

Spatial predictions of blue shark (*Prionace glauca*) catch rate and catch probability of juveniles in the Southwest Atlantic

Felipe C. Carvalho^{1,2*}, Debra J. Murie¹, Fábio H. V. Hazin³, Humberto G. Hazin³, Bruno Leite-Mourato^{3,4}, and George H. Burgess²

¹Program of Fisheries and Aquatic Sciences, School of Forest Resources and Conservation, University of Florida, 7922 NW 71st Street, Gainesville, FL 32653, USA

²Florida Program for Shark Research, Florida Museum of Natural History, University of Florida, 280 Dickinson Hall, Gainesville, FL 32611, USA

³Departamento de Pesca e Aquicultura, Universidade Federal Rural de Pernambuco, Rua Dom Manuel de Medeiros s/n, Dois Irmãos, Recife-PE CEP 52171-900, Brazil

⁴Departamento de Oceanografia, Universidade Federal de Pernambuco (UFPE), Cidade Universitária, 50670-901 Recife-PE, Brazil

*Corresponding Author: tel: +1 352 2733606; fax: +1 352 3923672; e-mail: fcorreia@ufl.edu.

Carvalho, F. C., Murie, D. J., Hazin, F. H. V., Hazin, H. G., Leite-Mourato, B., and Burgess, G. H. 2011. Spatial predictions of blue shark (*Prionace glauca*) catch rate and catch probability of juveniles in the Southwest Atlantic. – ICES Journal of Marine Science, 68: 890–900.

Received 15 July 2010; accepted 25 February 2011

Generalized regression analysis and spatial prediction was applied to catch per unit effort (cpue) data for blue shark (*Prionace glauca*) caught by the Brazilian tuna longline fleet between 1997 and 2008 (43 546 longline sets) to predict the effect of environmental, spatial, and temporal factors on catch distribution. In addition, the size distribution of blue sharks measured by on-board observers during the years 2006–2008 was used to model the proportion of juvenile blue sharks in the catches from a spatial perspective. Latitude was the most important factor influencing blue shark cpue in the Southwest Atlantic, with cpue spatial predictions suggesting two areas of higher catch probabilities. Latitude was also the most important factor influencing the proportion of juveniles in the catches. The spatial prediction map showed that juveniles were more frequently caught south of 35°S (~38°S). This information can assist in the design of management strategies either to exploit this predictable spatial distribution of the catch or to manage the fisheries in a spatially explicit manner if one component (i.e. juveniles) requires protective measures.

Keywords: blue shark, distribution, environmental variables, generalized additive models.

Introduction

There is growing concern about population depletion of apex fish predators and on the impacts this may have on marine ecosystems (Pauly *et al.*, 1998; Stevens *et al.*, 2000). These concerns are particularly grave in relation to sharks because their biological characteristics render them so vulnerable to overexploitation (Cailliet *et al.*, 2005). Reviews of world shark fisheries provided by Bonfil (1994) and Shotton (1999) documented areas where commercial catches of sharks have been declining, such as in the Northeast Atlantic (Pawson and Vince, 1999) and around Japan (Nakano, 1999).

The blue shark (*Prionace glauca*) is a carcharhinid and one of the widest ranging, large, open-ocean predators; it may well be the most abundant of all pelagic sharks in the global oceans (McKenzie and Tibbo, 1964; Draganik and Pelczarski, 1984; Nakano and Seki, 2003). Although blue sharks are caught with a variety of fishing gears in the Atlantic Ocean, pelagic longline fisheries that target tuna and swordfish account for most of their catches (Aires-da-Silva, 2008).

Management of large pelagic species such as blue sharks is difficult because their highly migratory nature results in them crossing national and international waters. Management of sharks, tuna, and billfish of the Atlantic Ocean therefore falls to the

International Commission for the Conservation of Atlantic Tunas (ICCAT). In 2008, ICCAT carried out a stock assessment for Atlantic blue shark (ICCAT, 2008). Although the general conclusion of the assessment was that blue shark stocks in the Atlantic Ocean seemed to be in a sustainable condition, probably exploited at levels below maximum sustainable yield, the results were interpreted with considerable caution owing to data deficiencies. In order to reduce the uncertainty involved in the stock assessment, ICCAT recognized the necessity of understanding better the geographic distribution of blue sharks to identify their main areas of occurrence relative to different size classes and to determine the influence of environmental factors on the catches.

Environmental factors influence the distribution of pelagic fishery resources such as tuna (Laevastu and Rosa, 1963; Sharp *et al.*, 1983), sharks, and swordfish (Bigelow *et al.*, 1999). Accurate stock assessments, especially for highly migratory species, require an ability to differentiate changes in abundance from altered catch vulnerability resulting from natural variability in oceanographic conditions (Brill *et al.*, 1999). Several authors have underscored the importance of incorporating environmental variables into stock assessment models (e.g. Ottersen and Sundby, 1995; Myers, 1998; Daskalov, 1999; Agnew *et al.*, 2002; Brander, 2003). However, the inclusion of spatial, temporal, and

environmental variables in the analysis of fishing performance and fish population dynamics remains complex (Bigelow *et al.*, 1999). According to Claireaux and Lefrançois (2007), a combination of these factors may affect the ability of a fish to grow, migrate, survive, and reproduce. Further, statistical analyses often assume a linear relationship between fishing performance and environmental variables, when actually they are very likely to be non-linear (Bigelow *et al.*, 1999). Despite the advantages of linear regression techniques in determining model parameters and their interpretation, the method has little flexibility because of its relatively restricted range of application (Chong and Wang, 1997). To overcome such difficulties, generalized additive models (GAMs) have been used to identify, characterize, and estimate the relationships between extrinsic factors and catch rates of certain fish species (Walsh *et al.*, 2002; Zagaglia *et al.*, 2004; Damalas *et al.*, 2007). GAMs (Hastie and Tibshirani, 1986) are semi-parametric extensions of GLMs (generalized linear models), and their major assumptions are that the functions are additive and the components smooth (Guisan *et al.*, 2002). The use of GAMs is normally justified when the effects of multiple, independent variables need to be modelled non-parametrically (Maunder and Punt, 2004).

Modelling spatial variation can also be used to better understand the influence of the marine ecosystem on species distributions and, consequently, can lead to the implementation of spatially explicit management and conservation measures. However, the use of spatial prediction techniques based on interpolation algorithms is generally data-intensive, requiring large quantities of well-distributed data. This requirement is rarely attainable with respect to fisheries, especially when the species of interest is not a target one. This problem was partially overcome by Lehmann *et al.* (2002a) with the development of a generalized regression analysis and spatial prediction (GRASP) method, which basically consists of GAMs used to generate predictions in a geographic-grid format. GRASP has solved a significant problem in spatial modelling because it has introduced a way of exporting statistical models to Geographic Information Systems (GIS) software (GIS, Arcview v.9.2, ESRI, CA, USA). With it, one can model statistical relationships between a variable of interest (e.g. blue shark catch) and environmental, spatial, and temporal variables, then make spatial predictions based on the predictor variables (Lehmann *et al.*, 2002b). GRASP can also aid in understanding the structure of a specific stock, such as predicting abundance and spatial distribution of individuals in different maturity stages and age classes. Assessing this type of information is crucial if fishery managers are to improve plans for sustainable harvesting (Laidig *et al.*, 2007).

In the present study, a GRASP analysis was applied to catch per unit effort (cpue) data on blue sharks to examine their distribution and abundance in relation to environmental factors in the Southwest Atlantic. Cpue data were available for blue sharks caught by the Brazilian pelagic longline fleet between 1997 and 2008. In addition, the size distribution of blue sharks caught in the pelagic longline fleet of Brazil was used to model the proportion (spatially) of juvenile blue sharks in the catches between 2006 and 2008.

Material and methods

Blue sharks were caught in Brazilian tuna longline sets distributed through a large part of the equatorial and Southwest Atlantic Ocean (Figure 1). The fishing area in the analysis was constrained

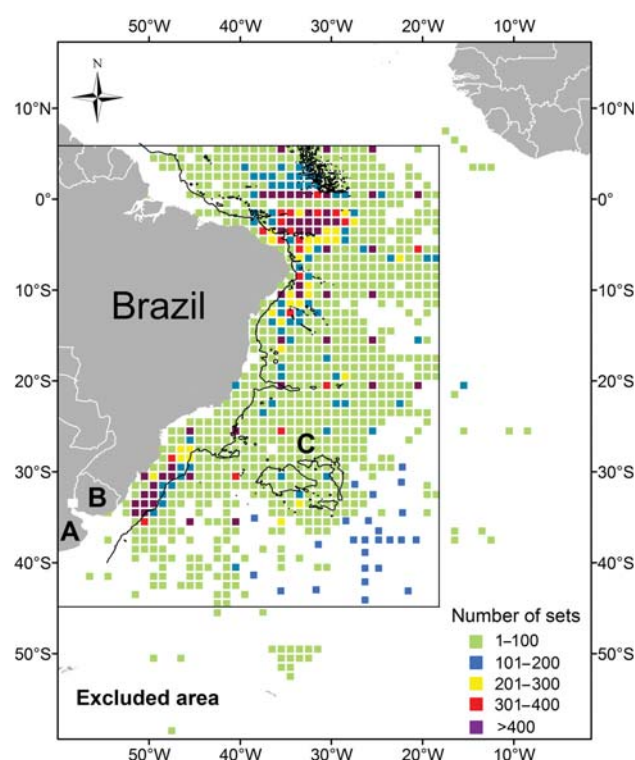


Figure 1. Spatial distribution of fishing sets by the Brazilian pelagic longline fleet in the Southwest Atlantic from 1997 to 2008: (A) Argentina, (B) Uruguay, and (C) Rio Grande Rise. The 3000-m isobath is shown by a solid black line.

to encompass most of the catch data, ranging from 55° to 15°W and from 5°N to 45°S (Figure 1). Within this general area, the equatorial waters from ~4°N to 20°S are mainly under the influence of the South Equatorial Current, which is a broad, west-flowing current that extends from the surface to a depth of 100 m (Mayer *et al.*, 1998). The area is also characterized by the presence of seamounts (Cadeia Norte do Brasil) and oceanic islands (Fernando de Noronha and Atol da Rocas), as well as by equatorial upwelling driven by the equatorial divergence (Mayer *et al.*, 1998; Travassos, 1999). The area south of 21°S is characterized by the presence of a convergence zone between the warm, coastal, south-flowing Brazil Current and the cold, north-flowing Malvinas (Falklands) Current (Garcia, 1997; Seeliger *et al.*, 1997). Further to the south is the Rio Grande Rise, a large seismic ridge with depths of 300–4000 m (Figure 1). The Rio Grande Rise, along with other seamounts and oceanic islands closer to the equator, represent important fishing grounds for commercially exploited pelagic species off Brazil (Azevedo, 2003). This is probably a consequence of greater biological productivity in the water around these rises and seamounts resulting from the interaction between oceanic currents and the bottom relief, creating areas of eddies and upwelling (Hekinian, 1982).

Catch data

Catch data were obtained from 49 656 longline sets made by the Brazilian pelagic tuna longline fleet, including both national and chartered vessels, from 1997 to 2008 (Table 1). Logbook data included records of individual fishing sets containing vessel identification, hour of the set, location of fishing ground (latitude and

Table 1. Annual number of fishing sets, hooks per set, total catch, and on-board observer coverage and measurement of blue sharks from 1997 to 2008 for the Brazilian pelagic longline fleet.

Year	Number of sets	Average number of hooks per set	Number of blue sharks caught	Number of observed sets	Number of blue sharks measured by observers
1997	1 497	1 785	4 580	0	0
1998	1 894	2 257	10 098	0	0
1999	4 664	2 002	9 367	0	0
2000	6 322	1 772	12 087	0	0
2001	6 627	2 017	27 244	0	0
2002	4 843	1 745	36 589	0	0
2003	2 540	1 080	10 831	0	0
2004	4 333	1 458	20 641	0	0
2005	4 413	1 390	27 313	0	0
2006	5 526	1 287	33 390	3 503	2 611
2007	4 749	1 154	37 753	1 754	5 743
2008	3 248	1 235	26 580	2 356	3 578

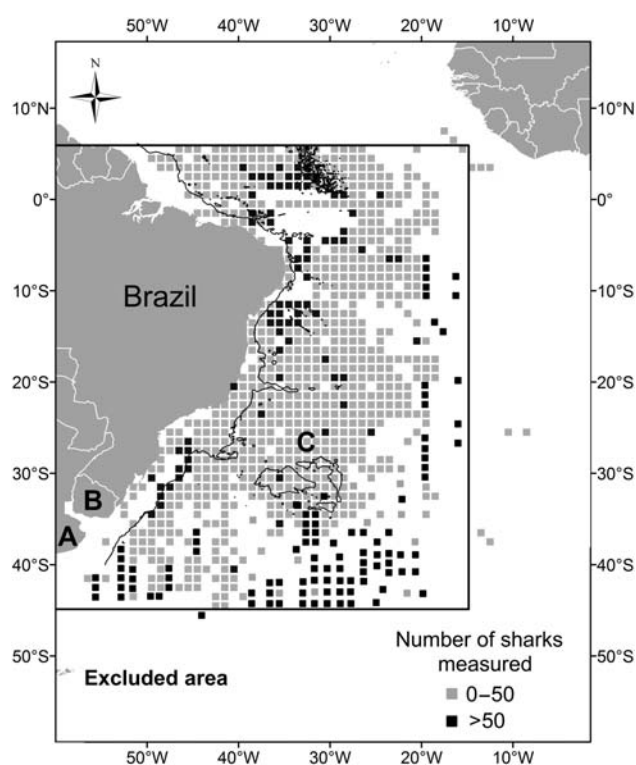


Figure 2. Spatial distribution and number of blue sharks measured by on-board observers on Brazilian pelagic longliners operating in the Southwest Atlantic from 2006 to 2008: (A) Argentina, (B) Uruguay, and (C) Rio Grande Rise. The 3000-m isobath is shown by a solid black line.

longitude), effort (number of hooks), date, and the number of fish caught with each set. Nominal cpue was calculated as the number of blue sharks caught per 1000 hooks per set.

Size class (fork length, FL, cm) information on blue sharks was obtained from the Brazilian on-board observer programme covering chartered longline fleets operating in the Southwest Atlantic, for the period January 2006 to December 2008. During those operations, 11 932 blue sharks were measured (Figure 2) over the same area as most of the total catch (Figure 1). To evaluate the spatial distribution by length, two FL classes were established following Mejuto and García-Cortéz (2004): juveniles, FL ≤ 119 cm, and

adults, FL > 119 cm. These data were then transformed into the proportion of juveniles and adults per $1 \times 1^\circ$ block, assuming a binomial distribution. Further, the mean FLs of sharks sampled by blocks of 5° latitude for the whole study area were calculated and checked for normality and homoscedasticity. A non-parametric Kruskal–Wallis test was used to compare FL means among regions.

Environmental and spatial variables

Environmental variables included in the GRASP model were sea surface temperature (SST), chlorophyll *a* (CHL) concentration, bottom depth at the fishing location, and distance from the nearest coast, plus year, month, and latitude and longitude of the catch. SST data for the period 1997–2008 were obtained from Advanced Very High Resolution Radiometer (AVHRR) sensors on board National Oceanic and Atmospheric Administration (NOAA) satellites. This dataset is produced and distributed by the Physical Oceanography Distributed Active Archive Center (PODAAC) of the Jet Propulsion Laboratory (JPL)/National Aeronautics and Space Administration (NASA) in Hierarchical Data Format (<http://www.jpl.nasa.gov/>).

The data on CHL concentration were obtained from Sea-viewing Wide Field-of-view Sensor (SeaWiFS) images, provided by the Goddard Space Flight Center of NASA (<http://oceancolor.gsfc.nasa.gov/SeaWiFS/>). Images were converted into numerical data (in mg m^{-3}) with the GDRA2XYZ programme provided by Phoenix Training Consultants (Phoenix Training Consultants, New Orleans, LA, USA). These data, with an original resolution of 9×9 km, were used to construct data based on $1 \times 1^\circ$ blocks by month, year, and latitude and longitude.

For SST and CHL, we used monthly averages for each year in the dataset. These data have an original resolution of 0.5° for SST and 9×9 km for CHL. To construct a database of $1 \times 1^\circ$ resolution by month, year, and latitude and longitude for both these environmental variables, the average values were calculated to a resolution of $1 \times 1^\circ$ around the location of each fishing set. These data were then matched with the length frequency and catch data.

As part of using remote-sensing to estimate SST and CHL, it is necessary to estimate values in a field of view that contains discontinuities, e.g. because of cloud cover. To reduce or eliminate effects of cloud cover on the estimates of SST and CHL, images with differing patterns of cover or cover acquired at different times

Table 2. Stepwise-selected GAMs for the spatial predictions of blue sharks, with RMSE values for the K-fold cross-validation.

Response variable	Final model	r^2 (%)	RMSE	Cross-validation
Model for cpue in Brazilian pelagic longline data				
Cpue (numbers per 1 000 hooks)	year + month + $s(\text{latitude}) + s(\text{longitude}) + s(\text{SST}) + s(\text{CHL})$	52	0.26	0.77
Model for proportion of juveniles in Brazilian pelagic longline catches				
Proportion of juveniles	month + $s(\text{latitude}) + s(\text{longitude}) + s(\text{CHL}) + s(\text{SST})$	44	0.29	0.61

(but within a short interval) are used to create composites that show cloud-free views of the ocean surface. A full description of this method can be found in McClain *et al.* (1985). The data used in our study were obtained via the JPL and SeaWiFS sites, which provided corrected data directly online.

The distance of the catch location from the Brazilian coast or oceanic islands was calculated according to the methodology proposed by Damalas *et al.* (2007). The method is based on locating the nearest land pixel (bottom depth >0) on a grid map, then estimating the distance between the two points (in km), after correcting for the spheroid shape of the Earth.

Generalized regression analysis and spatial prediction

The GRASP (version 3.2; Lehmann *et al.*, 2002a) extension for the software S-plus was used to model the spatial prediction of cpue (number of blue sharks caught per 1000 hooks) and the proportion of juveniles as a function of environmental variables. In the GRASP approach, spatial predictions are obtained through the relationships between a response variable (i.e. cpue or proportion of juveniles) and selected predictor variables (i.e. environmental and spatial factors) by fitting a GAM (Yee and Mitchell, 1991).

In the GRASP analysis, two types of distribution are used, a Poisson distribution with a log-link function for the Brazilian pelagic longline fleet cpue data, and a binomial distribution with the link function logit for the proportion of juveniles. Smoothing spline functions (natural cubic) were used to adjust the non-linear effects of the model (Cleveland and Delvin, 1988). A K-fold cross-validation procedure (Efron and Tibshirani, 1995) was used to evaluate the consistency of the final models (cpue and proportion of juveniles). For the K-fold cross-validation in the Poisson model, we used 5000 samples randomly chosen from the total fishing dataset (cpue) separate from the 44 506 longline sets used to generate the model. For the binomial model, 2500 samples were selected randomly from the size class data, again separate from the 11 932 measurements used to generate the model. Predictors were chosen using a stepwise procedure, going in both directions (forward and backward) from a full model and removing predictors according to an *F*-test ($\alpha = 0.05$). A root-mean-square error (RMSE) was used to provide a summary diagnostic of each model's goodness-of-fit in the K-fold cross-validation, with the lowest value of RMSE representing the best fit to the data.

The relative effect of each x_j variable over the dependent variable of interest was assessed using the distribution of partial residuals (Neter *et al.*, 1989). The relative influence of each factor was then assessed based on the values normalized with respect to the standard deviation of the partial residuals. The partial residual plots also contain the 95% confidence intervals, as well as tick marks on the abscissa showing the location and density of datapoints.

To build the spatial prediction maps for both models, we implemented the method developed by Lehmann *et al.* (2002a) using GRASP in S-Plus, which consists of exporting the results from the models to lookup-tables and making the prediction map in ArcView.

Results

Catch per unit effort

The final model for cpue of the Brazilian pelagic tuna longline fishery consisted of six of the eight input variables: latitude, longitude, SST, CHL (all as continuous variables), year, and month. This model explained 54% of the total deviance ($r^2 = 0.52$; Table 2). The RMSE and the K-fold cross-validation values indicated that predictions fitted reasonably well, with values of 0.26 and 0.77, respectively (Table 2). The relative contribution from each variable in the total explained deviance for the selected model showed that latitude (34%) and longitude (24%) were the most important factors, followed by year (15%) and month (10%). Among environmental variables, SST (9%) was the most significant, followed by CHL (8%).

Partial response curves showing the effects of predictor variables on the model indicated a much greater (cpue) probability of blue sharks being found between 20 and 40°S, decreasing northwards towards the equator (Figure 3). The influence of longitude on blue shark cpue was also positive between 60 and 55°W, decreased to a minimum at ~40°W, then increased and positively peaked at 20°W (Figure 3). The year variable reflected some inter-annual variability in the cpue data, but overall showed a positive influence after 2001. The factor month revealed relatively stable cpue from January through May (Figure 3); it then increased from June to August, when it peaked, before declining again through December. The influence of SST on blue shark cpue peaked at ~18°C, decreasing at lower or higher temperatures (Figure 3). Finally, the positive effect of CHL showed a bimodal distribution, with one peak at ~0.7 mg m⁻³ and a second, continuous, increase from 1.2 mg m⁻³ to a maximum of ~2.1 mg m⁻³ (Figure 3).

The map of cpue spatial predictions showed that spatial cpue probabilities were closely related to latitude, with two distinct areas of high-cpue probability (Figure 4), one close to the southern coast of Brazil and Uruguay, and the other larger one located more oceanically near the Rio Grande Rise (Figure 4). In addition, there was an area of moderate cpue probability off the central coast of Brazil around 10°S 20°W. By correlating the prediction map and the spatial distribution of fishing sets, areas of high cpue could be predicted from an area with many sets (oceanic region) and areas of low cpue from an area of few sets (close to the coast).

The proportion of juvenile blue sharks in the catch

Overall, the length frequency analysis revealed blue sharks of all sizes, from juveniles to adults, within the fishing area (Figure 5). Mean FL was not significantly different among 5° latitudinal

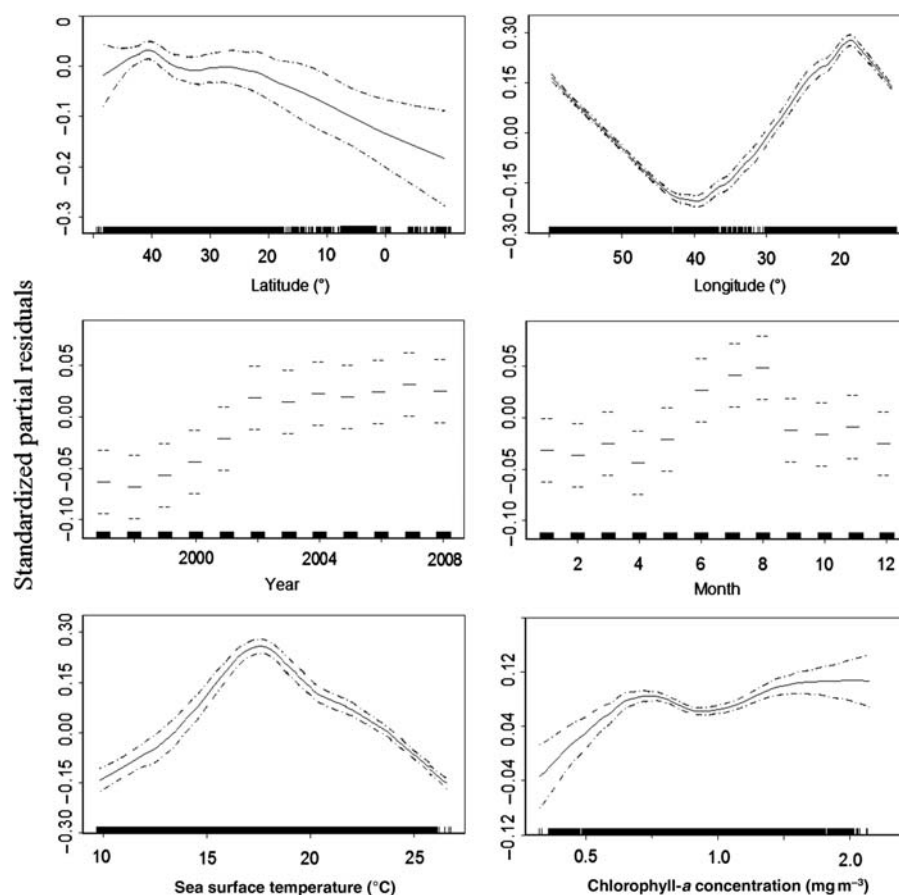


Figure 3. Partial response curves showing the effects of the predictor variables added to the model for the cpue of blue sharks caught by the Brazilian pelagic longline fleet operating in the Southwest Atlantic from 1997 to 2008. The dashed lines are 95% confidence limits, and tick marks on the abscissa show the location and density of datapoints.

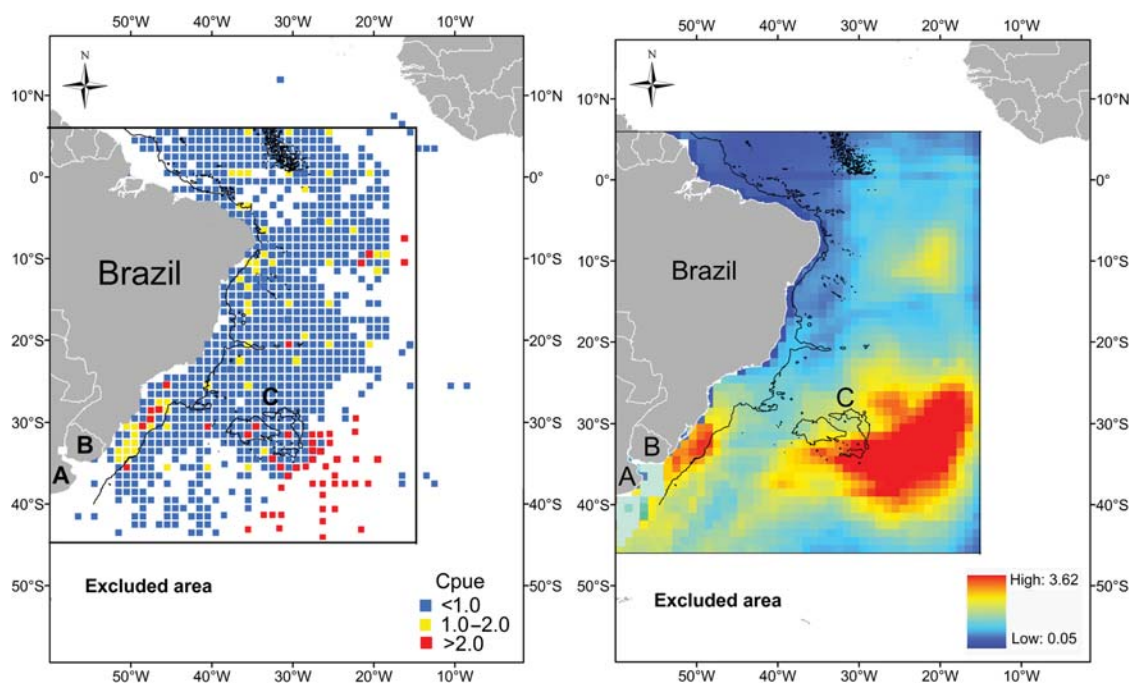


Figure 4. Spatial distribution of observed (left) and predicted (right) blue shark cpue (sharks per 1000 hooks) caught by the Brazilian pelagic longline fleet from 1997 to 2008 in the Southwest Atlantic. (A) Argentina, (B) Uruguay, and (C) Rio Grande Rise. The 3000-m isobath is shown by a solid black line.

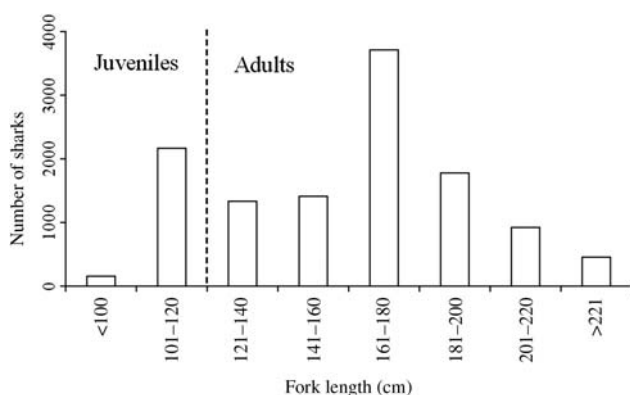


Figure 5. Number of blue sharks measured per FL size class by observers on board Brazilian pelagic tuna longline vessels between 2006 and 2008. The vertical dashed line indicates the size at first maturity (119 cm).

blocks between 5°N and 35°S, but did suggest that most sharks were adults (FL ≥ 120 cm; Figure 6; Kruskal–Wallis, $F = 4.16$, $p = 0.973$). The mean FL of sharks between 35.1 and 45°S, however, was significantly smaller and suggested to us that most of the blue sharks caught in higher latitudes to the south were juveniles, i.e. <120 cm (Kruskal–Wallis, $F = 3.01$, $p = 0.011$; Figure 6).

The final model for the proportion of juveniles in the catch explained 44% of the deviance and consisted of five variables (Table 2). Latitude (34%) and longitude (25%) were the most important factors, followed by month (17%). Among the environmental variables, SST (13%) was the most important, followed by CHL (11%).

Through partial response curves, the proportion of juvenile blue sharks was observed to be positively associated with higher latitude, particularly south of 30°S, and decreased to the north (Figure 7). The influence of longitude on the proportion of juvenile blue sharks was relatively stable from ~ 28 to 48°W, decreasing towards lower or higher longitudes. Month was associated with a larger proportion of juvenile blue sharks from May to August. The positive influence of SST on the proportion of juvenile blue sharks was highest between 12 and 14°C and was negatively associated with higher temperatures (Figure 7). The proportion of juvenile blue sharks in the catch was negatively associated with low CHL ($0.2\text{--}0.8\text{ mg m}^{-3}$) and positively associated with an increase in CHL $>1.2\text{ mg m}^{-3}$ (Figure 7).

The spatial prediction map for the proportion of juvenile blue sharks in the catch showed that juveniles had a much greater probability of being in the catches of pelagic longline sets south of 35°S and between 25 and 50°W (Figure 8). Overall, the proportion of juvenile blue sharks was very low over most of the Brazilian coast (5°N to 30°S) compared with more southern areas (Figure 8).

Discussion

Maury *et al.* (2001) noted that the relationship between cpue and species abundance is generally non-linear. Using GAMs, Bigelow *et al.* (1999) also observed strong non-linear correlations between catch indices and fishing and oceanographic variables for swordfish (*Xiphias gladius*) and blue shark in the North Pacific Ocean. Zagaglia *et al.* (2004) found this non-linearity too when analysing the relationship between cpue and environmental

variables for bigeye tuna (*Thunnus obesus*), yellowfin tuna (*T. albacares*), and albacore (*T. alalunga*) in the equatorial Southwest Atlantic.

It is also important to note that data can be spatially dependent or autocorrelated (Latimer *et al.*, 2006), and the use of models that ignore this dependence can lead to inaccurate parameter estimates and inadequate quantification of uncertainty. GRASP deals with spatial autocorrelation at the data stage, with correlations between the chosen predictors examined to allow the removal of correlated predictors. In this analysis, the results showed that correlation between predictors (i.e. latitude and SST) was not sufficiently high to justify removing any of the variables from the modelling process.

In this study, the spatial prediction of blue shark cpue achieved by the GRASP model fitted the data well because the variation explained by the predictors and the K -fold cross-validation values were 52% and 0.77, respectively. The model for the spatial distribution of the proportion of juveniles also showed good adjustment, with the variation explained by the predictor and the cross-validation values being 44% and 0.61, respectively. These cross-validation values were comparable with those reported in other studies that used GRASP, i.e. 0.94 (Lehmann *et al.*, 2002a), 0.65–0.98 (Lehmann *et al.*, 2002b), and 0.61–0.72 (Zaniewski *et al.*, 2002).

Several factors, e.g. marine currents, thermal fronts, latitude, distance from coast, and SST, influence the distribution and abundance of blue sharks (Compagno, 1984; Carey and Scharold, 1990; Hazin *et al.*, 1994; Bigelow *et al.*, 1999; Walsh and Kleiber, 2001). The GRASP model demonstrated a strong influence of spatial factors (latitude and longitude) in both the cpue and the size distribution of blue sharks in the Southwest Atlantic, similar to the results of the studies of Bigelow *et al.* (1999) and Walsh and Kleiber (2001) in the North Pacific Ocean. Montealegre-Quijano and Vooren (2010) noted higher cpue of blue sharks in higher latitudes ($>30^\circ\text{S}$) based on a large proportion of juveniles and adult males, and that adult females were more abundant at lower latitudes ($<25^\circ\text{S}$). Mourato *et al.* (2008) also observed greater cpue of blue sharks in higher latitudes. Compagno (1984) stated that the blue shark generally prefers relatively cold waters, between 7 and 16°C, although it does tolerate water $>21^\circ\text{C}$. For the North Pacific, Nakano and Nagasawa (1996) noted the presence of blue sharks in areas with SST ranging from 13 to 22°C. Bigelow *et al.* (1999) and Walsh and Kleiber (2001) reported high cpue values for North Pacific blue sharks where the SST was $\sim 16^\circ\text{C}$. In the North Atlantic, Casey and Hoenig (1977) reported blue shark catches where the SST was between 12 and 27°C. Stevens (1990) concluded that SST has a positive effect on the abundance of female blue sharks in the eastern North Atlantic. In southern Brazilian waters, the highest cpue of blue sharks was in colder water (Mourato *et al.*, 2008). Montealegre-Quijano and Vooren (2010) also showed that blue shark cpue increases with decreasing SST in the Southwest Atlantic, with females more abundant in warmer water ($>27^\circ\text{C}$), and a higher cpue for juveniles and males associated with colder water ($<18^\circ\text{C}$). Hazin (1993) also noted that the abundance of males in the equatorial Atlantic tended to decline with an increase in temperature, whereas that of females showed an inverse trend.

In this study, cpue was displayed as a dome-shaped response to SST, with a peak at 16–17°C, where the proportion of juveniles was higher at cooler temperatures. Off the south coast of Brazil, colder water is generally associated with the Subtropical

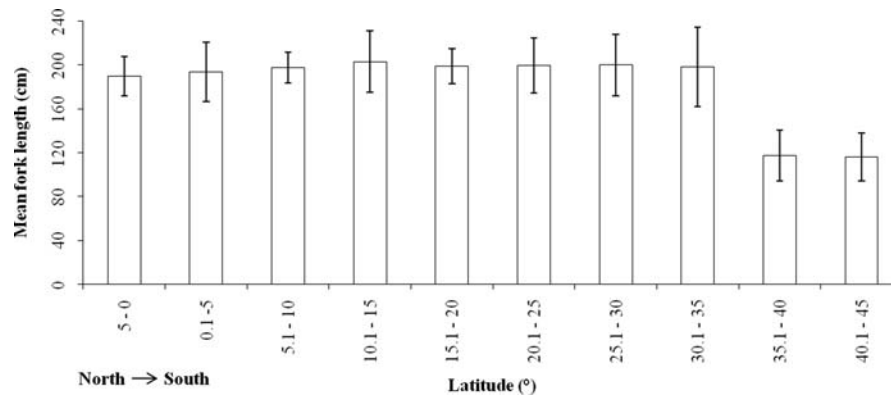


Figure 6. Mean FL (\pm s.e.) of blue sharks measured by observers on board Brazilian pelagic tuna longline vessels between 2006 and 2008, by blocks of 5° latitude. The horizontal dashed line indicates the size at first maturity (119 cm).

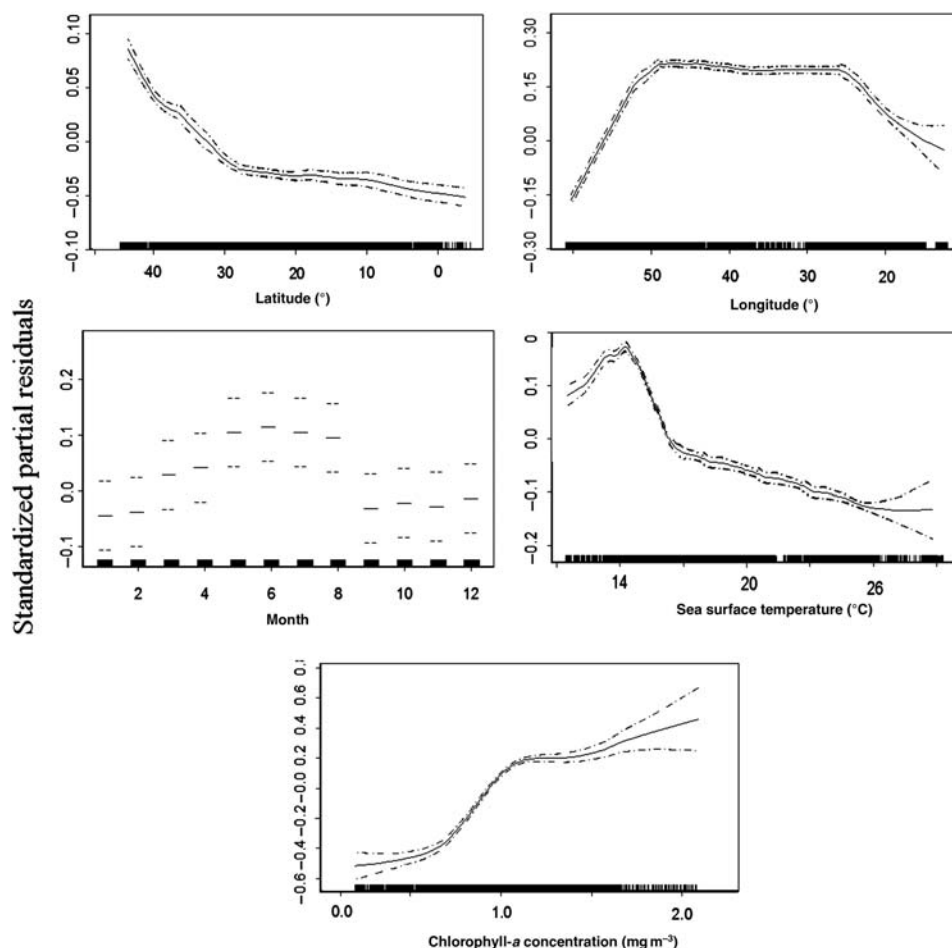


Figure 7. Partial response curves showing the effects of the predictor variables added to the model for the proportion of juvenile blue sharks caught by Brazilian pelagic longliners operating in the Southwest Atlantic from 2006 to 2008. The dashed lines represent 95% confidence limits, and tick marks on the abscissa show the location and density of datapoints.

Convergence (SC), the front of which moves north during the second and third quarters of the year (Olson *et al.*, 1988; Garcia, 1997). The SC is caused by the mixing of tropical warm water of the Brazil Current with cold water brought by the Malvinas Current. It is possible, therefore, that the higher cpue of blue sharks, as well as the larger proportion of juveniles, was related

to the position of the SC and the various biological phenomena associated with its front (i.e. upwelling), than to real changes in water temperature (Mourato *et al.*, 2008). According to Montu *et al.* (1997), the front of the SC is associated with water masses rich in nutrients that enhance phytoplankton development (higher CHL), which in turn promotes more primary and

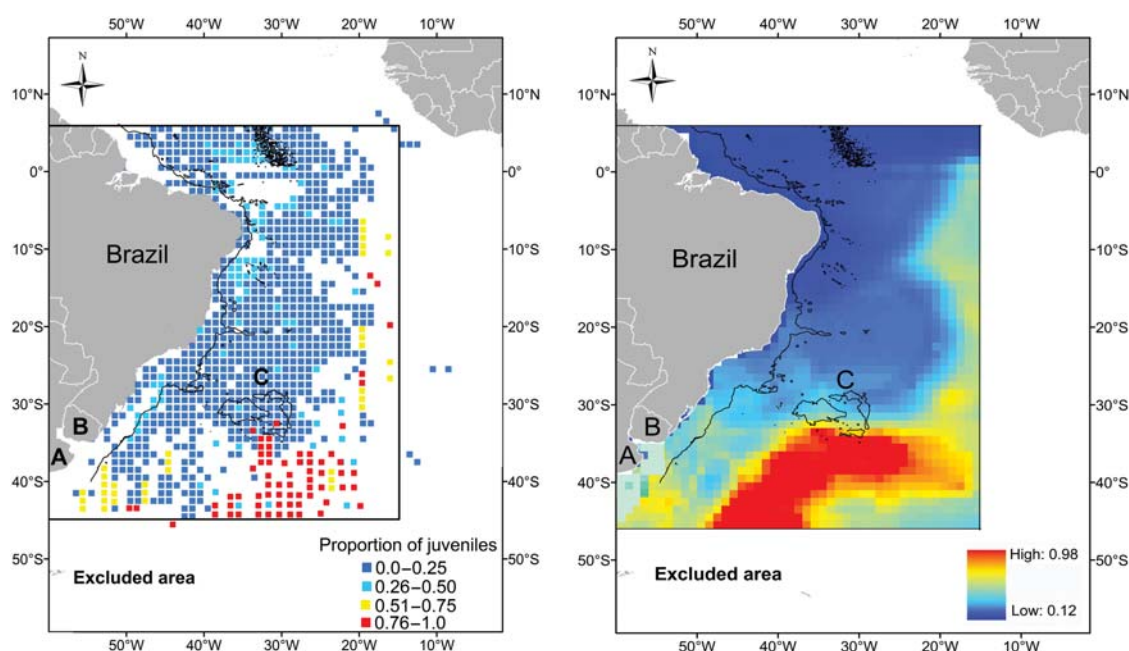


Figure 8. Spatial distribution of observed (left) and predicted (right) proportion of juvenile blue sharks in the catch of Brazilian tuna longliners operating in the Southwest Atlantic from January 2006 to December 2008. (A) Argentina, (B) Uruguay, and (C) Rio Grande Rise. The 3000-m isobath is shown by a solid black line.

secondary production. This phenomenon could increase the amount of potential prey for blue shark, e.g. squid (*Illex argentinus*; Vaske and Rincon, 1998), which stay in the region until the end of the third quarter of the year (Santos and Haimovici, 2002). This might also explain why high values of CHL had a notable influence on blue shark cpue and the proportion of juveniles. Coincidentally, both models suggested a higher cpue of blue sharks and proportion of juveniles during months when the SC was more intense in the area.

Some shark species tend to segregate by sex and/or size during their life cycle (Hoenig and Gruber, 1990), and this phenomenon has been broadly documented for blue sharks in the Atlantic Ocean (Hazin *et al.*, 1998; Kohler *et al.*, 2002; Fitzmaurice *et al.*, 2004), Pacific Ocean (Strasburg, 1958; Nakano, 1994), and Indian Ocean (Gubanov and Grigor'yev 1975). Stevens and Wayte (1999), for example, observed that blue shark body size decreased with increase in latitude. For the North Pacific, Nakano (1994) found a greater proportion of juveniles at higher latitude ($>35^{\circ}\text{N}$), in accord with the results of the spatial prediction map generated here for blue sharks in the Southwest Atlantic. In this study, the sex of the blue sharks measured was not recorded. However, it would be instructive for future work on sex-specific distribution patterns to collect information on sex in the future.

In the spatial prediction map for blue shark cpue, there were two areas of higher density, one close to shore and another in a more oceanic area, whereas a larger proportion of juveniles was only found offshore. As discussed above, the higher cpue and proportion of juveniles offshore could be related to the front of the SC and its regional influence on trophic dynamics. The areas of high abundance close to shore, in turn, might be explained by seasonal upwelling at the shelf break off the south coast of Brazil, Argentina, and Uruguay (Castelao *et al.*, 2004). This upwelling could also

attract blue sharks to an increased abundance of potential prey, similar to the situation described for the SC.

Another factor that might be leading to higher cpue and proportion of juvenile blue sharks in the area close to shore in southern latitudes is the Malvinas Current. According to Waluda *et al.* (2001), the Malvinas Current, which originates from the Antarctic Circumpolar Current, flows northwards along the continental shelf. It transports Subantarctic waters cold and rich in nutrients, maximizing production and the availability of food. Weidner and Arocha (1999) observed that other large oceanic predators tend to migrate from the tropics to this area, apparently attracted by the greater availability of nutrients and the associated increase in the prey base. In addition to the water enrichment resulting from nutrients brought in by the Malvinas Current and shelf break upwelling, the area may also receive an important input of nutrients from coastal discharge, such as from Lagoa dos Patos and the Plata River (Waluda *et al.*, 2001).

The most recent evaluation of blue shark stock status by ICCAT stated that current exploitation levels are sustainable (ICCAT, 2008). However, blue sharks are increasingly being caught by several fleets, particularly longliners pursuing swordfish as their main target species, such as those based in Santos and Itajai in the States of Sao Paulo and Santa Catarina of Brazil, respectively (UNIVALI/CTTMar, 2007), which provided the catch data used in this study. Such a trend could result in a significant increase in blue shark fishing mortality and the effects of this change on fishery operations are currently being analysed. Azevedo (2003) and Mourato *et al.* (2008) also observed a change in the spatial distribution of fishing effort in recent years, which could result in increased fishing pressure on blue shark stocks in the South Atlantic. Specifically, since 2000, longliners from the Santos and Itajai fleets that target swordfish have started to concentrate their effort in areas near the Rio Grande Rise, where blue shark

cpue was determined to be high. Such a change in fishing strategy would also probably increase the mortality of juveniles, because these waters seem to be an important habitat for juvenile blue sharks, as revealed by the spatial prediction map.

Acknowledgements

We thank the Brazilian Ministry for Fisheries and Aquaculture for funding the work, the Tropical Conservation and Development (TCD) Program and the Program of Fisheries and Aquatic Sciences of the University of Florida, for the TCD Fellowship and Graduate assistantship, respectively, provided to FCC, and the Florida Program for Shark Research for further financial assistance. Thanks are also due to John Carlson (US National Marine Fisheries Service, Panama City Laboratory), Daryl Parkyn (University of Florida Program of Fisheries and Aquatic Sciences), and two anonymous reviewers for thoughtful comments and suggestions on the submitted version of the paper.

References

- Agnew, D. J., Beddington, J. R., and Hill, S. L. 2002. The potential use of environmental information to manage squid stocks. *Canadian Journal of Fisheries and Aquatic Sciences*, 41: 1–23.
- Aires-da-Silva, A. 2008. Population dynamic of blue shark in the Northwest Atlantic Ocean. Doctoral thesis, University of Washington, Seattle, WA. 180 pp.
- Azevedo, V. G. 2003. Aspectos biológicos e dinâmica das capturas do tubarão-azul (*Prionace glauca*) realizadas pela frota espinheira de Itajaí-SC, Brasil. Master's thesis, Universidade de São Paulo, São Paulo, Brazil. 113 pp.
- Bigelow, A. K., Boggs, C. H., and He, X. 1999. Environmental effects on swordfish and blue sharks catch rates in the US North Pacific longline fishery. *Fisheries Oceanography*, 8: 178–198.
- Bonfil, R. 1994. Overview of world elasmobranch fisheries. *FAO Fisheries Technical Paper*, 341. 119 pp.
- Brander, K. 2003. Fisheries and climate. In *Marine Science Frontiers for Europe*, pp. 29–38. Ed. by G. Wefer, F. Lamy, and F. Mantoura. Springer, Berlin.
- Brill, R. W., Block, B. A., Boggs, C. H., Bigelow, K. A., Freund, E. V., and Marcinek, D. J. 1999. Horizontal movements and depth distribution of large adult yellowfin tuna (*Thunnus albacares*) near the Hawaiian Islands, recorded using ultrasonic telemetry: implications for the physiological ecology of pelagic fishes. *Marine Biology*, 133: 395–408.
- Cailliet, G. M., Musick, J. A., Simpfendorfer, C. A., and Stevens, J. D. 2005. Ecology and life history characteristics of chondrichthyan fish. In *Sharks, Rays and Chimaeras: the Status of the Chondrichthyan Fishes*, pp. 1–18. Ed. by S. L. Fowler, R. D. Cavanagh, M. Camhi, G. H. Burgess, G. M. Cailliet, S. V. Fordham, C. A. Simpfendorfer, et al. Cambridge University Press, Cambridge, UK. 314 pp.
- Carey, F. G., and Scharold, B. 1990. Movements of blue sharks (*Prionace glauca*) in depth and course. *Marine Biology*, 106: 329–342.
- Casey, J. G., and Hoenig, J. M. 1977. Apex predators in deepwater dumpsite. Baseline Report of Environmental Conditions in Deepwater Dumpsite. NOAA Dumpsite Evaluation Report, 77, Washington, DC. 54 pp.
- Castelao, R. M., Campos, E. J. D., and Miller, J. L. 2004. A modeling study of coastal upwelling driven by wind and meanders of the Brazil current. *Journal of Coastal Research*, 20: 662–671.
- Chong, Y. S., and Wang, J. L. 1997. Statistical modeling via dimension reduction methods. *Nonlinear Analysis, Theory, Methods and Applications*, 30: 3561–3568.
- Claireaux, G., and Lefrançois, C. 2007. Linking environmental variability and fish performance: integration through the concept of scope for activity. *Philosophical Transaction of the Royal Society*, 362: 2031–2041.
- Cleveland, W. S., and Delvin, S. J. 1988. Locally weighted regression: an approach to regression analysis by local fitting. *Journal of the American Statistical Association*, 83: 596–610.
- Compagno, L. J. V. 1984. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 1—Hexanchiformes to Lamniformes. *FAO Fisheries Synopsis*, 125. 249 pp.
- Damalas, D., Megalofonou, P., and Apostolopoulou, M. 2007. Environmental, spatial, temporal and operational effects on swordfish (*Xiphias gladius*) catch rates of eastern Mediterranean Sea longline fisheries. *Fisheries Research*, 84: 233–246.
- Daskalov, G. 1999. Relating fish recruitment to stock biomass and physical environment in the Black Sea using generalized additive models. *Fisheries Research*, 41: 1–23.
- Draganik, B., and Pelczarski, W. 1984. The occurrence of the blue shark, *Prionace glauca*, in the North Atlantic. *Reports of the Sea Fisheries Institute Gdynia*, 19: 61–75.
- Efron, B., and Tibshirani, R. J. 1995. Cross-validation and the bootstrap: estimating the error rate of the prediction rule. *Technical Report University of Toronto*, 176. 134 pp.
- Fitzmaurice, P., Green, P., Kierse, G., Kenny, M., and Clarke, M. 2004. Stock discrimination of the blue shark, based on Irish tagging data. *ICCAT Collective Volume of Scientific Papers*, 58: 1171–1178.
- Garcia, C. A. E. 1997. Coastal and marine environments and their biota. In *Subtropical Convergence Environments: the Coast and Sea in the Southwestern Atlantic*, pp. 129–136. Ed. by U. Seeliger, C. Odebrecht, and J. P. Castello. Springer, Berlin.
- Gubanov, Y. P., and Grigor'yev, V. N. 1975. Observations on the distribution and biology of the blue shark *Prionace glauca* (Carcharhinidae) of the Indian Ocean. *Journal of Ichthyology*, 15: 37–43.
- Guisan, A., Edwards, T. C., and Hastie, T. 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecological Modeling*, 157: 89–100.
- Hastie, T. J., and Tibshirani, R. J. 1986. Generalized additive models. *Statistical Science*, 1: 297–318.
- Hazin, F. H. V. 1993. Fisheries oceanographical study of tunas, billfishes and sharks in the southwestern equatorial Atlantic Ocean. PhD thesis, University of Fisheries, Tokyo. 286 pp.
- Hazin, F. H. V., Boeckmann, C. E., Leal, E. C., Lessa, R. P. T., Kihara, K., and Otsuka, K. 1994. Distribution and relative abundance of the blue shark, *Prionace glauca*, in the southwestern equatorial Atlantic Ocean. *Fishery Bulletin US*, 92: 474–480.
- Hazin, F. H. V., Zagaglia, J. R., Broadhurst, M. K., Travassos, P. E. P., and Bezerra, T. R. Q. 1998. Review of a small-scale pelagic longline fishery off northeastern Brazil. *Marine Fisheries Review*, 60: 1–8.
- Hekinian, R. 1982. *Petrology of the Ocean Floor*. Elsevier, New York. 393 pp.
- Hoenig, J. M., and Gruber, S. M. 1990. Life-history patterns in the elasmobranchs: implications for fisheries management. In *Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of the Fisheries*, pp. 1–6. Ed. by H. L. Pratt, S. Gruber, and T. Taniuchi. Report of the US Department of Commerce, Washington, DC.
- ICCAT (International Commission for the Conservation of Atlantic Tunas). 2008. Report of the 2008 inter-sectional meeting of the ICCAT shark species group: shark stock assessment. *ICCAT Collective Volume of Scientific Papers*, 17: 1–89.
- Kohler, N. E., Turner, P. A., Hoey, J. J., Natanson, L. J., and Briggs, R. 2002. Tag and recapture data for three pelagic shark species: blue shark (*Prionace glauca*), shortfin mako (*Isurus oxyrinchus*) and porbeagle (*Lamna nasus*) in the North Atlantic Ocean. *ICCAT Collective Volume of Scientific Papers*, 54: 1231–1260.

- Laevastu, T., and Rosa, J. 1963. The distribution and relative abundance of tunas in relation to their environment. FAO Fisheries Report, 6: 1835–1851.
- Laidig, T. E., Chess, J. R., and Howard, D. F. 2007. Relationship between abundance of juvenile rockfishes (*Sebastes* spp.) and environmental variables documented off northern California and potential mechanisms for the covariation. Fishery Bulletin US, 105: 39–48.
- Latimer, A. M., Wu, S., Gelfand, A. E., and Silander, J. A. 2006. Building statistical models to analyze species distributions. Ecological Applications, 16: 33–50.
- Lehmann, A., Leathwick, J. R., and Overton, J. M. 2002b. Assessing New Zealand fern diversity from spatial predictions of species assemblages. Biodiversity and Conservation, 11: 2217–2238.
- Lehmann, A., Overton, J. M., and Leathwick, J. R. 2002a. GRASP: generalized regression analysis and spatial prediction. Ecological Modelling, 157: 189–207.
- Maunder, M. N., and Punt, A. E. 2004. Standardizing catch and effort data: a review of recent approaches. Fisheries Research, 70: 141–159.
- Maury, O., Gascuel, D., Marsac, F., Fonteneau, A., and De Rosa, A. 2001. Hierarchical interpretation of nonlinear relationships linking yellowfin tuna (*Thunnus albacares*) distribution to the environment in the Atlantic Ocean. Canadian Journal of Fisheries and Aquatic Sciences, 58: 458–469.
- Mayer, D. A., Molinari, R. L., and Festa, F. G. 1998. The mean and annual cycle of upper layer temperature fields in relation to Sverdrup dynamics within the gyres of the Atlantic Ocean. Journal Geophysical Research, 103: 545–566.
- McClain, E. P., Pichel, W. G., and Walton, C. C. 1985. Comparative performance of (AVHRR) based multichannel sea surface temperatures. Journal of Geophysical Research, 90: 1587–1601.
- McKenzie, R. A., and Tibbo, S. N. 1964. A morphometric description of blue shark (*Prionace glauca*) from Canadian Atlantic waters. Journal of Fisheries Research, 21: 865–866.
- Mejuto, J., and García-Cortéz, B. 2004. Reproductive and distribution parameters of the blue shark, *Prionace glauca*, on the basis of on-board observations at sea in the Atlantic, Indian and Pacific Oceans. ICCAT Collective Volume of Scientific Papers, 58: 951–973.
- Montealegre-Quijano, S., and Vooren, C. M. 2010. Distribution and abundance of the life stages of the blue shark *Prionace glauca* in the southwestern Atlantic. Fisheries Research, 101: 168–179.
- Montu, M., Duarte, A. K., and Gloeden, I. M. 1997. Zooplankton. In Subtropical Convergence Environments, pp. 40–43. Ed. by U. Seeliger, C. Odebrecht, and J. P. Castello. Springer, Berlin.
- Mourato, B., Amorim, A. F., Arfelli, C. A., Hazin, F. H. V., Hazin, H. G., and Carvalho, F. C. 2008. Influence of environmental, spatial and temporal factors on blue shark, *Prionace glauca*, catch rate in the southwestern Atlantic Ocean. Arquivos de Ciencias do Mar, 41: 34–46.
- Myers, R. A. 1998. When do environment–recruit correlations work. Reviews in Fish Biology and Fisheries, 8: 285–305.
- Nakano, H. 1994. Age, reproduction and migration of blue shark in the North Pacific Ocean. Bulletin of the National Research Institute of Far Seas Fisheries, 31: 141–255.
- Nakano, H. 1999. Fishery management of sharks in Japan. In Case Studies of the Management of Elasmobranch Fisheries, pp. 552–579. Ed. by R. Shotton. FAO Fisheries Technical Paper, 378.
- Nakano, H., and Seki, M. P. 2003. Synopsis of biological data on the blue shark, *Prionace glauca*, Linnaeus. Bulletin of the Fisheries Research Agency, 6: 18–55.
- Nakano, N., and Nagasawa, K. 1996. Distribution of pelagic elasmobranchs caught by salmon research gillnets in the North Pacific. Fisheries Science, 62: 860–865.
- Neter, J., Wasserman, W., and Kutner, M. H. 1989. Applied Linear Regression Models, 2nd edn. Irwin Homewood, New York. 300 pp.
- Olson, D. B., Podesta, G. P., Evans, R. H., and Brown, O. B. 1988. Temporal variations in the separation of Brazil and Malvinas Currents. Deep Sea Research, 35: 1971–1990.
- Ottersen, G., and Sundby, S. 1995. Effects of temperature, wind and spawning stock biomass on recruitment of Arcto-Norwegian cod. Fisheries Oceanography, 4: 278–292.
- Pauly, D., Trites, E., and Christensen, V. 1998. Diet composition and trophic levels of marine mammals. ICES Journal of Marine Science, 55: 467–481.
- Pawson, M., and Vince, M. 1999. Management of shark fisheries in the Northeast Atlantic. In Case Studies of the Management of Elasmobranch Fisheries, pp. 1–46. Ed. by R. Shotton. FAO Fisheries Technical Paper, 378.
- Santos, R. A., and Haimovici, M. 2002. Cephalopods in the trophic relations off southern Brazil. Bulletin of Marine Science, 71: 753–770.
- Seeliger, U., Odebrecht, C., and Castello, J. P. 1997. Subtropical Convergence Environments: the Coast and Sea in the Southwestern Atlantic. Springer, Berlin. 308 pp.
- Sharp, G. D., Csirke, J., and Garcia, S. 1983. Modelling fisheries: what was the question? In Proceedings of the Expert Consultations to Examine Changes in Abundance and Species Composition of Neritic Fisheries Resources, pp. 1177–1214. Ed. by G. D. Sharp, and J. Csirke. FAO Fisheries Report, 219.
- Shotton, R. (ed.). 1999. Case studies of the management of elasmobranch fisheries. FAO Fisheries Technical Paper, 378: 480–920.
- Stevens, J. D. 1990. Further results from a tagging study of pelagic sharks in the north-east Atlantic. Journal of the Marine Biological Association of the UK, 70: 707–720.
- Stevens, J. D., Bonfil, R., Dulvy, N. K., and Walker, P. A. 2000. The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. ICES Journal of Marine Science, 57: 476–494.
- Stevens, J. D., and Wayne, K. 1999. Overview of world elasmobranch fisheries. FAO Fisheries Technical Paper, 341. 119 pp.
- Strasburg, D. W. 1958. Distribution, abundance and habitats of pelagic sharks in the central Pacific Ocean. Fishery Bulletin US, 58: 335–361.
- Travassos, P. 1999. l'Étude des relations thons-environnements dans l'Océan Atlantique intertropical ouest: cas de l'albacore (*Thunnus albacares*, Bonnaterre 1788), du germon (*Thunnus alalunga*, Bonnaterre 1788) et du thon obèse (*Thunnus obesus*, Lowe 1839). PhD thesis, Université Paris. 240 pp.
- UNIVALI/CTTMar. 2007. Boletim estatístico da pesca industrial de Santa Catarina – ano 2006 e panorama 2001/2006. Itajai-SC. 80 pp.
- Vaske, T., and Rincon, G. 1998. Conteúdo estomacal dos tubarões azul (*Prionace glauca*) e anequim (*Isurus oxyrinchus*) em águas oceânicas no sul do Brasil. Revista Brasileira de Biologia, 3: 445–452.
- Walsh, W. A., and Kleiber, P. 2001. Generalized additive model and regression tree analyses of blue shark (*Prionace glauca*) catch rates by the Hawaii-based longline fishery. Fisheries Research, 53: 115–131.
- Walsh, W. A., Kleiber, P., and McCracken, M. 2002. Comparison of logbook reports of incidental blue shark catch rates by Hawaii-based longline vessels to fishery observer data by application of a generalized additive model. Fisheries Research, 58: 79–94.
- Waluda, C. M., Rodhouse, P. G., Podesta, G. P., Trathan, P. N., and Pierce, G. J. 2001. Surface oceanography of the inferred hatching grounds of *Illex argentinus* (Cephalopoda: Ommastrephidae) and influences on the recruitment variability. Marine Biology, 139: 671–679.
- Weidner, D., and Arocha, F. 1999. South America: Atlantic, part A, section 2 (segment B). Brazil. In US National Marine Fisheries Service (NMFS) Report. World Swordfish Fisheries: an Analysis

- of Swordfish Fisheries, Market Trends, and Trade Patterns, 4, pp. 237–628. NMFS, Silver Spring, MD.
- Yee, T. W., and Mitchell, N. D. 1991. Generalized additive models in plant ecology. *Journal of Vega Science*, 2: 587–602.
- Zagaglia, C. R., Lorenzetti, J. A., and Stech, J. L. 2004. Remote sensing data and longline catches of yellowfin tuna (*Thunnus albacares*) in the equatorial Atlantic. *Remote Sensing of Environment*, 93: 267–281.
- Zaniewski, A. E., Lehmann, A., and Overton, J. 2002. Predicting species distribution using presence-only data: a case study of native New Zealand ferns. *Ecological Modelling*, 157: 259–278.