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Corrigenda

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This article has been modified to correct the third affiliation by removing the word "Albania," which was included by mistake. Additionally, an extra line of keywords at the end of the summary, not belonging to this article, has also been removed.

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Habitat modelling of the southern right whale (*Eubalaena australis*) in the breeding area of southern Brazil

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Summary: Southern right whales migrate seasonally between breeding and feeding grounds, and the southern coast of Brazil is one of their key breeding areas in the Atlantic Ocean. Recent observations suggest a notable decline in whale occurrences in this region since 2015. Since 2015, the occurrence and abundance patterns of right whales in Brazil have changed. To better understand past habitat use and establish a baseline for comparing future distribution trends, we modelled whale distribution using data from aerial surveys conducted between 2003 and 2012, covering the area from Palhoça, Santa Caterina to Torres, Rio Grande do Sul, Brazil. Generalized additive models were employed to assess the influence of environmental and spatio-temporal variables on whale distribution. Our results revealed that whale abundance follows a four-year cycle, which differs from the established three-year reproductive cycle. Higher whale numbers were observed in shallow areas (<10 metres deep) with gentle slopes and near river mouths. The Ribanceira/Ibiraquera region exhibits the highest concentration of whales. These findings provide critical insights into historical habitat preferences and serve as a valuable reference point for evaluating ongoing and future changes in the species' spatial distribution along the Brazilian coast, thereby supporting the development of targeted conservation strategies and more effective management plans for southern right whales in the region.

Keywords: cetaceans; habitat use; distribution; kernel; generalized additive models; hurdle models.

Modelado de hábitat de la ballena franca austral (*Eubalaena australis*) en el área de reproducción del sur de Brasil

Resumen: Las ballenas francas australes migran estacionalmente entre áreas de reproducción y alimentación, siendo la costa sur de Brasil una de sus principales zonas de reproducción en el océano Atlántico. Observaciones recientes sugieren un notable descenso en los avistamientos de ballenas en esta región desde 2015. Desde ese año, los patrones de ocurrencia y abundancia de las ballenas francas en Brasil han cambiado. Para comprender mejor el uso histórico del hábitat y establecer una línea de base que permita comparar las tendencias de distribución futuras, modelamos la distribución de las ballenas utilizando datos de relevamientos aéreos realizados entre 2003 y 2012, abarcando el área desde Palhoça (SC) hasta Torres (RS), Brasil. Se emplearon modelos aditivos generalizados para evaluar la influencia de variables ambientales y espaciotemporales sobre la distribución de las ballenas. Nuestros resultados revelaron que la abundancia de ballenas sigue un ciclo de cuatro años, diferente del ciclo reproductivo de tres años previamente establecido. Se observaron mayores concentraciones de ballenas en áreas someras (menos de 10 metros de profundidad), con pendientes suaves y cercanas a desembocaduras de ríos. La región de Ribanceira/Ibiraquera presentó la mayor concentración de individuos. Estos hallazgos aportan información clave sobre las preferencias históricas de hábitat y constituyen una referencia valiosa para evaluar los cambios actuales y futuros en la distribución espacial de la especie a lo largo de la costa brasileña, apoyando así el desarrollo de estrategias de conservación específicas y planes de manejo más eficaces para la ballena franca austral en la región.

Palabras clave: cetáceos; uso del habitat; distribución; kernel; modelos aditivos generalizados; modelos hurdle.

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INTRODUCTION

The southern right whale, *Eubalaena australis* (Desmoulins 1822), migrates from high latitude feeding grounds to low latitude breeding grounds during the austral winter (Burnell and Bryden 1997). The southern Brazilian coast is a breeding ground for the southwest Atlantic population of southern right whales, which includes Argentina, Uruguay and Brazil (Cummings 1985, Payne 1986, Simões-Lopes et al. 1992, Groch et al. 2005, Costa et al. 2007, Seyboth et al. 2015, Agrelo et al. 2021, Renault-Braga et al. 2018, 2021, Groch and Renault-Braga 2021). In Brazil, right whales were historically found from Bahia State (13.017°S) in northeast Brazil to Rio Grande do Sul (33.766°S), the southernmost state of the country. Currently, they are primarily concentrated along the southern coast of Brazil, particularly between Florianopolis (27.768°S) and Laguna in Santa Catarina State (Renault-Braga et al. 2018; Renault-Braga et al. 2021). While there are regular sightings of southern right whales off the coast of Rio Grande do Sul, especially near Torres (29.367°S) (Danilewicz et al. 2016), their occurrence along other parts further north from Santa Catarina coast is sporadic and limited to occasional records (Lodi et al. 1996, Rossi-Santos et al. 2003, Santos et al. 2001, Figueiredo et al. 2017).

Recent studies have investigated the distribution and abundance of southern right whales in southern Brazil using photo-identification techniques (Groch 2005, Renault-Braga et al. 2021). The population of southern right whales visiting Brazil has been estimated at 397 mature females, with an annual growth rate of 4.8% (±1,2%) (Renault-Braga et al. 2021, 2023). However, these studies have also revealed some concerning trends. Since 2015, a significant decline in whale numbers has been recorded in the region, except in 2018 and 2021 (Renault-Braga et al. 2021). Notably, the 2020 aerial survey reported the lowest number of whales since 2004 (Renault-Braga et al. 2021).

Southern right whales follow a triannual reproductive cycle (Groch et al. 2005), and disruptions to this cycle are often associated with unsuccessful reproduction. Studies have shown that climatic phenomena are associated with the reproductive success of southern right whales in Brazil (Seyboth et al. 2016). Breeding success depends on the whales' body condition, which is directly influenced by foraging success. Foraging, in turn, is affected by climate-driven changes in the abundance of the whales' primary prey, krill (*Euphausia superba*) (Seyboth et al. 2016). Reproductive failure may cause southern right whales to alter their reproductive cycle, leading to intervals that are longer than the species' typical pattern. The species' reproductive cycle typically consists of one year of lactation, one year of rest, and one year of pregnancy. However, the resting year may be extended to two or more years in cases in which the female does not accumulate sufficient energy reserves to support reproduction. This recent changes in whales' occurrence in Brazil may be linked to previously unsuccessful reproduction.

Arriving at breeding grounds with insufficient nutritional reserves may alter distribution and residency patterns in southern right whales. In years of lower energy accumulation, individuals may spend less time in breeding areas and tend to avoid regions with suboptimal conditions, potentially intensifying competition for areas with higher reproductive suitability. This competition can increase the likelihood of calf loss and, consequently, disrupt regular reproductive cycles. In contrast, during years of higher nutritional intake, avoiding competition may be energetically advantageous, as remaining in intermediate-quality areas could reduce overall energetic costs. Moreover, extended residency in breeding grounds may not only facilitate energy-efficient movement between optimal and suboptimal areas but also play a key role in calf motor development, particularly swimming proficiency. Alternatively, it is important to consider that local habitat alterations may contribute to changes in the species' distribution patterns. Studies in Península Valdés, Argentina, have documented shifts in southern right whale distribution within breeding grounds, with evidence of nursery area reconfiguration and abandonment of previously used sites, likely in response to environmental changes and anthropogenic disturbances (Rowntree et al. 2001).

Considering these findings, we propose establishing a baseline of data that describe the spatial and seasonal factors influencing the distribution and abundance of southern right whales in Brazil during the period preceding the observed changes for future comparisons, analysing a dataset spanning from 2003 to 2012. This dataset provides valuable information, as it represents a period during which no major changes in the species' distribution patterns had yet been observed. All studies conducted to assess the southern right whale population in Brazil—from 1987 to 2003 by Groch et al. (2005), and from 2003 to 2012 by Renault-Braga et al. (2018)—indicated a consistent increase in the number of individuals over the years. However, between 2015 and 2017, this abundance declined significantly, reaching levels like those observed in the 1990s (Renault-Braga et al. 2021). Considering this context, to investigate the distribution patterns and the spatial and seasonal factors driving the distribution of southern right whales in Brazil prior to the observed decline in occurrence, we employed habitat modelling methods. On the Brazilian coast, the abundance of southern right whales has been linked to specific factors, including temperature gradients, beach morphotype, bay mouth width, latitude, coast linearity, and seabed type (Seyboth et al. 2015, Renault-Braga et al. 2021).

This study analyses the distribution and relative abundance of southern right whales in relation to environmental values, but we also add temporal variables. The inclusion of temporal variables enables us to assess whether abundance patterns follow the expected trends of the species' reproductive cycles over time, as well as to infer the timing of arrival and departure of whales in the breeding area. Detecting changes in these cycles may indicate increased rates of reproductive failure and allow us to investigate whether the duration of stay in breeding grounds is associated with the mothers' nutritional status (i.e. in years of reduced food availability, reproductive females may remain for shorter periods in the breeding area). Our objective aims to establish a baseline for understanding whale distribution before recent changes in seasonal variation and will provide a foundation for future comparisons with more recent data.

MATERIALS AND METHODS

Data collection

Aerial surveys

The abundance and distribution of southern right whales were assessed through 34 systematic aerial surveys conducted by the Brazilian Right Whale Project between 2003 and 2012. Data were collected by trained observers aboard a helicopter (Bell Jet Ranger), following survey tracks 500 m offshore and parallel to the coastline. Surveys were conducted at an average speed of 100 km h^{-1} and an altitude of 300 m.

The study area extended along the coastline from Torres, Rio Grande do Sul (29.367°S), to Palhoça, Santa Catarina (29.907°S). This region is characterized by a series of bays with sandy or clayey substrates, interspersed with rocky headlands from the northern boundary up to Santa Marta Cape (Carvalho and Rizzo 1994, Pereira et al. 2009). Within this northern section, coves with dissipative morphodynamics are predominant (Silveira et al. 2011). Farther south, the region transitions into a continuous sandy coastline. The slope throughout the study area is gentle, remaining below 3°, and numerous river mouths are distributed along the entire coastline (Fig. 1).

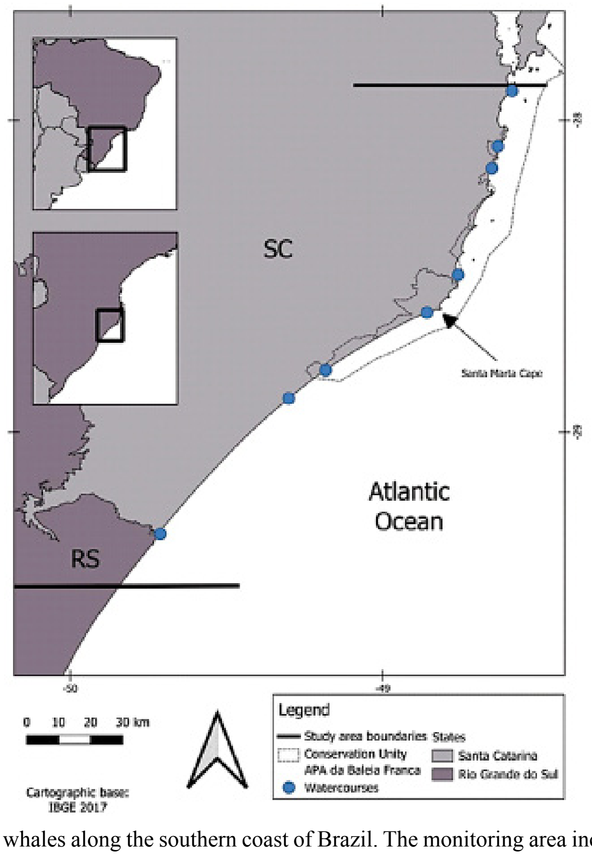

Fig. 1. – Study area for southern right whales along the southern coast of Brazil. The monitoring area includes the Right Whale Environmental Protection Area Conservation Unit. Watercourses, shown in the figure, are highlighted due to the potential environmental impact resulting from waste input associated with urban occupation.

Sampling effort and sighting data

Whale search efforts followed standardized protocols. Three observers were in the aircraft in addition to the pilot (one in front and two in the rear). The main observer sat beside the pilot, on the port side of the aircraft, because of the larger field-of-view in this position. This observer was responsible for searching and recording data such as whale numbers, group composition, GPS location and whale behaviour. The observer behind the pilot searched for whales on the starboard side, took photographs for photo identification and observed whale behaviour and group composition. The third observer sat next to the photographer and beside the main observer, and searched for whales on the port side of the aircraft. The search for whale groups was performed by naked eye. Whenever a whale or group of whales was spotted, they were approached at a minimum height of 100 m, the number of whales was counted, and group composition and GPS position were recorded.

When a whale or group of whales was spotted, the helicopter hovered at an altitude of 100 m to record the latitude and longitude of their location using GPS and to determine group composition. Photographs were taken for photo-identification and to confirm group composition when uncertainties arose. To minimize positional bias, GPS data were recorded simultaneously with photo-identification, as the helicopter needed to be directly above the whales for accurate identification. Sightings were categorized into three categories based on composition: adults without calves, adults with calves, and subadults.

Survey routes were recorded using GPS, and any deviations from the planned route for photo-identification purposes were excluded from the analysis, as no active search for whales was conducted during these deviations. The routes were divided into five-kilometre segments (to follow the evolution of the explanatory variables), each treated as a sampling unit, with the number of whales per segment representing the abundance. The central point of each segment was extracted, and explanatory variables were associated with this point. If the final stretch of the route exceeded 2.5 km, which is half of a standard segment, it was treated as a new segment; segments shorter than 2.5 km were merged with the previous segment.

Explanatory variables

Environmental variables, including geographic and climatological information (Table 1), were imported into ArcGIS 9.2 (ESRI, Redlands, CA) using the UTM 22S projection (WGS 1984). Spatial variables (latitude) and temporal variables (month and year) were also incorporated into the analysis.

Tabla. 1. – Explanatory variables used to model the distribution of southern right whales in the breeding area of southern Brazil.

Explanatory variable	Unit	Resolution	Transformation	Model reference
Month	-	-		month
Sea surface temperature	°C	4 km		SST
Year	-	-		year
Bathymetry	Metres	1:300000		bat
Slope	Degree	1:300000		slope
Seabed surface	Categorical	-		subst
Latitude	Decimal degree	-		lat
Ribanceira–Ibiraquera distance	Metres	-		riba_dist
Watercourse distance	Metres	-	log	river_dist

Note: Not all variables were included in the construction of the final model.

Sea surface temperature (SST) data were obtained from the MODIS platform (http://oceancolor.gsfc.nasa.gov) at eight-day intervals, with temperature values recorded in degrees Celsius with 5 km resolution. Bathymetric data were sourced from digitized nautical charts provided by the Brazilian Navy Centre of Hydrography (scale 1:300,000), and slope data were derived by converting the bathymetric surface using the Slope tool in ArcMap.

Ribanceira/Ibiraquera Bay, located in Imbituba, Santa Catarina, is recognized as the primary area for right whale occurrences in Brazil (Seyboth et al. 2015, Renault-Braga et al. 2018). The distance to Ribanceira/Ibiraquera Bay was used as an explanatory variable because this bay represents the area with the highest abundance of right whales, suggesting that it offers the best environmental conditions for them during the breeding season. It is assumed that these better conditions become progressively less favourable as the distance from this core area increases, thus justifying the inclusion of this variable as a spatial gradient of habitat suitability. Studies conducted in Argentina indicate that the distribution of right whales exhibits a density-dependent pattern, with densities of three individuals per square kilometre being sufficient to trigger the expansion into new occupancy areas (Suyero et al. 2018). We therefore assume that, once a certain density of individuals is reached, whales begin to occupy surrounding areas around Ribanceira/Ibiraquera Bay. The midpoint of the bay was selected to assess its influence on distance. Euclidean distances were calculated between each sample unit and the bay's midpoint. To avoid overlap with land, a semicircle was delineated (using half of the Euclidian distance as measurement of the radius), and the arc length of this semicircle was used to measure distances from Ribanceira/Ibiraquera Bay.

Distances to watercourses were calculated using the same method. Watercourses carry various effluents resulting from anthropogenic activities, which may in some way affect the use of these areas along the coastal region. The geographic positions of watercourses were identified using georeferenced images, and only those with mouth widths ≥50 m were included in the analysis.

Data analysis

Data exploration

Boxplots were used to identify outliers, and pair plots were employed to detect collinearity between variables (defined as r≥|0.7|, Pearson's correlation) (Zuur et al. 2009) (Supplementary Material, Figs S1-S2). A high correlation was observed between month and SST (r=0.75), as well as between distance from Ribanceira/Ibiraquera Bay and latitude (r=–0.96). To determine which of these correlated variables to include in the models, we conducted simple generalized additive model (GAM) analysis, modelling the number of whales with each explanatory variable individually, and selected the variable with the highest explanatory power. The variables chosen were month (13.3%; SST: 9.54%) and distance from Ribanceira/Ibiraquera Bay (6.79%; latitude: 5.05%). Although substrate type showed collinearity with latitude, it did not exhibit collinearity with the distance from Ribanceira/Ibiraquera Bay. Therefore, this variable was retained in the analysis. The distance to watercourses initially displayed outliers, as indicated by the boxplots. These outliers were addressed by applying a log transformation to the variable.

Statistical models

The number of whale sightings was modelled using a suite of GAMs (Zuur et al. 2009). Due to overdispersion in the response variable, the model was structured with a negative binomial distribution and a log link function. Smoothing was performed using thin plate regression splines. Model selection was guided by the Akaike information criterion (AIC), with a backward selection method applied to identify the model with the lowest AIC score. The final model was validated by assessing residuals (Figs S3-S5) and testing for spatial autocorrelation using variogram analysis performed with the geoR package 1.6-34 (Ribeiro and Diggle 2001) and a temporal autocorrelation plot (Fig. S6). To account for differences in sampling effort, the segment length of each sampling unit was included as an offset. All modelling procedures were implemented in R (version 3.0.2) (R Development Core Team 2010) using the *mgcv* package (version 1.7-26) (Wood 2001).

In addition to the regular models, we tested hurdle models to address the excess of zeros in the response variable, as identified during exploratory analysis. We chose to apply and compare methods that address excess zeros with standard models, since hurdle models work separately, indicating that the processes influencing presence/absence may be different from those influencing abundance (Welsh et al. 1996). Therefore, it is recommended to compare the goodness-of-fit (AIC) of both approaches to select the final model (Warton 2005). Hurdle models combine two statistical approaches (Zuur et al. 2009): a binomial model, which estimates the probability of presence; and a zero-truncated model, which models abundance using only the non-zero observations (Zuur et al. 2009). The same protocols used for the regular GAM models were applied to the hurdle models, with two key distinctions: the binomial model employed a binomial distribution, and the zero-truncated model used a gamma distribution. It is important to recognize that in hurdle models, the final interpretation should integrate the variables selected by both (binomial and gamma) models.

Non-significant variables selected by the hurdle model were not excluded from the analysis if they were selected by the negative binomial model, and the model selection was guided by the lowest AIC, even if non-significant variables were included.

RESULTS

Whale counting

Across 34 aerial surveys covering a total of 7047.5 kilometres, 1642 whales were sighted. Each survey consisted of 36 to 43 sampling units, resulting in a total of 1489 sampling unit segments included in the analysis (Table 2).

Tabla. 2. – Survey effort and total number of southern right whale sightings in the breeding area of southern Brazil.

Year	Surveys	Segments	Total distance (km)	Total whales
2003	4	172	866.50	153
2004	5	217	1089.75	128
2005	4	175	875.57	129
2006	4	176	878.53	238
2007	5	219	881.45	277
2008	3	87	435.71	118
2009	1	44	219.23	60
2010	3	134	667.65	142
2011	3	132	465.69	204
2012	3	133	667.41	193
2013	3	134	667.65	142

Generalized additive models

The five best-fitting models are summarized in Table 3. The selected model identified the following variables as significant predictors: month, year, bathymetry, slope, distance from Ribanceira/Ibiraquera bay and distance from watercourses.

Tabla. 3. – Best negative binomial generalized additive models explaining variation in the presence of southern right whales with the selected explanatory variables. Deviance explained and Akaike information criterion values are also presented. The selected model is highlighted in bold. * Variables with p<0.05; ** Variables with p<0.01.

Model	Explained deviance	AIC
month **+ year + bat** + slope* + riba_dist** + river_dist****	**27%**	**3759.1**
month** + year** + slope** + riba_dist** + river_dist**	25.4%	3785.6
month** + year** + riba_dist** + river_dist**	24.9%	3796.1
month* + year* + bat* + slope + riba_dist*	25.2%	3797.9
month** + year** + bat** + riba_dist**	24.8%	3798.8

The response curves of the best-fitting model are presented in Figure 2. The month curve peaks in September, followed by a decline. The year curve reveals an abundance cycle with peaks occurring approximately every four years and a slight upward trend in whale abundance over recent years. The bathymetry curve indicates that whale occurrences are highest at depths between 2 and 5 m, with a decline at deeper depths. The slope curve demonstrates a linear negative relationship with whale abundance. The curve for distance from Ribanceira/Ibiraquera Bay highlights higher whale abundance near this area, while the distance from watercourses curve shows a concave shape.

Although the dataset contained many zeros, the graphical analysis of GAM residuals (Fig. S3) indicates a reasonable fit, with no evidence of spatial autocorrelation in the variogram residuals of the selected model (Fig. 3). This suggests that the model performs well.

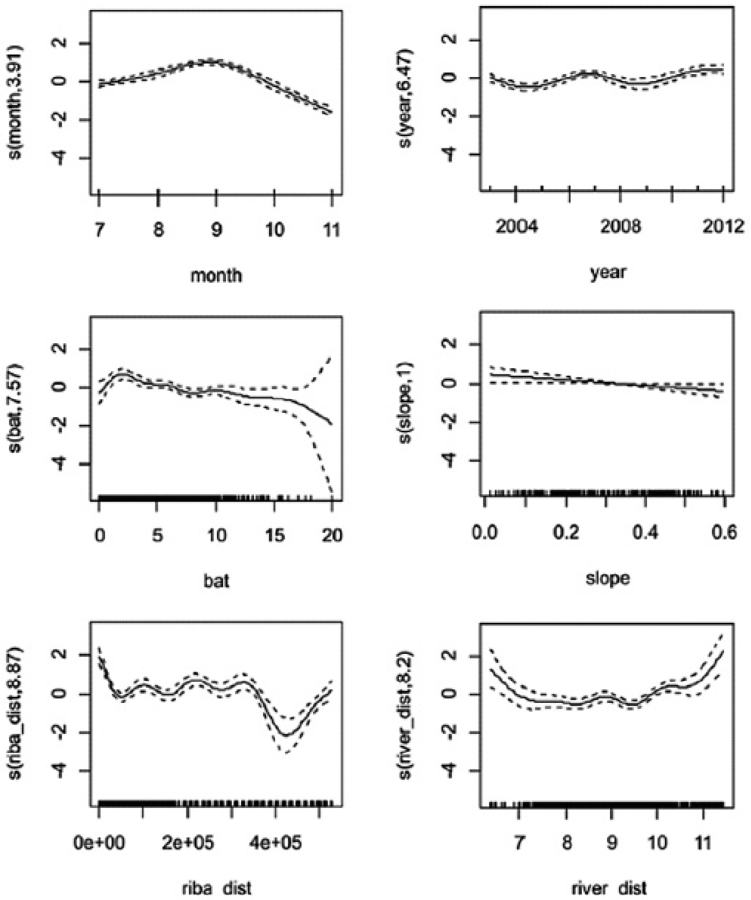

Fig. 2. – Model terms for the negative binomial generalized additive model of southern right whale counts. Estimated smooth functions (solid lines) with 95% confidence interval (dashed lines) are shown for each explanatory variable. y-axis, fitted function with estimated degrees of freedom in parenthesis; x-axis, variable range with rug plots indicating sampled values

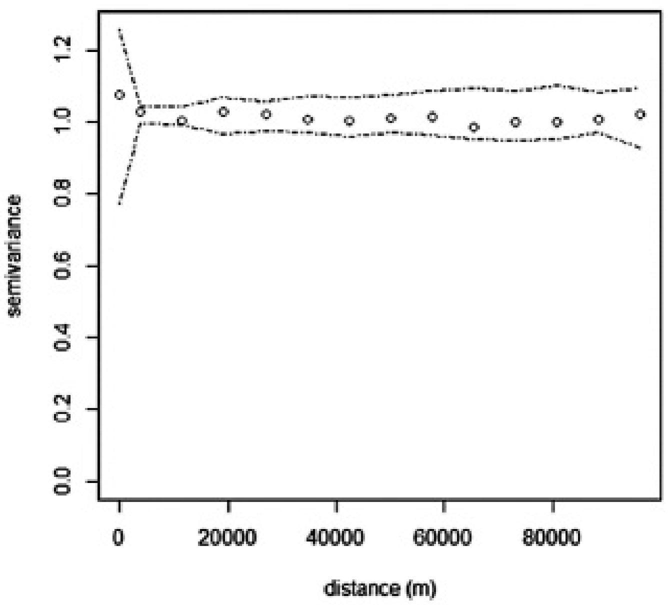

Fig. 3. – Binned variogram with Monte Carlo envelope of deviance residuals from the selected negative binomial generalized additive model for aerial survey data collected between 2003 and 2012.

Generalized additive hurdle model

Binominal model (presence/absence)

The five best-fitting binomial hurdle models are summarized in Table 4. The final model identified the following variables as predictors: month, year, bathymetry, slope, distance from Ribanceira/Ibiraquera Bay and distance from watercourses.

Tabla. 4. – Best binomial hurdle generalized additive models explaining variation in the presence of southern right whales with the selected explanatory variables. Deviance explained and Akaike information criterion values are also presented. The selected model is highlighted in bold. * Variables with p<0.05; ** Variables with p<0.01.

Model	Explained deviance	AIC
month **+ year + bat** + slope + riba_dist** + river_dist**	**13.5%**	**1521.4**
month **+ year** + bat** + slope + riba_dist** + river_dist + subst	13.3%	1522.5
month **+ year** + bat** + slope + riba_dist** + subst	12.6%	1525.4
month **+ year** + bat** + riba_dist*	12.7%	1526.6
month **+ year** + riba_dist** + river_dist*	12.4%	1531.6

The response curves of the best-fitting binomial model are shown in Figure 4. The variables month, slope, distance from Ribanceira/Ibiraquera Bay and distance from watercourses exhibit trends consistent with the response curves estimated by the negative binomial GAM model. The response curve for year displays a clear linear positive relationship, indicating an increase in the occurrence of southern right whales over time. For bathymetry, the curve shows the highest occurrence of whales in areas with depths up to 10 m, followed by a linear decline in occurrence beyond this depth (Fig. 4).

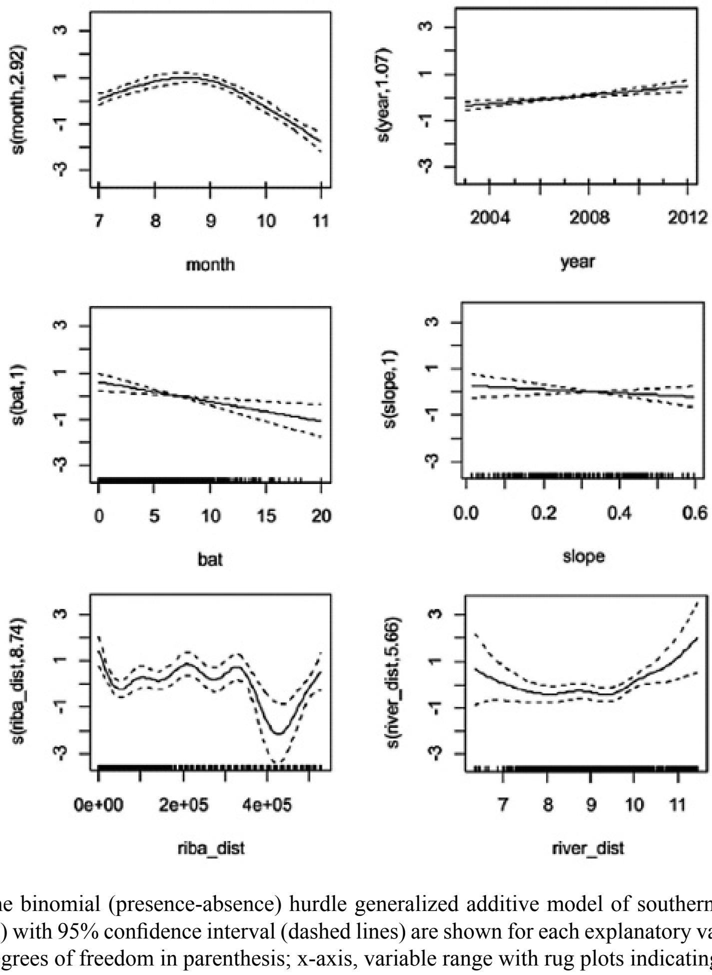

Fig. 4. – Model terms for the binomial (presence-absence) hurdle generalized additive model of southern right whale presence. Estimated smooth functions (solid lines) with 95% confidence interval (dashed lines) are shown for each explanatory variable. y-axis, fitted function with estimated degrees of freedom in parenthesis; x-axis, variable range with rug plots indicating sampled values.

Tabla. 5. – Best binomial hurdle generalized additive models explaining variation in the presence of southern right whales with the selected explanatory variables. Deviance explained and Akaike information criterion values are also presented. The selected model is highlighted in bold. * Variables with p<0.05; ** Variables with p<0.01.

Model	Explained deviance	AIC
month **+ riba_dist**	**22.3%**	**-4704.4**
month **+ slope + riba_dist**	22.7%	-4704.1
month **+ bat + riba_dist**	22.5%	-4703.1
month **+ riba_dist** + river_dist	22.3%	-4702.7
month **+ year + riba_dist**	22.3%	-4702.6

Gamma model (count component)

The five best-fitting gamma models are summarized in Table 5. The final model retained only two variables: month and distance from Ribanceira/Ibiraquera Bay. The response curve for month shows an increase in the number of whales from July to September, followed by a decline. This trend aligns with the patterns observed in the negative binomial GAM model. For distance from Ribanceira/Ibiraquera Bay, the response curve indicates a decrease in the number of whales as the distance from this area increases (Fig. 5).

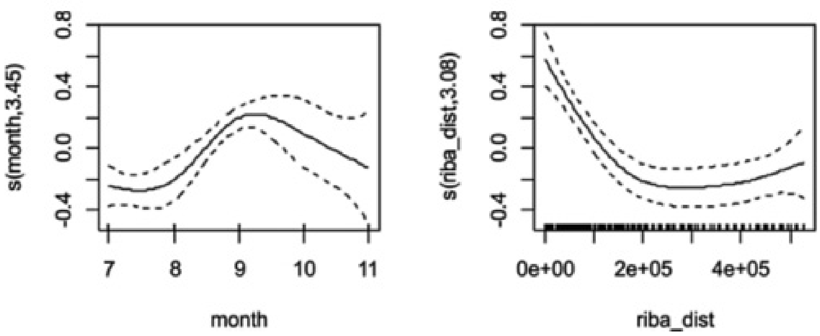

Fig. 5. – Model terms for the gamma hurdle generalized additive model of southern right whale counts. Estimated smooth functions (solid lines) with 95% confidence interval (dashed lines) are shown for each explanatory variable. y-axis, fitted function with estimated degrees of freedom in parenthesis; x-axis, variable range with rug plots indicating sampled values.

DISCUSSION

GAMs have proven to be valuable tools for understanding species-environmental interactions. This method has been widely used and has proven effective in modelling right whale distribution patterns in several breeding grounds (e.g. Keller et al. 2012, Gowan and Ortega-Ortiz 2014, Renault-Braga et al. 2021). In this study, GAMs were shown to be effective tools, and all explanatory variables tested have been previously identified in other studies investigating the distribution of right whales (Cummings 1985, Payne 1986, Best 1990, 2000, Elwen and Best 2004a, 2004b, Keller et al. 2006, Rayment et al. 2012, Seyboth et al. 2015, Renault-Braga et al. 2021, 2021b)

In our study, both the negative binomial and hurdle GAM models identified the same explanatory variables. However, there were notable differences between the two components of the hurdle model, as the gamma model selected only two variables. It is important to recognize that the hurdle model consists of two parts: the binomial model, which estimates the probability of presence/absence, and the gamma model, which models abundance. Therefore, the final interpretation should integrate the variables selected by both models.

Although both the negative binomial and hurdle models selected similar explanatory variables, the interpretation of these models reveals distinct biological implications. The negative binomial model directly relates whale counts to environmental variables, suggesting an association that may be nonlinear, as observed for variables such as month, year, bathymetry, Ribanceira/Ibiraquera and watercourse distances inputs. On the other hand, the hurdle model separates the processes defining whale occurrence (presence/absence) and abundance when present, allowing for the consideration that different ecological or behavioural mechanisms may influence these stages. For example, whale presence may be primarily driven by large-scale environmental conditions or cultural fidelity to specific bays. Fidelity to feeding areas has been previously observed (Valenzuela et al. 2009). Moreover, the high resighting rate of southern right whales in Brazil supports the existence of some degree of fidelity to the reproductive area (Renault-Braga et al. 2023). Regarding abundance (from hurdle), more localized factors may shape distribution patterns, such as areas better suited for calf breeding or areas used to avoiding anthropogenic disturbances. The selection of fewer variables by the gamma component of the hurdle model may reflect these specific conditions necessary to sustain larger aggregations of whales. Therefore, integrating both modelling approaches provides complementary insights, allowing a more detailed understanding of the environmental and possibly behavioural factors influencing the distribution of southern right whales along the Brazilian coast.

All variables in the final negative binomial model were significant in explaining the occurrence of right whales in Brazil. Although the final binomial hurdle model included slope and distance from watercourses, these variables were not significant in explaining the presence/absence of whales.

The month variable was significant in all models. The smooth curves of this variable reveal a clear seasonal pattern of southern right whale occurrence, consistent with previous research (e.g. Groch 2005). In the Brazilian calving grounds, the reproductive season begins in July, peaks in early September and ends in mid-November (Groch et al. 2005). The response curve for abundance, observed in both the negative binomial and gamma hurdle models, peaks in September. Studies in a South African breeding ground have shown that the peak of births occurs in mid-August (Best 1994). After giving birth, whales are likely to reduce their movements between bays to conserve energy and protect their calves, which explains the expected reduction in whale presence adjacent to the bays after calving. On the other hand, the birth of calves leads to an increase in whale abundance and, consequently, in whale density. Research conducted in Argentina indicates that when bay areas reach densities near three whales per km², significant changes are detected in adjacent areas (Sueyro et al. 2018). It was therefore expected that the presence would increase after the birth of the calves. We did not test the density of whales in our models. It is possible that whale densities in the bays of the Brazil have not yet reached the threshold of three whales per km². Furthermore, the presence of mature whales migrating to mate significantly decreases as the season progresses (Groch et al. 2005), which is consistent with our findings. Studies have described a positive relationship between the size of the occurrence area and the number of mature adult whales (males and females in non-calving year) in the region (Renault-Braga, 2014). This increase in the occurrence area appears to be associated with the greater movement of this whales' class along the bays, as they search for potential mates (Renault-Braga 2014). As a result, a reduction in the presence of whales along the bays would be expected.

Southern right whales typically follow a triennial reproductive cycle (Payne 1986, Burnnel and Bryden 1997, Groch et al. 2005), though deviations from this cycle are not uncommon and may be linked to individual reproductive failures (Best et al. 2001, Leaper et al. 2006). Our results indicate an abundance oscillation occurring approximately every four years, which could suggest an unusually high number of females experiencing interrupted reproductive cycles due to calf loss or failure to conceive (Best et al. 2001). This triennial reproductive cycle consists of one year of rest, followed by one year of gestation and one year of lactation. However, reproductive failure can extend the resting phase if the female does not conceive during the expected breeding period, thereby lengthening the overall cycle. The failure to conceive is likely a response to the poor nutrition of the female, and previous studies (Seyboth et al. 2016) have shown that the reproductive cycle of right whales in Brazil is strongly influenced by prey biomass in their feeding grounds, which can be affected by climate phenomena such as El Niño. Climate change has also been associated with changes in survival rates of right whales in Argentina (Agrello et al. 2021). Although we cannot confirm that the observed changes in occurrence cycles in Brazil are directly related to these climate phenomena, we strongly recommend further investigation into the potential correlation between climate change and these fluctuations in reproductive cycle.

Our results suggest an overall increase in whale abundance over the years. Mark-recapture studies in the Brazilian calving grounds have indicated a 4.8% annual population growth rate (Renault-Braga et al. 2021b). Although the best-fitting gamma hurdle model did not select the year variable, suggesting that the number of whales per unit area has not changed significantly over time, the selection of this variable by the binomial hurdle model indicates that new areas have been progressively occupied by whales. This finding aligns with a recent study, which reported the expansion of the population into new areas with higher densities of whales in the region (Renault-Braga et al. 2018).

The bathymetry curve in both the negative binomial and binomial hurdle models clearly indicates a preference for shallower waters, specifically those less than 10 m deep, which is consistent with findings from Argentina and South Africa (Payne 1986, Elwen and Best 2004a). Shallower areas may provide several advantages for females, such as avoiding mating males and offering protection against predators (Payne 1986, Elwen and Best 2004c, Sironi et al. 2008). In breeding areas, North Atlantic right whales tend to prefer waters ranging from 10 to 20 m deep (Keller et al. 2012). In our study area, the coastline from Santa Marta Cape to the northern boundary is more irregular, with the 10 m isobath located just outside the coves, exposing these areas to stronger wave action and winds. Avoiding such conditions may help conserve energy and offer better protection for calves.

The slope variable was selected in both the negative binomial GAM and binomial hurdle models. The curves from both models describe a negative linear relationship between whale abundance and occurrence and increasing slope. In South Africa, southern right whales also show a preference for areas with low slopes (Elwen and Best 2004a, 2004b). A study in Brazilian calving grounds found that beach morphotype (dissipative, reflective or intermediate) significantly influenced the distribution of right whales (Seyboth et al. 2015). Most bays north of Santa Marta Cape were classified as dissipative, characterized by factors such as beach slope and surf zone. Although the region from Torres, Rio Grande do Sul, to Santa Marta Cape, Santa Catarina, shares similar characteristics, we considered these areas comparable due to their slope values, which are closest to those of dissipative bays (slope<3°).

Our results show a decline in whale abundance as we move farther from Ribanceira/Ibiraquera Bay. The gamma hurdle model best represents this trend, as it accounts for whale abundance. Historically, Ribanceira/Ibiraquera Bay has the highest number of right whales in the Brazilian breeding area. This bay offers favourable characteristics for southern right whales, such as shallow depths, sandy substrates, and proximity to river mouths. Other bays in the region share these characteristics but do not support the same whale densities, suggesting the presence of an unexamined variable, possibly behavioural, that could explain this pattern. Despite this, both the negative binomial and binomial hurdle models identify other areas, away from Ribanceira/Ibiraquera Bay, as regions with above-average whale presence.

Baleen whales are known to exhibit site fidelity to their breeding areas (Hoelzel 1998), and southern right whales have also demonstrated fidelity between breeding and feeding grounds. Calves may learn to prefer specific bays from their mothers, resulting in intergenerational site fidelity (Valenzuela et al. 2009). However, we lack information on whale abundance in Ribanceira/Ibiraquera Bay prior to the hunting period, as historical whale catches were not categorized by bay. The high whale density observed in this bay post-hunting, from the 1980s to the present, corresponds to the recovery of whale populations. As result, we cannot assume that recent site fidelity to this area reflects a long-standing historical pattern. To better understand individual site fidelity in Brazil, further studies involving genetics, photo-identification and telemetry are essential.

In South Africa, whale abundance has been positively correlated with proximity to river mouths, which are believed to offer potential benefits such as skin exfoliation and the removal of external parasites (Elwen and Best 2004b). On the other hand, we do not dismiss the possibility that freshwater input may induce physical and chemical changes in the water, potentially influencing whale preference for these areas. We must consider that these chemical changes may be an anthropogenic consequence, due to the high level of urbanization in the region, as we would also expect a greater amount of pollutant compounds being carried by the local watercourses. A resident population of bottlenose dolphins (*Tursiops truncatus*) in the estuarine system of Laguna, which is located within our study area, has shown a chronic skin condition that has been associated with chemical pollution and environmental degradation in the region (Daura-Jorge and Simões-Lopes 2011). While the negative binomial model suggests a decline in whale abundance as distance from river mouths increases, this trend is not significant in the hurdle model curve. However, this curve does not provide biological insights that would help explain the preference for these areas. Along the coastline, numerous streams discharge into the bays, though these streams were not included in the modelling due to their narrow mouths. These streams may, nevertheless, provide a sufficient freshwater supply to meet whales' needs.

The moderate explanatory power of the selected models suggests that one or more key variables influencing the distribution and abundance of southern right whales in the region may be missing. Behavioural and cultural factors likely contribute to these missing variables (e.g. Hastie et al. 2004), but they are difficult to measure and incorporate objectively in such models. Southern right whales display some degree of philopatry to feeding areas (Valenzuela et al. 2009), and photo-identification studies confirm site fidelity to breeding areas in both South Africa (e.g. Best 2000) and Brazil (e.g. Groch 2005). Therefore, a comprehensive understanding of whale distribution in the region would ideally consider not only environmental factors but also cultural and behavioural aspects. Southern right whales are considered capital breeders, relying on energy reserves accumulated during the feeding season and undergoing prolonged fasting throughout the reproductive phase (Roman et al. 2025). Consequently, identifying local variables that would indicate a predator-prey relationship is not necessary for a study at this local scale.

The recent changes in distribution patterns and occurrences of right whales in Brazil, not included in this study, are concerning, particularly results for the year 2016, which saw the lowest number of whales within an 18-year dataset (Renault-Braga et al. 2023). How the demographic parameters of this population will behave in the coming years will directly influence the species' distribution patterns in the region. Our results establish a baseline for future assessments of distributional changes in southern right whales along the Brazilian coast. These data will be critical for disentangling the drivers of recent shifts (Renault-Braga et al. 2022), whether they stem from regional-scale processes, such as habitat degradation or changes in local environmental conditions within breeding grounds, or from broader, global-scale phenomena, including climate-driven alterations in prey availability and productivity in feeding areas.

SUPPLEMENTARY MATERIAL

The following supplementary material is available through the online version of this article:

Fig. S1. Boxplots showing the distribution of explanatory variables used in the models.

Fig. S2. Pair plots illustrating the relationships among explanatory variables used in the models. These plots were used to assess collinearity and guide variable selection.

Fig. S3. Residuals of the selected negative binomial generalized additive models.

Fig. S4. Residuals of the selected binomial generalized additive hurdle models.

Fig. S5. Residuals of the selected gamma generalized additive hurdle models.

Fig. S6. Temporal autocorrelation plot of whale abundance in Brazilian calving grounds from 2003 to 2013.

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AUTHORS' CONTRIBUTION STATEMENT

Eduardo Pires Renault-Braga: Conceptualization, Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing. **Karina R. Groch**: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Writing – review & editing. **Eduardo Resende Secchi**: Conceptualization, Investigation, Methodology, Writing – review & editing. **Luciano Dalla Rosa**: Conceptualization, Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing.

REFERENCES

Agrelo M., Daura-Jorge F., Rowntree VJ., et al. 2021. Ocean warming threatens southern right whale population recovery. Sci. Adv. 7(42): eabh2823. https://doi.org/10.1126/sciadv.abh2823

Best P.B. 1990. Trends in the inshore right whale population off South Africa, 1969-1987. Mar. Mam. Sci. 6(2): 93-108. https://doi.org/10.1111/j.1748-7692.1990.tb00232.x

Best P.B. 1994. Seasonality of reproduction and length of gestation in southern right *whales Eubalaena australis*. J. Zoo. 232: 175-189. https://doi.org/10.1111/j.1469-7998.1994.tb01567.x

Best P.B. 2000. Costal distribution, movements and site fidelity of right whales *Eubalaena australis* off South Africa, 1969–1998. S. A. J. Mar. Sci. 22: 43-55. https://doi.org/10.2989/025776100784125618

Best P., Brandão A., Butterworth D.S. 2001. Demographic parameters of southern right whales off South Africa. J. Cetacean Res. Manage. (Special Issue 2): 161-169. https://doi.org/10.47536/jcrm.vi.296

Burnell S.R., Bryden M.M. 1997. Costal residence periods and reproductive timing in south right whale *Eubalaena australis*. J. Zoo. London. 241: 613-621. https://doi.org/10.1111/j.1469-7998.1997.tb05736.x

Carvalho V.C., Rizzo H. 1994. A zona costeira brasileira: subsídios para uma avaliação ambiental. Brasília, Ministério do meio ambiente. 211 pp.

Costa P., Piedra M., Franco P. et al. 2007. Distribution and habitat use patterns of southern right whales, *Eubalaena australis*, off Uruguay. J. Cetacean Res. Manage. 9(1): 45-51. https://doi.org/10.47536/jcrm.v9i1.691

Cummings WC. 1985. Right Whales: *Eubalaena glacialis* (Muller, 1776) and *Eubalaena australis* (Desmoulins, 1982). In: Ridgway, S.H. and Harrison, R. (eds), Handbook of Marine Mammals. Volume 3, The Sirenians and Baleen Whales. Academic Press Inc., London, pp. 275-304.

Danilewicz D., Moreno I.B., Tavares M., et al. 2016. Southern right whales (*Eubalaena australis*) off Torres, Brazil: Group characteristics, movements, and insights into the role of the Brazilian-Uruguayan wintering ground. Mamm. 81(3): 225-234. https://doi.org/10.1515/mammalia-2015-0096.

Daura-Jorge F.G., Simões-Lopes P.C. 2011. Lobomycosis-like disease in bottlenose dolphins *Tursiops truncatus* of the estuarine system of Laguna, southern Brazil: associated factors and pathologic characteristics. Dis. Aquat. Org. 93: 163-170. https://doi.org/10.3354/dao02293

Elwen S.H., Best P. 2004a. Environmental factors influencing the distribution of southern right whales (*Eubalaena australis*) on the south coast of South Africa I: Broad scale patterns. Mar. Mam. Sci. 20(3): 567-582. https://doi.org/10.1111/j.1748-7692.2004.tb01180.x

Elwen S.H., Best P. 2004b. Environmental factors influencing the distribution of southern right whales (*Eubalaena australis*) on the south coast of South Africa II: Within Bay Distribution. Mar. Mam. Sci. 20(3): 583-601. https://doi.org/10.1111/j.1748-7692.2004.tb01181.x

Elwen S.H., Best P, 2004c. Female southern right whale *Eubalaena australis*: Are there reproductive benefits associated with their costal 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. et al. 2017. Southern Right Whales (*Eubalaena australis*) in an Urbanized Area off the Southwestern Atlantic Ocean: Updated Records and Conservation Issues. Aqu. Mamm. 43(1): 52-62. https://doi.org/10.1578/AM.43.1.2017.52

Gowan T.A., Ortega-Ortiz J.G. 2014. Wintering Habitat Model for the North Atlantic Right Whale (*Eubalaena glacialis*) in the Southeastern United States. Plos One. 9(4): e95126. https://doi.org/10.1371/journal.pone.0095126

Groch K.R. 2005. Biologia populacional e ecologia comportamental da baleia franca austral, *Eubalaena australis* (Desmoulins, 1822), CETACEA, MYSTICETI, no litoral sul do Brasil. PhD thesis, Universidade Federal do Rio Grande do Sul, Porto Alegre, RS. 168 pp.

Groch K.R., Palazzo Jr J.T., Flores P.A.C., et al. 2005. Recent rapid increases in right whale (*Eubalaena australis*) population off southern Brazil. Lat. Ame. J. Aqu. Mamm. 4(1): 41-47. https://doi.org/10.5597/lajam00068

Groch K.R., Renault-Braga E.P. 2021. A baleia do sul do Brasil: Uma gigante no nosso litoral. Imbituba/SC, Carbo: 136 pp.

Hoelzel A. 1998. Genetic structure of cetacean populations in sympatry, parapatry, and mixed assemblages: implications for conservation policy. J. Hered. 89: 451-458. https://doi.org/10.1093/jhered/89.5.451

Keller C.A., Ward-Geiger L.I., Brooks W.B., et al. 2006. North Atlantic right whale distribution in relation to sea-surface temperature in the southeastern United States calving ground. Mar. Mam. Sci. 22(2): 426–445. https://doi.org/10.1111/j.1748-7692.2006.00033.x
Keller C.A., Garrison L., Baumstark R., et al. 2012. Application of habitat model of the North Atlantic right whale in the southeastern United States. End. Spe. Res. 18: 73-87. https://doi.org/10.3354/esr00413
Leaper R., Cooke J., Trathan P., et al. 2006. Global climate drives southern right whales (*Eubalaena australis*) population dynamics. Biol. Lett. 2: 289-292. https://doi.org/10.1098/rsbl.2005.0431
Lodi L., Sciciliano S., and Bellini C. 1996. Ocorrência e conservação de baleias-francas-do-sul, *Eubalaena australis*, no litoral do Brasil. Pap. A. Zoo. 39(17): 307-328. https://doi.org/10.11606/0031-1049.1994.39.p307-328
Payne R. 1986. Long-term behavioral studies of the southern right whales (*Eubalaena australis*). Rep. Int. Whal. Comm. (Sp. Issue 10): 161-168.
Pereira M.D., Schettini C.A.F., Omashi C.Y. 2009. Caracterização de feições oceanográficas na plataforma de Santa Catarina através de imagens orbitais. R. Bra. Geof. 27(1): 81-93. https://doi.org/10.1590/S0102-261X2009000100007
Rayment W., Davidson A., Dawson S., et al. 2012. Distribution of southern right whales on the Auckland Islands calving grounds. N. Z. J. Mar. Freshwater Res. 46(3): 431-436. https://doi.org/10.1080/00288330.2012.697072
Renault-Braga E.P. 2014. Distribuição espaço-temporal da baleia-franca-austral – *Eubalaena australis* (Desmoulins, 1822) – no sul do Brasil. PhD thesis, Univ. Federal do Rio Grande, 115 pp.
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*, of southern Brazil. Mar. Ecol. 39(3): e12506. https://onlinelibrary.wiley.com/doi/abs/10.1111/maec.12506.
Renault-Braga E.P., Groch K.R, Simões-Lopes P.C. 2021a. Is there spatial segregation between reproductive groups of southern right whales along the coastline of southern Brazil? Mar. Mam. Sci. 37(3): 1008-1021. https://doi.org/10.1111/mms.12797
Renault-Braga E.P., Groch K.R., Simões-Lopes P.C. 2021b. Numerical population estimates update for Southern Right Whales in Brazil. Papers submitted to the 75 IWC , SC/68C/CMP/10.
Renault-Braga E.P., Groch K.R., Simões-Lopes P.C. 2022. Predicting the breeding hotspots of the southern right whale, *Eubalaena australis* (Cetartiodactyla: Mysticeti), along the southern Brazilian coastline. Sci. Mar. 86(2): e031. https://doi.org/10.3989/scimar.05223.031
Renault-Braga E.P., Groch K.R., Simões-Lopes P.C. 2023. How many are they? Estimates of demographic patterns of reproductive females of southern right whale (*Eubalaena australis*) in the southern coast of Brazil. Mar. Ecol. 44(2): e12744. https://doi.org/10.1111/maec.12744
Ribeiro P.J., Diggle P.J. 2001. geoR: A package for geostatistical analysis. R News. 1: 15-18. https://doi.org/10.32614/CRAN.package.geoR
Roman J., Estes J.A., Morissette L., et al. 2025. Migrating baleen whales transport high-latitude nutrients to low-latitude ecosystems. Nat. Commun. 16: 12345. https://doi.org/10.1038/s41467-025-56123-2
Rossi-Santos M., Wedekin L.L., Souza-Lima R.S. 2003. Distribution and habitat use of small cetaceans of Abrolhos Bank, eastern Brazil. Lat. Ame. J. Aqu. Mamm. 5(1): 23-28. https://doi.org/10.5597/lajam00088
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 in their long-range movements. J. Cetacean Res. Manag. (Spec. Iss. 2): 133–143. https://doi.org/10.47536/jcrm.vi.298
Santos C.O.M., Siciliano S., Souza S.P.D.E. et al. 2001. Occurrence of southern right whale along southeastern Brazil. J. Cetacean Res. Manage. (Special Issue 2): 153-156
Seyboth E., Groch K.R., Secchi E.R. et al. 2015. Habitat use by southern right whales, *Eubalaena australis* (Desmoulins, 1822), in their main northern most calving area in the western South Atlantic. Mar. Mam. Sci. 31: 1521–1537. https://doi.org/10.1111/mms.12241.
Seyboth E., Groch K.R., Dalla Rosa L., et al. 2016. Southern right whale (*Eubalaena australis*) Reproductive success is influenced by krill (Euphausia superba) density and climate. Sci. Rep. 6: 28205. https://doi.org/10.1038/srep28205
Silveira L.F., Klein A.H.F. Tessler M.G. 2011. Classificação morfodinâmica das praias do Estado de Santa Catarina e do litoral norte do Estado de São Paulo utilizando sensoriamento remoto. B. J. Aqu. Sci. Tech. 15(2): 13-28. https://doi.org/10.14210/bjast.v15n2.p13-28
Simões-Lopes P.C., Palazzo Jr J.T., Both M.C; et al. 1992. Identificação, movimentos e aspectos biológicos da baleia franca austral (*Eubalaena australis*) na costa sul do Brasil. In: 3° Reunión de Trabajo de Expertos en Mamíferos Acuáticos de América del Sur, Montevideo (Uruguai).
Sironi M., López J.C., Bubas R. et al. 2008. Predation by killer whales (*Orcinus orca*) on southern right whales (*Eubalaena australis*) of Patagonia, Argentina: effects on behavior and habitat choise. J. Cetacean Res. Manage. SC/60/BRG29.
Sueyro N., Crespo E.A., Arias M. et al. 2018. Density-dependent changes in the distribution of Southern Right Whales (*Eubalaena australis*) in the breeding ground Peninsula Valdés. PeerJ. 6(6): e5957. https://doi.org/10.7717/peerj.5957
Valenzuela L., Sironi M., Rowntree V.J. et al. 2009. Isotopic and genetic evidence for culturally inherited site fidelity to feeding grounds in Southern right whales (*Eubalaena australis*). Mol. Eco. 18: 782-791. https://doi.org/10.1111/j.1365-294X.2008.04069.x
Warton D.I. 2005. Many zeros does not mean zero inflation: comparing the goodness-of-fit of parametric models to multivariate abundance data. Environmet. 16(3): 275-289. https://doi.org/10.1002/env.702
Welsh A.H, Cunningham R.B, Donnelly CF, et al. 1996. Modeling the abundance of rare species: statistical models for counts with extra zeros. Ecol. Model. 88(1-3): 297–308. https://doi.org/10.1016/0304-3800(95)00113-1
Wood S.N. 2001. Mgcv: GAMs and generalized ridge regression for R. R News. 1: 20-25.
Zuur A.F., Ieno E.N., Walker N., et al. 2009. Mixed effects models and extensions in ecology with R. New York, Springer. 572 pp. https://doi.org/10.1007/978-0-387-87458-6