Blue shark (*Prionace glauca*) occurrence and relative abundance in the western South Atlantic Ocean influenced by spatiotemporal variability, environmental variables, and oceanographic processes

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ABSTRACT

The aim of this study was to evaluate spatiotemporal patterns in the distribution and relative abundance of blue sharks and their relationship with environmental variables and oceanographic processes in the southwestern Atlantic Ocean. We modeled data on catch records from the Brazilian pelagic tuna longline fleet using generalized additive models (GAMs). The distribution of *Prionace glauca* was influenced by salinity, chlorophyll-a and temperature. Our models showed that both the catch per unit of fishing effort (CPUE) and the probability of presence increased mainly between March and August. The CPUE was also influenced by ocean depth and sea surface height, and the probability of occurrence by ocean fronts and slope. The highest CPUE values and probability of occurrence of blue sharks tended to occur mainly in parts of the continental slope off Brazil and at the Rio Grande Rise, characterized by the presence of seamounts. Such hotspots for *P. glauca* could potentially be considered in fisheries management plans.

1. Introduction

Most habitat studies are concerned with patterns of abundance and distribution of species and how these patterns vary over time and space (Gotelli, 2009). Identifying the distribution of species and their associations with specific habitat features is necessary for conservation and management (Reese et al., 2011). Studies in marine ecosystems, however, demonstrate the complexities involved in such associations within these heterogeneous environments (Ainley et al., 2009; Reese et al., 2011).

In marine ecosystems, the relationship between species distribution and environmental factors, in addition to their spatiotemporal dynamics, has been addressed by numerous studies, including for highly migratory species such as oceanic elasmobranchs (e.g., Coelho et al., 2018; Mourato et al., 2008). In southern Brazil, elasmobranchs constitute an important component of the marine megafauna in both diversity and abundance (Chelotti and Santos, 2020; Vooren and Oddone, 2019).

In recent decades, population declines in oceanic sharks have been widely attributed to pelagic longline fisheries (Worm et al., 2013). Elasmobranchs can be caught by various types of fishing gear (Dulvy et al., 2017), such as bottom trawls, longlines and gillnets, intentionally or as bycatch (Stevens et al., 2000; Costa and Chaves, 2006), but most catches occur as bycatch on pelagic longlines targeting swordfish (*Xiphia gladius*) and tuna (*Thunnus* spp) (Coelho et al., 2018; Hazin et al., 2008).

In the South Atlantic Ocean, most pelagic shark catches also occur in surface longline fisheries targeting tuna and swordfish (Bonfil, 1994). The catch composition of the Brazilian tuna longline fleet and the relative proportion of various elasmobranch species change markedly with fishing area, effort strategy, and season (Hazin et al., 2008; Mourato et al., 2011) due to the environmental preferences of these species throughout its life cycle, which affects its geographic distribution (Rivera, 2004).

One of the most caught species of pelagic longline fishers in southern Brazil is the blue shark *Prionace glauca* (Amorim et al., 1998;

FURG/SEMA, 2020; Lucena-Frédou et al., 2015; Mourato et al., 2011). *Prionace glauca* is a large oceanic pelagic predator (Campana et al., 2005) with a cosmopolitan distribution (Chang and Liu, 2009) that occurs in tropical and temperate waters of all oceans between 60°N and 50°S (Abascal et al., 2011; Compagno et al., 2005). The abundance of *P. glauca* varies seasonally with some environmental characteristics (Carvalho et al., 2011; Damalas and Megalofonou, 2010), such as changes in sea surface temperature (Montealegre-Quijano and Vooren, 2010), chlorophyll-a concentration (Mourato et al., 2008) and sea level anomalies (Selles et al., 2014). Furthermore, oceanic fronts influence the distribution and abundance of this species (Compagno, 1984; Montealegre-Quijano and Vooren, 2010).

Although *P. glauca* is mainly oceanic, it can occasionally be found near the coast in areas where the continental shelf is narrow (Nakano and Seki, 2003). In general, ocean waters are less productive with lower diversity than coastal areas (Pikitch et al., 2008), but there are productivity hotspots in the open ocean (Worm et al., 2003), generally associated with marine fronts (Lucifora et al., 2012) or physiographic structures such as seamounts (Morato et al., 2010; Worm et al., 2003). These areas of high productivity can vary seasonally according to oceanographic conditions, often causing species inhabiting these regions to have to migrate or move long distances (Block et al., 2001).

In addition, seamounts are also areas of recognized productivity responsible for the aggregation of great biodiversity in deep-sea regions (Morato et al., 2010), which can potentially influence the abundance and diversity of elasmobranchs (e.g., Klimley et al., 2008), noting that the probability of catching these species increases near seamounts (Morato et al., 2010). In this regard, the Rio Grande Rise (RGR) is a region of seamounts in the Southwest Atlantic (Montserrat et al., 2019). The topographic features of the RGR probably cause turbulent submarine flows and upwelling foci that favor high biological productivity (e. g., Boehlert, 1988), attracting higher trophic level predators such as *Prionace glauca* (Carvalho et al., 2010).

The abundance and species richness in seamounts and on the continental slope, one of the richest and most productive regions of the ocean, have been proposed to be similar and respond to the same environmental variables, but there are still few studies that support this theory (Clark et al., 2010). Therefore, considerable attention has been directed to the identification of areas of higher occurrence of some species and the biophysical relationships associated with these ecologically important areas (Reese and Brodeur 2006; Reese et al., 2011; Sydeman et al., 2006).

The objective of this study was to evaluate spatiotemporal patterns in the distribution and relative abundance of blue sharks and their relationship with oceanographic processes and environmental variables in the western South Atlantic Ocean using a long time series ranging from 2002 to 2018. Another goal was to identify areas of greatest importance for blue sharks within the region.

2. Materials and methods

2.1. Study area

The study area comprises the epipelagic oceanic zone of the western South Atlantic, between 18°S–40°S and 20°W-55°W (Fig. 1), composed of the continental slope and the international oceanic region, which includes the Rio Grande Rise. The area is governed by the western branch of the South Atlantic anticyclone, formed from the meeting of the Brazil Current, a mass of tropical water, which borders the Brazilian coast toward the south, transporting warm and saline waters, with the Malvinas Current, of subantarctic origin, which flows northward, carrying cold, nutrient-rich waters (Stramma and England, 1999). The confluence of these two water masses constitutes the western end of the subtropical convergence of the South Atlantic, which results in the formation of a subtropical water mass with its own characteristics, thus marking a seasonal variation in temperature (Piola et al., 2000). This
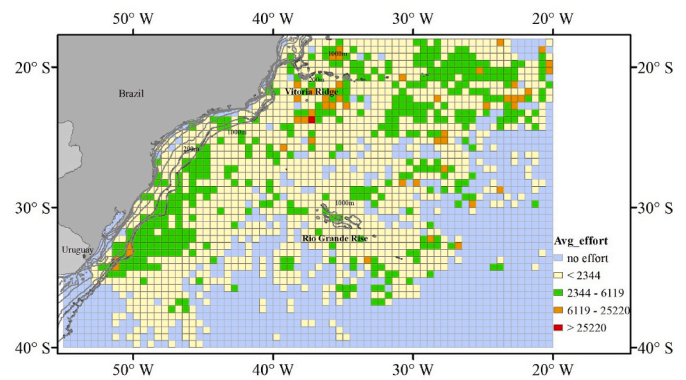

Fig. 1. Study area and spatial distribution of the average monthly fishing effort (number of hooks) carried out by the Brazilian pelagic longline fleet from 2002 to 2018 in the western South Atlantic Ocean (18°S-40°S and 20°W–55°W). Grid cells correspond to 0.5 × 0.5°.

seasonal variation is known as the Central Water of the South Atlantic (Garcia, 1997), which penetrates the coastal region over the continental shelf during the summer and retreats to areas farther away from the coast during the winter (Pires-Vanin et al., 1993).

Along the Brazil Current, there are places with recurrent vortex formation: Vitória (20°S), Cabo de São Tomé (22°S) and Cabo Frio (23°S) (Calado et al., 2006). Under the highly stable and permanently stratified oligotrophic waters of the South Atlantic Subtropical Gyre is the Rio Grande Rise. In this area, the main reservoir of new nutrients is the Central Water mass of the South Atlantic, the formation of vortices and the circulation of the Taylor Column (Montserrat et al., 2019), in addition to the upwelling of the deep water masses of Antarctica (Boebel et al., 1997), resulting in local increases in productivity (Montserrat et al., 2019).

2.2. Data collection

Catch and fishing effort data recorded in logbooks of the Brazilian pelagic tuna longline fleet, including both national and chartered vessels, were obtained from the National Database of Tuna and Tuna-like Species Fishing (BNDA) of the Brazilian Government. In addition, we obtained catch and fishing effort data registered in logbooks of the pelagic longline fleet based in Rio Grande do Sul State, collected in the framework of the "Blue Shark Project" (FURG/SEMA, 2021). This project is coordinated by the Laboratory of Demersal and Cephalopod Fishery Resources of the Federal University of Rio Grande - FURG. Data from the BNDA for the period 2002 to 2018 and those from the "Blue Shark Project" between 2017 and 2018 were analyzed.

The Brazilian pelagic longline fisheries is characterized by subsurface sets that start at dusk and night l harvesting a multi-specific catch, with tuna (*Thunnus* sp), swordfish (*Xiphias gladius*) or, sometimes, sharks as the main target species. Logbook data included records of individual fishing sets, including flag identification, effort (number of hooks), date, schedules of the longline set, location of fishing grounds (latitude and longitude) and the number of blue sharks caught in each set. For the study area, a grid of 0.5 × 0.5° cells was created. In each cell, the number of individuals and total monthly effort were calculated. Each geographical cell where there was fishing effort was our sampling unit (Fig. 1).

2.3. Environmental and physiographic variables

The data used in the statistical modeling included environmental variables derived from remote sensing and from monthly temporal resolution and static physiographic variables (Table 1). Sea surface temperature (SST; °C) and chlorophyll-a concentration (chloa; mg m^{-3})

Table 1

Environmental and physiographic variables obtained for the study area, including their codes, units, resolutions and transformations, when applicable. Not all variables were considered together in the modeling process (see Section 2.4 methodology for more details).

Covariate	Code	Unit	Temporal resolution	Transformation
Sea Surface Temperature	SST	°C	Monthly	–
Chlorophyll a concentration	logchloa	mg m^{-3}	Monthly	log
Sea Surface Salinity	SSS		Monthly	–
Sea surface height anomalies	SSH	m	Monthly	–
Depth	depth	m	–	–
Slope	sqrtslope	degree	–	sqrt
Distance to the coast	sqrtland_cost	km	–	sqrt
Distance 200-m isobath	sqrtdis200	km	–	sqrt
Distance 500-m isobath	sqrtdis500	km	–	sqrt
Distance 1000-m isobath	sqrtdis1000	km	–	sqrt
Distance to ocean fronts	sqrtfront	km	–	sqrt
Latitude	lat	decimal degrees	–	–
Longitude	long	decimal degrees	–	–

raster data at a 9-km resolution were obtained from the Moderate Resolution Imaging Spectroradiometer (MODIS) onboard the Aqua satellite (available at https://oceancolor.gsfc.nasa.gov). Salinity (SSS) and sea surface height (SSH; m) were selected from the 'Ocean product' section of the Copernicus database, of the European Union (EU) Copernicus Marine Environment Monitoring Service (CMEMS) (http://marine.copernicus.eu). Salinity was based on the Multi Observation Global Ocean Sea Surface Salinity and Sea Surface Density model at 0.25° spatial resolution, and SSH was based on Global Ocean Gridded L4 Sea-Surface Heights at 0.25° spatial resolution. The average values of the environmental variables were extracted using the *Zonal Statistics* tool in the *Spatial Analyst Tools* of ArcGIS 10.6.1 software (ESRI, Redlands, CA, USA) to obtain a single value of each variable for each month in each cell of the grid.

Bathymetric values were obtained from the *General Bathymetric Chart of the Oceans* (GEBCO Compilation Group, 2020) at a global 15 arc-second grid. The bathymetric slope and 200 m, 500 m and 1000 m contour lines originated from the digital elevation models (DEMs) using *Spatial Analyst's slope* and *contour* tools, respectively. Minimum distances from the midpoint of each grid cell to the contour lines and coast were calculated with the *Near* tool.

Ocean fronts were identified in the monthly SST raster images using the Marine Geospatial Ecology Tools (MGETs) (Roberts et al., 2010) in ArcGIS, which implements the Cayula and Cornillon (1992) single-image edge detection algorithm. Custom settings in the algorithm parameters included an average temperature difference of ≥0.4 °C, a histogram window size of 32 × 32, and a histogram window range of 16 pixels. The ocean fronts in the output rasters were converted to polylines, and distances were then calculated from the midpoint of each grid cell to the nearest front.

2.4. Exploratory data analysis

An exploratory data analysis was performed to identify outliers and other potential problems in the data that could affect the fit of the models (Ieno and Zuur, 2015). Relationships between explanatory variables (environmental and physiographic variables) were examined to avoid correlation and collinearity and to reduce overfitting, with generalized additive models (GAMs) being very sensitive to collinearity (Zuur et al., 2009).

Pair plots with Pearson rank correlation were produced, and when pairs of covariates with high correlation values (Pearson correlation |r| > 0.7) were identified (Dormann et al., 2013), only one of the variables was included at a time in the modeling process. Additionally, multicollinearity among the predictor variables was evaluated by calculating the variance inflation factor (VIF) with a cutoff value of 5. One variable was removed at a time, and the VIF values were recalculated, repeating the process until all values were less than 5 (Zuur et al., 2009), using the *vif* function in the *car* package (Fox and Weisberg, 2019) in R language (R Core Team, 2020).

Due to the high correlation, four pairs of covariates were not considered at the same time in the models: distance to isobath 500 m with distance to isobath 1000 m; distance to isobath 200 m with distance to the coast; lat-long with distance to the cost and lat-long with distance to isobath 200 m. Chlorophyll-a concentration values were logtransformed, and the slope and the different distances were square-root transformed to adjust the distribution of the values.

2.5. Statistical models

GAMs (Wood, 2017; Zuur, 2012) were applied to identify the spatiotemporal dynamics and oceanographic features associated with the relative abundance and presence of *Prionace glauca*. GAMs are semiparametric extensions of linear models (GLMs), in which the effect of each predictor variable on the response variable is modeled with more flexibility by means of an unspecified *f* function (Hastie and Tibshirani, 1990). Two types of models were constructed, with the Tweedie and binomial distributions.

In the Tweedie model, the response variable was the monthly total capture per unit of effort (CPUE) (Campos and Andrade, 1998) in each grid, calculated as:

CPUE = (Monthly number of individuals/Monthly effort in number of hooks) x 1000　　　　(1)

The Tweedie distribution was chosen because of its ability to handle continuous data, including many low or zero values (16.5%) and few large observations (35%) (Shono, 2008; Tweedie, 1984). Furthermore, fitting exponential family dispersion models (Tweedie) is an alternative method to reduce the overdispersion of the final model fit (Gelfand and Dalal, 1990; Hazin et al., 2011).

Therefore, we assume that Y_i, the CPUE of blue sharks in each grid cell, follows a Tweedie distribution with mean μ_i and dispersion parameter σ^2,

$$Y_i \sim Tweedie(\mu_i, \sigma^2) \qquad (2a)$$

In the presence-absence model, we assume the response variable, Y_i, represents the presence of blue sharks in each grid cell by month and year, and it follows a binomial distribution with probability p_i,

$$Y_i \sim Binomial(1, p_i) \qquad (2b)$$

The general structure of the models was as follows:

$$g(\mu_i) = \alpha + \sum f_i(x_i) \qquad (3)$$

where $g(\mu_i)$ is the link function (log for Tweedie family; logit for the binomial family), μ_i is the expected response variable, α is the intercept, f_i are smooth functions (thin plate regression splines) and xi are the covariates.

The explanatory variables considered for both models were: a) spatial (latitude and longitude); b) temporal (month and year); and c) environmental and physiographic (see section 2.3). For the selection of the final models, manual *backward stepwise* selection was used, which

consisted of building the complete model and then removing each predictor variable based on the F test with 95% confidence ($p < 0.05$), lower Akaike information criterion (AIC) values (Akaike, 1974), explained deviance and checking the distribution of residuals (Supporting Material, Fig. S1 and S2). During each step, the variable with the highest p value was removed, and the AIC was recalculated for the reduced model. This iterative process was repeated while the variable removal lowered the AIC (Wood, 2017).

Only longitude and latitude were treated as interaction terms because their combination is more meaningful as area information. The degrees of freedom of the smooth function of this interaction were restricted, and the number of basis functions (k) was defined as $k = 100$ for the Tweedie model and $k = 200$ for the binomial model. Model selection was based on the lowest AIC value (Akaike, 1974). Each GAM was fitted using *thin plate regression splines.* The models were developed using the *gam* function in the *mgcv* package in R (Wood, 2017).

Model evaluation for both Tweedie and binomial models was performed through 5 times cross validation (Efron and Tibshirani, 1995) based on training and test datasets created by a random selection of 80% and 20% of each dataset, respectively (Elith and Leathwick, 2009). To know the predictive performance of the Tweedie model, the root mean square error (RMSE) was calculated using the *caret* package in R. For the binomial model, the area under the receiver operating curve (AUC), commonly used in species distribution modeling (Elith et al., 2006), was then calculated using the *PresenceAbsence* package in R (Freeman and Moisen, 2008). This index is tabulated in a confusion matrix indicating true positive (VP), false positive (FP), false negative (FN) and true negative (VN) predictions (Brodie et al., 2015). The AUC ranges from 0 to 1, with a value of 0.5 indicating as good as random performance, values between 0.7 and 0.9 considered useful, and values > 0.9 as excellent (Fielding and Bell, 1997). From the confusion matrix, specificity was obtained, which indicates the proportion of correctly predicted absences, and sensitivity, which indicates the proportion of correctly predicted observed occurrences (Lezama-Ochoa et al., 2020).

The dependence of prevalence on specificity and sensitivity was corrected with the true skill statistic (TSS). The TSS is an alternative measure of model accuracy, but it is threshold-dependent and not affected by the size of the validation set applied to presence-absence predictions. The TSS ranges from -1 to $+1$, where values of 0 or less indicate no predictive ability and $+1$ indicates perfect agreement. The calculation is TSS = sensitivity + specificity -1 (Allouche et al., 2006). The area under the curve (AUC) and TSS are used in combination when assessing the predictive power of a squared deviation from the mean (SDM) (Pearson et al., 2006).

2.6. Prediction maps

Predictions of the spatial distribution of *P. glauca* CPUE and probability of presence for the entire study area were obtained from the final GAM models using the *predict.gam* function of the *mgcv* package (Wood, 2017). The spatial prediction maps for both models were built at a resolution of $0.5 \times 0.5°$ for the entire period (2002–2018) using the ArcGIS program (ESRI, Redlands, CA, USA). The monthly predictions of CPUE and probability of occurrence of *P. glauca* were averaged over four quarters to represent the seasonal variation. Thus, spatial maps were created considering the first quarter (January–March), second quarter (April–June), third quarter (July–September) and fourth quarter (October–December), adjusting to the final model. Areas with a higher probability of occurrence of blue sharks were considered potential hotspots.

3. Results

The number of geographical cells with fishing effort per year ranged from 127 to 1473 (mean = 579). However, the total number of blue sharks captured per year ranged from 5964 to 64747 (mean = 22841),

and the CPUE values ranged from 6.7 to 21.5 (mean = 15.77). The percentage of positive captures was high (86.44%) for the total period (2002–2018) (Supporting Material Table S1).

3.1. Tweedie model

The selected Tweedie model for the CPUE explained 30.9% of the total deviation with an adjusted R^2 of 0.21 (Table 2). The value of the parameter p, which shows the maximization of likelihood, analyzed in this distribution was estimated at 1.50, which demonstrates a composition between the Poisson and gamma distributions. All model variables were significant (F test, p < 0.05) (Fig. 2).

Salinity had a positive effect on blue shark CPUE, with values between 31 and 36.2 and the highest peak at approximately 32.5. SST also had a significantly positive effect on CPUE between 14 and 24 °C, with the highest values at approximately 17 °C. The effect of ocean depth on blue shark catches was positive between 1100 and 4900 m. CPUE showed a decreasing trend with increasing chlorophyll values, having a negative effect above 0.07 mg m^{-3}. Negative SSH values and values between 0.1 and 0.21 had a positive influence on CPUE (Fig. 2).

The effect of the month on blue shark CPUE was positive between March and August, with a peak in May. From September, the effect was negative, with the lowest CPUE values between October and November. The year covariate presented positive cycles of approximately 4–5 years, alternating with negative cycles of 2–4 years. The blue shark CPUE had the highest values in 2008–2009, 2014–2015 and from 2018 onward, and the relative trend has increased. The lowest values were observed between 2002 and 2006 and between 2011 and 2012. The effects of the interaction between latitude and longitude on the CPUE were positive between 29°–40°S and 28°–36° and 45°–49°W, with the highest values being concentrated between 35°–36°S and 31°–33°W (Fig. 2).

3.2. Binomial model

The selected binomial model explained 26.9% of the total deviation with an adjusted R^2 of 0.26 (Table 2). All model variables were significant (F test, p < 0.05). (Fig. 3). The probability of the presence of *P. glauca* is higher between April and August, with a peak in July and a cyclical interannual variation with three peaks between 2005–2006, 2010 and 2014–2015. The lowest probability was observed in 2017. Regarding the oceanographic variables, *P. glauca* is more likely to occur in areas with salinity values between 32 and 35 and above 37, with chlorophyll concentrations <0.07 mg m^{-3} and >1.23 mg m^{-3}, and in areas with slopes between 0.64 and 1.21° and above 2.25°. SST values between 20°–26 °C and above 28 °C and greater distances to ocean fronts also corresponded to a higher probability of occurrence. The model also suggests a higher probability of the presence of *P. glauca* between 30°S–40°S near the Rio Grande Rise (31°–37°W) and near the continental shelf (41°–47°W). The model was able to predict the presence of *P. glauca* well (cross-validation values: AUC: 0.81; sensitivity:

Table 2
Summarized results of final selected GAM models for catch rates and presence-absence data of blue sharks, *Prionace glauca*, in pelagic longline fisheries in the western South Atlantic Ocean.

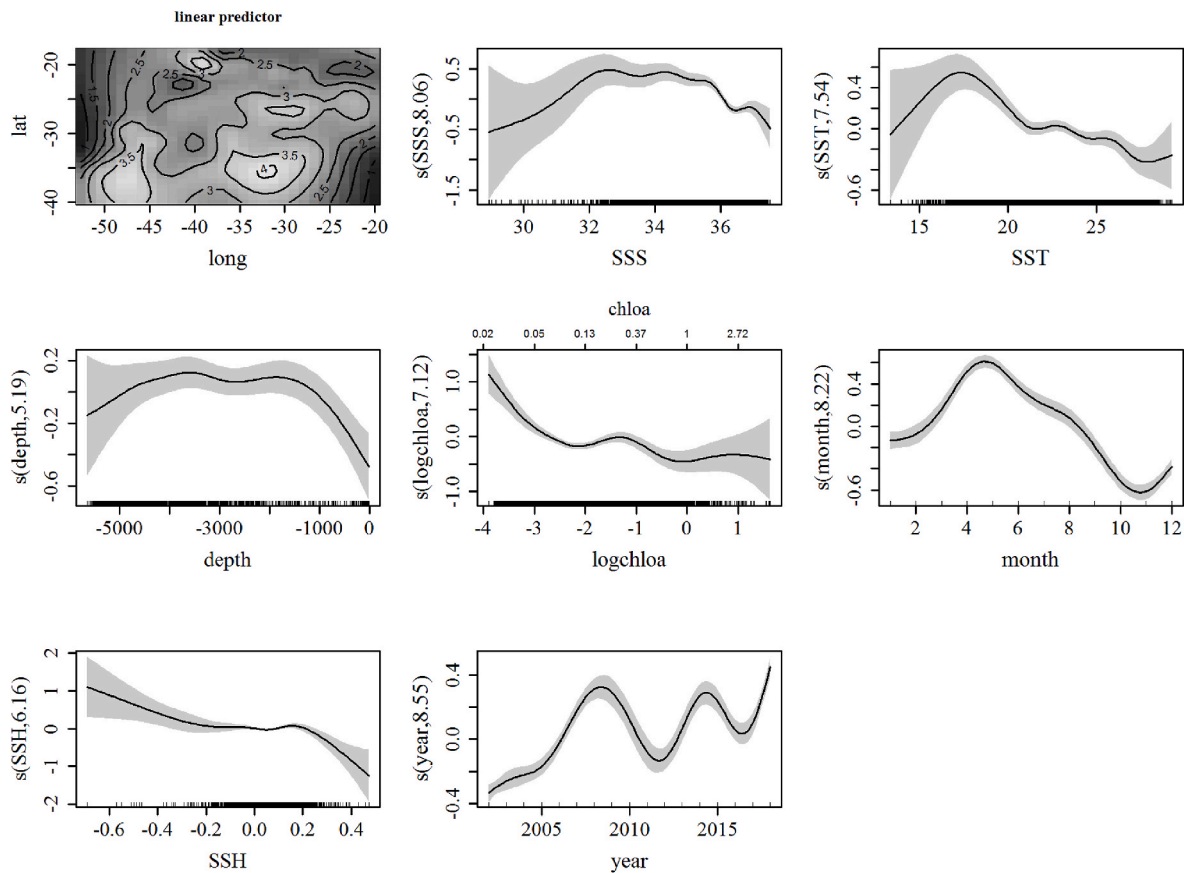| Error distribution	Final model	R-sq (adj)	% Deviance explained	RMSE	AUC
Tweedie	CPUE ~ s(long, lat) + s (SSS) + s(SST) + s (depth) + s(logchloa) + s(month) + s(SSH) + s (year)	0.21	30.9	21.9	–
Binomial	PA ~ s(long, lat) + s (year) + s(month) + s (logchloa) + s(SSS) + s(sqrtslope) + s(SST) + s (sqrtfront)	0.26	26.9	–	0.81

Fig. 2. Model terms for the Tweedie generalized additive model (GAM) of blue shark CPUE. Estimated smooth functions (solid lines) with 95% confidence intervals (shaded areas) are shown for each explanatory variable. Untransformed values are provided on the upper x-axis of transformed variables to facilitate interpretation.

0.98; specificity: 0.31; TSS: 0.29) and identified the most important areas for the species.

3.3. Prediction maps

The observed and predicted spatial distributions of the CPUE are shown in Fig. 4. The observed CPUE map showed three areas of greatest capture: an area close to the continental slope (CSL), a second close to the Rio Grande Rise (RGR) and a third close to the Vitoria-Trindade Chain (CVT) (Fig. 4A). The predicted CPUE tends to increase with latitude and is greater in the CSL of the southern coast of Brazil and Uruguay, between 26°–36°S and around the RGR. Two areas with high predicted catches stand out in the CSL, one between 29°–31°S and 47°–49°W and another between 33°–34°S and 48°–52°W (Fig. 4B).

Considering the seasonal analysis (Fig. 5), the highest predicted blue shark CPUE values (≥21) occurred in the RGR and adjacent areas in January–March and October–November (Fig. 5, A and D). In the CSL area, prediction values were higher in April–June and July September, between 28°–32°S and 34°–36°S (Fig. 5B and C).

The prediction map for blue shark probability of presence (Fig. 6) showed that the species is more likely to be caught in the southern portion of the CSL, with two areas of greater probability: one between 26°–31°S and 35°–48°W and another between 32°–35°S and 49°–52°W; in areas close to the RGR and in some oceanic regions to the north of the study area.

In the seasonal predictions, the CSL area presented a high probability of the presence (hotspots) of *P. glauca* throughout the year. However, in the first and fourth quarters, despite their persistence, the size of the hotspot area seems to be smaller. The northern oceanic region presented higher probabilities of presence in the first quarter (19°–21°S and 25°–30°W). Finally, the RGR showed a small area of high probabilities in the first and fourth quarters (Fig. 7).

4. Discussion

This study explored habitat preferences and hotspots of blue sharks in the western South Atlantic Ocean based on a long time series (2002–2018) of catch records of pelagic longline fisheries. Both CPUE and presence-absence data were modeled as a function of spatial, temporal, physiographic and environmental covariates, including oceanographic processes, using generalized additive models (GAMs).

4.1. Environmental and physiographic variables

The CPUE and the presence of blue sharks were positively affected by salinity. In the Mexican Pacific, salinity was the most influential factor affecting the CPUE of adults and juveniles in coastal oceanic waters, as they occurred mainly in waters with low temperatures and salinities (14°–15 °C and 33.6–34.6, respectively) (Vögler et al., 2010).

Blue shark has a wide thermal tolerance but prefers a much narrower temperature range (Queiroz et al., 2005). Our results suggest that the highest CPUE of this species was in colder waters, reaching a peak at approximately 17 °C (see Tweedie model, Fig. 2); however, the probability of occurrence was higher in warm waters above 28 °C (see binomial model, Fig. 3). In a study in the Eastern Mediterranean, blue sharks were most often recorded in cooler waters, but locally dense concentrations were more likely to occur in relatively warm areas (Damalas and Megalofonou, 2010).

Other studies carried out in the western South Atlantic also recorded higher blue shark catches in relatively cold waters (<22 °C) (Kotas et al., 1999; Mourato et al., 2008; Montealegre-Quijano and Vooren, 2010; Carvalho et al., 2011). However, CPUE is also influenced by the life stage
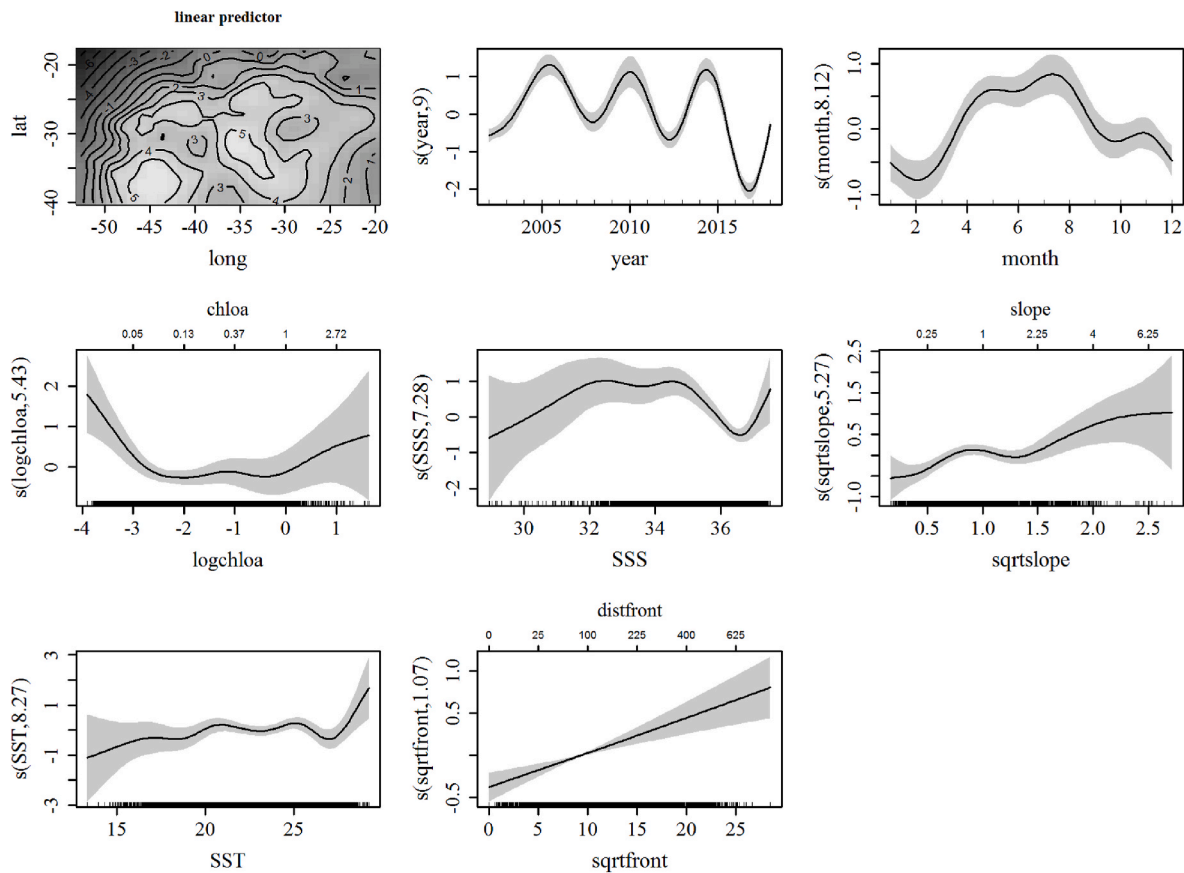
Fig. 3. Model terms for the binomial generalized additive model of blue shark presence-absence. Estimated smooth functions (solid lines) with 95% confidence intervals (shaded areas) are shown for each explanatory variable. Untransformed values are provided on the upper x-axis of transformed variables to facilitate interpretation.
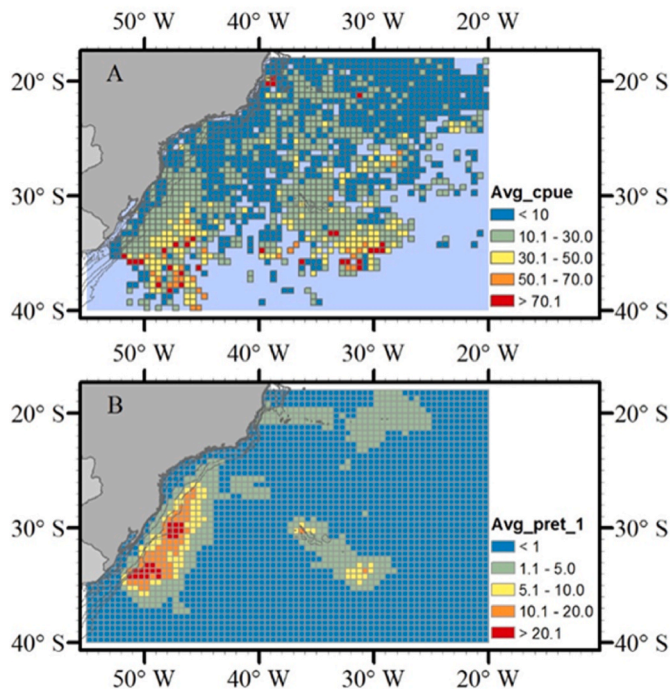

Fig. 4. Average observed (A) and predicted (B) spatial distributions of the CPUE of *Prionace glauca* in the western South Atlantic Ocean for the period between 2002 and 2018.

structure of catches, thus indicating that, for example, in this region, adult females are more abundant in warmer waters (>27 °C) in the second quarter, whereas small juveniles are highly abundant in cooler waters (<18 °C) in particular areas in the third and fourth quarters (Montealegre-Quijano and Vooren, 2010). Additionally, in the South Atlantic, Coelho et al. (2018) observed an increase in the abundance of males in colder waters south of 20°S, while females showed an inverse trend. Thus, the higher CPUE of *P. glauca* in colder waters, suggested by the Tweedie model, is expected to be related mostly to the capture of juveniles and males, while the greater probability of occurrence of blue sharks in warm waters, suggested by the binomial model, could be related to the higher presence of females.

In addition to salinity and temperature, the distribution and abundance of *P. glauca* may also be affected by productivity due to the probability of greater abundance and residence times in areas with optimal environmental conditions (Mitchell et al., 2014). Thus, high concentrations of chlorophyll-a, a proxy for ocean productivity, would be expected to have a positive effect on the blue shark CPUE. However, despite the blue shark's preference for cold waters, which tend to be more eutrophic, in our study, both the CPUE and the probability of occurrence showed a negative correlation with the increase in chlorophyll a concentration (>0.07 mg m^{-3}). Nevertheless, the probability of occurrence apparently increased with chlorophyll values above 1.5 mg m^{-3}, but the confidence bands were wide in this case.

Previous studies conducted in the region had similar results. Mourato et al. (2008) observed that the highest range of chlorophyll concentrations (>0.9 mg m^{-3}) had a negative effect on blue shark CPUE. Nevertheless, the capture of juvenile blue sharks had a negative association with low chlorophyll values (<0.8 mg m^{-3}) and a positive association with increasing chlorophyll values (Carvalho et al., 2011). In southern
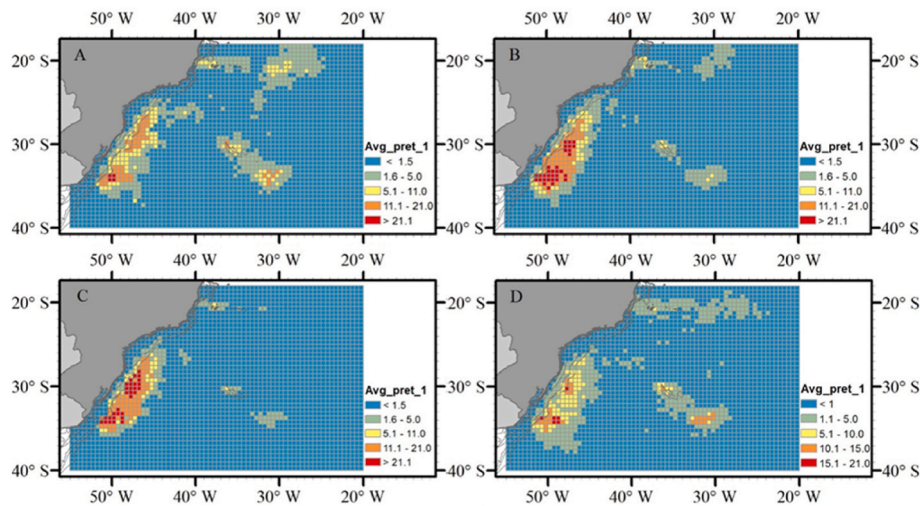
Fig. 5. Average variation by quarter of the year in the predicted spatial distribution of CPUE of *Prionace glauca* for the period 2002–2018 in the western South Atlantic Ocean. (A) January–March, (B) April–June, (C) July–September and (D) October–December.
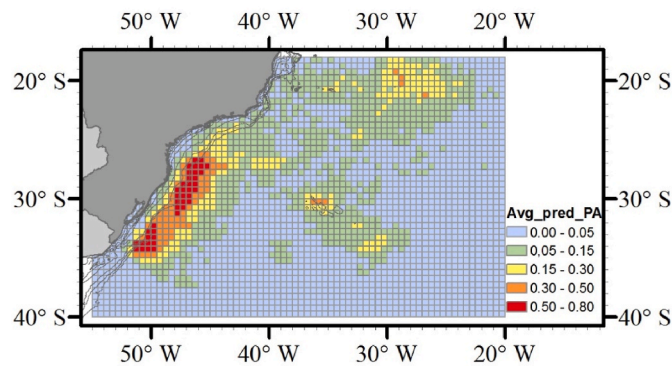

Fig. 6. Prediction map of the probability of the presence of *Prionace glauca* in pelagic longline catches between 2002 and 2018 in the western South Atlantic Ocean.

Portugal, a low correlation was found between blue shark space use and chlorophyll concentration (Queiroz et al., 2012), and in the North Atlantic, there was a positive relationship between chlorophyll values and CPUE at lower levels of chlorophyll, and there was a marked decline in the CPUE of blue sharks at higher chlorophyll levels (Mitchell et al., 2014).

Sea level height anomalies (SSHs) (Kahru et al., 2007) and ocean fronts (Mitchell et al., 2014; Queiroz et al., 2012) are oceanographic processes that are also linked to productivity, influencing the spatial and temporal patterns of abundance and diversity of pelagic fish. In this study, negative SSH values were found to have a positive effect on the CPUE (Tweedie model) of *P. glauca*. SSH is used as a proxy for upwelling and eddies (Gründlingh, 1995); negative values denote cyclonic eddies, upwelling, shallow mixed layers (Domokos et al., 2007) or cold sides of thermal fronts (Marín-Enríquez et al., 2017), being areas of higher productivity. However, a decrease in the probability of occurrence (binomial model) of blue sharks was observed with increasing distance to oceanic fronts, and this covariate was not selected in the final CPUE model. This result, as well as the low catch rates with increasing
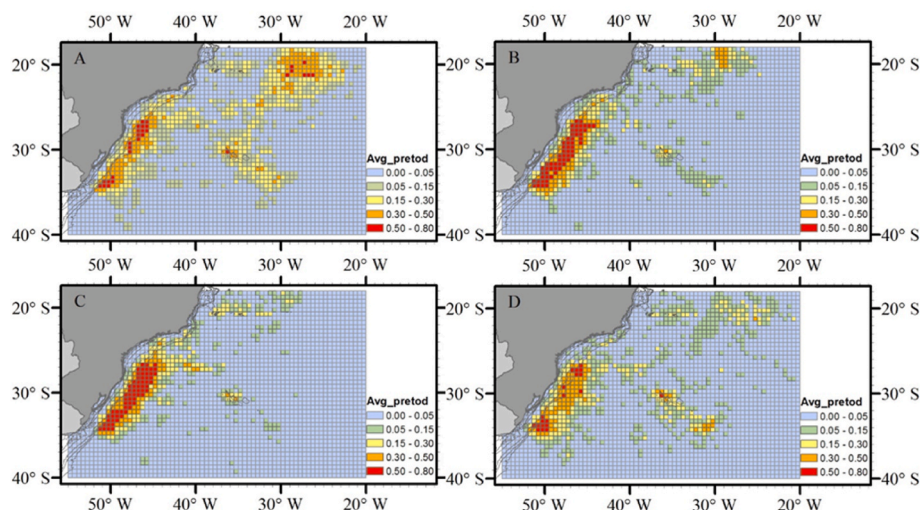

Fig. 7. Variation by quarter of the year of the predicted spatial distribution of the probability of the presence of *Prionace glauca* from 2002 to 2018 in the western South Atlantic Ocean. (A) First quarter (January–March), (B) Second quarter (April–June), (C) Third quarter (July–September) and (D) Fourth quarter (October–December).

chlorophyll concentration, is contrary to what would be expected, given the importance of productivity for prey and blue shark abundance and distribution.

In the North Atlantic, blue shark CPUE was lower with increasing ocean front density, but when lagged front density was analyzed, it exhibited a positive correlation with capture (Mitchell et al., 2014), suggesting a delay between the evolution of oceanographic processes (ocean fronts, vortices, upwelling), the subsequent increase in productivity and the attraction of higher trophic levels, including blue shark prey such as squid and small pelagic fish (Kahru et al., 2007). However, our results could also be influenced by the spatial and temporal resolution of the SST raster images used in the identification of oceanic fronts. Using monthly images, ocean features with long retention times that are persistent over time are examined (e.g., Ullman and Cornillon, 1999), which could mask more dynamic oceanic features that are of short period (Miller, 2009), such as some fronts and eddies. Furthermore, the response variables were also combined monthly for each grid cell.

Another factor that can influence the distribution of species and their spatial patterns is depth (Starr et al., 2012). *P. glauca* is a species distributed mainly from the sea surface to depths of approximately 445 m (Rochman et al., 2021), although deeper dives up to 1160 m have been recorded (Queiroz et al., 2012). The results of the Tweedie model showed that blue shark catch rates were higher in the epipelagic realm of waters between 1100 m and 4000 m depth, confirming the preference of this species for oceanic waters, as in other studies (e.g., Bigelow et al., 1999; Mourato et al., 2008). The binomial model showed that the highest probability of blue shark occurrence was in areas with slopes between 0.64 and 1.21° and above 2.25°. Slope describes the rate of change in elevation over distance; low slope values correspond to a flat ocean floor (or areas of sediment deposition), while higher values indicate potential rocky ledges (Lauria et al., 2015). In general, habitats associated with deeper waters and with a high slope gradient have a high probability of occurrence of different species, such as tunas (e.g., *Thunnus albacares*) (Gonzáles-Andrés et al., 2016).

4.2. Temporal and spatial variables

Regarding the month covariate, our models showed that both the CPUE and the probability of occurrence increased mainly between the months of March and August. Previous studies in the western South Atlantic observed an increase in blue shark catches between January and August (Carvalho et al., 2011; Kotas et al., 1999; Mourato et al., 2008). For the year covariate, the Tweedie model exhibited CPUE cycles with positive peaks approximately four to five years apart, and an increasing relative trend. The binomial model also showed a probability of occurrence with cyclic interannual variation, with three peaks during this study. Likewise, Carvalho et al. (2011) observed interannual variability in CPUE data.

In relation to the spatial interaction term longitude-latitude, the highest CPUE values and probability of occurrence of blue sharks occurred in latitudes higher than 30°S. The abundance of this species is known to increase at higher latitudes (Nakano and Seki, 2003; Hazin and Lessa, 2004). For the North Pacific, Nakano (1994) found a higher proportion of juveniles at higher latitudes (>35°N). In the South Atlantic, Mourato et al. (2008) also observed the highest CPUE values of blue sharks at higher latitudes (>30°S). In addition, a greater abundance of juveniles and males was observed at higher latitudes and of females at lower latitudes (Montealegre-Quijano and Vooren, 2010; Carvalho et al., 2011; Coelho et al., 2018). Looking at specific regions, the highest CPUE values and probability of occurrence of blue sharks tended to occur in parts of the continental slope (CSL) and in the Rio Grande Rise (RGR). These areas can also be identified in the spatial prediction maps.

RGRs are composed of seamounts (Camboa and Rabinowitz, 1984), which, as has been observed in other areas, act as biological hotspots and support unusually large populations of fish (Queiroz et al., 2005),

including oceanic species (Klimley et al., 2008). Many fish species occur in these areas to feed due to increased productivity resulting from the upwelling of deep, nutrient-rich waters and hydrographic retention mechanisms such as eddies (Morato and Clark, 2007), providing enhanced foraging opportunities for top predators (Litvinov, 2007).

Seamounts often have distinct geomagnetic signatures (Klimley, 1993), enabling blue sharks to detect these fields and thus use these areas as meeting points for copula aggregations (Litvinov, 2007). However, there are no year-round observations to confirm the permanent or seasonal nature of such aggregations, but long-term aggregations of large pelagic sharks can seriously influence seamount populations through predation on a wide variety of fish, squid and crustaceans (Litvinov, 2007).

The shelf dynamics in the coastal and oceanic regions south-southeast of Brazil are influenced, during the winter and spring periods (Odebrecht and Castello, 2001), by the penetration of waters of sub-Antarctic origin transported to the north by a coastal branch of the Malvinas Current (Da Silva et al., 1996). These cold and low salinity waters of the region, with warm and saline waters of tropical origin, are transported by the Brazil Current, increasing the biological productivity of the region due to the contribution of nutrients (Waluda et al., 2001). This high productivity in the area may attract blue sharks due to a greater abundance of potential prey (Carvalho et al., 2011).

4.3. Prediction maps and hotspots of occurrence

The observed CPUE spatial distribution is influenced by the effort distribution as a function of the target species and is linked to the environmental conditions of the areas in question (Azevedo, 2003). The surface longline fleet has its operations with greater fishing effort on the slope break and adjacent oceanic region, in the Trindade-Vitória Chain and in the Rio Grande Rise, the latter being characterized as an important area for the surface longline fishery, targeting swordfish, tuna, dolphinfish and sharks (Azevedo, 2003; Carvalho et al., 2011).

In turn, two similar areas within the CSL showed the highest predicted catches and the highest probability of presence of blue sharks. Although they varied slightly by season and even merged in some maps, this region of the CSL was persistent in the predictions for both types of models, appearing in all quarters and with higher values in autumn and winter, suggesting that these two areas or the larger merged area might be considered hotspots for blue sharks in the western South Atlantic.

Other apparent blue shark hotspots in the study area include the area over the RGR, as evidenced by the consistent predictions in both types of models, including the overall and seasonal models, and especially in summer and spring. In addition, the northern Oceanic Region (NOR) of the study area also presented some groups of cells with relatively high prediction values, especially for the probability of presence of blue sharks in the overall and summer prediction maps.

These results provide information about the factors that influence the presence and catches of the blue shark in the Western South Atlantic Ocean. Highlighting important areas of abundance that deserve greater attention might contribute to the assessment of blue shark (*Prionace glauca*) stocks in the Atlantic Ocean, aiming at the adoption of more efficient fisheries management and conservation measures for the species (ICCAT, 2016).

Mesoscale hydrographic features, such as fronts and eddies, and others affiliated with bathymetric structures, such as canyons, sills, seamounts and banks, or coastal topography are particularly important as hotspots (Sydeman et al., 2006). Sharks can actively select and aggregate in these space-use hotspots characterized by higher productivity (Queiroz et al., 2016). In the southwestern Indian Ocean, consistent local hotspots of *P. glauca* abundance were found, which occur where stable mesoscale anticyclonic activity is characterized by positive sea level anomaly values and higher concentrations of chlorophyll are present (Selles et al., 2014). However, in the southwestern Atlantic, porbeagle (*Lamna nasus*) hotspots were identified considering the high

seasonality and the repetitive use of habitats over the months (Cortés and Waessle, 2017).

4.4. Concluding remarks

Our results provide a contribution to the understanding of the factors that affect blue shark catches in the western South Atlantic Ocean, considering a large time series and using generalized additive models (GAMs). In addition to environmental factors, oceanographic processes such as ocean fronts, upwellings and eddies can influence the distribution of *P. glauca* and, consequently, be used to identify areas with higher importance for the species. GAMs are a suitable approach in the analysis of factors related to the availability and predictions of blue sharks. Despite this, it is possible that the explanatory power of our Tweedie and binomial models was limited by the large volume of data and by using the grid cell as a sampling unit with a monthly temporal resolution. Finally, it is important to consider that the blue shark is a species that presents size and sex segregation, with different habitat preferences, which ideally should be considered when modeling and for fisheries management and conservation. Another factor that should also be considered is prey availability, which has been identified as a factor that can influence shark distribution patterns; therefore, its inclusion in spatial prediction models might improve predictive accuracy.

CRediT authorship contribution statement

M.R.M., L.D.R conceived and designed the study. **M.R.M.** completed the analyses and wrote the original and final manuscript. **L.G.C., B.M.** provided data. All authors reviewed and approved the manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The authors do not have permission to share data.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.marenvres.2022.105842.

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