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Distribution patterns and population structure of the blue shark (*Prionace glauca*) in the Atlantic and Indian Oceans

Rui Coelho[1] | Jaime Mejuto[2] | Andrés Domingo[3] | Kotaro Yokawa[4] | Kwang-Ming Liu[5] | Enric Cortés[6] | Evgeny V. Romanov[7] | Charlene da Silva[8] | Fábio Hazin[9] | Freddy Arocha[10] | Aldrin Masawbi Mwilima[11] | Pascal Bach[12] | Victoria Ortiz de Zárate[13] | William Roche[14] | Pedro G. Lino[1] | Blanca García-Cortés[2] | Ana M. Ramos-Cartelle[2] | Rodrigo Forselledo[3] | Federico Mas[3] | Seiji Ohshimo[4] | Dean Courtney[6] | Philippe S. Sabarros[12] | Bernardo Perez[13] | Ciara Wogerbauer[14] | Wen-Pei Tsai[15] | Felipe Carvalho[9] | Miguel N. Santos[1]

[1]Portuguese Institute for the Ocean and Atmosphere (IPMA), Olhão, Portugal

[2]Instituto Español de Oceanografía (IEO), C.O. A Coruña, A Coruña, Spain

[3]Dirección Nacional de Recursos Acuáticos (DINARA), Laboratorio de Recursos Pelágicos, Montevideo, Uruguay

[4]National Research Institute of Far Seas Fisheries (NRIFSF), Shizuoka-City, Shizuoka, Japan

[5]Institute of Marine Affairs and Resource Management, National Taiwan Ocean University, Keelung, Taiwan

[6]National Oceanographic and Atmospheric Administration, National Marine Fisheries Service (NOAA-NMFS), Southeast Fisheries Science Center, Panama City Laboratory, Panama City, FL, USA

[7]Centre Technique d'Appui à la Pêche Réunionnaise (CAP RUN – Hydrô Réunion), Le Port, Île de la Réunion

[8]Department of Agriculture, Forestry and Fisheries; Branch: Fisheries Research and Development, Inshore Research, Cape Town, South Africa

[9]Departamento de Pesca e Aquicultura, Universidade Federal Rural de Pernambuco (UFRPE), Recife, Brasil

[10]Instituto Oceanográfico de Venezuela, Universidad de Oriente, Estado Sucre, Venezuela

[11]Ministry of Fisheries and Marine Resources, National Marine Information Resource Center, Windhoek, Namibia

[12]Institut de Recherche pour le Développement (IRD), UMR 248 MARBEC, Sète Cedex, France

[13]Instituto Español de Oceanografía (IEO), C.O. Santander, Santander, Spain

[14]Inland Fisheries Ireland, Dublin 24, Ireland

[15]Department of Fisheries Production and Management, National Kaohsiung Marine University, Kaohsiung, Taiwan

Correspondence
Rui Coelho, Portuguese Institute for the Ocean and Atmosphere (IPMA), Olhão, Portugal.
Email: rpcoelho@ipma.pt

Present addresses
Felipe Carvalho, NOAA Pacific Islands Fisheries Science Center, Honolulu, HI, USA

Miguel N. Santos, International Commission for the Conservation of Atlantic Tunas (ICCAT), Madrid, Spain

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Abstract

The blue shark (*Prionace glauca*) is the most frequently captured shark in pelagic oceanic fisheries, especially pelagic longlines targeting swordfish and/or tunas. As part of cooperative scientific efforts for fisheries and biological data collection, information from fishery observers, scientific projects and surveys, and from recreational fisheries from several nations in the Atlantic and Indian Oceans was compiled. Data sets included information on location, size and sex, in a total of 478,220 blue shark records collected between 1966 and 2014. Sizes ranged from 36 to 394 cm fork length. Considerable variability was observed in the size distribution by region and season in both oceans. Larger blue sharks tend to occur in equatorial and tropical regions, and smaller specimens in higher latitudes in temperate waters. Differences in sex ratios were also detected spatially and seasonally. Nursery areas in the Atlantic seem to occur in the temperate south-east off South Africa and Namibia, in the south-west off southern Brazil and Uruguay, and in the north-east off the Iberian Peninsula and the Azores. Parturition may occur in the tropical north-east off West Africa. In the Indian Ocean, nursery areas also seem to occur in temperate waters, especially in the south-west Indian Ocean off South Africa, and in the south-east off south-western Australia. The distributional patterns presented in this study provide a better understanding of how blue sharks segregate by size and sex, spatially and temporally, and improve the scientific advice to help adopt more informed and efficient management and conservation measures for this cosmopolitan species.

KEYWORDS
Atlantic Ocean, fishery observer programmes, Indian Ocean, pelagic fisheries, size distribution, spatial distribution

1 | INTRODUCTION

The blue shark (*Prionace glauca*, Carcharhinidae) is one of the widest ranging of all pelagic shark species, found throughout tropical and temperate seas from latitudes of about 60°N to 50°S (Last & Stevens, 2009). It is a pelagic species mainly distributed from the sea surface to depths of about 350 m, even though deeper dives down to 1,000 m have been recorded (Campana et al., 2011). The blue shark is an oceanic species capable of long-range migrations (e.g. Campana et al., 2011; da Silva, Kerwath, Wilke, Meÿer, & Lamberth, 2010; Queiroz et al., 2005), but can also occasionally occur closer to shore, especially in areas where the continental shelf is narrow (Last & Stevens, 2009). The sporadic presence of blue shark recruits has been described very close to shore in some areas (e.g. north-east Atlantic, Mejuto, García-Cortés, Ramos-Cartelle, & Abuin, 2014).

Blue sharks are captured by a variety of fishing gears, but most catches that have been reported take place as by-catch in pelagic longlines targeting tunas (*Thunnus* spp.) and/or swordfish (*Xiphias gladius*), where it is the most prevalent shark captured (Castro, Serna, Macías, & Mejuto, 2000; Coelho, Fernandez-Carvalho, Lino, & Santos, 2012; Hazin, Broadhurst, Amorin, Arfelli, & Domingo, 2008; Mejuto, 1985; Mejuto & García-Cortés, 2005; Mejuto, García-Cortés, Ramos-Cartelle, & Serna, 2009; Romanov, Bach, & Romanova, 2008). Depending on the fisheries, areas and seasons, blue shark catches can be very significant in the overall catch and in some specific cases can account for more than 50% of the total fish catch and around 85–90% of the total elasmobranch catch (Coelho et al., 2012).

In the Atlantic, the average blue shark landings reported to ICCAT (International Commission for the Conservation of Atlantic Tunas) over the last few years (2010–2014) were approximately 64,000 t, of which approximately 58% were from the North and 42% from the South Atlantic. Overall, this represents approximately 8.5% of the total pelagic fish landings in weight for the Atlantic, considering that the average annual landings (all species combined) reported to ICCAT during the same period were approximately 756,000 t (Anon., 2014). In the Indian Ocean, the average annual blue shark landings reported to IOTC (Indian Ocean Tuna Commission) over the 2010–2014 period were approximately 28,000 t (Anon., 2015a), which represents approximately 1.6% of the total pelagic fish landings considering an average annual landing (all species combined) reported to IOTC of approximately 1,700,000 t for the same period (Anon., 2015a). However, compared to the Atlantic Ocean, the catch and landings of blue shark in the Indian Ocean are likely considerably higher than the reported values due to under-reporting and lack of species-specific identification for many shark species in some fisheries. Over the same period (2010–2014), the reported landings of "sharks *nei*—not elsewhere included" for the Indian Ocean were approximately 47,000 t (Anon. 2015a), which considering the prevalence of blue shark in pelagic gear catches is likely composed of a large proportion of blue sharks.

Understanding the spatio-temporal dynamics of marine species is extremely important for fisheries management and conservation, as it allows a better understanding of the species distribution and potential impacts by fisheries. Some previous studies have focused on the distribution of catch rates of blue shark in specific areas of the Atlantic, including the works of Hazin, Boeckmann, Leal, Lessa et al. (1994), Mejuto and García-Cortés (2005), Domingo, Mora, and Cornes (2002), Montealegre-Quijano and Vooren (2010) and Carvalho et al. (2011) in the south-west Atlantic; Cortés, Brown, and Beerkircher (2007) and Tavares, Ortiz, and Arocha (2012) in the western North Atlantic; Megalofonou, Damalas, and DeMetrio (2009) in the Mediterranean; and Vandeperre, Aires-da-Silva, Santos et al. (2014), Vandeperre, Aires-da-Silva, Fontes et al. (2014) in the Central North Atlantic. Previous studies have also investigated size distributions of blue sharks in broad areas of the North and South Atlantic, such as Mejuto and García-Cortés (2005), and in more specific areas of the Atlantic, such as Tavares et al. (2012) off Venezuela in the Caribbean Sea and adjacent waters, Carvalho et al. (2010) in the south-west Atlantic, and da Silva et al. (2010) off the Atlantic–Indian confluence zone. For the Indian Ocean, the currently available information on blue shark is still very scarce and includes mainly observations on biological aspects and distribution (e.g. Gubanov & Grigor'yev, 1975; Selles et al., 2014), and size, sex, catch rates and reproductive parameters (Mejuto & García-Cortés, 2005).

Ecological risk assessment (ERA) methods have been used by some t-RFMOs (tuna Regional Fisheries Management Organizations) to provide indicators of the vulnerability of pelagic shark species to fishing gears. In 2012, a semi-quantitative ERA for pelagic sharks was developed in the Indian Ocean, where the blue shark received a medium vulnerability ranking as they were characterized to be the most productive shark species but also highly susceptible to pelagic longline gear (Murua et al., 2012). In the Atlantic, ERAs for pelagic sharks were conducted in 2008 and 2012, and also showed that the blue shark had an intermediate vulnerability level, also characterized by high productivity within the pelagic sharks and high susceptibility to pelagic longline fishing gear (Cortés et al., 2010, 2015).

The latest stock assessments of blue shark for the Atlantic were carried out by ICCAT in 2015. For the North Atlantic stock, all scenarios indicated that the stock was not overfished and that overfishing was not occurring, but due to the high levels of uncertainty, the possibility of the stock being overfished and overfishing occurring was not completely ruled out (Anon., 2015b). For the South Atlantic, the scenarios and models varied from predicting that the stock was not overfished and that overfishing was not occurring, to less optimistic cases where the stock could be overfished and overfishing could be occurring. The high uncertainty in catch estimates and deficiency of some important biological parameters, particularly for the South Atlantic, were identified as obstacles for obtaining more reliable estimates of the current stock status (Anon., 2015b). The latest stock assessment conducted for the Indian Ocean by IOTC also took place in 2015, and from the various model runs, there was a suggestion that the stock could be subject to overfishing but not yet overfished; however, there was high uncertainty in the results, and as such, the stock status remained uncertain (Anon., 2015c). As in most pelagic species, there is still considerable uncertainty in the stock status advice for blue shark currently provided both for the Atlantic and Indian Oceans.

To date, an oceanic-wide and fleet-combined study on the size-structure and distribution patterns of blue shark is lacking. However, this type of information is needed to provide better management advice for the populations at an oceanic-level scale. Research efforts have been carried out in recent years by scientists both in the Atlantic and Indian Oceans, in collaboration with the major fishing fleets, to provide and analyse such scientific data in support of management advice. This includes the provision of size-based data for length-based, age-structured integrated stock assessment models that have been used more recently by the t-RFMOs.

The main goal of this study is therefore to provide a review of the detailed size distribution data available for the blue shark from the major oceanic fleets that target tunas and/or swordfish in the Atlantic and Indian Oceans, especially pelagic longline fisheries that can have relatively high catch rates of blue sharks. Additional data from recreational fisheries and scientific projects and surveys were also used. The specific objectives of this review are to: (i) analyse the size distribution and seasonal patterns of the blue shark in the Atlantic and Indian Oceans; (ii) provide time-series trends of the size distribution in each region; (iii) analyse the distribution of sex ratios at oceanic-wide scales; (iv) characterize the main areas of concentration of particular life stages including juveniles/immature and adults/mature specimens; and (v) model the expected size distribution over oceanic-wide scales in the Atlantic and Indian Oceans.

2 | MATERIALS AND METHODS

2.1 | Data collection

Blue shark records and data were collected mainly by national scientific observers on-board commercial vessels. Additional data were obtained from detailed logbooks and port samplers working on national data collection programmes, and from scientific projects from several fishing nations in the Atlantic and Indian Oceans, mainly surveying pelagic longline fisheries. Most of the data came from the commercial drifting pelagic longlines, including shallow night setting longlines targeting swordfish in both temperate and tropical regions, deeper day setting longlines targeting tropical tunas in more tropical regions, and deeper setting longlines in high latitudes of the North Atlantic targeting bluefin tuna (*Thunnus thynnus*; ICCAT, 2006–2016). Additional data used came from artisanal pelagic longlines in the Bay of Biscay, from scientific pelagic longline surveys carried out by some nations between the 1960s and 1980s (Japan and USSR), and from tagging undertaken by angling charter vessels off Ireland (Green et al., 2009). A summary of the data collected, compiled and used for this study is provided in Table 1. A limitation of this study is that the majority of the data collected came from fishery-dependent sources, which affected the length compositions and detection of blue sharks (see Discussion for more details).

Data were collected across a wide geographical range in the two oceans. In the Atlantic, the two hemispheres were separated at the 5°N parallel, as recommended in the ICCAT Manual for shark species (ICCAT, 2006–2016; Figure 1). Furthermore, each hemisphere was divided into four areas (NW, NE, SW, SE) taking into consideration the ICCAT sampling areas for sharks (ICCAT, 2006–2016) as well as the distribution patterns of the fleets and the characteristics of the distributions of sizes of blue sharks in the sample. For the Indian Ocean, only one blue shark stock was considered as used by the IOTC, divided into four areas (NW, NE, SW, SE) based mainly on the characteristics of the distributions of sizes of blue sharks in the sample and distribution of the fleets (Figure 1).

For captured specimens, data on size, sex, capture location and date were recorded. The size measurement most often taken was the fork length (FL), but there were some exceptions as some of the national programmes record other measurements (e.g. TL—total length; PCL—pre-caudal length; LW—live or round weight; DW—dressed weight). In those cases, all sizes and weights were converted to FL using equations available at the national research institutes (Table 2).

TABLE 1 Summary of the data compiled and analysed for this study by fleet and gear type, with information on the sample size in number of specimens (*N*), the size range of the specimens (FL—fork length, cm) and the range of years in each data set

Ocean	Country/fleet	Gear	Activity	Sample (*N*)	Size range (FL, cm)	Years range
Atlantic	Brazil	Pelagic longline	Commercial	6,242	43–320	2004–2008
	EU.Spain	Pelagic longline	Commercial	99,053	41–310	1993–2013
	EU.Spain	Artisanal longline	Commercial	26,889	69–310	1998–2001
	EU.Ireland	Rod and reel	Recreational	3,520	40–240	1970–2013
	EU.Portugal	Pelagic longline	Commercial	87,490	45–370	1997–2013
	Japan	Pelagic longline	Commercial	33,206	42–328	1997–2014
	Namibia	Pelagic longline	Commercial	11,578	38–352	2004–2013
	Taiwan	Pelagic longline	Commercial	59,107	40–394	2004–2013
	Uruguay	Pelagic longline	Commercial	69,157	36–305	1998–2012
	USA	Pelagic longline	Commercial	2,685	41–335	1992–2014
	Venezuela	Pelagic longline	Commercial	1,376	50–355	1994–2013
	South Africa	Pelagic longline	Commercial	521	107–265	2012–2014
Indian	EU.France	Pelagic longline	Commercial	305	89–300	2007–2014
	EU.France	Pelagic longline	Research	53	100–270	2003–2011
	EU.Portugal	Pelagic longline	Commercial	15,276	80–299	2011–2014
	Japan	Pelagic longline	Commercial	39,978	41–369	1992–2014
	Japan	Pelagic longline	Research	4,163	62–307	1967–2002
	Taiwan	Pelagic longline	Commercial	10,275	51–350	2004–2013
	USSR	Pelagic longline	Research	2,975	57–311	1966–1989
	South Africa	Pelagic longline	Commercial	4,371	70–322	2012–2014

2.2 | Data analysis

Size-frequency distributions by area and trends in mean size distributions were analysed and plotted by year, area, sex and quarter of the year. Size data were tested for normality with Kolmogorov–Smirnov normality tests with the Lilliefors correction (Lilliefors, 1967), and for homogeneity of variances with Levene tests (Levene, 1960). Specimen sizes were compared among regions, sexes and quarters of the year using nonparametric *k*-sample permutation tests (Manly, 2007).

Sex ratios were calculated and mapped over a 5° × 5° (latitude × longitude) grid for both the Atlantic and Indian Oceans. The comparison among areas was carried out with contingency tables and Pearson's chi-squared tests. The sex ratios were also compared among seasons of the year and size-classes (categorized by the 20th percentiles of the data), taking into account the various regions, using Cochran–Mantel–Haenszel (CMH) chi-squared tests. This allowed the detection of seasonality and size-related effects in the sex ratios conditional to each of the regions analysed.

The proportions of immature versus mature specimens in each region and season were calculated. In the Atlantic, the median sizes at maturity (FL) used to define immature and mature specimens were based on the ICCAT Shark Working Group report (Anon., 2014) as follows: North Atlantic: females = 182.1 cm FL, males = 197.0 cm FL; South Atlantic: females = 173.8 cm FL, males = 175.5 cm FL. For the Indian Ocean, the median sizes at maturity (FL) were defined according to the IOTC Executive Summary for blue shark produced by the IOTC Scientific Committee (Anon., 2015d) as follows: females = 194 cm FL; males = 201 cm FL. The kernel densities of the distribution of young juvenile (age <= 1), immature (juveniles of all age classes) and adult sharks in the Atlantic and Indian Oceans were calculated on a 5° × 5° grid. Kernel densities were estimated on this grid using bivariate normal distributions (Wand, 1994). For plotting the densities of young juveniles (ages 0 and 1), the size-at-age definitions of Skomal and Natanson (2003) were used, specifically age 0 females: 60.9 cm FL; age 0 males: 66.1 cm FL; age 1 females: 97.0 cm FL; and age 1 males: 97.4 cm FL.

A generalized additive model (GAM) with a Gaussian error structure and identity link function was used to predict the expected blue shark size distributions as a function of location (latitude and longitude) and quarter of the year in each ocean. The predictors in this model were given by the smooth functions of latitude and longitude plus a parametric component for the quarters. The smooth terms for the location covariates were estimated by maximum likelihood with thin plate regression splines (Wood, 2003). The significance of the model parameters was tested with likelihood ratio tests comparing nested models, including the significance of the interactions between latitude, longitude and quarter of the year. Goodness of fit was assessed with Akaike information criterion (AIC; Akaike, 1973) and with the final deviance explained. A residual analysis was carried out for model validation. The expected mean sizes were mapped along the study area in each ocean and for each quarter of the year.

The analysis for this study was carried out using the R language for statistical computing version 3.2.0. (R Core Team, 2015). Additional packages used included the following libraries: "car" (Fox & Weisberg,

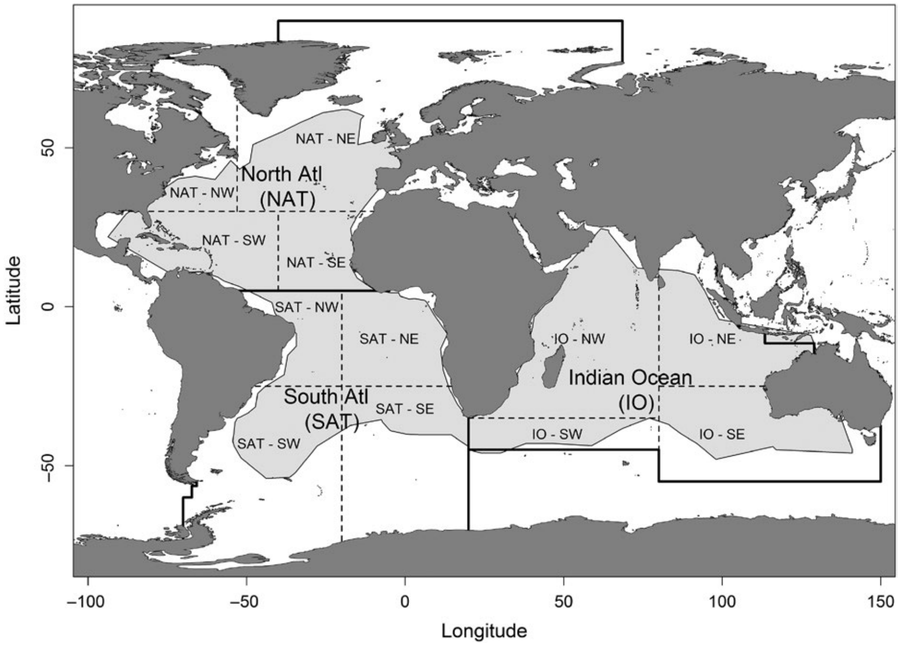

FIGURE 1 Location of the study area in the Atlantic and Indian Oceans with the limits of the size sample distributions shaded in the light grey area. The stock and region nomenclature used and the spatial distribution of the samples are also indicated. Specifically, the ICCAT and IOTC stock management units for sharks are identified as solid black lines (North Atlantic, South Atlantic and Indian Ocean), and the four areas (quadrants) within each stock as defined for this study are identified with dashed lines

2011), "classInt" (Bivand, 2013), "ggplot2" (Wickham, 2009), "gmodels" (Warnes, Bolker, Lumley, & Johnson, 2013), "KernSmooth" (Wand, 2015), "lme4" (Bates, Maechler, Bolker, & Walker, 2013), "maps" (Becker, Wilks, Brownrigg, & Minka, 2013), "mapplots" (Gerritsen, 2013), "maptools" (Bivand & Lewin-Koh, 2013), "mgcv" (Wood, 2006, 2011), "perm" (Fay & Shaw, 2010), "plyr" (Wickham, 2011), "rgdal" (Bivand, Keitt, & Rowlingson, 2013), "scales" (Wickham, 2012) and "shapefiles" (Stabler, 2013).

3 | RESULTS

3.1 | Spatial distribution

A total of 478,220 blue sharks were recorded and used for this work, with 400,824 from the Atlantic and 77,396 from the Indian Ocean. Specimens ranged in size from 36 to 394 cm FL in the Atlantic, and from 41 to 369 cm FL in the Indian Ocean, covering most of the known size range of the species. A summary of the sample size (N) and specimen size ranges by ocean and fleet is provided in Table 1, and the distribution map of the sample in both oceans is shown in Figure 2.

Size data were not normally distributed (Lilliefors test: $D = 0.036$, $p < .001$), and the variances were heterogeneous among regions (Levene test: $F = 2005.2$, $df = 11$, $p < .001$), quarters (Levene test: $F = 250.8$, $df = 11$, $p < .001$) and sexes (Levene test: $F = 12.584$, $df = 1$, $p < .001$). Using univariate nonparametric statistical tests revealed that sizes significantly differ among regions (permutation test: chi-squared = 138440, $df = 12$, $p < .001$), quarters (permutation test: chi-squared = 5484.8, $df = 3$, $p < .001$) and sexes (permutation test: chi-squared = 1358, $df = 1$, $p < .001$).

Considerable variability was observed in the size distributions of both male and female blue sharks among areas (Figures 1–3). However, with the areas structured as described above, blue shark size distributions within each area were mostly unimodal except for slight evidence of bimodal distributions in some areas (NAT-NE and NAT-SW; Figure 3). In the Atlantic, smaller specimens tended to be captured in more temperate waters (NAT-NE, SAT-SW; Figure 3), while larger specimens tended to be captured more frequently in tropical waters, especially between West Africa and the Caribbean Sea(NAT-SE, NAT-SW and SAT-SE; Figure 3). Similarly, in the Indian

TABLE 2 Morphometric relations (length–length, length–weight and weight–weight) from unpublished data available at national institutes, used to convert and standardize the measurements used in this study. The measurements are fork length (FL), total length (TL), pre-caudal length (PCL), live or round weight (LW) and dressed weight (DW). All size data are in cm and all weight data are in kg. Data come from IPMA (Portuguese Institute for the Ocean and Atmosphere), NRIFSF (National Research Institute of Far Seas Fisheries) and YugNIRO (Southern Scientific Research Institute of Marine Fisheries and Oceanography; E. Romanov, unpublished data)

Ocean	Relation	Equation	Source
Atlantic	Live to dressed weight	DW = 0.0068 + LW * 0.4167	IPMA
	Fork length to live weight	LW = 0.0000015 * FL^3.2907	IPMA
	Total to fork length	FL = −1.122 + TL * 0.829	NRIFSF
	Total to pre-caudal length	PCL = −2.505 + TL * 0.762	NRIFSF
Indian	Pre-caudal to fork length	FL = 0.9095 + PCL * 1.0934	YugNIRO
	Total to fork length	FL = 3.6291 + TL * 0.8215	YugNIRO

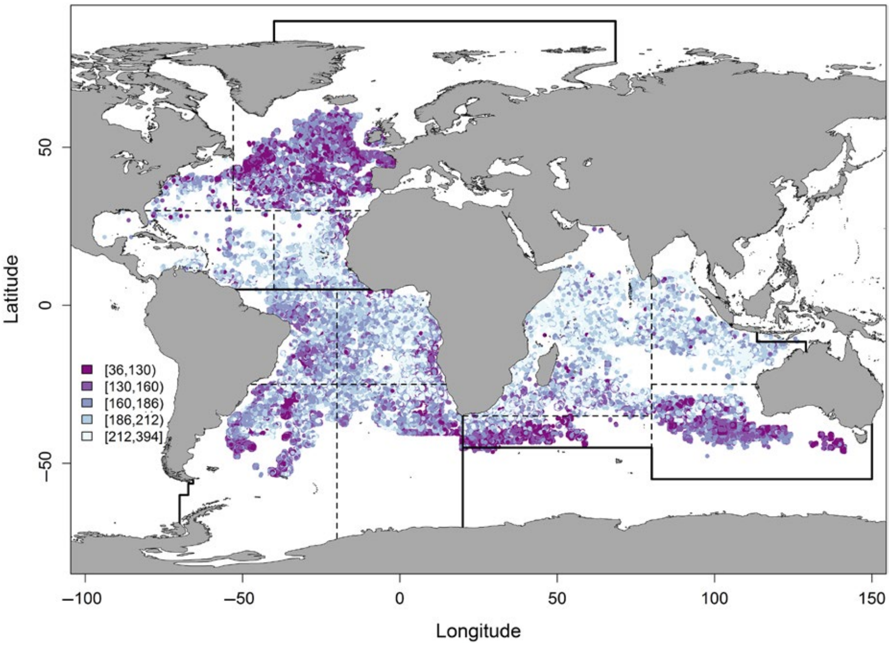

FIGURE 2 Location and size distribution of samples (FL, cm) of blue shark (*Prionace glauca*) recorded for this study in the Atlantic and Indian Oceans. The categorization of size-classes was carried out using the 0.2 quantiles of the data (values in the legend represent the lower and upper limits of each size-class). The ICCAT and IOTC stock management units for sharks are identified as solid black lines (North Atlantic, South Atlantic and Indian Ocean). The four areas (quadrants) within each stock as defined for this study are identified with dashed lines. [Colour figure can be viewed at wileyonlinelibrary.com]

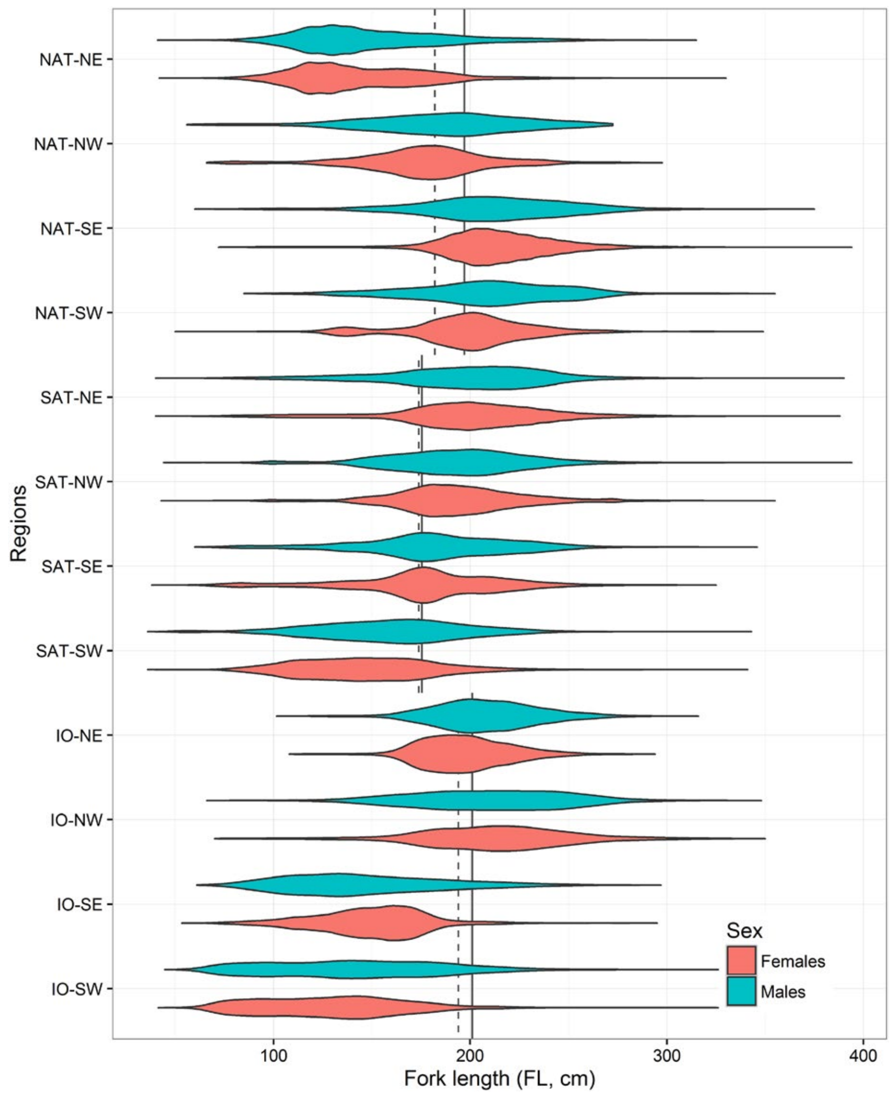

FIGURE 3 Size-frequency distributions of male and female blue shark (*Prionace glauca*) caught in the different regions of the Atlantic and Indian Oceans. NAT = North Atlantic, SAT = South Atlantic and IO = Indian Ocean. Within each major area, there are four quadrants as defined for this study (NW, NE, SW and SE, see Figure 1). The vertical lines represent median size at maturity in each region (solid lines = males, dashed lines = females). [Colour figure can be viewed at wileyonlinelibrary.com]

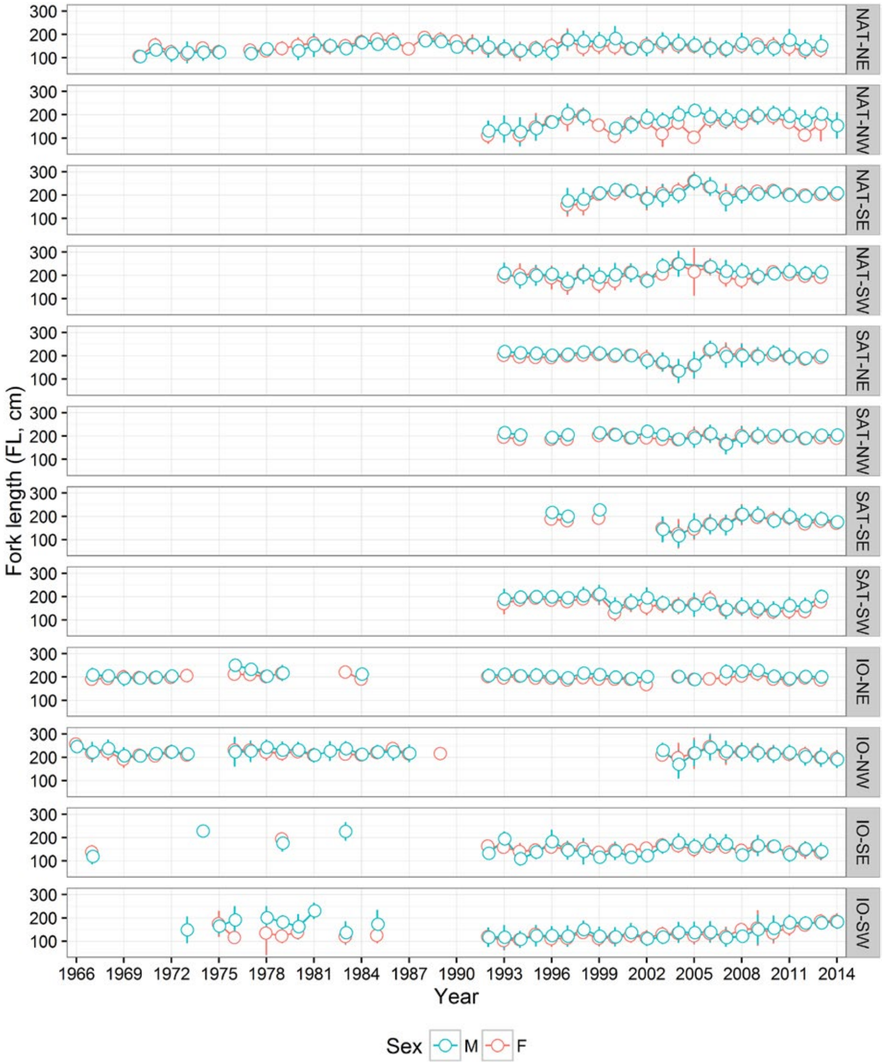

FIGURE 4 Time series of the mean size of blue shark (*Prionace glauca*) by sex caught in the different regions of the Atlantic and Indian Oceans. NAT = North Atlantic, SAT = South Atlantic and IO = Indian Ocean. Within each major area, there are four quadrants as defined for this work (NW, NE, SW and SE, see Figure 1). The error bars are 95% confidence intervals. [Colour figure can be viewed at wileyonlinelibrary.com]

Ocean, smaller specimens also tended to be captured in more temperate waters (IO-SE and IO-SW, Figure 3), while larger specimens were captured more frequently in tropical waters (IO-NE and IO-NW; Figure 3). These general trends tended to be common for both males and females. However, in some areas, there were more marked differences in the size-frequency distribution of each sex with the males being noticeably smaller than the females (IO-SE; Figure 3).

3.2 | Annual and seasonal variability

There were differences in time series of the mean sizes among regions, with some regions showing relatively more stable trends than others. The time series were relatively stable in the NAT-NE and SAT-NW (Figure 4). In contrast, higher variability was found in the NAT-NW and NAT-SE (Figure 4).

No major trends in the time series were noticeable for most regions. However, in some cases, such as the IO-SW, there were relatively pronounced trends with larger blue shark sizes in the 1970s (research cruise data), followed by a period with smaller sizes between 1992 and 2006, and then another period with larger sizes in more recent years (Figure 4).

Seasonality and sex also influence the size of blue sharks caught. In some areas, similar trends were observed for males and females throughout the year. For example, in the SAT-NE, IO-SE and IO-SW, both male and female sizes tended to decrease throughout the year (Figure 5). In contrast, in the IO-NW, both male and female sizes tended to increase along the quarters of the year (Figure 5).

3.3 | Sex ratios

Of all blue sharks with sex recorded (417,552 specimens), 352,797 were from the Atlantic and 64,755 from the Indian Ocean. In the Atlantic, 165,229 specimens (46.8%) were females and 187,568 (53.2%) were males, representing an overall sex ratio of 1.14 males for each female. In the Indian Ocean, 32,819 specimens (50.7%) were females and 31,936 (49.4%) were males representing an overall sex ratio very close to 1:1, specifically 1.03 females for each male.

In the Atlantic, both spatial and seasonal variability in sex ratios was evident when calculated and mapped over a 5° × 5° grid for each quarter of the year (Figure 6). In the temperate north-east Atlantic, there were more females in the higher latitudes (north of 45°N), especially evident in quarters 3 and 4. In contrast, in lower latitudes of temperate

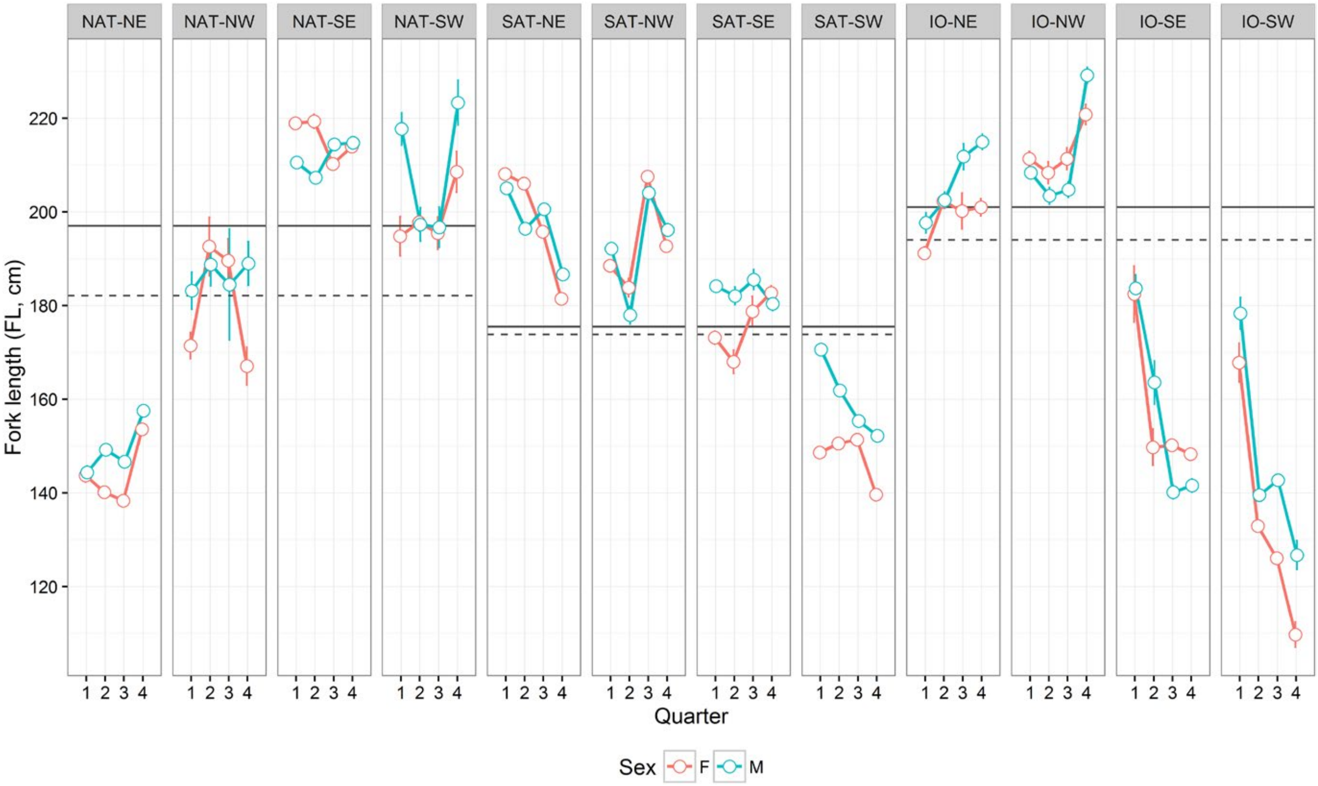

FIGURE 5 Mean size of male and female blue shark (*Prionace glauca*) by sex and quarter of the year caught in several regions of the Atlantic and Indian Oceans. NAT = North Atlantic, SAT = South Atlantic and IO = Indian Ocean. Within each major area, there are four quadrants as defined for this work (NW, NE, SW and SE, see Figure 1). The error bars are 95% confidence intervals. The horizontal lines represent median size at maturity in each region (solid lines = males, dashed lines = females). [Colour figure can be viewed at wileyonlinelibrary.com]

north-eastern waters, between 20 and 40°N, there were in general more males, especially in quarters 2 and 3. In temperate waters of the NAT-NW, there was high variability in the sex ratios, while in tropical waters in the central Atlantic, there was a large concentration of females, particularly in quarter 3. In the South Atlantic, between 0 and 20°S, the sex ratios were highly variable, while in waters south of 20°S, there were in general more males, both in the south-west and south-east Atlantic and especially in quarters 1, 2 and 3. In the area of the Gulf of Guinea (north-east quadrant of the South Atlantic), there was a tendency for the presence of more males in quarters 3 and 4. The differences observed in the Atlantic sex ratios were significant when compared among the geographic areas as defined in Figure 1 (proportion test: chi-squared: 3,501.5, $df = 7$, $p < .001$) and seasons conditionally within each area (CMH test: chi-squared = 1,808.1, $df = 3$, $p < .001$). There were also significant differences detected in the sex ratios comparing sizes tested conditionally within the each area (CMH test: chi-squared = 1,518.5, $df = 4$, $p < .001$).

Similarly, in the Indian Ocean, there was also evidence of variability in the sex ratios when calculated and mapped over a 5° × 5° grid for each quarter of the year (Figure 7). In general, there were more females recorded in southern latitudes both in the south-eastern and the south-western Indian Ocean, especially south of 40°S. In contrast, there was a tendency for the presence of more males immediately to the north of this parallel, in waters between ca. 40°S and 30°S, also both in the SE and SW Indian Ocean. The sex ratios in southern tropical waters were more variable, with more females in quarters 1 and 2, and more males in quarter 3, especially in the eastern areas. In the tropical North Indian Ocean (north of the equator), there were in general more males throughout the year in most areas. The differences in the sex ratios observed in the Indian Ocean were significant when compared among the geographic areas as defined in Figure 1 (proportion test: chi-squared: 3,755.9, $df = 3$, $p < .001$) and seasons within each area (CMH test: chi-squared = 956.5, $df = 3$, $p < .001$). There were also significant differences detected in the sex ratios comparing sizes tested conditionally within each area (CMH test: chi-squared = 696.3, $df = 4$, $p < .001$).

3.4 | Distribution of life stages

Considerable variability was observed in the distribution of young juvenile and adult specimens in both oceans when considering regions and quarters. In the Atlantic, more immature blue sharks, including young-of-the-year (age 0) and very small juveniles (age 1), were captured in the north-east (Gulf of Biscay), central east (Azores Islands and waters west of the Azores) and south-west (off southern Brazil and Uruguay) regions (Figure 8), while adults were more abundant in the equatorial and tropical Eastern Atlantic, in the Gulf of Guinea and closer to the Cabo Verde Archipelago (Figure 9). In the Indian Ocean, the densities of juveniles were higher in the south-west off South Africa, and south-east off Australia (Figure 8), while adults were

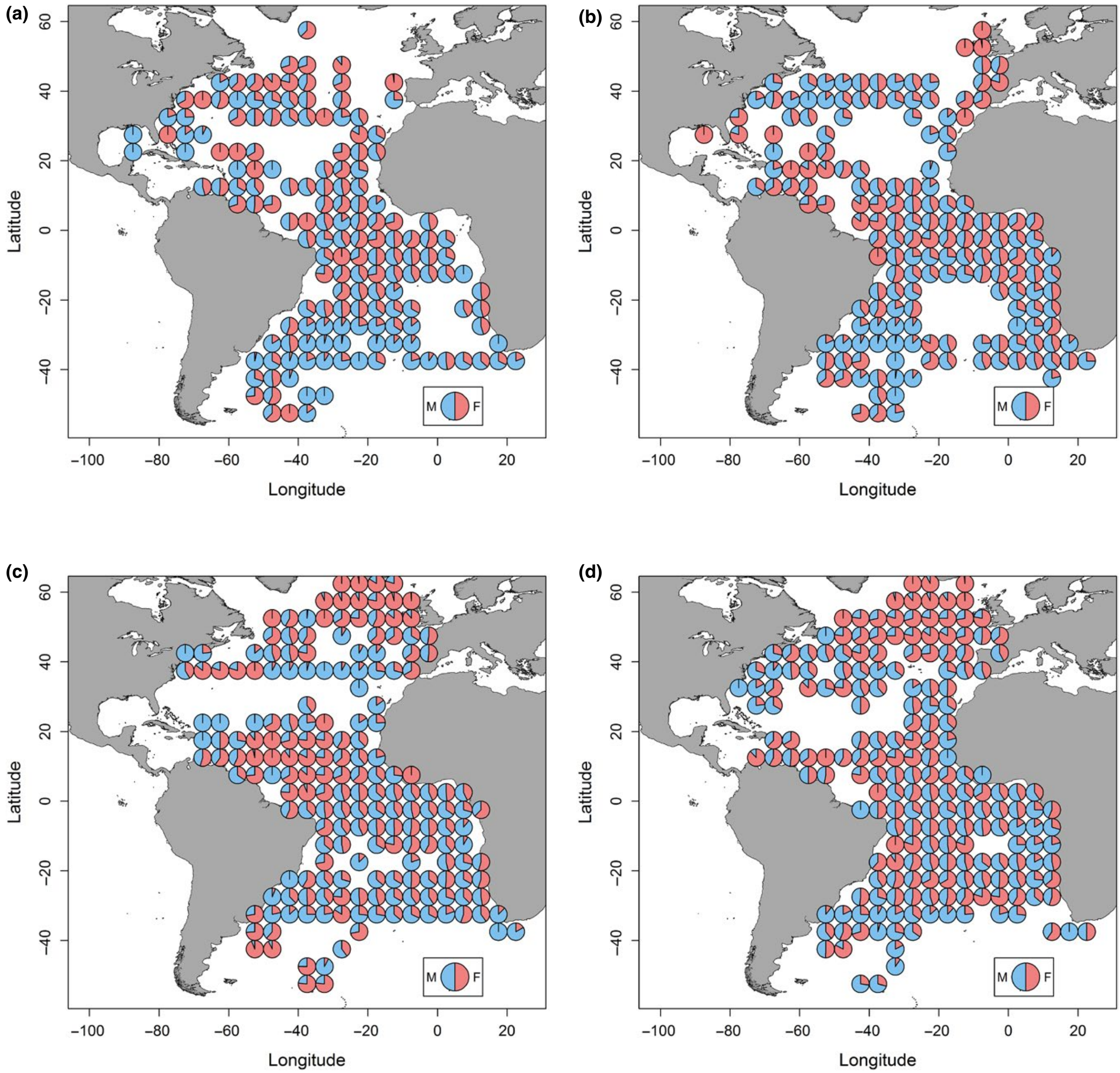

FIGURE 6 Blue shark (*Prionace glauca*) sex ratios recorded in 5° × 5° (latitude × longitude) squares during this study in each quarter of the year (a = quarter 1, b = quarter 2, c = quarter 3, d = quarter 4) for the Atlantic Ocean. Circle sizes are fixed and not proportional to sample size within each 5° × 5° square. [Colour figure can be viewed at wileyonlinelibrary.com]

distributed along wider areas, including the eastern Indian Ocean, closer to Indonesia (Figure 9).

3.5 | Modelling size distribution

There was also considerable variability in the expected size distributions of blue shark both in the Atlantic and Indian Oceans when taking into consideration the catch location and quarter of the year. In the Atlantic, the larger blue sharks were predicted to occur mainly along the equatorial and tropical regions, particularly in the Central Eastern Atlantic, along Equatorial waters and in the Gulf of Mexico. By contrast, the smaller specimens were predicted to occur mainly in higher latitudes both in the northern and southern hemispheres, especially in the north-east and south-west regions of the Atlantic (Figure 10). Similarly, in the Indian Ocean, the larger mean blue shark sizes were also predicted mainly along the equatorial and tropical regions, while the smaller specimens were predicted to occur in higher latitudes and more temperate waters of the Southern Indian Ocean (Figure 11). In the Indian Ocean, there was also some variability with longitude, with the larger specimens predicted to occur mainly in the north-west and medium sizes in the north-east regions (Figure 11). For both the Atlantic and Indian Oceans, the final estimated GAMs considered the nonparametric smooth terms for location (latitude and longitude, with interactions) and the parametric term of quarter used as a fixed factor. The total deviance explained by the final models was 43.2% for the Atlantic and 46.5% for the Indian Ocean. The residual analysis

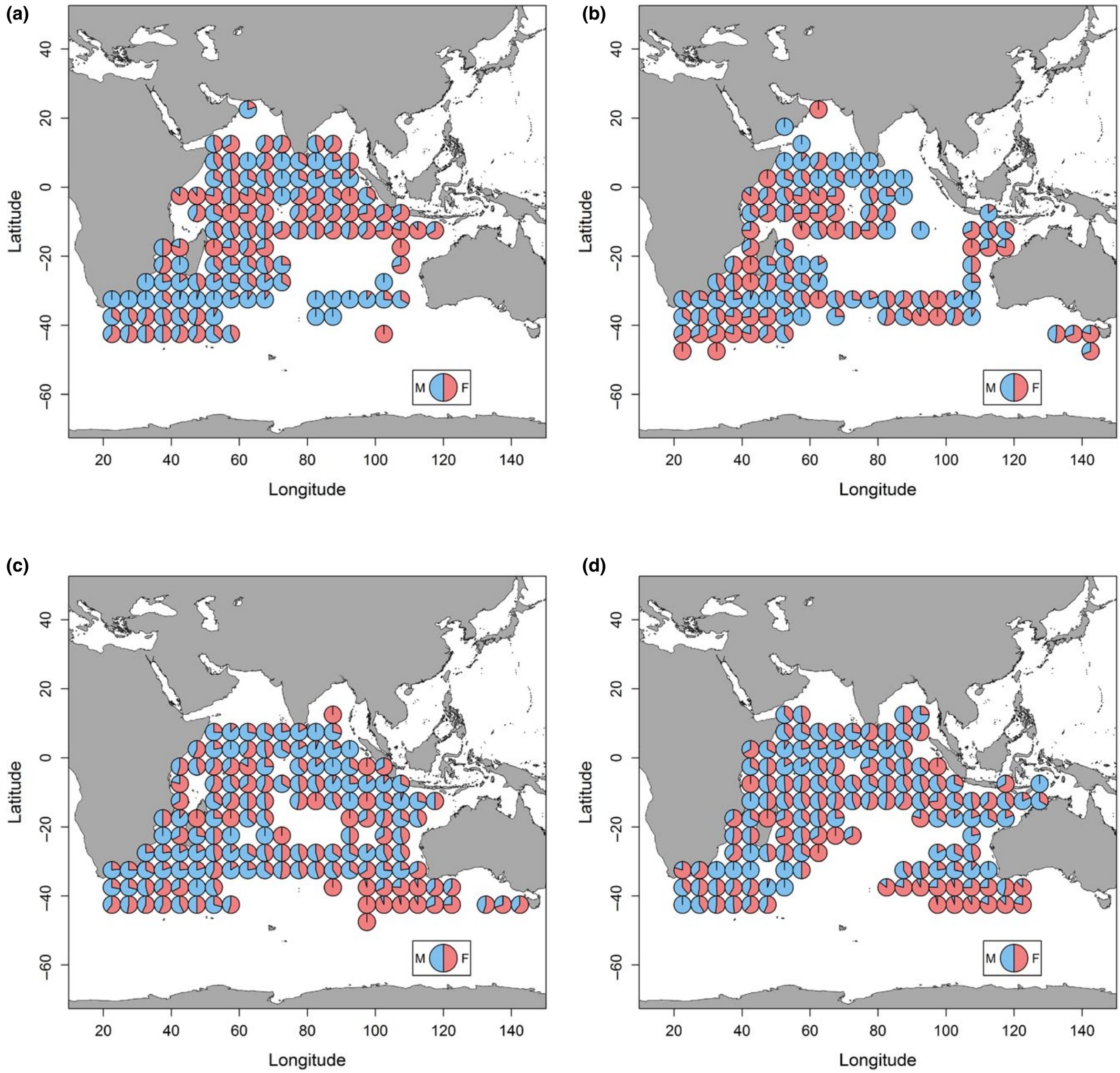

FIGURE 7 Blue shark (*Prionace glauca*) sex ratios recorded in 5° × 5° (latitude × longitude) squares during this study in each quarter of the year (a = quarter 1, b = quarter 2, c = quarter 3, d = quarter 4), for the Indian Ocean. Circle sizes are fixed and not proportional to sample size within each 5° × 5° square. [Colour figure can be viewed at wileyonlinelibrary.com]

revealed no major trends or patterns in the residuals that could be considered problematic.

4 | DISCUSSION

This work provides the most comprehensive study on blue shark population structure and size distribution patterns ever carried out in the Atlantic and Indian Oceans, including data from scientific fishery observer programmes, fishery-independent sampling programmes and surveys, projects and research cruises. The results provide an important contribution to the study of the spatial and seasonal dynamics of the most widely distributed and captured pelagic shark in oceanic waters. In terms of geographical coverage and distribution, records of blue sharks ranging from 62°N to 54°S in the Atlantic and from 25°N to 48°S in the Indian Ocean were provided. The previously reported global area of distribution of blue shark ranged from about 60°N to 50°S (Last & Stevens, 2009). As such, this general wide latitudinal range of distribution is confirmed, and we also expand the previously reported values in both hemispheres, especially for the Atlantic.

Significant differences were found in the length-frequency distributions, sex ratios and proportions of immature and mature specimens across subregions of the Atlantic and Indian Oceans. Of particular importance is to note the clear latitudinal stratification of blue sharks in both oceans, with the larger mature specimens tending to occur along

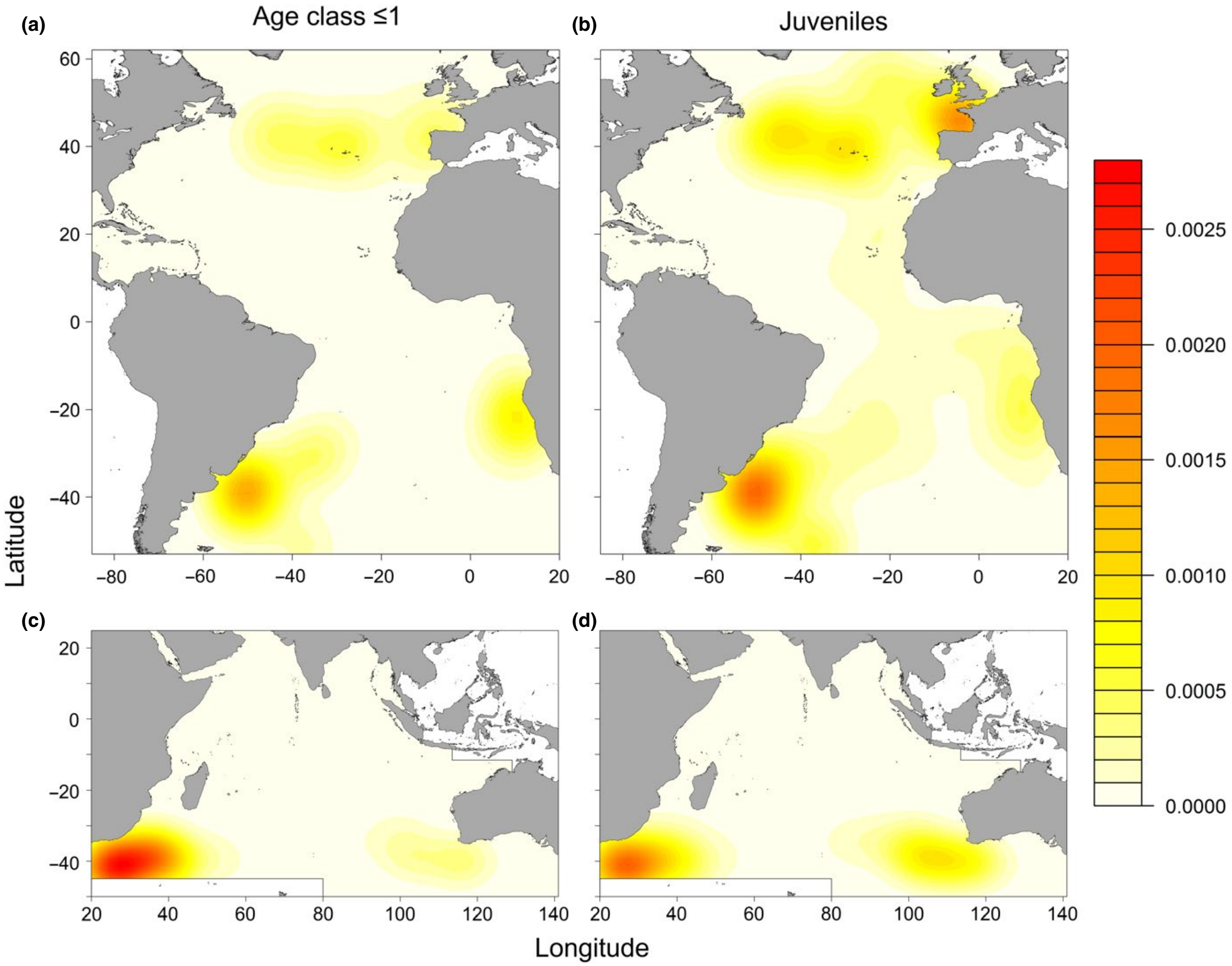

FIGURE 8 Kernel density distributions for young-of-the-year and small juveniles (age classes 0 and 1, see text in Methods for definitions) in the Atlantic (a) and Indian Oceans (c); and juveniles of all age classes of blue shark (*Prionace glauca*) in the Atlantic (b) and Indian Oceans (d). [Colour figure can be viewed at wileyonlinelibrary.com]

the equatorial and tropical regions of both oceans, and the smaller-sized immature specimens occurring mainly in temperate waters in higher latitudes. In the Atlantic, immature sharks occur both in the temperate north and temperate south, especially in the north-east and in the south-west Atlantic, while in the Indian Ocean immature sharks occur in temperate southern waters, as the Northern Indian Ocean does not have a temperate water system. This general size segregation corroborates the patterns previously described by Mejuto and García-Cortés (2005) for blue shark in these oceans. However, this general latitudinal gradient is opposite to the patterns found in some other pelagic shark species. One example is the bigeye thresher (*Alopias superciliosus*) in the Atlantic Ocean, where the smaller and younger sharks tend to concentrate predominantly in the tropical regions, while the larger specimens seem to prefer temperate areas of the northern and southern Atlantic (Fernandez-Carvalho et al., 2015).

There are also longitudinal gradients in size distribution along both oceans. In the Atlantic, the larger specimens were predicted to occur mainly in the north-west and south-east equatorial and tropical regions, especially in the Gulf of Guinea and in the central and western tropical Atlantic, while immature sharks occurred mainly in the north-east and south-west. Again, these results corroborate the previous findings from Mejuto and García-Cortés (2005). Similarly, in the Indian Ocean, the larger specimens were also predicted to occur mainly in the tropical north-western area. In the south-western Indian Ocean, trophic ecology studies have shown an ontogenic shift in the diet of blue shark, with the larger specimens displaying more offshore tropical foraging habitats (Rabehagasoa et al., 2012).

In general, the movement of sharks can be influenced by migration of prey (e.g. Carey, Scharold, & Kalmijn, 1990), water temperature (e.g. Nakano, 1994), reproductive state, sex and size segregation (e.g. Kohler, Turner, Hoey, Natanson, & Briggs, 2002; Montealegre-Quijano & Vooren, 2010; Nakano & Seki, 2003; Pratt, 1979; Strasburg, 1958). The reasons for the specific differences detected in the blue shark distribution patterns seem to be mainly related to migratory and habitat segregation patterns, which are in turn related to spatio-temporal changes in growth and reproductive stages. Specifically for the South

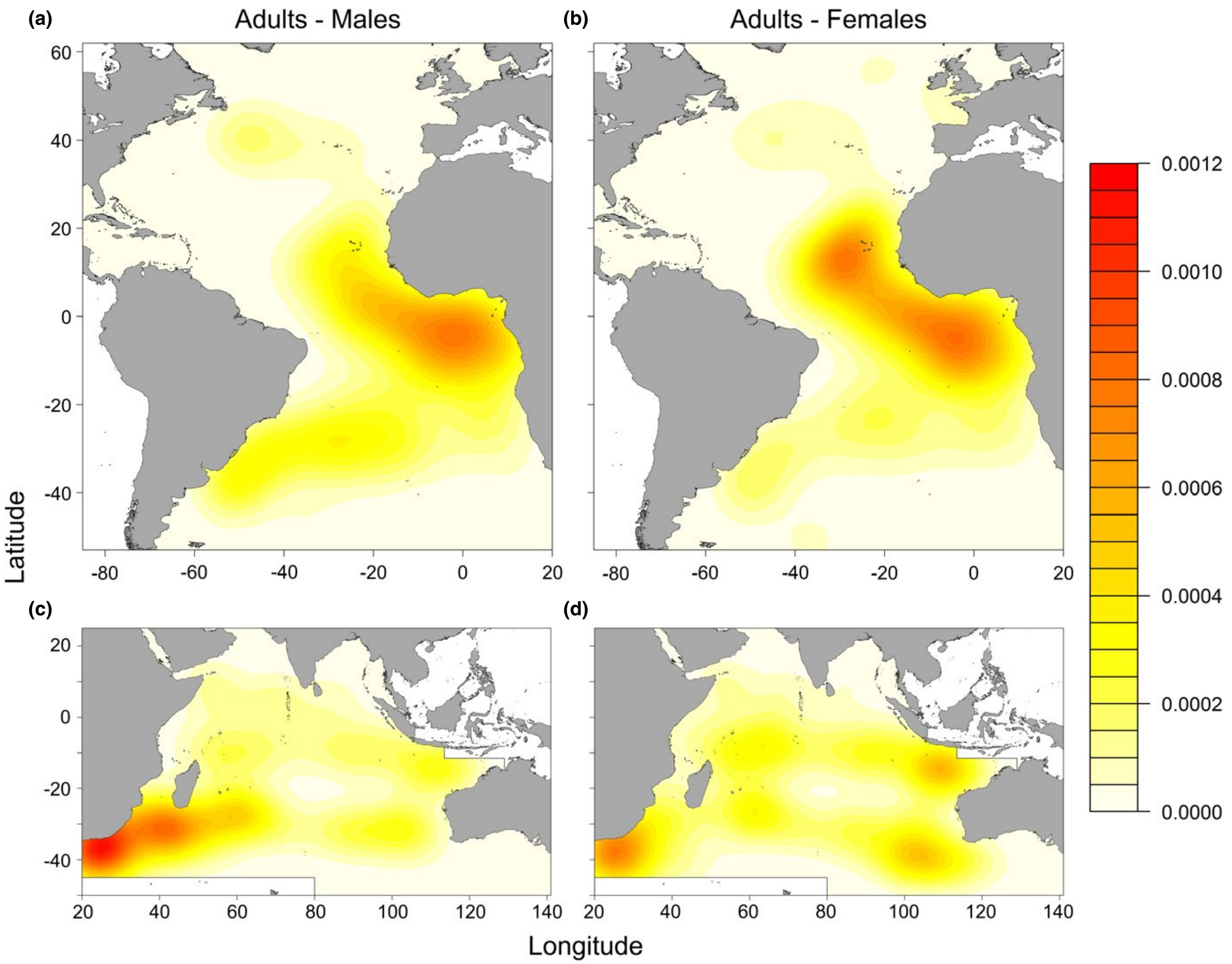

FIGURE 9 Kernel density distributions for adult male (a,c) and female (b,d) blue shark (*Prionace glauca*) in the Atlantic (a,b) and Indian Oceans (c,d). [Colour figure can be viewed at wileyonlinelibrary.com]

Atlantic, Hazin, Pinheiro, and Broadhurst (2000) hypothesized that adult blue sharks copulate off south-eastern Brazil from December to February, and ovulation and fertilization take place off north-eastern Brazil three to four months later (Hazin, Boeckmann, Leal, Otsuka, & Kihara, 1994). Pregnant females would then move across the Atlantic to the Gulf of Guinea where early pregnancy stages are found from June to August (Castro & Mejuto, 1995). Finally, parturition would likely take place in more temperate waters off South Africa (da Silva et al., 2010; Hazin et al., 2000), as confirmed by the presence of neonate sharks with umbilical scars and females with post-parturition scars. The patterns in the size distribution reported in our study lend some support to this hypothesis, as the larger specimens are found in tropical and equatorial areas, especially in the Gulf of Guinea, while smaller specimens, including young age 0 and 1 juveniles, occur in more temperate waters off Namibia and South Africa in the south-east Atlantic. However, a high density of smaller-sized specimens in temperate south-west waters off southern Brazil and Uruguay was also found, which is not fully concordant with the previous hypothesis. Still, in general, the presence of small juvenile blue sharks has been associated with colder and more productive waters (Mejuto & García-Cortés, 2005), which would justify this prevalence of small juveniles in the temperate and more coastal waters of the south-west Atlantic. Based on our study, the main nursery grounds for blue shark in the South Atlantic would therefore be in temperate waters of the south-east Atlantic off South Africa and Namibia, and also in the south-west Atlantic off southern Brazil and Uruguay.

For the North Atlantic, Pratt (1979) suggested that mating takes place off southern New England in late May and early June, and that the embryos take 9–12 months to develop and are born from April to July. Based mainly on tagging data, Stevens (1990) added that adult sharks in the north-west Atlantic could move offshore into the Gulf Stream or south along the margins of the Gulf Stream into the Caribbean. Nursery areas for the species in the North Atlantic have been proposed in the Mediterranean Sea and off the Iberian Peninsula, and in the Central North Atlantic off the Azores Islands (Aires-da-Silva, Ferreira, & Pereira, 2008; Vandeperre, Aires-da-Silva, Santos et al., 2014, Vandeperre, Aires-da-Silva, Fontes et al., 2014). The size distribution patterns reported in our study corroborate and expand these

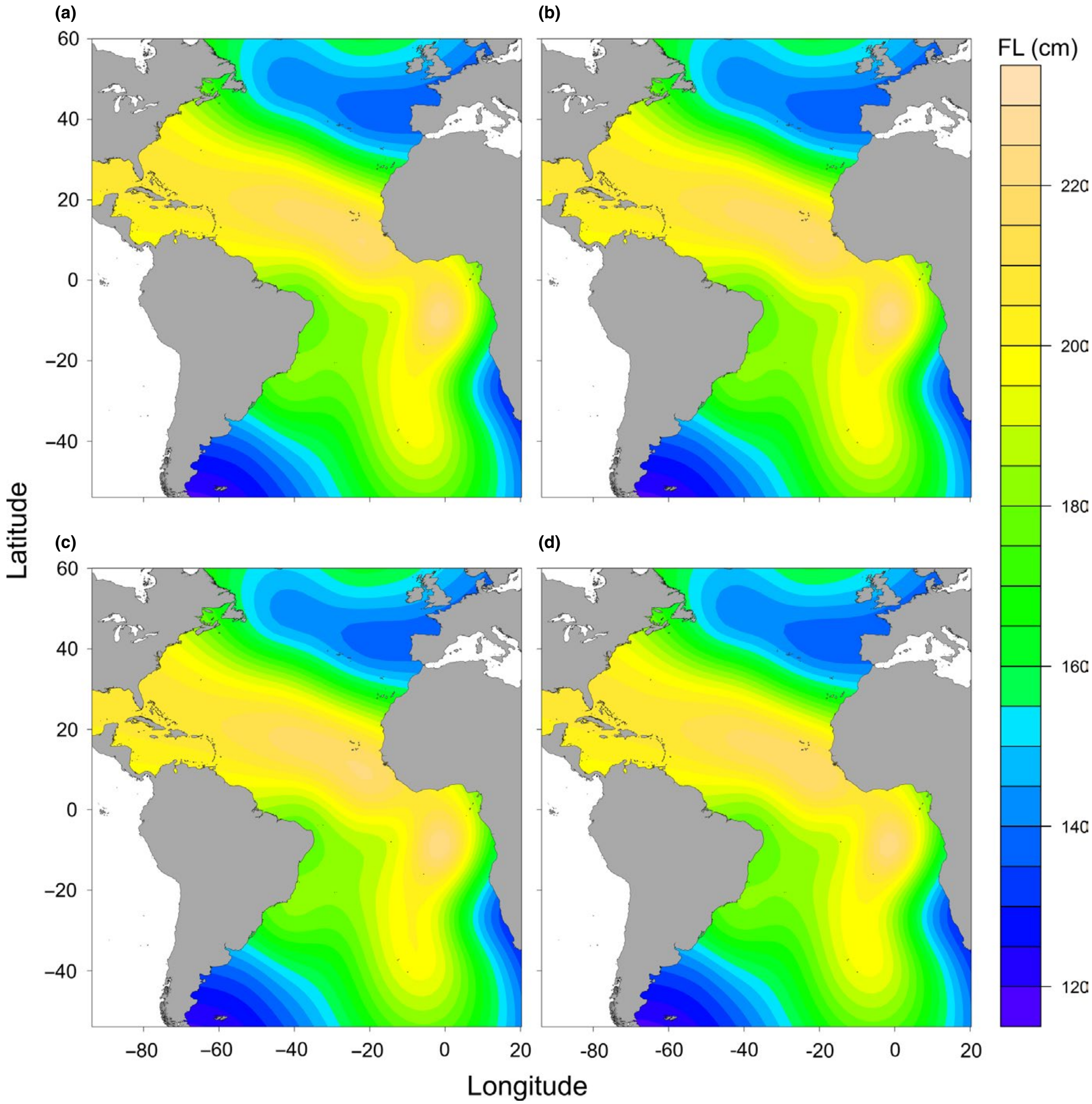

FIGURE 10 Prediction of the size distribution of blue shark (*Prionace glauca*) caught in the Atlantic Ocean by quarter of the year (a = quarter 1, b = quarter 2, c = quarter 3, d = quarter 4), from a Generalized Additive Model (GAM). The size range considered was 36–394 cm FL, and the sexes are modelled together. [Colour figure can be viewed at wileyonlinelibrary.com]

previous hypotheses, as in the North Atlantic the main areas for aggregation of large mature adult specimens appear to be in the tropical Northeast, while large aggregations of smaller immature sharks were detected particularly in the temperate Northeast and Central North Atlantic. Areas of particular abundance for young-of-the-year and small juveniles are mainly off the Iberian Peninsula and in the Bay of Biscay in the north-east Atlantic, and off the Azores Islands and west of the Azores in the Central North Atlantic, which confirms that these areas may be the main nursery grounds for the blue shark in the North Atlantic. Our study also pinpointed a large concentration of adult specimens, especially large females, in the tropical Northeast region around the Cabo Verde Islands and off West Africa, in a region that had been previously reported by Nakano and Stevens (2008) as an important area of concentration for pregnant females. Litvinov (2006) suggested a finer-scale heterogeneity of the sex-specific distribution of blue sharks, describing dense aggregations of adult males in certain slope and seamount areas, where the males' prevalence could reach 80%–90%. Litvinov (2006) hypothesized the functional role of such

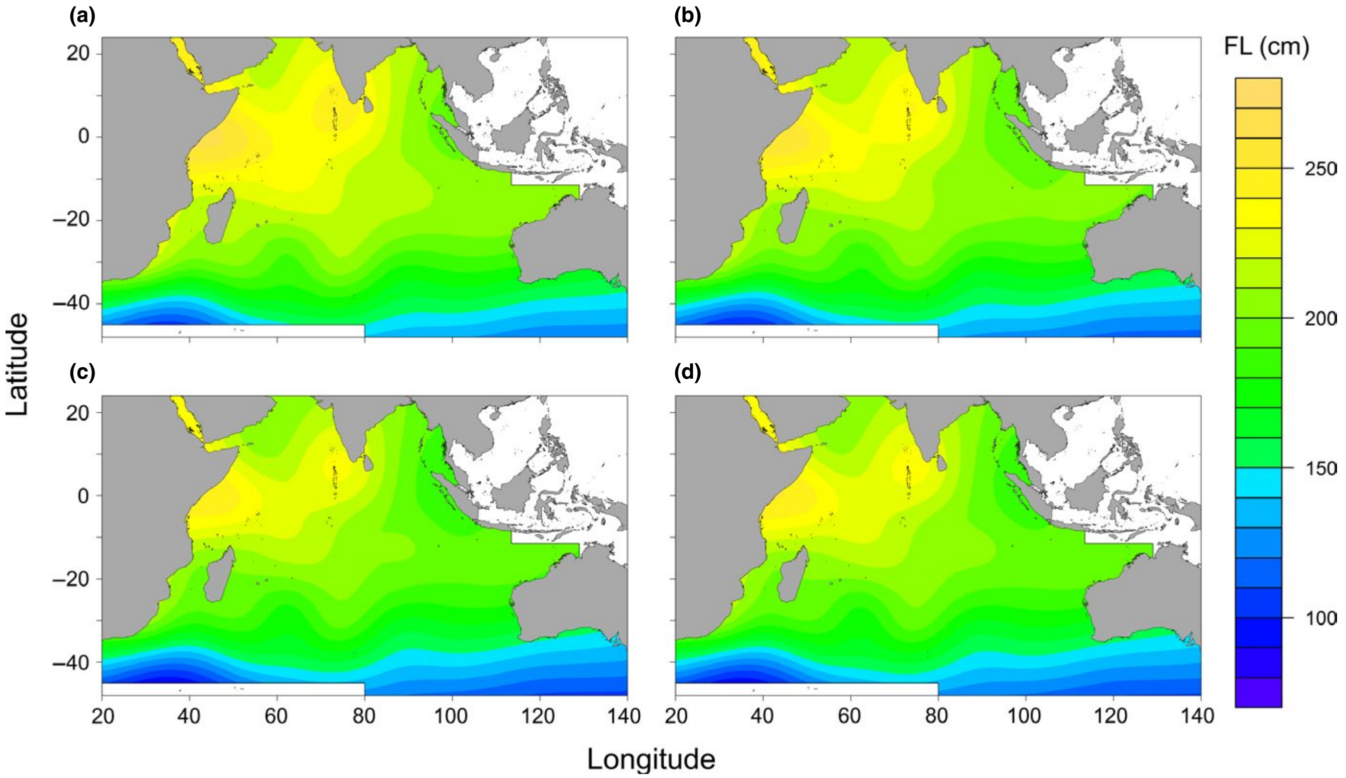

FIGURE 11 Prediction of the size distribution of blue shark (*Prionace glauca*) caught in the Indian Ocean by quarter of the year (a = quarter 1, b = quarter 2, c = quarter 3, d = quarter 4), from a Generalized Additive Model (GAM). The size range considered was 41–369 cm FL, and the sexes are modelled together. [Colour figure can be viewed at wileyonlinelibrary.com]

male aggregations with the increasing probabilities to copulate with mature females passing on their migratory routes.

Limited work has led to few hypotheses on the large-scale distribution of blue shark in the Indian Ocean to date, with the exception of some analyses restricted mainly to the Indian/Atlantic confluence zone (da Silva et al., 2010). In fact, there may be some connectivity between the south-east Atlantic and south-west Indian Oceans, as has been described for other pelagic sharks (e.g. da Silva-Ferrette et al., 2015; for the crocodile shark (*Pseudocarcharias kamoharai*, Pseudocarchariidae). Our results suggest that immature sharks, including young-of the year, juvenile and pre-adult sharks, concentrate mainly in temperate waters of the south-west Indian Ocean off South Africa, and in the south-east Indian Ocean off south-western Australia, implying that these may be the two main nursery grounds for the species in the Indian Ocean. Larger mature and adult blue sharks are more widely spread along the Indian Ocean, including in more tropical and equatorial waters, but there is also a large concentration of adults in the south-west temperate region, which combined with the presence of young specimens, may represent a parturition ground for the blue shark in the Indian Ocean. A predominance of females in early pregnancy stages has also been described for the north-west Indian Ocean (Gubanov & Grigor'yev, 1975), especially during the first half of the year.

For the Pacific Ocean, and particularly in the North Pacific, Nakano (1994) suggested that mating takes place in early summer at 20–30°N, and that pregnant females then move north to parturition grounds in more temperate waters at 35–45°N. The pupping and nursery areas are located in these colder water regions, where there is a larger prey biomass for the juveniles, which can remain there for 5–6 years prior to maturity (Nakano & Nagasawa, 1996). By contrast, adults occur mainly from equatorial waters to areas south of the nursery grounds (Nakano & Stevens, 2008). These results for the Pacific are similar to what is now described in this work especially for the Atlantic, with the adults occurring mainly along equatorial and tropical waters and the small juveniles in colder temperate waters of both hemispheres.

A limitation of our study was that the data used were mostly fishery dependent, obtained from multiple fishing fleets, with different fishing *métiers* that target different species. As a result, the size ranges and abundance reported by each fleet for each region may also be affected by area coverage and gear selectivity (e.g. hook shape and size, bait type, use of wire leaders, targeting, day/night fishing and depth of hooks). In terms of the set depth of the hooks, it has been shown that the vertical catch rate patterns of blue shark do not seem to cluster on particular depth ranges, as is more commonly observed in tunas and billfishes (Nakano, Okazaki, & Okamoto, 1997; Yokawa, Saito, Kanaiwa, & Takeuchi, 2006). However, the influence of depth in the catch-at-size is still not completely understood. The other variables, such as hook and bait type, use of wire leaders and targeting, have been shown to affect shark catch rates.

It is also important to note that most of the data used in this work come from oceanic pelagic longlines, set in oceanic waters and targeting mainly swordfish or tunas, with the exception of the data from the artisanal longlines in the Bay of Biscay, which operate in a much more coastal region. As such, the results obtained provide mainly a vision of the fraction of the blue shark population that is present in oceanic waters and available to, and selected by, these fishing gears. One important result from this study is that the capture of very small specimens (young juveniles) was in general low in oceanic waters. This can be due either to the very small sharks occurring mainly in more coastal waters, that is not being present in high numbers in oceanic waters, or possibly due to fishing gear selectivity, that is, small juveniles also occurring in oceanic waters but not captured by these oceanic pelagic longlines. In this sense, Nakano and Stevens (2008) pointed out that juvenile blue sharks remain in the nursery areas and do not take part in extensive migrations until reaching a size of about 130 cm. Mejuto et al. (2014) noted the presence of small recruits in very coastal areas of the northeast Atlantic (off north-west Spain), suggesting that these very small juveniles may, in fact, prefer more coastal and productive waters of the temperate regions. Therefore, small juvenile blue sharks may not be present in high abundances in oceanic waters, making that component of the population less susceptible to oceanic fisheries.

Even with the limitations inherent to the fisheries-dependent nature of the data, our study provides an important improvement on the understanding of the spatio-temporal dynamics and population structure of blue shark populations in the Atlantic and Indian Oceans. While our study provides a general overview of the distribution patterns at oceanic-wide scales, a limitation is the fact that the analyses and models used focus on major large-scale, spatio-temporal effects over entire ocean-basin areas. There are likely other finer-scale effects and local variability patterns affecting distribution that are not captured in our large-scale models and analyses. Therefore, while this study is important as a general overview providing the general and major trends in the Atlantic and Indian Oceans, it is important to emphasize the need to continue conducting more detailed and local analyses for specific regions of these oceans. Blue sharks are revealed to occur from temperate to tropical regions of the Atlantic and Indian Oceans, and this is also the case in the Pacific Ocean (Nakano & Seki, 2003), indicating that the blue shark is likely one of the most thriving and widely distributed fish among the highly migratory species.

In conclusion, the distribution patterns presented in this study provide a better understanding of different aspects of the blue shark distribution and dynamics in the Atlantic and Indian Oceans. The results have been provided to the ICCAT Shark Species Group and the IOTC Working Party on Ecosystems and Bycatch and have been incorporated, to some extent, in the latest blue shark stock assessments carried out by these t-RFMOs. We expect that this and further similar analyses will continue to be used in future stock assessments of this and other shark species, as they allow the use of more adequate stock assessment models, with inclusion of both biological and spatial-seasonal dynamics of the species, and ultimately help managers adopt more informed and efficient management and conservation measures.

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