

Predicting the breeding hotspots of the southern right whale, *Eubalaena australis* (Cetartiodactyla: Mysticeti), along the southern Brazilian coastline

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Summary: To predict the potential breeding hotspots of southern right whales in southern Brazil, we used a Maxent model with a “presence-only” dataset. The dataset was obtained from a systematic aerial survey and public records of the Programa de Monitoramento de Cetáceos da Baía de Santos and Sistema de Apoio ao Monitoramento de Mamíferos Marinhos. Because of spatial autocorrelation, 528 records out of 3028 were used in the modelling process. The explanatory variables used in the models were coastal distance, linearity, slope and substrate type. The models were created separately for unaccompanied adults (Ad) and mother-calf pairs (Fe). Both models showed good accuracy according to their area under the curve values (Ad=0.974; Fe=0.958). Coastal distance was the most relevant explanatory variable for the unaccompanied adult model (54%), whereas coastal linearity was more relevant for the mother-calf pair model (82%). The estimated area for mother-calf pairs was more restricted to coastal areas than that for unaccompanied adults, possibly owing to the high number of shelter areas for calves near the coast. This is the first study to predict the potential breeding hotspots of southern right whales in Brazil and its results will allow for a more directed management of these whales and provide further research opportunities.

Keywords: Southern right whale; *Eubalaena australis*; Brazil; breeding ground; habitat modelling; MaxEnt; presence-only data.

Predicción de los “hotspots” de reproducción de la ballena franca austral, *Eubalaena australis* (Cetartiodactyla: Mysticeti), en la costa sur de Brasil

Resumen: Para predecir los posibles “hotspots” de reproducción de las ballenas francas en el sur de Brasil, utilizamos un modelo Maxent con un conjunto de datos de “solo presencia”. El conjunto de datos se obtuvo de un estudio aéreo sistemático y registros públicos del “Programa de Monitoreo de Cetáceos da Baía de Santos” y el “Sistema de Apoio ao Monitoramento de Mamíferos Marinhos”. Debido a la autocorrelación espacial, se usaron 528 registros de 3028 en el proceso de modelado. Las variables explicativas empleadas en los modelos fueron la distancia costera, la linealidad, la pendiente y el tipo de sustrato. Los modelos se crearon por separado para adultos no acompañados (Ad) y parejas madre-cría (Fe). Ambos modelos mostraron una buena precisión de acuerdo con sus valores de AUC (área bajo la curva: Ad=0,974; Fe=0,958). La distancia costera fue la variable explicativa más relevante para el modelo de adulto no acompañado (54%), mientras que la linealidad costera fue más relevante para el modelo de pareja madre-cría (82%). El área estimada para las parejas madre-cría estaba más restringida a las áreas costeras en comparación con el área prevista para los adultos no acompañados, posiblemente debido a la gran cantidad de áreas de refugio para las crías cerca de la costa. Este es el primer estudio que predice los posibles “hotspots” de reproducción de las ballenas francas en Brasil y sus resultados permitirán una gestión más dirigida de estas ballenas y brindarán más oportunidades de investigación.

Palabras clave: ballena franca austral; *Eubalaena australis*; Brasil; área reproductiva; modelado de habitat; MaxEnt; datos de “solo presencia”.

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INTRODUCTION

Migratory baleen whales have an extensive ecological niche, and the environmental conditions that define this niche are extremely diverse. Baleen whales usually migrate seasonally between feeding and calving grounds (Corkeron and Connor 1999). The southern right whale, *Eubalaena australis* (Desmoulins, 1822), is a baleen whale that lives in the southwest Atlantic Ocean, breeds in Argentina and Brazil in winter and spring (Rowntree et al. 2001) and feeds around the South Georgia Islands in summer and autumn (Zerbini et al. 2017). Another species, the humpback whale, *Megaptera novaeanglia* (Borowski, 1781), breeds in northeastern Brazilian coastal areas and has also been tracked to the South Georgia Islands for feeding (Zerbini et al. 2006). This information shows the large gradient that defines this species' ecological niche, because environmental conditions between these two regions, such as sea surface temperature, are substantially different.

Recently, studies that predict the distribution patterns of animals have increased, as these patterns provide basic information to determine management and conservation strategies. Habitat modelling approaches are frequently used and show effective results in predicting cetacean distribution (Redfern et al. 2006), including that of baleen whales. Regression models, such as generalized additive models and linear models, have been effectively used to understand species distribution patterns. However, for these models to be effective and produce unbiased results, the data must be obtained with several, well-delimited standard protocols. When data do not follow these assumptions or when presence-only data are available (i.e. repository, opportunistic and collection data), other methods such as maximum entropy are more appropriate (Elith et al. 2011). In studies on migratory baleen whales, the ecological conditions for predicting their distribution in feeding areas are different from those for breeding and calving areas (Redfern et al. 2006). Whale distribution in feeding areas is mainly defined by prey distribution (Friedler et al. 2006). In breeding areas, whales fast, and their distribution may be related to areas that increase calf survival.

The southern right whale is a migratory baleen whale that breeds along the Brazilian coast (Palazzo and Carter 1983, Lodi et al. 1996). Because of whaling activity on the Brazilian coast from 1602 to 1976 (Morais et al. 2017), the species occurrence is currently reduced. It is distributed mainly along the Santa Catarina state coast, with sporadic records in the southeastern and northeastern Brazilian coasts (Ellis 1969, Figueiredo et al. 2017, Morais et al. 2017).

Several bays have shown a higher whale density than that shown in records from previous research, which appears to be linked to the current population growth rate (Groch et al. 2005, Renault-Braga et al. 2018, Renault-Braga, et al. 2021a). Therefore, some regions where species occurrence is frequent may reach the carrying capacity in a few years, which would force some whales to search for other areas with similar

oceanographic conditions relatively soon. Predicting these potential areas will allow us to conduct research and conservation programmes.

Therefore, our objective was to predict future potential occupation areas (here, potential breeding hotspots) of right whales in Brazil, using habitat modelling approaches and a 16-year dataset of southern right whale occurrences.

MATERIALS AND METHODS

Study area

To predict the right whale breeding hotspots, we delimited the southern Brazilian coast, which includes three states (Paraná, Santa Catarina and Rio Grande do Sul) (25.0319°S to 33.727°S). We delimited this area because it is the boundary of the major occurrence areas for the species (Renault-Braga et al. 2018). A 20-km buffer from the coastline was created using Arc-Map 10.4 (ESRI). This resulted in a total analysed area of 23027 km², which was the region where potential hotspots were predicted (Fig. 1).

Maximum entropy model

The maximum entropy model (Maxent) was used to identify potential breeding hotspots of the southern right whale. This is a presence-only method that allows the use of datasets without a systematic survey (Elith et al. 2011). To avoid bias, Maxent generates a "pseudo-absence" background dataset inside a delimited space (Philips and Dudík 2008, Philips et al. 2009). Maxent has previously been used to identify hotspots for several vertebrate groups, including marine mammals (Nachtsheim et al. 2017, Lobo et al. 2021).

MAXENT 3.4.1 was used with default configurations to generate models with 10 replicates per whale class (adults unaccompanied by calves and adults accompanied by calves, assumed to be and referred to as mother-calf pairs). The maximum number of background points for "pseudo-absence" was set at 10000. The average output from the 10 replicates was assumed to be the final model. The replicate run type was set for cross validation. The regularization multiplier parameter that affects how focused or closely fitted the output distribution is was set to 1 as the default. Model accuracy was evaluated using the area under the curve (AUC) value, for which values near 1.0 indicate better accuracy (Philips et al. 2004). For presence-only data, the AUC method is the most suitable method for evaluating models (Merow et al. 2013). The jackknife test was used to test the contribution of each explanatory variable to the model.

Dataset

Southern right whale records were acquired from three different sources; however, the main data were obtained from systematic aerial surveys. Records from Sistema de Apoio ao Monitoramento de Mamíferos

Marinhos (SIMMAM) (<http://simmam.acad.univali.br/site/>) and a public dataset of the Projeto de Monitoramento de Cetáceos na Bacia de Santos (PMC-BS) were also used.

The dataset used for this analysis consisted of 50 aerial surveys using helicopters conducted in 2003-2018 from Cabo Frio (22.220°S) to Chuí (32.115°S). The aerial surveys were obtained from a systematic study that had been conducted by Projeto Baleia Franca and the Instituto Australis from 2003 to 2018. They had standard protocols for data collection (see Renault-Braga et al. 2018), but the coverage area and seasonality changed over time. The survey tracks were parallel to the coastline and were 500 m offshore. Surveys were conducted at a mean speed of 100 km/h and an altitude of 300 m, and only on days with optimal conditions of low wind speed (<10 knots), low sea state (≤ 3 Beaufort Sea Scale), adequate daylight (8:00 to 16:00 local time) and good visibility (horizon line visible). When a whale or a group of whales was spotted, the latitude and longitude position was recorded and

photographs were taken for individual identification. Group composition was recorded as follows: adults unaccompanied and adults with calves (here assumed to be, and hereafter called, “mother-calf” pairs). After data collection, the helicopter resumed the survey at the last point, before deviating from the route.

The datasets from both SIMMAN and PMC-BS used in this study were public datasets available on the project website. SIMMAN is a GIS platform that stores information on the sightings, bycatches and strandings of marine mammals in Brazil. It allows for information sharing from research in Brazil (<http://simmam.acad.univali.br/site/>). If species identification was possible in the sightings category (i.e. by photograph or when the data were classified as reliable by the SIMMAN system), the data were inserted into our dataset. PMC-BS is a systematic study conducted in oceanic areas from Cabo Frio (22.220°S) to Florianópolis (27.381°S) to evaluate the effect of oil exploration on cetaceans in Brazilian waters (<https://www.comunicabaciadesantos.com.br/programa-ambiental/projeto-de-monitoramen->

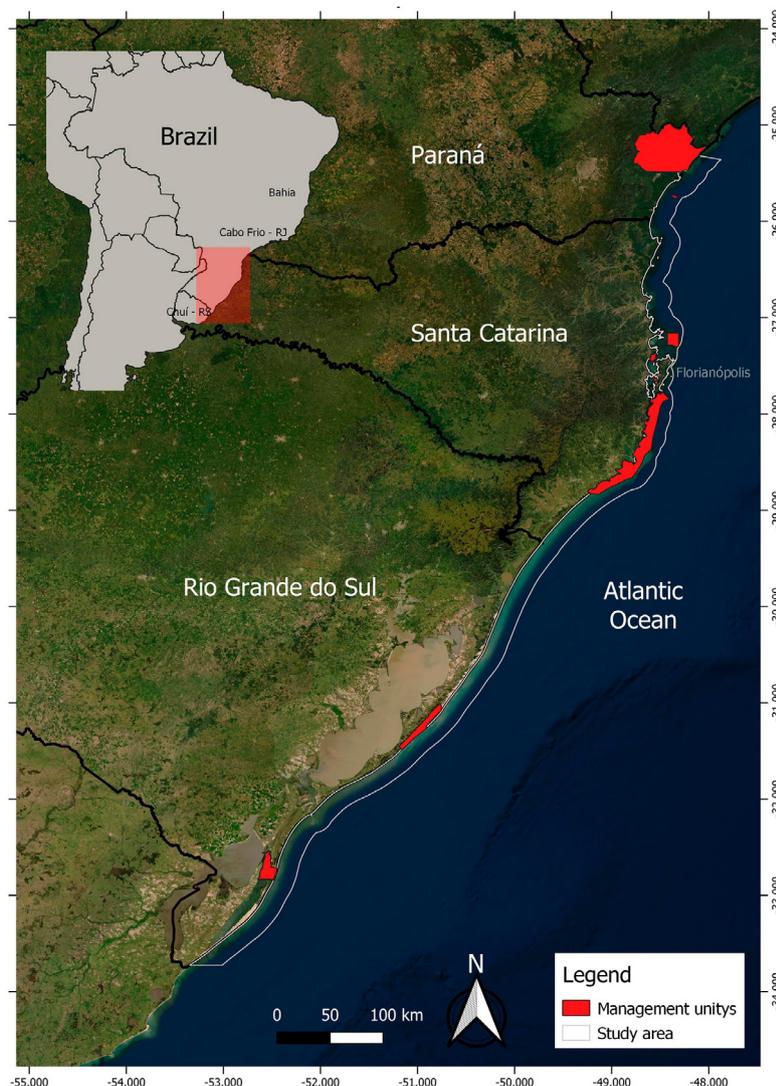


Fig. 1. – Study area with the 11 federal management units along the southern coast of Brazil. Red polygons represent the managements units. The white polygon represents the area where the hotspots will be predicted.

[to-de-cetaceos-pmc.html](https://doi.org/10.1007/s12572-020-10000-0) accessed on 20/03/2020). The data on southern right whales in the PMC-BS dataset were considered only if it was determined that the data came from a systematic study (nautical and aerial dedicated surveys and passive acoustic monitoring) with trained researchers.

To avoid bias owing to spatial autocorrelation, the sightings were filtered and 25% of all data were randomly selected for each whale category; these sightings were plotted with ArcMap 10.4 (ESRI) and a buffer of 1 km was generated. Finally, the full dataset was plotted in ArcMap 10.4 (ESRI) and all sightings that overlapped with these generated buffers were excluded from the analysis (except the sightings that originated in the buffer) (adapted from Lobo et al. 2021).

Habitat variables

All explanatory variables used in this study were previously identified in other studies to explain the distribution of right whales (Table 1). We focused on static variables because dynamic oceanographic variables, such as sea surface temperature, may have a strong influence on latitude, producing biased results. Additionally, the occurrence of historical southern right whales reaches the northwest coast of Brazil, in Bahia State (Lat 12.993°S) (Lodi et al. 1996), suggesting that right whales can support a large gradient of these variables.

The coastal distance was estimated as the linear distance between the core point of each cell and coastline using the “near” tool in ArcMap. The bathymetric raster

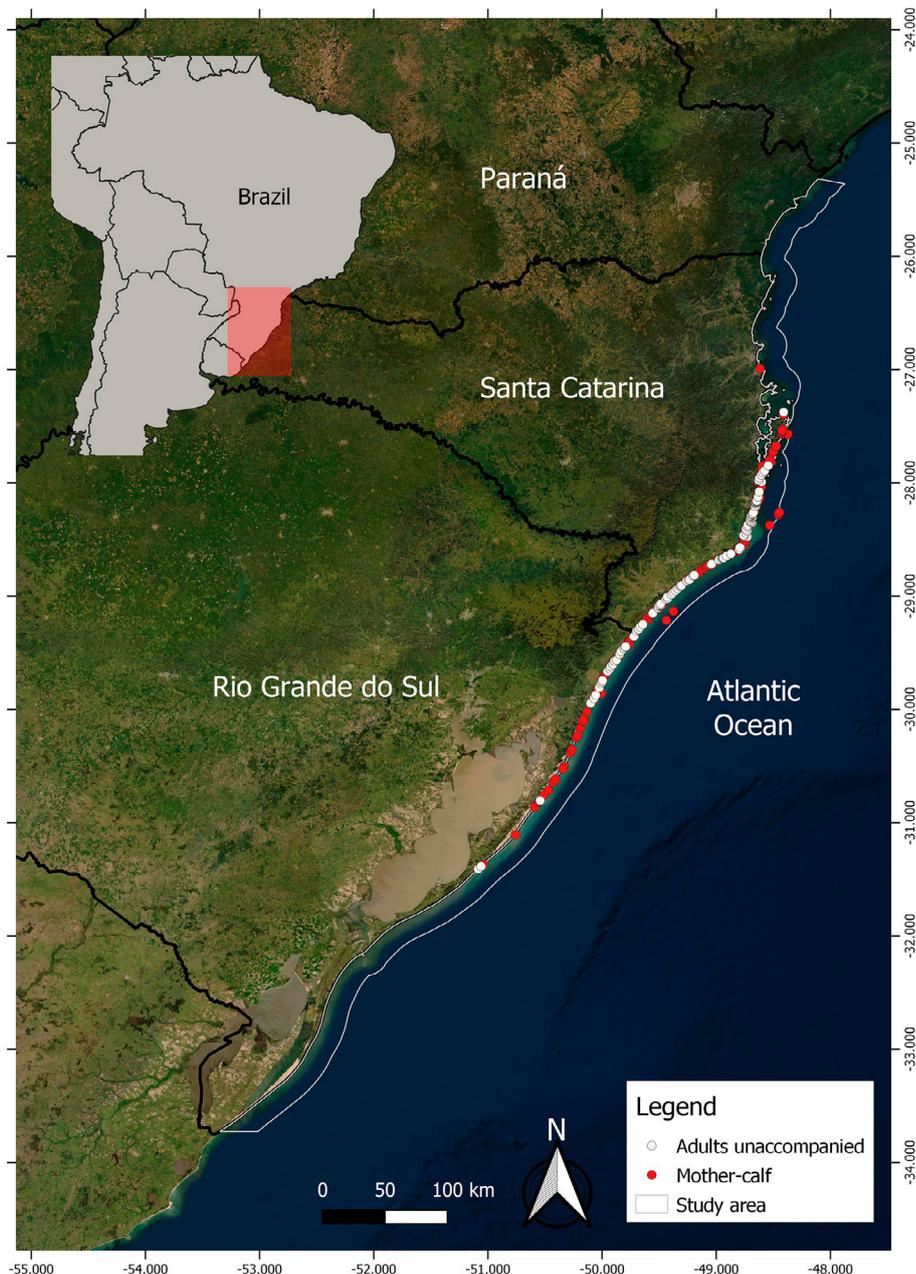


Fig. 2. – Dataset of southern right whales’ presence in the study area in southern Brazil after data sorting (110 unaccompanied adults and 418 mother-calf pairs).

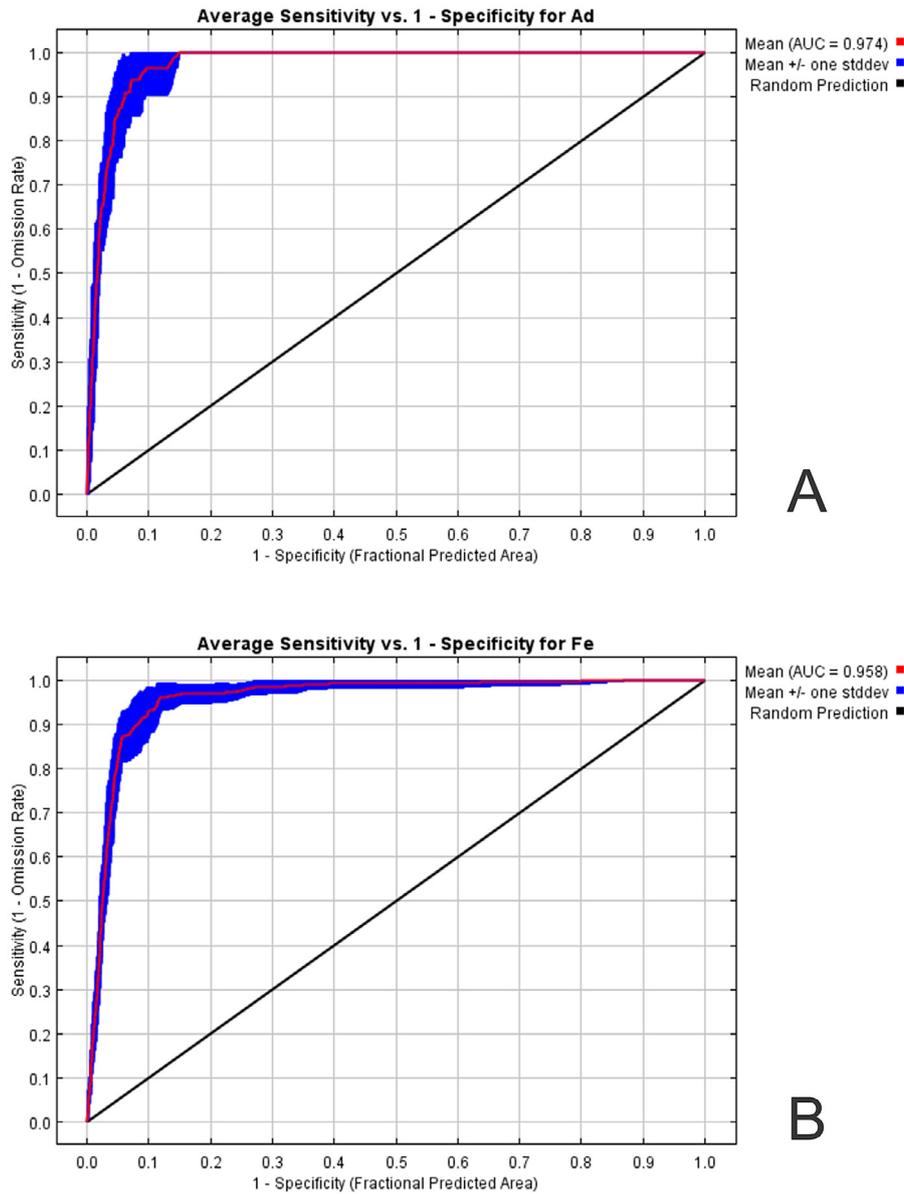


Fig. 3. – ROC curve of the average model to predict breeding hotspots of unaccompanied adults (A) and mother-calf pairs (B) of southern right whales in southern Brazil. This curve generates an AUC of 0.971(±0.004) for unaccompanied whales and 0.958(±0.012) for mother-calf pairs.

Table 1. – Explanatory variables used to build the models to identify probable breeding hotspots of southern right whales in southern Brazil.

Explanatory variable	Unit	References	Model reference	Colinearity
Coast distance	Metres	Elwen and Best 2004a, Rayment et al. 2015	dist_coast	
Bathymetry	Metres	Elwen and Best 2004a, Elwen and Best 2004b, Keller et al. 2012, Rayment et al. 2015	bat	Slope (Fig. 8)
Slope	Degree	Elwen and Best 2004a, Elwen and Best 2004b, Santo 2012, Rayment et. al. 2015, Seyboth et al. 2015	slope	Bathymetry (Fig 8)
Coastline linearity	Index	Santo 2012	coast_lin	-
Substrate Type	Categorical	Elwen and Best 2004b	sediment	-

was created with a point-of-depth dataset obtained from the Projeto Batimetria do Serviço Geológico do Brasil (<http://www.cprm.gov.br>) using triangulated irregular network interpolation. The bathymetric slope was calculated based on the same raster generated for bathymetry and “slope” tools in ArcMap 10.1 (ESRI). The coastline was divided into 4 km latitudinal intervals to generate a coastal linearity raster. For each latitudinal interval, the coast was overlaid on a straight line. The ratio of the size of the estimated straight coastline and that of the actual coastline was used to generate a value for coastal linearity. Offshore areas (>1.5 km from the coast) were considered open and exposed, so their coastal linearity indices were set to one (1 – real coastline is

equal to the estimated straight coastline, which represents an exposed area). The substrate type was obtained from georeferenced images using a regional atlas of morphology and sedimentology (Martins and Correa 1996).

Each variable was converted into raster formats in ArcMap 10.4 (ESRI) with a resolution of 500×500 m. Data exploration of explanatory variables was conducted according to Zuur et al. (2010). Pair plots were used to identify collinearity ($r \geq 0.7$) (Zuur et al. 2009). Bathymetry and slope showed collinearity ($r = 1.0$). In the final model, we used the variable that contributed the most from the full model according to the jackknife test, and the slope showed a higher contribution.

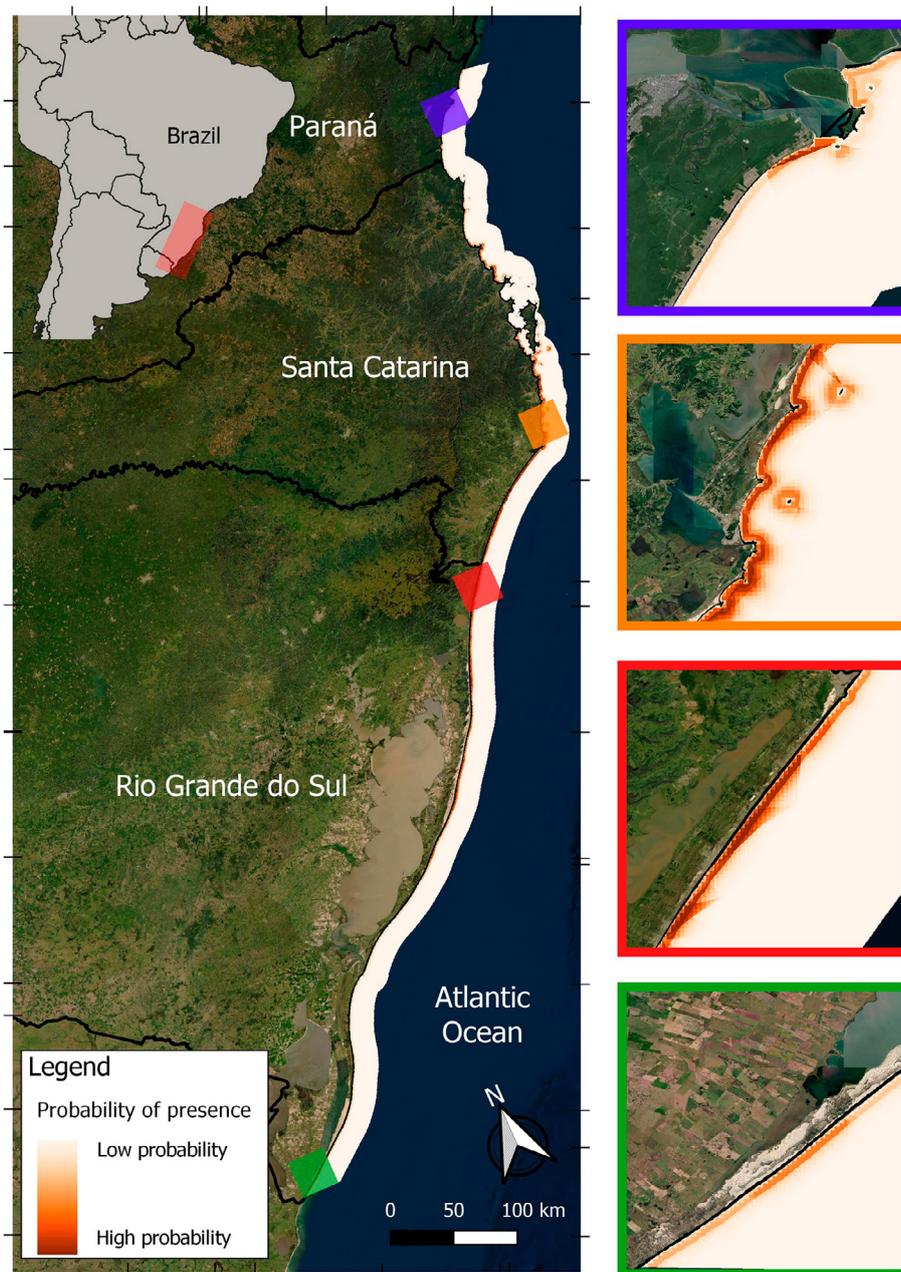


Fig. 4. – Predicted hotspots of unaccompanied adults of southern right whales along the southern Brazilian coast.

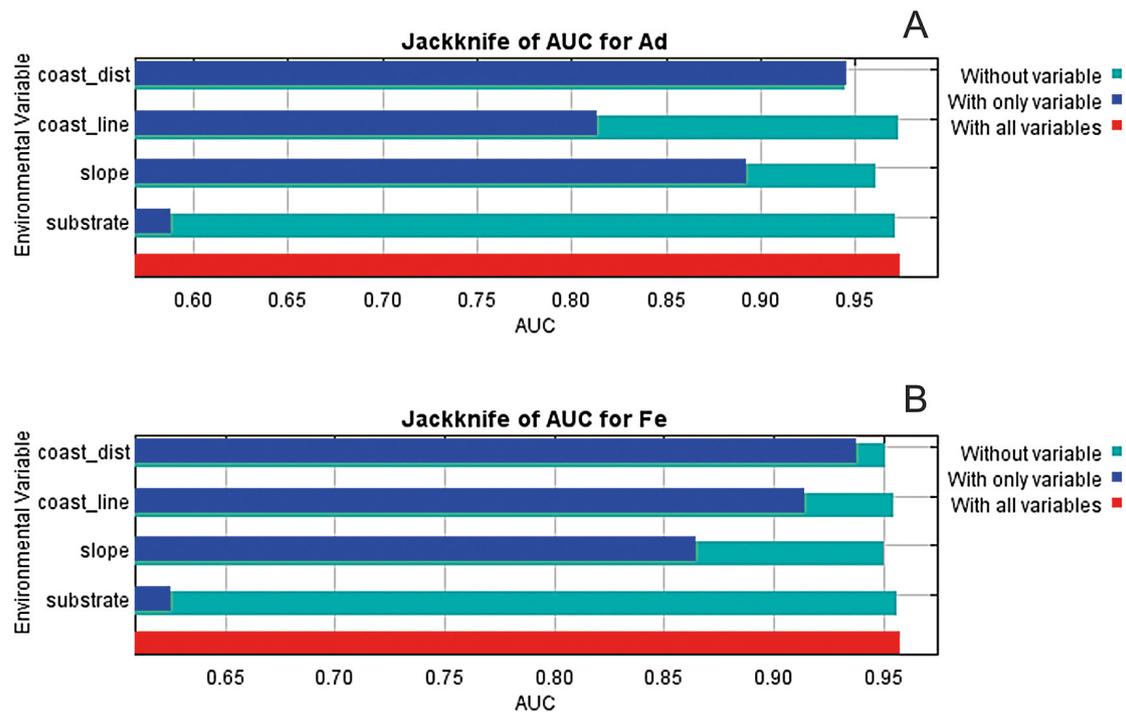


Fig. 5. – Jackknife test of the model for unaccompanied adults (A) and mother-calf pairs (B) of right whales in southern Brazil. Coast distance showed 54% of model contribution, coast linearity 19.3%, slope 24.5% and substrate type 2.2% for unaccompanied adults. Coast linearity showed 82% of model contribution, slope 11.6%, coast distance 4.6% and substrate type 1.7% for mother-calf pairs.

RESULTS

Southern right whale sight data

The dataset contained 3010 records from systematic aerial surveys, 16 records from SIMMAM and 2 records from PMC-BS. After data sorting, we used 528 records of southern right whales to run our models, of which 110 were unaccompanied adults and 418 were mother-calf pairs (Fig. 2).

Unaccompanied adults

All four variables were used in the model and demonstrated good accuracy ($AUC=0.974\pm 0.004$) (Fig. 3A). The prediction of the hotspot map showed a coastal preference along most of the coastline and some coastal islands (Fig. 4).

Coastal distance, slope and coastal linearity were the variables that most contributed to the model for unaccompanied adults, at 54%, 24.5%, and 19.3%, respectively. Substrate type was the variable that least contributed to the model (2.2%). However, the jackknife test showed that the absence of any of the variables decreased the AUC value of the model (Fig. 5A).

Mother-calf pairs

All four variables were used in the model and demonstrated good accuracy ($AUC=0.958\pm 0.012$) (Fig. 3B). The prediction map generated by the model

indicated potential hotspots along all coastal areas of the delimited study polygon, but with an occurrence closer to the coast than in the results obtained for the unaccompanied adults (Fig. 6).

Coastal linearity showed the highest contribution (82%) to the model, followed by slope (11.6%), coastal distance (4.6%) and substrate type (1.7%). As described for the unaccompanied adults, the jackknife test showed that the absence of any of the variables decreased the AUC value of the model (Fig. 5B).

DISCUSSION

Historically, southern right whales have existed in Brazil from the south of Bahia State (12.993°S) to the Rio Grande do Sul State (33.743°S) (Lodi et al. 1996). Currently, distribution is limited to southern Brazil, mainly in Santa Catarina state, with sporadic sightings near the north- and southeastern coasts (Lodi et al. 1996, Figueiredo et al. 2017, Renault-Braga et al. 2018). Previous studies have modelled factors that influence right whale distribution in Brazilian breeding grounds (Seyboth et al. 2015), but this is the first study to predict potential breeding hotspots.

Maxent, a “presence-only” model, allowed us to use a dataset of southern right whale sightings that also includes oceanic and neritic areas, even though coastal distribution in the breeding area is a pattern already observed in other breeding grounds (Best 1990, Danilewicz et al. 2016). However, the limited records regarding oceanic areas may be sporadic or represent whales on migratory routes (Zerbini et al. 2017).

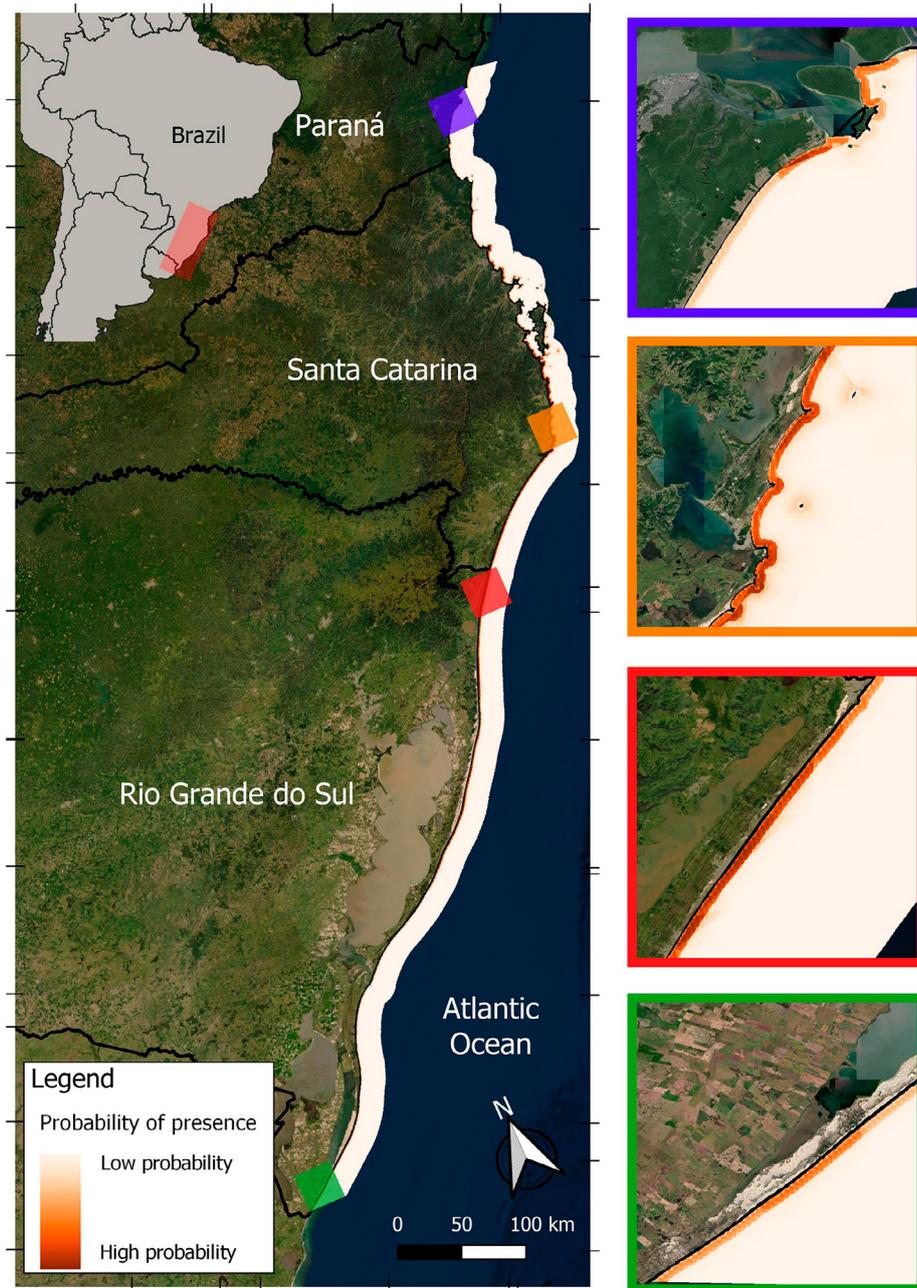


Fig. 6. – Predicted hotspots of mother-calf pairs of southern right whales along the southern Brazilian coast.

The model prediction did not reveal any unsuitable areas along the entire coastal region of the study area (Figs 5 and 6). Currently, stranding events and sightings confirm the occurrence of right whales in Paraná (Instituto Australis, unpublished data) and Rio Grande do Sul (Danilewicz et al. 2016, Greig et al. 2001). The factors influencing whale preferences for Santa Catarina over Paraná and Rio Grande do Sul are unknown. For mother-calf pairs, sheltered areas can be advantageous for calf development, as well as for mothers who fast during the breeding season to save energy (Payne 1986). This may explain the preference for Santa Catarina over Rio Grande do Sul. Santa Catarina has an irregular coastline forming sev-

eral bays that may confer protection against wind and waves, whereas Rio Grande do Sul and Paraná have a straight coastline. The seasonality of the species on the southern coast of Santa Catarina is well documented (Groch 2005, Seyboth et al. 2015, Renault-Braga et al. 2018), whereas from Florianópolis to the north, its occurrence is sporadic but more prevalent than in Paraná and Rio Grande do Sul.

Whaling in Brazil collapsed the right whale population in the 19th century (Morais et al. 2017). The last whaling station in Santa Catarina was closed in 1829 (Ellis 1969), and in the 1950s, when the population had shown some recovery, whaling was reinstated until 1973, when the last right whale was captured in Brazil

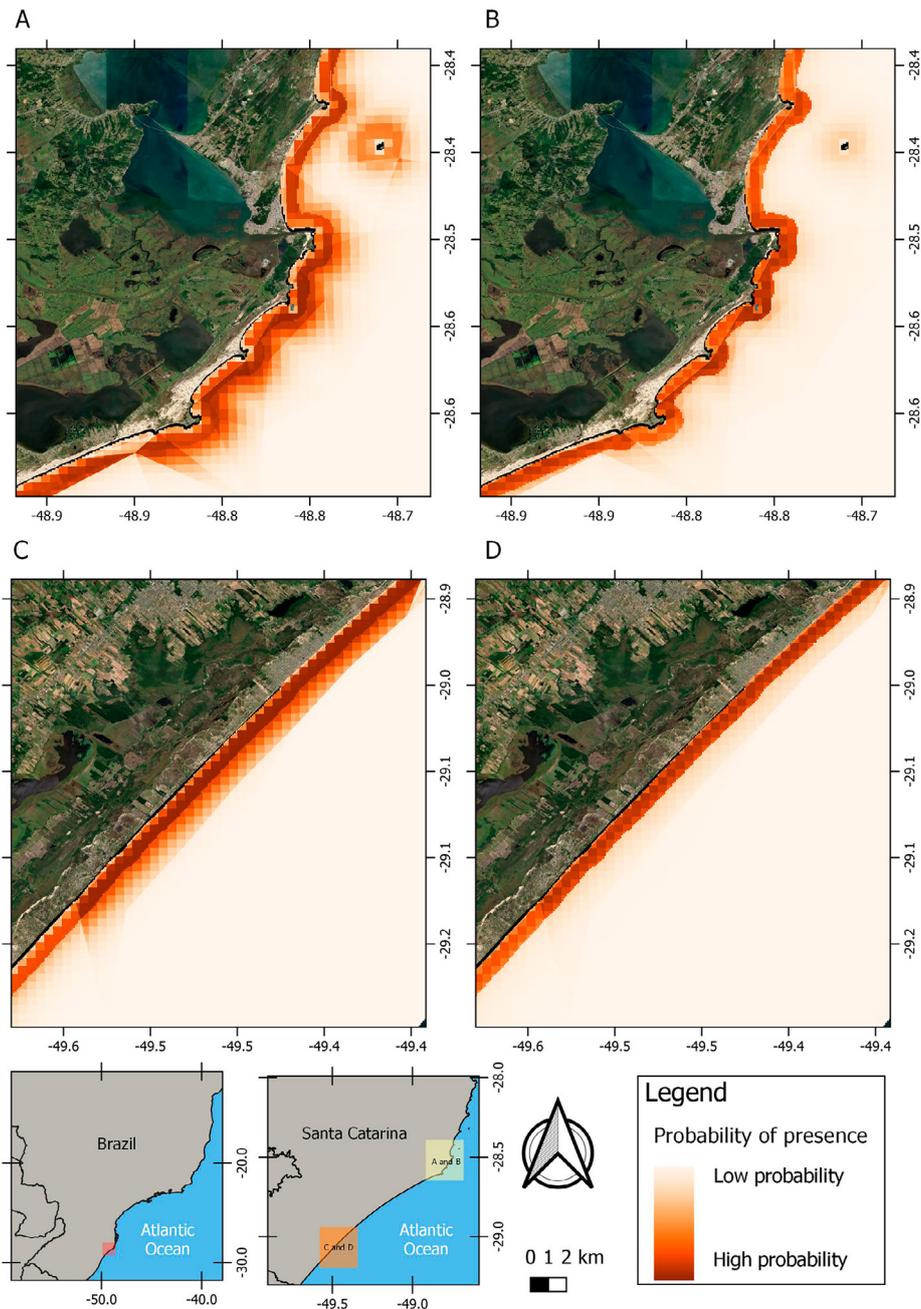


Fig. 7. – Predicted hotspots of southern right whales in southern of Brazil. A and B represent an area of several bays, whereas C and D represent a straight coastline. A and C are predictions of unaccompanied adults and B and D are predictions of mother-calf pairs.

(Palazzo and Carter 1983). Whaling has been officially illegal in Brazil since 1986, and since then, the population has shown some recovery. Right whales show some philopatry to their breeding grounds (Rowntree et al. 2001, Groch et al. 2005), which appears to be transferred by the mother to the calf (Valenzuela et al. 2009). The greater occurrence of right whales between Florianópolis (27.768°S) and Torres (29.367°S) may be related to philopatry of the breeding grounds. It is possible that social information (Oro 2020) regarding the use of areas different from Santa Catarina was lost or severely reduced owing to intense whaling in other regions. However, the recent recovery that has been noted in the Brazilian breeding population (Renault-Braga

et al. 2021a) may cause some bays to reach the carrying capacity, forcing whales to disperse to other bays. This process will possibly result in the gradual recovery of the previous distribution before the whaling impact. In Argentine breeding grounds, mother-calf pairs avoid bays with densities higher than three whales per square kilometre (Sueyro et al. 2018). Although this pattern has not been investigated in Brazil, new areas of occurrence have been reported in recent years (Renault-Braga et al. 2018), suggesting expansion.

Prediction maps showed that hotspots for mother-calf pairs were more coastal than those for unaccompanied adults. The predicted area classified the coastline into two environments: one area formed by

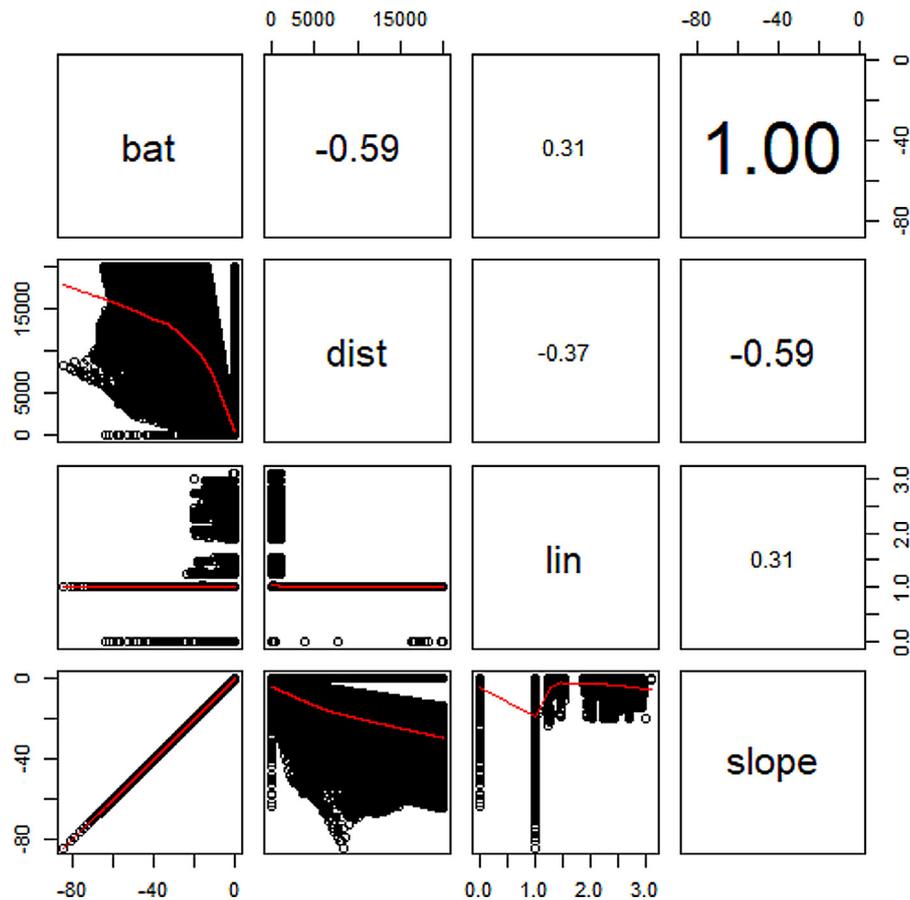


Fig. 8. – Correlation plot of the explanatory variables used to build the models to identify probable breeding hotspots of southern right whales in southern Brazil.

several bays; and one with a straight coastline and consequently more exposure to wind and waves (Fig. 7). This pattern of mother-calf pairs being more coastal than unaccompanied adults occurs in both environments (coast with several bays and straight coastline). There are several advantages for mothers to stay near the coast, such as protection of their calves against waves and wind (Best 1990, Elwen and Best 2004a, Rayment et al. 2015). In breeding areas, right whales have a fasting period. Therefore, they must develop strategies to save energy, mainly for mothers, because nursing calves increase their energy requirements. In addition, mothers must stay longer in breeding areas during calf development than unaccompanied adults (Groch 2005). Therefore, mothers may select sheltered areas to increase their survival and that of their calves (Elwen and Best 2004a, Payne 1986). Proximity to the coast also reduces predation, as these areas are usually shallow and consequently limit predator attack.

The model indicated a higher contribution of unaccompanied adults at further distances from the coast. However, for mother-calf pairs, the model showed a higher contribution to coastal linearity. Factors that are directly related to coastal characteristics, such as coastal linearity, were more influential in whales that were more coastal, justifying the higher contribution of coastal linearity to the model for the mother-calf pair.

Coastal linearity is directly related to the protection of bays against the action of waves and wind, but it has limited influence in areas further away from the coast, where there is little protection. Thus, coastal distance showed more contribution power for models of unaccompanied whales, who possibly frequent areas with little or no protection from the coast.

Staying close to the coast for some species, such as right whales, can create problems if the chosen area is near cities with activities that may impact whales, such as ship collisions (Laist et al. 2001, Conn and Silber 2013), underwater noise disturbances (Clark et al. 2009, Sousa-Lima and Clark 2008, Rolland et al. 2012) and gillnet fishery interactions (Pontalti and Danielski 2011). In the predicted hotspots of the study areas, there are five harbours (from north to south: Paranaguá, São Francisco do Sul, Itajaí, Imbituba and Rio Grande), three of which (Paranaguá, Itajaí and Rio Grande) are commercially active with large ships and maritime traffic. Currently, only the Imbituba harbour has a management plan for the presence of right whales, providing a land-based systematic study throughout its breeding season. Collision can be avoided by reducing vessel speed (Bezamat et al. 2015), and systematic studies can inform vessels of whale presence.

Preference for gently sloping bays is a pattern observed in right whale breeding grounds in South Africa

and New Zealand (Elwen and Best 2004a, Rayment et al. 2015). Slope is a factor used to classify bay morphotypes (Pereira et al. 2009). Right whales are more frequent in dissipative bays (gentle slopes) that reduce the wave force (Seyboth et al. 2015) and consequently save energy for whales.

Substrate type was the variable with the lowest contribution in both models. Despite previous studies indicating that sediment could explain southern right whale distribution (Elwen and Best 2004b), in Brazilian breeding grounds this variable shows no relationship with whale distribution patterns (Renault-Braga et al. 2021b). In South Africa, right whales prefer areas with sandy substrates and avoid rocky regions (Elwen and Best 2004a). In southern Brazil, there is limited substrate variability, with only sand, silt and clay as soft sediments.

The southern right whale is the only locally endangered whale species that breeds in coastal Brazil (ICMBio 2018). This study provides a foundation for management and development strategies for research and conservation, directing these actions to predicted breeding hotspots.

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REFERENCES

- Best P.B. 1990. Trends in the inshore right whale population off South Africa, 1969-1987. *Mar. Mamm. Sci.* 6: 93-108. <https://doi.org/10.1111/j.1748-7692.1990.tb00232.x>
- Bezamat C., Wedekin L.L., Simões-Lopes P.C. 2015. Potential ship strikes and density of humpback whales in the Abrolhos Bank breeding ground, Brazil. *Aquat. Conserv.* 25: 712-725. <https://doi.org/10.1002/aqc.2523>
- Clark C.W., Ellison W.T., Southall B.L., et al. 2009. Acoustic masking in marine ecosystems: Intuitions, analysis, and implications. *Mar. Ecol. Prog. Ser.* 395: 201-222. <https://doi.org/10.3354/meps08402>
- Conn P.B., Silber G.K. 2013. Vessel speed restrictions reduce risk of collision-related mortality for North Atlantic right whales. *Ecosphere* 44: 1:16. <https://doi.org/10.1890/ES13-00004.1>
- Corkeron P.J., Connor R.C. 1999. Why do baleen whales migrate? *Mar. Mamm. Sci.* 15: 1228-1245. <https://doi.org/10.1111/j.1748-7692.1999.tb00887.x>
- Danilewicz D., Moreno IB., Tavares M., Sucunza F. 2016. Southern right whales (*Eubalaena australis*) off Torres, Brazil: group characteristics, movements, and insights into the role of the Brazilian-Uruguayan wintering ground. *Mammalia* 81: 1-10. <https://doi.org/10.1515/mammalia-2015-0096>
- Eliith J., Phillips S.J., Hastie T., et al. 2011. A statistical explanation of MaxEnt for ecologists. *Diversity Distrib.* 17: 43-57. <https://doi.org/10.1111/j.1472-4642.2010.00725.x>
- Ellis M. 1969. A baleia no Brasil colonial. Melhoramentos, São Paulo/SP.
- Elwen S.H., Best P.B. 2004a. Environmental factors influencing the distribution of southern right whales on the south coast of South Africa I: broad scale patterns. *Mar. Mamm. Sci.* 20: 567-582. <https://doi.org/10.1111/j.1748-7692.2004.tb01180.x>
- Elwen S.H., Best P.B. 2004b. Female southern right whale *Eubalaena australis*: Are there reproductive benefits associated with their coastal distribution off South Africa? *Mar. Ecol. Prog. Ser.* 269: 289-295. <https://doi.org/10.3354/meps269289>
- Figueiredo G.C., Santos C.O.M., Siciliano S., Moura J.F. 2017. Southern right whales *Eubalaena australis* in an urbanized area off the southwestern Atlantic Ocean: updated records and conservation issues. *Aquat. Mamm.* 43: 52-62. <https://doi.org/10.1578/AM.43.1.2017.52>
- Greig A.B., Secchi E.R., Zerbini A.N., Dalla Rosa L. 2001. Stranding events of southern right whales, *Eubalaena australis*, in southern Brazil. *J. Cetacean Res. Manag.* 2: 157-160.
- Groch K.R. 2005. Biologia populacional e ecologia comportamental da Baleia Franca Austral, *Eubalaena australis* Desmoulins, 1822, CETACEA, MYSTICETI, no litoral do Brasil. PhD thesis, Univ. Fed. do Rio Grande do Sul, 169 pp.
- Groch K.R., Palazzo Jr. J.T., Flores P.A., et al. 2005. Recent rapid increases in the right whale *Eubalaena australis* population off southern Brazil. *Lat. Am. J. Aquat. Mamm. (LAJAM)* 4: 41-47. <https://doi.org/10.5597/lajam00068>
- ICMBio. 2018. Livro Vermelho da Fauna Brasileira Ameaçada de Extinção volume ii - mamíferos. at https://www.icmbio.gov.br/portal/images/stories/comunicacao/publicacoes/publicacoes-diversas/livro_vermelho_2018_vol2.pdf
- Keller C.A., Garrison L., Baumstark R., et al. 2018. Application of a habitat model to define calving habitat of the North Atlantic right whale in the southeastern United States. *Endang. Species Res.* 18: 73-87. <https://doi.org/10.3354/esr00413>
- Laist D.W., Knowlton A.L., Mead J.G., Colete A.S., Podesta M. 2001. Collision between ships and whales. *Mar. Mamm. Sci.* 17: 35-75. <https://doi.org/10.1111/j.1748-7692.2001.tb00980.x>
- Lobo A.J., Wedekin L.L., Sobral-Souza T., Pendu Y.L. 2021. Potential distribution of Guiana dolphin (*Sotalia guianensis*): a coastal-estuarine and tropical habitat specialist. *J. Mammal.* 102: 308-318. <https://doi.org/10.1093/jmammal/gyaa153>
- Lodi L., Siciliano S., Bellini C. 1996. Ocorrência e conservação de baleias-francas-do-sul, *Eubalaena australis*, no litoral do Brasil. *Papeis Avulsos de Zoologia* 3917: 307-328.
- Martins L.R., Corrêa I.C.S. 1996. Atlas Morphology and sedimentology of the southwest Atlantic coast zone and continental shelf from Cabo Frio Brazil to Península Valdés Argentina. UFRGS-IG-CECO, Porto Alegre.
- Morais I.O.B., Danilewicz D., Zerbini N.A., Bortolotto G.A. 2017. From the southern right whale hunting decline to the humpback whaling expansion: a review of whale catch records in the tropical western South Atlantic Ocean. *Mammal Rev.* 47: 11-23. <https://doi.org/10.1111/mam.12073>
- Merow C., Smith M.J., Silander Jr. J.A. 2013. A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography* 36: 001-012. <https://doi.org/10.1111/j.1600-0587.2013.07872.x>
- Nachtsheim D.A., Jerosch K., Hagen W., et al. 2017. Habitat modelling of crabeater seals (*Lobodon carcinophaga*) in the Weddell Sea using the multivariate approach Maxent. *Polar Biol.* 40: 961-976. <https://doi.org/10.1007/s00300-016-2020-0>
- Oro D. 2020. Perturbation, behavioural feedbacks, and population dynamics in social animals: when to leave and where to go. Oxford University Press, Oxford, 176 pp. <https://doi.org/10.1093/oso/9780198849834.001.0001>
- Palazzo J.T., Carter L.A. 1983. A caça de baleias no Brasil. *Agapan*, Porto Alegre, 25 pp.
- Payne R. 1986. Long-term behavioral studies of the southern right whale *Eubalaena australis*. *Rep. IWC.* 10 (Special Issue): 161-168.
- Pereira M.D., Schettini C.A.F., Omachi C.Y. 2009. Caracterização de feições oceanográficas na plataforma de Santa Catari-

- na através de imagens orbitais. *Rev. Bras. Geof.* 271: 81-93. <https://doi.org/10.1590/S0102-261X2009000100007>
- Philips S.J., Dudík M. 2008. Modeling of species distribution using MAXENT: new extensions and comprehensive evaluation. *Ecography* 31: 161-175. <https://doi.org/10.1111/j.0906-7590.2008.5203.x>
- Philips S.J., Dudík M., Schapire R.E. 2004. A maximum entropy approach to species distribution modeling. *Proc. of the 21^o Int. Con. on Mac. Lea.*, pp. 655-662. <https://doi.org/10.1145/1015330.1015412>
- Philips S.J., Dudík M., Elith J., et al. 2009. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecol. Appl.* 19: 181-197. <https://doi.org/10.1890/07-2153.1>
- Pontalti, M. Danielski M. 2011. Right whale, *Eubalaena australis* Cetacea, Mysticeti, entanglement records in the reproductive season of 2010 in Santa Catarina, Brazil. *Biotemas* 24: 109-112. <https://doi.org/10.5007/2175-7925.2011v24n2p109>
- Rayment W., Dawson S., Webster T. 2015. Breeding status affects fine-scale habitat selection of the southern right whales on their wintering grounds. *J. Biogeogr.* 42: 463-474. <https://doi.org/10.1111/jbi.12443>
- Redfern J.V., Ferguson M.C., Becker E.A., et al. 2006. Techniques for cetacean-habitat modeling. *Mar. Ecol. Prog. Ser.* 310: 71-295. <https://doi.org/10.3354/meps310271>
- Renault-Braga E.P., Groch K.R., Flores P.A.C., et al. 2018. Area usage estimation and spatiotemporal variability in distribution patterns of southern right whales, *Eubalaena australis*, in southern Brazil. *Mar. Ecol. (Berl.)* 39: e12506. <https://doi.org/10.1111/maec.12506>
- Renault-Braga E.P., Groch K.R., Simões-Lopes P.C. 2021a. Numerical population estimates update for Southern Right Whales in Brazil. *Rep. IWC. SC/68C/CMP*.
- Renault-Braga E.P., Groch K.R., Simões-Lopes P.C. 2021b. Is there spatial segregation between reproductive groups of southern right whales along the coastline of southern Brazil? *Mar. Mamm. Sci.*: 10.1111/mms.12797. <https://doi.org/10.1111/mms.12797>
- Rolland R.M., Parks.S.E., Hunt K.E., et al. 2012. Evidence that ship noise increases stress in the right whales. *Proc. R. Soc. B.* 279: 2363-2368. <https://doi.org/10.1098/rspb.2011.2429>
- Rowntree V.J., Payne R.S., Schell D.M. 2001. Changing patterns of habitat use by southern right whales (*Eubalaena australis*) on their nursery ground at Península Valdés, Argentina, and their long-range movements. *J. Cetacean Res. Manag.* 2(Special Issue): 133-143. <https://doi.org/10.47536/jcrm.vi.298>
- Santo SME. 2012. Estudo da distribuição da baleia franca austral *Eubalaena australis* Desmoulins, 1822 Cetartiodactyla, Balaenidae, de acordo com fatores ambientais na costa sul brasileira. Ph.D. thesis, Uni. Fed. Santa Catarina, 123 pp.
- Seyboth E., Groch K.R., Secchi E.R., Dalla-Rosa L. 2015. Habitat use by southern right whales, *Eubalaena australis* Desmoulins, 1822, in their main northern calving area in the western South Atlantic. *Mar. Mamm. Sci.* 314: 1521-1537. <https://doi.org/10.1111/mms.12241>
- Sousa-Lima, R.S., Clark C.W. 2008. Modeling the effect of boat traffic on the fluctuation of humpback whale singing activity in the Abrolhos National Marine Park, Brazil. *Can. Acoust.* 36: 174-181.
- Sueyro N., Crespo E.A., Arias M., Coscarella M.A. 2018. Density-dependent changes in the distribution of Southern Right Whales *Eubalaena australis* in the breeding ground Península Valdés. *PeerJ* 6: e5957. <https://doi.org/10.7717/peerj.5957>
- Valenzuela L.O., Sironi M., Rowntree V.J., Seger J. 2009. Isotopic and genetic evidence for culturally inherited site fidelity to feeding grounds in southern right whales (*Eubalaena australis*). *Mol. Ecol.* 18: 782-791. <https://doi.org/10.1111/j.1365-294X.2008.04069.x>
- Zerbini A.N., Andriolo A., Heide-Jorgensen M.P., et al. 2006. Satellite-monitored movements of humpback whales *Megaptera novaeangliae* in the Southwest Atlantic Ocean. *Mar. Ecol. Prog. Ser.* 313: 295-304. <https://doi.org/10.3354/meps313295>
- Zerbini A.N., Fernandez A., Andriolo A., et al. 2017. Satellite tracking of Southern right whales *Eubalaena australis* from Golfo San Matías, Río Negro Province, Argentina. *Rep. IWC. SC/67B/CMP/17*.
- Zuur A.F., Ieno E.N., Waljer N., et al. 2009. Mixed effects models and extensions in ecology with R. Springer, New York, 572 pp. <https://doi.org/10.1007/978-0-387-87458-6>
- Zuur A.F., Ieno E.N., Elphick C.S. 2010. A protocol for data exploration to avoid common statistical problems. *Methods Ecol. Evol.* 1: 3-14. <https://doi.org/10.1111/j.2041-210X.2009.00001.x>