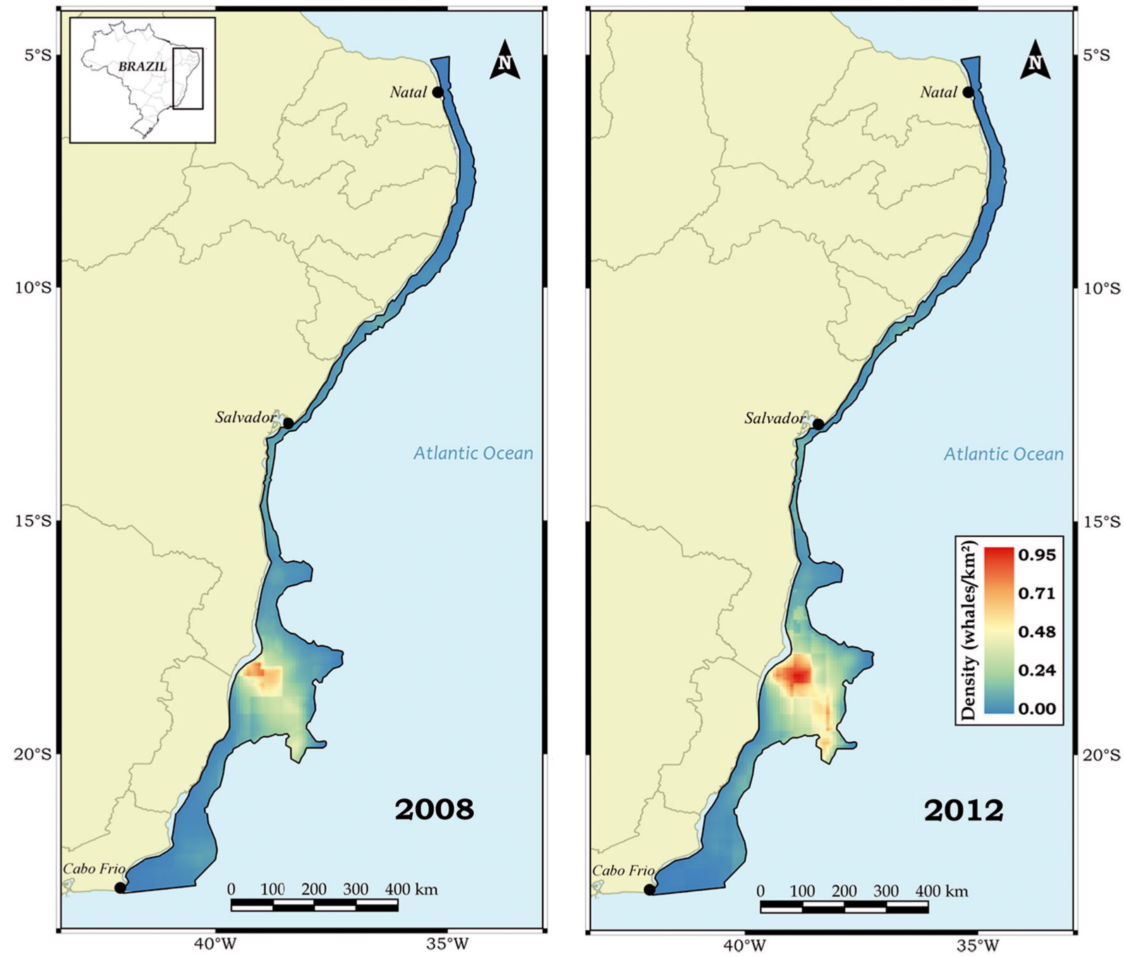

Fig. 4. Density surface maps for 2008 and 2012. Predictions were made with the abundance estimation model (AEM)

the study area, with SST and geographic position being the most powerful explanatory terms. The effect of year was not selected in the spatial models, suggesting that differences in the distribution patterns from 2008 to 2012 were better explained by the variation in the spatial covariates than by temporal changes between survey years.

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

Migratory whales show marked differences in habitat preferences according to different age classes, sexes, reproduction-related individual characteristics and/or group composition (Craig & Herman 2000, Ersts & Rosenbaum 2003, Elwen & Best 2004a, Oviedo & Solís 2008, Cartwright et al. 2012, Craig et al. 2014, Rayment et al. 2015), and for specific group types (Elwen & Best 2004b, Félix & Botero-Acosta 2011) when in breeding areas. However, the passing mode data collection procedure adopted here prevented more specific data on individual whales, such as sex, age class or accurate group composition, from being obtained. Because of this, results presented here are representative of the population as a whole, not of any particular sex, age or group type. Although some of the results may be consistent with what could be expected for habitat preferences of breeding and/or calving animals in the area, such as the importance of shelter as a predictor of density, it is not possible to make robust inferences for specific reproductive stages. A study to investigate the distribution and habitat use of WSA humpback whales based on data from satellite tagging of individual whales (Zerbini et al. 2006) is underway, and is expected to provide information on predictors of distribution and habitat use in relation to sex and group composition. Because the procedure of attaching tags requires close proximity to the animals, collection of individual and group information is possible at the moment of tagging.

Spatial modelling

The covariates retained in the models explained a high proportion of the variation in whale density across the surveyed area (deviance explained = 54.1 % for HUM; 66.8 % for AEM). In addition to this increase in explained deviance, the residual autocorrelation (observed in the HUM) was no longer apparent in the AEM (ACF plots; Figs. S2 & S3), in which SST was substituted by the geographic position (although the auto-correlation in the residuals of the HUM was not high and required no further action; see Wood 2006 for concerns about residual autocorrelation of GAMs). It is likely, therefore, that the bivariate smooth for easting/northing included in the AEM is acting as a proxy for unmodelled environmental or social characteristics. For example, because it was highly correlated with SST, which was not included in the AEM, easting/northing may be representing not only SST but also some other environmental feature(s). This may explain the increase in percentage of explained deviance when SST is substituted by easting/northing in the AEM.

Shelter (a combination of SST and wind speed) was created as an environmental feature that could be important to whales that are calving, for example, to represent conditions that may be related to energy saving for the calf (Corkeron & Connor 1999). Because the effects of wind speed on detectability have been accounted for in the estimation of the detection probability, no confounding with the effects of wind in the shelter variable is expected. The response variables in the detection function model and the habitat use/abundance estimation spatial models are completely different: in the detection process, it is the perpendicular distance (in relation to the trackline); in the spatial models the response variable is abundance (corrected count per segment). Furthermore, wind speed may influence both the detectability of animals and how animals use their habitat, which is supported by the present results. Indeed, a major advantage of DSMs using data from distance sampling surveys is that the effects of variables on detectability and on abundance can be teased apart.

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

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

Habitat use

The main reasons for SST to be considered an important factor in explaining the distribution of migratory whales in their breeding grounds are likely related to presence of calves, which are not as efficient in conserving their body temperature as older animals (Corkeron & Connor 1999). SST was the most important variable selected in the HUM, and it was highly correlated with geographic position (northing/easting). The overall relation between whale density and SST was positive, peaking at 24 to 25°C. This result for SST may reflect habitat selection of calving females for the reason stated above. The habitat use of North Atlantic right whales in their calving grounds off the south-eastern US was also observed to be strongly related to SST (Keller et al.

2006); however, differences in species characteristics (e.g. latitudinal range) should be taken into account in any comparison. Trudelle et al. (2016) did not find a relationship between SST and humpback whale movements in their Madagascar coastal breeding area, possibly because of the relatively low variation in SST in the area. Although a temporal change in distribution was not supported by our models, long-term monitoring should provide important insights on this, as the effects of climate change (Walther et al. 2002), for example, may impact the distribution of marine animals.

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

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

The relationships between whale density and environmental covariates revealed by our models are consistent with what could be expected for mothers, which may prefer a secure environment for the development of their calves in sheltered waters. However, Trudelle et al. (2016) noted that while the movements of female humpback whales in a breeding area off the coast of Madagascar are influenced by environmental features such as depth and distance to the shore, male movements are probably more influenced by social factors, such as female occurrence. Despite the fact that their distribution may also be influenced by the presence of other males (Herman 2017), adult males are indeed likely to seek receptive females, not those that are about to or have just given birth. Calving females may prefer shallow waters, where the chances of being harassed by males are lower; their habitat selection may be driven primarily by avoidance of males (Craig et al. 2014). Humpback whale groups containing calves have been found significantly more frequently in shallower waters than groups without calves in Brazilian breeding grounds (Martins et al. 2001, Zerbini et al. 2004). Thus, bathymetric features may also be related to what may represent shelter for whales.

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

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

The estimated negative effect on predicted whale numbers of current speeds greater than 0.2 m s^{-1} is not very well supported by the data (95% confidence interval widens with increasing current speed). In a study that supports the importance of the current for large whales in breeding areas, Trudelle et al. (2016) found that differences in current speed between shelf and oceanic waters influenced the movement patterns of humpback whales in their Madagascar breeding area. Whales of both sexes swam faster in slower currents, and the authors suggested that when animals are engaged in mate-searching-related movements close to the coast, the current speed probably does not have an important effect. Therefore, data on the behavioural status and/or movements of individual animals are likely needed to better understand the effects of current speed on habitat use of humpback whales off the coast of Brazil. In addition, the resolution of this covariate (5 d bins and 0.33 × 0.33° of latitude/longitude; Table 1) was likely unable to capture fine-scale variability, particularly around complex coastlines.

Implications for conservation and management

The predicted distributions support previous work showing that WSA humpback whales have a strong preference for the Abrolhos Bank region during their breeding season in coastal waters of Brazil (Siciliano 1997, Andriolo et al. 2010, Wedekin 2011, Martins et al. 2013, Pavanato et al. 2017). However, other areas also had relatively high predicted densities, such

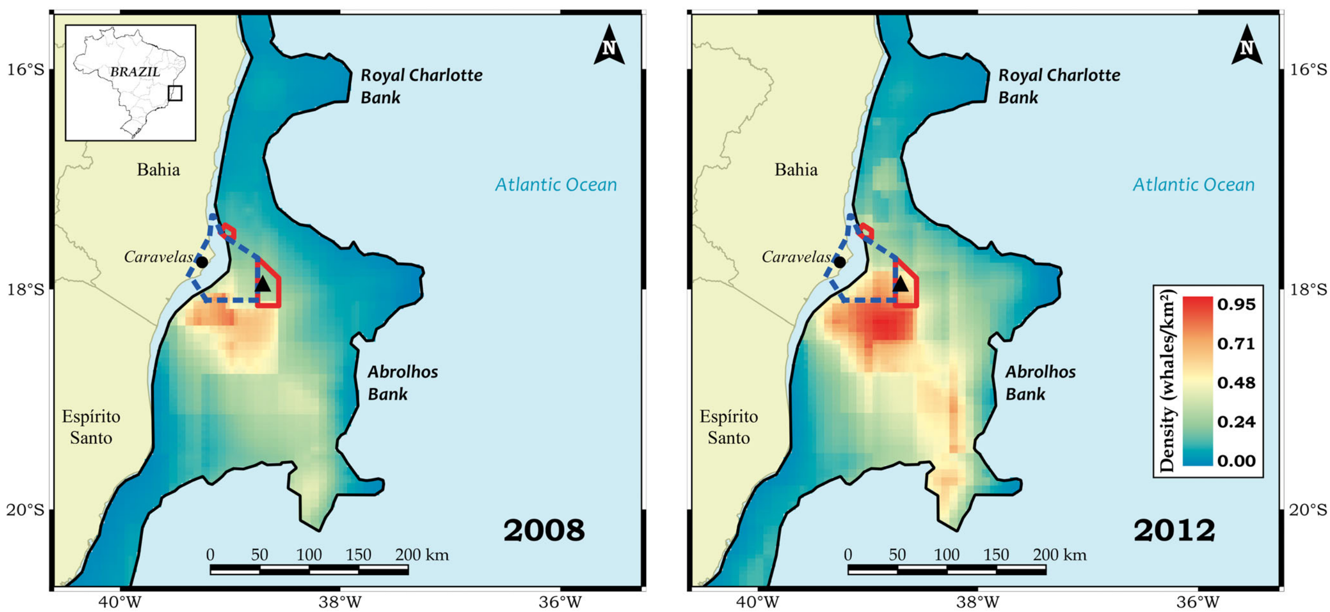

Fig. 5. Density surface maps for 2008 and 2012 for the Abrolhos Bank region. Predictions were made with the abundance estimation model (AEM). Black triangles indicate the location of the Abrolhos Archipelago. Red polygons represent the Abrolhos Marine National Park, and dashed blue polygons represent the Ponta da Baleia marine protected area

as near Salvador and off the coasts of Sergipe and Alagoas States (Figs. S5 & S6). Little is known about their distribution or habitat use in these areas (Zerbini et al. 2004, Baracho-Neto et al. 2012), but relatively recent observations indicate that the distribution of WSA humpback whales in Brazil may be broader than currently recognized (e.g. Wedekin et al. 2014, Bortolotto et al. 2016c, Pavanato et al. 2017).

The Abrolhos Archipelago is included in the Abrolhos Marine National Park, which is a national 'Conservation Unit' area of 880 km^2 (ICMBio 2017). According to the Brazilian Ministry of Environment (www.mma.gov.br) this is a federal conservation unit of 'integral protection' where only scientific research and educational, recreational and small-scale ecotourism activities are permitted. All of these activities are regulated by the Chico Mendes Institute for Biodiversity Conservation (ICMBio), the federal body responsible for protected areas in Brazil. Commercial activities are therefore mostly limited to those related to small-scale ecotourism. The nearby Environmental Protection Area of Ponta da Baleia is regulated by Bahia State and is in the category of 'sustainable use area' (INEMA 2017). These protected areas cover a very small portion of the area predicted to have the highest concentration of animals (Fig. 5). Our results support the conclusions of Castro et al. (2014), who used satellite-tracked movement data to show that MPAs only cover a very small portion of the areas most used by WSA humpback whales in their breeding grounds.

The Abrolhos Bank is a region of high biodiversity (Werner et al. 2000), and expanding the area under protection could benefit not only cetaceans but also other marine organisms, such as the unique coral reefs in the area (Francini-Filho & de Moura 2008). Because most humpback whale births are expected to occur on or near Abrolhos Bank (Martins et al. 2001), expanding the protected area during the period when whales are consistently present (winter–spring), could reduce the risk of anthropogenic impact, especially for calves that are more vulnerable to disturbance (Schaffar et al. 2013). To conserve marine species in the area, past management actions have included the cancellation of seismic and other oil and gas exploitation activities on the Bank during the humpback whale breeding season (Engel et al. 2004, Marchioro et al. 2005). However, there is increasing interest from the oil and gas industry to explore for oil on the Bank (http://app.anp.gov.br). Because young animals are more vulnerable to stressors (Schaffar et al. 2013, Ott et al. 2016, Dunlop et al. 2017), and we did not include group composition in this study, future studies aiming to provide information for conservation should investigate the distribution of different group types at a finer scale and include potential stressors and displacement factors associated with human presence in the marine environment, with special attention to the Abrolhos Bank region.

Abundance estimates presented here (14 264, CV = 0.084 for 2008 and 20 389, CV = 0.071 for 2012) provide additional confirmation that the WSA humpback whale population is growing (Zerbini et al. 2011). A new population status assessment in the framework of Zerbini et al. (2011) is currently underway, which will take the present results and new catch history data (de Morais et al. 2017) into account to provide an updated understanding of this population's recovery, more than 4 decades after whaling ceased in 1973 in this area.

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

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