



Using pop-up satellite archival tags to inform selectivity in fisheries stock assessment models: a case study for the blue shark in the South Atlantic Ocean

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Carvalho, F., Ahrens, R., Murie, D., Bigelow, K., Aires-Da-Silva, A., Maunder, M. N., and Hazin, F. Using pop-up satellite archival tags to inform selectivity in fisheries stock assessment models: a case study for the blue shark in the South Atlantic Ocean. – ICES Journal of Marine Science, doi: 10.1093/icesjms/fsv026.

Received 5 September 2014; revised 15 January 2015; accepted 30 January 2015.

Selectivity has traditionally been well estimated internally in stock assessment models when length or age composition data are available. However, in stock assessment, temporal or spatial variation in fishery or stock structure can lead to misspecification of the selectivity pattern, which can contribute substantially to the uncertainty in stock assessment results. Consequently, generating auxiliary information to help stock assessment scientists avoid unrealistic specifications of selectivity patterns should be encouraged. Here, we combine data from pop-up satellite archival tags (PSATs) deployed on blue sharks in the South Atlantic Ocean, and information on maximum pelagic longline fishing depths, to introduce an alternative approach for estimating selectivity of fishing gear. Further, we present how this externally estimated tag-based selectivity can be used to inform the most appropriate form of selectivity curves (e.g. asymptotic or dome-shaped) in a spatially structured stock assessment model for the South Atlantic blue shark population. The estimated tag-based selectivity showed substantially different selectivity patterns within the area of the assessed stock, in one area the depth range of the longline gear is inhabited mostly by adults, which is consistent with an asymptotic selectivity. In another area, the overlap shifts to younger ages, with older sharks located in deeper waters, consequently the expected selectivity is more dome-shaped. To account for this variability in the stock assessment model, we assigned fishing fleets with different selectivity patterns. The form of the selectivity curve assigned for each fleet was based on the tag-based selectivity estimates for the area of where that fleet operates. The assessment model demonstrated relatively good fit to the data and that the estimated management quantities were robust. This study provides additional evidence that externally derived estimates of selectivity using PSATs data can assist implementing stock assessments that capture some of the spatial variability of pelagic fish species.

Keywords: Atlantic Ocean, blue shark, PSATs, selectivity, spatial variability, stock assessment.

Introduction

Most of the world's catches of sharks are taken incidentally by various types of fishing gear targeting other species, constituting bycatch that is either discarded at sea or landed for sale (Bonfil,

1994; Vannuccini, 1999). Over the past decade, there has been a growing global concern regarding bycatch of sharks in fishing operations (Clarke *et al.*, 2007). However, the historically low economic value of shark products compared with other fish has resulted in

research and conservation of sharks being given a lower priority than traditionally higher-value fish species (Barker and Schlessel, 2005).

The blue shark (*Prionace glauca*) is possibly the most wide-ranging shark species occurring in temperate, subtropical, and tropical waters (Henderson et al., 2001), with high bycatch rates in pelagic longline fisheries (Compagno et al., 2005). Several studies have reported declines in the abundance of blue shark (Baum and Myers, 2004; Campana et al., 2005), possibly as a result of the heavy fishing pressure. In the Southwest Atlantic Ocean, off the coast of Brazil, blue sharks are taken by fleets targeting tuna and swordfish with pelagic longline gear (Carvalho et al., 2010). Historically, Brazil has been responsible for a substantial portion of blue shark catches in the South Atlantic, which placed it as a major contributor to the fishing mortality of this species. Between 2002 and 2012, for instance, Brazil ranked third in the number of blue sharks landed by country, behind only that of Spain and Portugal (ICCAT, 2012).

Carvalho et al. (2010) analysed the distribution and relative abundance of blue sharks in the Southwestern Atlantic Ocean based on catch-per-unit-effort (cpue) and length frequencies of blue sharks caught by the Brazilian pelagic tuna longline fleet between 1978 and 2009. Blue shark cpue showed a relatively stable trend from 1978 to 1995. In 1995, a sharp increase in blue shark cpue was observed, which could have been attributed to the introduction of monofilament gear in 1995/1996 to target swordfish, followed by a gradual increase in the market value of blue shark over time. Based upon length frequency distributions of over 11 000 blue sharks caught by the pelagic longline fishery in the Southwest Atlantic Ocean, there is a clear spatial variability of the sizes of the individuals caught by this fishery (Carvalho et al., 2011). Overall, the spatial distribution of blue sharks by size showed a general tendency of adults to concentrate in lower latitudes and juveniles to be more common in higher latitudes. However, it is still unclear if the spatial variability of the blue shark lengths found by Carvalho et al. (2011) is simply due to gear selectivity or if the proportion of the population by length actually varies spatially. If the latter is true, then this difference in the spatial structure of the population can strongly affect selectivity. In stock assessment, misspecification of the selectivity pattern can generate errors in the estimates of biomass (Kimura, 1990; Ichinokawa et al., 2014; Lee et al., 2014; Wang et al., 2014), spawning-stock biomass (SSB; Punt et al., 2002; Radomski et al., 2005), exploitation rate (Radomski et al., 2005), and the ratio of stock biomass in the first year to stock biomass in the final year of analysis (Yin and Sampson, 2004). It is common practice in stock assessments to assume asymptotic selectivity unless there is clear evidence that certain sizes or ages are not being selected by the fishery (Cope and Punt, 2011). However, using an asymptotic selectivity for all fisheries might cause estimates of fishing mortality to be biased toward higher values. Alternatively, if selectivity were to be assumed to be dome-shaped for all fisheries, its estimation within a stock assessment model may not be possible due to the likelihood that the dome-shape would confound estimates of mortality. Recent research indicates that some degree of dome-shaped selectivity is to be expected in many situations, due to incomplete mixing of individuals and spatial heterogeneity in fishing intensity (Sampson, 2014; Waterhouse et al., 2014). Therefore, collection of auxiliary information that may help to determine the most appropriate form of the selectivity curves in stock assessment should be encouraged (Crone et al., 2013).

Tagging data alone have been used to estimate selectivity externally of stock assessment models. Typically, selectivity estimation

studies are primarily designed to make use of conventional tagging data, which rely on fishery recaptures (Myers and Hoening, 1997; Cadrin, 2006; Bacheler et al., 2010). The deployment of pop-up satellite archival tags (PSATs), on commercially exploited fish species has become more common over the past decade. These tags potentially provide much more information on temporal- and spatial-specific movements than conventional tags. Perhaps their greatest advantage is that they provide fishery-independent information about the location and movement of tagged fish between tagging and pop-off locations (Sippel et al., 2015).

For highly migratory species, PSATs have been used primarily for studying spatial-temporal behaviour and ecology (Sippel et al., 2015). However, data from PSATs have also been used to directly incorporate habitat variation in the cpue standardization process (Hinton and Nakano, 1996; Maunder et al., 2006a, b), and more recently in models to inform fisheries management (Taylor et al., 2011; Eveson et al., 2012). We are unaware of any studies that used depth data returned from PSATs to specifically estimate selectivity for highly migratory species in longline fisheries.

Using PSATs data and information on maximum pelagic longline fishing depths, the present study examined the spatial variability of the South Atlantic blue shark and the vulnerability of this species to pelagic longline fishing. The specific objectives of this manuscript include: (i) combine data obtained from PSATs and information on maximum pelagic longline fishing depths with regression models to introduce an alternative approach for estimating selectivity of South Atlantic blue shark to pelagic longline fishing gear; and (ii) to present how this externally estimated tag-based selectivity can be used to inform the most appropriate form of selectivity curves in spatially structured stock assessment models. For this purpose, a statistical catch-at-age stock assessment model for the South Atlantic blue shark was implemented in AD Model Builder (ADMB, Fournier et al., 2012). Additionally, biological reference points estimated in the assessment were used to indicate the current status of the South Atlantic blue shark stock.

Material and methods

Three sequential procedures were used to present how externally estimated tag-based selectivity can be used to inform the most appropriate form of selectivity curves in a spatially structured stock assessment model: (i) depth profiles of 16 blue sharks tagged in two different geographic areas of the South Atlantic Ocean were analysed as well as their overlap with pelagic longline fishing gear depth; (ii) these data were fit to regression models to construct selectivity curves for each area separately; and (iii) standardized cpue indices, catch, and catch-at-age data were used to implement a statistical catch-at-age model (SCAM). The SCAM includes two different pelagic longline fishing fleets, each with a different selectivity pattern, as a proxy for spatial structure (Area). Externally estimated tag-based selectivity curves were used to inform the most appropriate form of selectivity curves for each fleet used in the SCAM (Figure 1).

Data

Catch and effort

For the SCAM, the total blue shark catches per year in the South Atlantic were estimated by the ratio of sharks to tuna method developed by the ICCAT shark working group (ICCAT, 2005; Carvalho et al., 2014; Figure 2). Blue shark cpue was obtained from 37 665

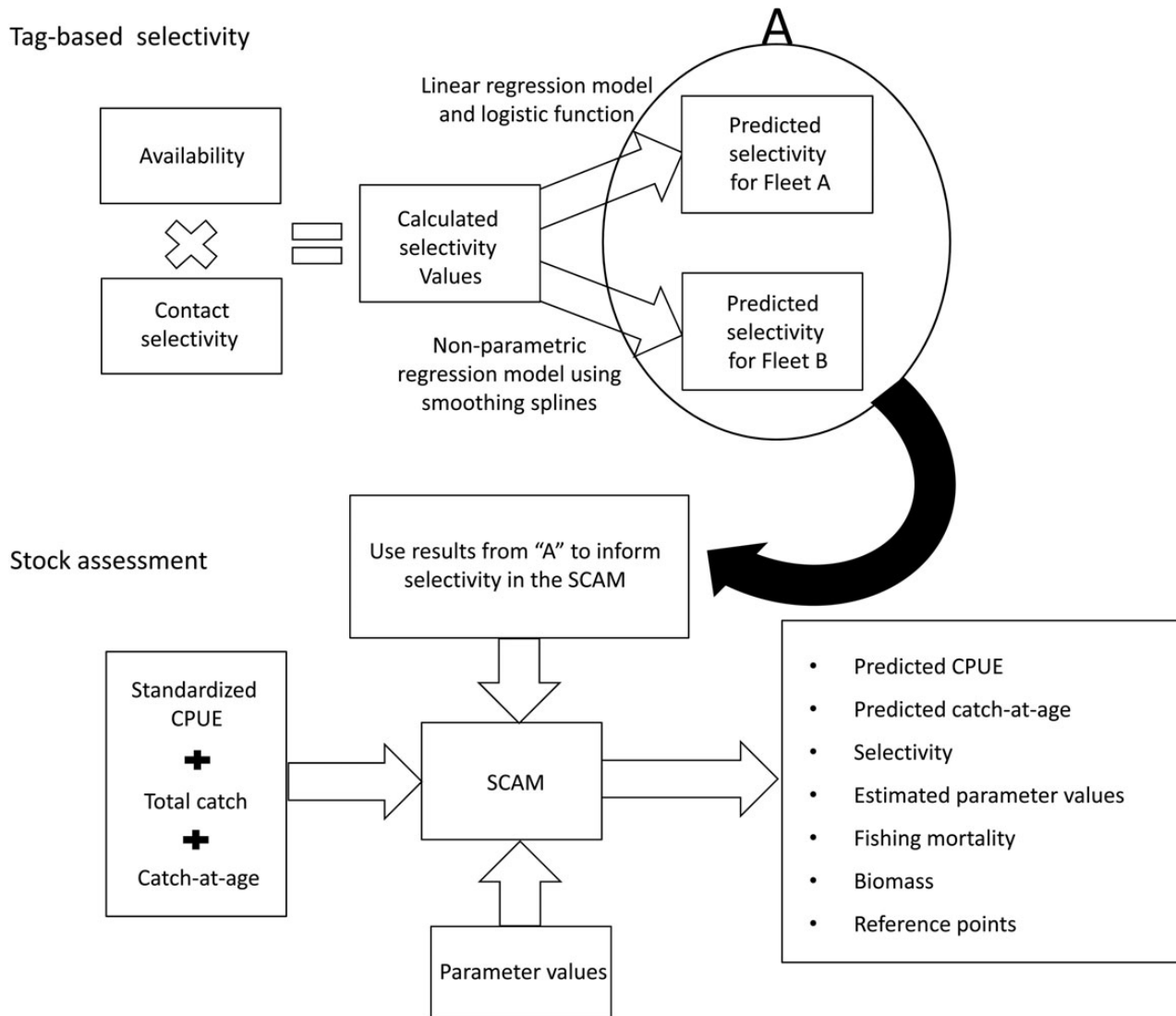


Figure 1. Schematic figure describing the procedure to use PSATs data to inform selectivity in a statistical catch-at-age stock assessment model.

longline sets made by two Brazilian tuna longline fleets, represented here as Fleet A and Fleet B. Longline sets from both fleets were distributed throughout a wide area, ranging from 10°E to 50°W longitude and between 10°N and 45°S latitude (Figure 3). Both Fleets used the same pelagic longline gear configuration and had the same targeting practices. Fleet A is based in the coastal cities of northeast Brazil, including Recife, Natal, and Cabedelo, and its major fishing ground is located in the Equatorial Atlantic. This area (Area I) is characterized by the presence of seamounts, oceanic islands, and upwelling driven by the equatorial convergence (Figure 3). Fleet B is based in the South of Brazil, in the cities of Santos, Itajaí, and Rio Grande. The major fishing ground for this fleet is near the Rio Grande Rise, a large seismic ridge situated between the Mid-Atlantic Ridge and the Brazilian continental shelf (Area II; Figure 3). Fisheries logbooks from both fleets were made available by the Ministry of Fisheries and Aquaculture within the Brazilian government. The logbooks contained details for each vessel operating within the fishery and included: date, time, start and end coordinates of the set, total number of hooks, and the total number of individuals caught for each set.

Size frequency

Fork length information was obtained from the Brazilian on-board observer programme. In all, 16 341 blue sharks were measured from 2002 to 2012 across Areas I and II. Age frequencies were obtained by back-transforming the lengths into ages using the von Bertalanffy relationship provided by Lessa *et al.* (2004).

Tagging

PSATs are archival tags that have the capacity to transmit stored information to a satellite. PSATs are attached to the fish externally and log temperature, depth (pressure), and light intensity after the fish is released, the later can then be used to calculate latitude and longitude of the fish position. The tags detach after a programmed interval and transmit their recorded information through the ARGOS satellite system to a land station then ultimately to the researcher via the Internet. In the present study, tagging was spatially and temporally stratified to match the fishing areas for Fleets A and B. Between March 2009 and April 2012, a total of ten mature males and females and six immature male and female blue sharks caught in

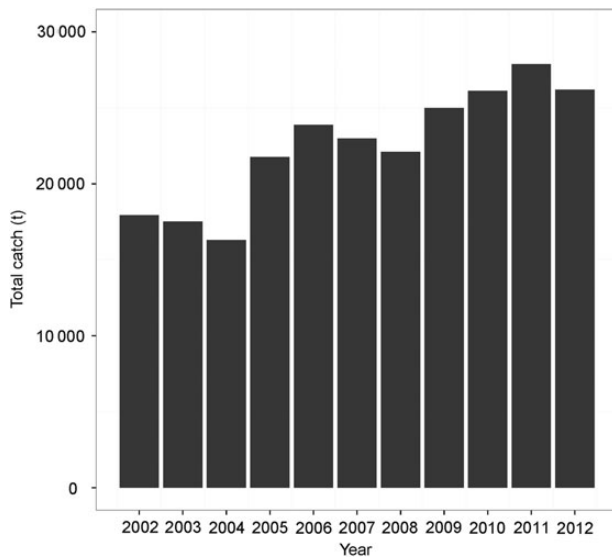


Figure 2. Annual catches (2002–2012) of blue sharks in the South Atlantic Ocean estimated by ICCAT using the ratio of sharks landed to the total landings of all tuna, swordfish, and billfish.

Areas I and II from longline vessels were tagged with PSATs model MK10 (Wildlife Computers, WA, USA; Table 1). Age-at-maturity was assumed as 5 years, following Lessa *et al.* (2004). The ages of tagged blue sharks ranged from 3 to 11 years, obtained by back-transforming the lengths into ages. PSATs were programmed to record depth, temperature, and light intensity every 60 s and stored as summary data over set intervals of 6 h. Tags were programmed to detach after 3 or 7 months after tagging. Minimum and maximum temperature bins (12 bins total) were programmed to sample temperatures >12 and $<30^{\circ}\text{C}$, while depth bins (12 bins total) were programmed to sample the minimum depth of <1 m (or 0) and maximum depth up to 500 m. Light intensity records were post-processed using the global positioning software WC-GPE2 (Wildlife Computers) to provide raw geolocations (GLS, Global Location System) of tagged fish. We applied the Kalman Filter State–Space Model augmented with SST (UKFSST; Nielsen *et al.*, 2006) to the raw tracks to predict the Most Probable Track (MPT). Time-at-depth data for each of the 16 blue sharks tagged were aggregated into 10 m bins and expressed using boxplots. All 16 tags successfully detached and transmitted data on the movements and habitat variables. PSATs attachment time for the 16 individuals averaged 106.1 ± 43.8 days with a maximum attachment time of 209 d (Table 1). Movement errors for latitude and longitude estimates for the PSATs were low (longitude: ranging from 0.04° to 0.58° ; latitude: ranging from 0.35° to 1.47°) and similar to those found in other movement studies using Kalman Filter methods (e.g. Musyl *et al.*, 2011). The positional error associated with these light-based estimates should not be a concern for this study because the MPT was only used to determine if a particular individual was in Area I or in Area II during a specific time. In addition, UKFSST predicted location estimates, including positional error, showed that all individuals, except one, stayed in one of the two assigned areas during the entire track (see the “Results” section for details). Swimming depth data from predicted locations that could not be assigned, without error, to one of the areas (e.g. the estimated location point is in Area I but its error range reaches Area II) were not incorporated in the time-at-depth analysis.

Depths of pelagic longline gear set

To delineate the maximum effective fishing depth for the configuration of pelagic longline gear used by Fleets A and B, a total of 154 Temperature Depth Recorders (TDRs) (Model LTD-1100; Lotek Wireless, St John’s, Newfoundland, Canada) were deployed in 411 fishing sets (Fleet A = 193 and Fleet B = 218) between January 2010 and December 2011. TDRs were attached to the lower end of the middle branch within each hook basket, following the methodology of Kerstetter and Graves (2006).

Data analyses

Selectivity from tagging data

To compare the vertical habitat utilization of blue sharks across the Southwest Atlantic Ocean, we calculated time-at-depth boxplots by age group in each of the two areas using vertical data from the PSATs. To construct the selectivity curves based on tagging data, availability was considered as the proportion of time that an age-specific blue shark occupies the depth range of the longline fishing gear and assumed to range from 0 to 100 m in depth in both areas (see the “Results” section for details).

The time-at-depth analysis suggests that there is a trend in the age of sharks caught across depth in both areas. In Area I (Fleet A), the depth range of the longline gear is inhabited mostly by adults, which is consistent with an asymptotic selectivity. On the other hand, in Area II (Fleet B), the overlap shifts to younger ages, with older sharks located in deeper waters. Consequently, the expected selectivity for Fleet B is more dome-shaped. For Fleet A, a simple asymptotic logistic curve was chosen to model the shark selectivity. To estimate the selectivity for Fleet A based on tagging data first we multiplied the contact selectivity by the availability for each observed age available from tagging. Contact selectivity was assumed to be equal to 1.0 for all tagged individuals from 3 to 16 years old and 0.0 for individuals younger than 3 years. Given the calculated selectivity values, we used a simple linear regression model and a logistic function to estimate the probability that a fish of age a is caught.

To allow for a decrease in selectivity at older ages for Fleet B, a general non-parametric regression model was used to fit the availability from tagging data obtained in Area II. In this form of regression analysis, the predictor does not take a predetermined form (e.g. asymptotic) but is constructed according to information derived from data. One way that this relationship can be modelled is by constructing smoothing splines. Splines are implemented in non-parametric modelling to allow some degree of bending on a curved line between fixed points (Thorson *et al.*, 2013).

Stock assessment

cpue indices

For calculating time-series with relative indices of abundance useful for stock assessment, it is first necessary to adjust the data for the impacts of factors other than the changing abundances of the species over time. This process is commonly referred as cpue standardization (Maunder and Punt, 2004). The most common method is the application of generalized linear models (GLMs). One challenge when modelling data from shark populations is that the datasets of bycatch species often have a large proportions of fishing sets with zero-catches. One way to overcome this problem is using the GLM with statistical distributions that allow for a large proportion of zero observations (Maunder and Punt, 2004). The Tweedie distribution recently proposed by Shono (2008) has become popular in cpue standardization for bycatch species. To generate relative

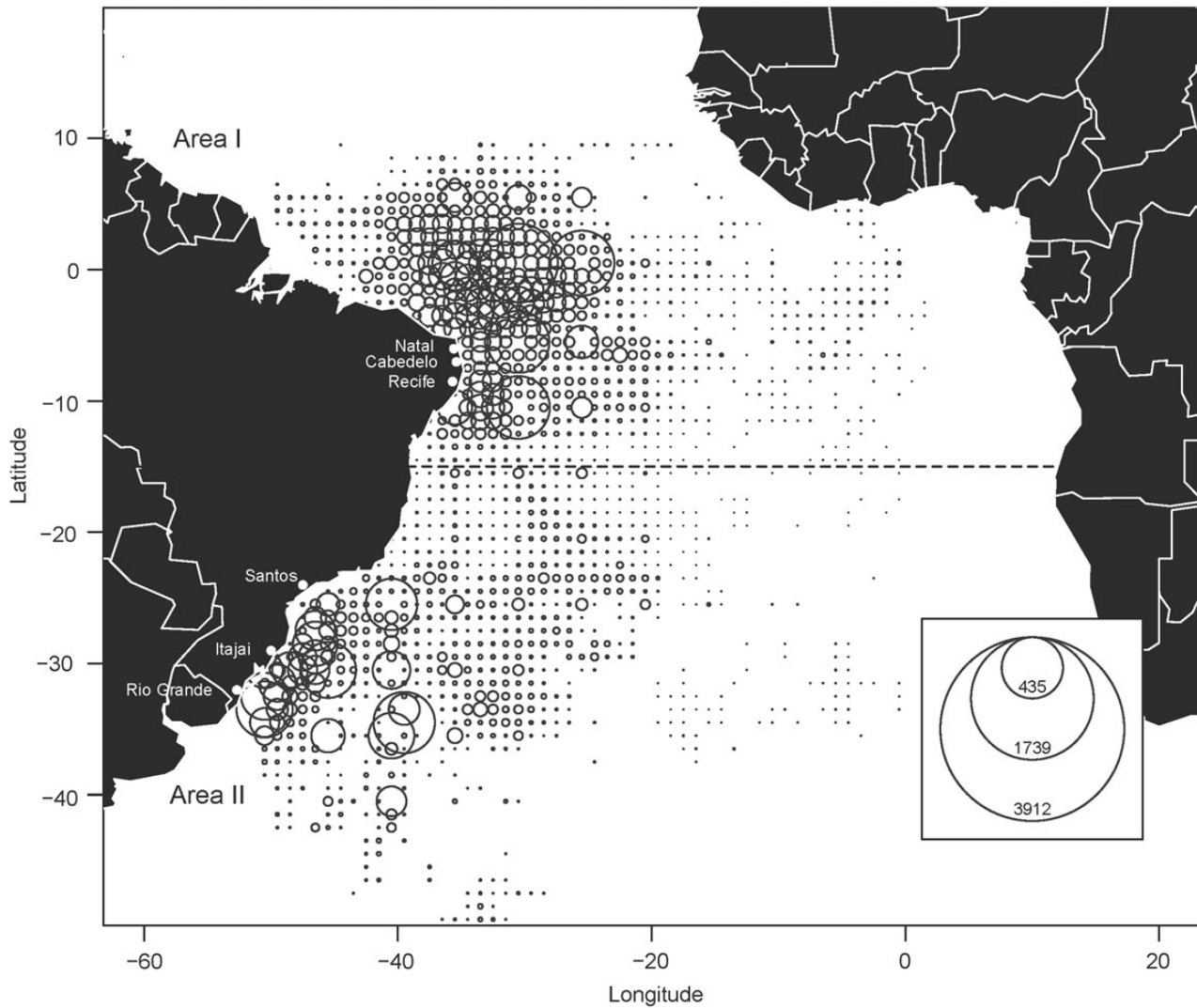


Figure 3. Distribution of fishing effort in the number of hooks/100 by the Brazilian longline Fleets A and B between 2002 and 2012 in Areas I and II, respectively.

Table 1. Summary data for 16 blue sharks tagged with pop-off satellite-tags in the South Atlantic Ocean

| ID | Age (years) | Sex | Area | Tagging date | Programmed release days | Pop-up date | Days at liberty | GLS locations (n) |
|----|-------------|-----|------|------------------|-------------------------|-------------------|-----------------|-------------------|
| 1 | 3 | F | I | 21 May 2009 | 90 | 09 August 2009 | 81 | 56 |
| 2 | 10 | F | I | 22 May 2009 | 210 | 16 December 2009 | 205 | 141 |
| 3 | 7 | F | I | 12 May 2011 | 180 | 07 July 2011 | 57 | 34 |
| 4 | 9 | M | I | 12 May 2011 | 180 | 20 June 2011 | 40 | 31 |
| 5 | 8 | M | I | 14 May 2011 | 180 | 07 September 2011 | 117 | 83 |
| 6 | 4 | M | I | 18 May 2011 | 180 | 25 September 2011 | 131 | 95 |
| 7 | 5 | F | I | 19 May 2011 | 180 | 03 September 2011 | 108 | 71 |
| 8 | 3 | M | I | 01 July 2011 | 180 | 24 October 2011 | 116 | 70 |
| 9 | 4 | F | II | 14 January 2009 | 180 | 09 May 2009 | 106 | 62 |
| 10 | 8 | F | II | 16 January 2009 | 90 | 19 March 2009 | 63 | 41 |
| 11 | 3 | M | II | 22 January 2009 | 90 | 29 March 2009 | 67 | 38 |
| 12 | 3 | F | II | 11 December 2010 | 180 | 02 April 2011 | 113 | 74 |
| 13 | 5 | M | II | 13 December 2010 | 180 | 29 April 2011 | 138 | 82 |
| 14 | 11 | F | II | 05 November 2011 | 90 | 30 December 2011 | 56 | 37 |
| 15 | 10 | F | II | 06 November 2011 | 210 | 28 April 2012 | 175 | 119 |
| 16 | 10 | M | II | 13 November 2011 | 210 | 14 March 2012 | 123 | 68 |

F, female; M, male. Tagging occurred in two geographic areas, I and II.

abundance indices for Fleets A and B, cpue standardizations were performed using the GLM. In all, 20 228 and 17 437 longline sets were used to standardize blue shark cpue for Fleets A and B, respectively. The number of zero blue shark catches was relatively high in the datasets (56% in Fleet A; 51% in Fleet B) and a Tweedie distribution with a log-link function was therefore used in the GLM, following [Carvalho et al. \(2014\)](#). For the cpue standardization, the response variable considered was catch per unit effort (cpue), measured as the number of fish per 1000 hooks deployed. Models were constructed separately for each fleet, the explanatory variables considered were: year (2002–2012), quarter of the year (4), depth, and the target. The variables year, quarter of the year, and target were included as factors in the model, whereas depth was a continuous variable. Estimates of the bathymetry for each fishing set location (x -variable = depth) were obtained from bathymetry data downloaded from the NOAA National Geophysical Data Center, Geophysical Data System (<http://www.ngdc.noaa.gov/mgg/bathymetry/relief.html>). The target factor was developed using the methodology proposed by [Carvalho et al. \(2014\)](#), which uses cluster analysis to account for changes in target species of the Brazilian pelagic tuna longline fleet between 2002 and 2012. After the cluster analysis, percentages of the species and species groups were calculated for each cluster. These clusters comprised the target species factor in the GLM. Here, as in [Carvalho et al. \(2014\)](#), the cluster analyses resulted in the separation of the catch into six different clusters representing fishing or target strategies. The models used the following formulae:

$$E[Y](= E[CPUE] = \mu) = \exp\{\text{intercept} + \text{year} + \text{quarter of the year} + \text{depth} + \text{target}\}$$

$$\text{Var}[Y](= \phi \text{var}[\mu]) = \sigma^2 \mu^p,$$

where μ is the location parameter, σ^2 the diffusion parameter, and p the power parameter ([Shono, 2008](#)).

The selection of predictors was evaluated exclusively on AIC. The GLMs were computed in the R Project for Statistical Computing version 2.14.1 (R Development Core Team 2012) using functions available in library “tweedie” ([Dunn, 2011](#)).

Statistical catch-at-age model

There are several age-structured stock assessment methods; however, one of the most commonly used in stock assessment for many exploited fish stocks is statistical catch-at-age analysis ([Quinn and Deriso, 1999](#)). SCAMs are based on the age structure of a fished population and generally consist of two submodels, one describing the population dynamics of the stock and a second that predicts observed data, given the estimated population each year ([Fournier and Archibald, 1982](#)).

An estimate of historical blue shark abundance in the South Atlantic Ocean was reconstructed using a modified SCAM that was originally developed by [Frisk et al. \(2010\)](#). Our SCAMs use the “areas-as-fleet” approach and include the Brazilian pelagic longline Fleets A and B. The biological parameters used for the calculations, as well as subscripts, input data, and estimated parameters, are shown in [Table 2](#), and the model equations are shown in [Tables 3 and 4](#). The model considered annual time intervals, the period from 2002 and 2012, and ages 2 through 16 (age 16 was an aggregate class that included all sharks of age 16 and older). The model produced estimates of fishing mortality rates, abundance, total biomass, and SSB (i.e. the biomass of mature females in the population). Calculated harvest management points were based on Maximum Sustainable

Table 2. Definition of subscripts, input data, and input parameters used in the SCAM

| | |
|---|--|
| Indices | |
| Index for age | a |
| Age of plus group | A |
| Index for time | t |
| Index for fishery | f |
| Data | |
| Fishery observed catch | $C_{t,f}$ |
| Fishery relative abundance | $i_{t,f}$ |
| Fishery age proportions | $P_{a,t,f}$ |
| Life-history information | |
| Instantaneous mortality rate | $M = 0.2 \text{ year}^{-1}$ |
| von Bertalanffy growth parameters | $L_\infty = 352.1$ $k = 0.16 \text{ year}^{-1}$ $t_0 = -1.01$ |
| Allometry for length–weight | $w = \alpha l^\beta$ $\alpha = 1.901 \times 10^{-6}$ $\beta = 3.134$ |
| Age-at-50% maturity | $a_h = 5 \text{ years}$ |
| Standard deviation in age-at-maturity | $y_h = 0.65$ |
| Calculated parameters | |
| Average recruitment | \bar{R} |
| Average fishing mortality | F |
| Reproductive rate in equilibrium conditions | $\phi_E; \phi_e$ |
| Vulnerable biomass | $\phi_B; \phi_b$ |
| Equilibrium recruitment | R_0 |
| Virgin biomass | B_0 |
| Equilibrium biomass | B_e |
| Abundance-at-age in year t | $N_{a,t}$ |
| Model predicted catch-at-age | $C_{a,t,f}$ |
| Instantaneous total mortality rate | $Z_{a,t}$ |
| SSB | S_t |
| Maximum survival rate from egg to age 1 | s_0 |
| Asymptotic limit | b |
| Model predicted proportions of catch-at-age | $\hat{P}_{a,t,f}$ |
| Model predicted total catch | $\hat{C}_{t,f}$ |
| Total number of individuals | T_t |
| Total vulnerable biomass | B_t |
| Model predicted abundance index | $\hat{l}_{t,f}$ |
| Estimated parameters | |
| Age-at-50% vulnerability | a_f |
| Maturity-at-age | m_a |
| Vulnerability-at-age for each fishery | $v_{a,f}$ |
| Standard deviation in vulnerability-at-age | \hat{y}_f |
| Unfished age-1 recruits | R_0 |
| Recruitment compensation | k |
| Equilibrium fishing rate | F_e |
| Recruitment deviations | ω_t |

Upper and lower case subscripts indicate unfished and fished conditions, respectively.

Yield (MSY), using the stock assessment model in equilibrium with a given F and F_{MSY} , that maximizes the yield. The fishing mortality rate that maximizes yield (F_{MSY}) is calculated numerically using a Newton–Raphson approach to solve the instantaneous catch equation ([Martell et al., 2008](#)) assuming steady state conditions. Given an estimate of F_{MSY} , other reference points are derived based on equilibrium recruitment at F_{MSY} and per recruit incidence functions.

To estimate vulnerability-at-age for Fleet A, a standard logistic function was used. To estimate vulnerability-at-age for Fleet B, a dome-shaped selectivity was used. To implement a dome-shaped selectivity, an additional penalty weight was added to the objective function that controls how much curvature there is and limits how much

Table 3. Notation for estimated parameters, age-schedule calculations

| | |
|--|-------|
| Biology | |
| $l_a = l_\infty e^{-k(a-t_0)}$ | T3.1 |
| $w_a = \alpha l_a^\beta$ | T3.2 |
| $m_a = \{1 + e^{[(a_n - a)/y_n]}\}^{-1}$ | T3.3 |
| $v_{a,f} = \{1 + e^{[(a_f - a)/y_f]}\}^{-1}$ | T3.4 |
| Survivorship | |
| $S_a = \begin{cases} 1 & a = 1 \\ S_{a-1}e^{-M} & a > 1 \\ S_a/(1 - e^{-M}) & a = A \end{cases}$ | T3.5 |
| $\widehat{S}_a = \begin{cases} 1 & a = 1 \\ S_{a-1}e^{-M_{a-1} - F_e v_{a-1}} & A > a > 1 \\ S_a/(1 - e^{-M - F_e v_a}) & a = A \end{cases}$ | T3.6 |
| $\phi_E = \sum_{a=1}^A S_a m_a$ $\phi_e = \sum_{a=1}^A \widehat{S}_a m_a$ | T3.7 |
| $\phi_B = \sum_{a=1}^A S_a m_a v_a$ $\phi_b = \sum_{a=1}^A \widehat{S}_a m_a v_a$ | T3.8 |
| $R_e = R_0((k - \phi_e/\phi_E)/(k - 1))$ $\phi_E/\phi_e < k, \quad k > 1$ | T3.9 |
| where k is given by: $4h/(1 - h)$ | |
| $B_0 = R_0 \phi_b$ $B_e = R_e \phi_b$ | T3.10 |
| Initial state | |
| $N_{a,t} = R_e \widehat{S}_a e^{(\omega_t - a)}$ | T3.11 |
| State dynamics | |
| $C_{a,t,f} = F_{a,t,f} N_{a,t} W_a v_a (1 - e^{-Z_{a,t}})/Z_{a,t}$ | T3.12 |
| $Z_{a,t} = M + F_{a,t,f} v_a$ | T3.13 |
| $S_t = \sum_{a=1}^A N_{a,t} m_a$ | T3.14 |
| $N_{a,t} = \begin{cases} (s_0 S_t / (1 + b S_t)) e^{\omega_t - 0.5 t^2} & a = 1 \\ N_{a-1,t-1} e^{-Z_{a,t}} & a > 1 \\ N_{a,t-1} e^{-Z_{a,t}} & a = A \end{cases}$ | T3.15 |
| $s_0 = k/\phi_E$ | T3.16 |
| $b = (k - 1)/R_0 \phi_E$ | T3.17 |
| $\hat{P}_{a,t,f} = (C_{a,t,f} / \sum_a C_{a,t,f}) W_a$ | T3.18 |
| $\hat{c}_{t,f} = \sum_a C_{a,t,f} W_a$ | T3.19 |
| $T_t = \sum_{a=1}^A N_{a,t} v_{a,f}$ | T3.20 |
| $B_t = \sum_{a=1}^A N_{a,t} v_{a,f} W_a$ | T3.21 |

Upper and lower case subscripts indicate unfished and fished conditions, respectively.

dome-shaping can occur. To penalize the curvature, the square of the second differences of the vulnerabilities-at-age were added to the objective function. The selectivity pattern for each fleet used within the SCAM was chosen based on the shape of the tag-based selectivity.

It was assumed that each individual's growth followed a von Bertalanffy equation (T3.1) (Lessa *et al.*, 2004). Natural mortality (M) was assumed to be age-independent and time-invariant and was fixed at a constant 0.2 year⁻¹, based on the ICCAT 2008 assessment. The mortality parameters, along with the age-specific information, were used to derive parameters for the Beverton–Holt stock recruitment relationship, in which equilibrium and unfished conditions were assumed. A commonly used parameterization of the Beverton–Holt stock recruitment model, the so-called steepness parameterization, was applied.

The SCAM was developed and implemented using ADMB (Fournier *et al.*, 2012). A Bayesian approach was used to obtain posterior probability estimates for the parameter values and quantities of interest. The model was fitted to standardized cpue indices, total commercial catch, and catch-at-age data. To improve model convergence, informative prior distributions were used on some model parameters. A beta prior (0.9, s.d. = 0.2) was assigned for the steepness parameter (h) of the Beverton–Holt stock–recruitment relationship. This value is based on previous blue shark stock assessments in the North Pacific (Kleiber *et al.*, 2009) and Atlantic

Table 4. Residuals and likelihoods

| | |
|--|-------|
| Residuals | |
| Abundance index | |
| $l_t = \ln(I_{t,f}) - \ln(B_t)$ | T4.1 |
| where l_t is given by: | |
| $l_{t,f} = q_{t,f} B_t e^{\epsilon_t}$ | |
| $q_{t,f} = \exp \sum_{\tau \leq t} \ln(I_{\tau,f}) - \ln(B_\tau)$ | |
| Recruitment | |
| $\delta_t = \ln(N_{1,t}) - \ln(R_t)$ | T4.2 |
| Age proportions | |
| $v_{a,t,f} = \ln(Q_{a,t,f}) - \ln(\hat{Q}_{a,t,f})$ | T4.4 |
| where $\hat{Q}_{a,t,f} = (V_{a,t,f} / \sum_a V_{a,t,f})$ and $V_{a,t,f} = N_{a,t} v_{a,f}$ | |
| $\eta_{a,t} = \ln(P_{a,t,f}) - \ln(\hat{P}_{a,t,f}) - (1/A) \sum_{a=1}^A \ln(P_{a,t,f}) - \ln(\hat{P}_{a,t,f})$ | T4.5 |
| Negative log-likelihoods | |
| Catch | |
| $l_c = \ln(\sigma_{c,f}) + \sum_{t=1}^T (c_{t,f} - \hat{c}_{t,f})^2 / 2\sigma_{c,f}^2$ | T4.6 |
| Abundance index | |
| $l_{i,f} = \ln(\sigma_{i,f}) + \sum_{t=1}^T (\epsilon_{t,f}^2 / 2\sigma_{i,f}^2)$ | T4.7 |
| Recruitment | |
| $l_\omega = \ln(\tau) + \sum_{t=1}^T (\omega_t^2 / 2\tau^2)$ | T4.8 |
| Age proportions | |
| $l_Q = (A - 1)T \ln(1/((A - 1)T)) \sum_{a=1}^A \sum_{t=1}^T v_{a,t}^2$ | T4.9 |
| $l_P = (A - 1)T \ln(1/((A - 1)T)) \sum_{a=1}^A \sum_{t=1}^T \eta_{a,t}^2$ | T4.10 |
| Age-specific selectivity constraints | |
| Curvature penalty | |
| $\lambda_f^2 \sum_{a=2}^{A-1} (v_{f,a} - 2v_{f,a-1} + v_{f,a-2})^2$ | T4.11 |
| Dome-shaped penalty | |
| $\begin{cases} \lambda_f^2 \sum_{a=1}^{A-1} ([v]_{f,a} - v_{f,a+1})^2 & v_{f,a+1} < v_{f,a} \\ 0 & v_{f,a+1} \geq v_{f,a} \end{cases}$ | T4.12 |
| where λ_f^1 and λ_f^2 are the relative weights | |

Oceans (ICCAT, 2008). Recruitment deviations (ω_t) were assumed to be lognormally distributed, with an unknown variance to be estimated from the data (Maunder *et al.*, 2006a). The parameters ω_t represent the process error component in the model. Other parameters have the default ADMB uniform prior on the scale that the parameter is estimated on from $-\text{inf}$ to inf .

Regarding the initial conditions of the stock used in the model, it was assumed that the first year for which annual catch data were available might not have corresponded to the first year of (appreciable) exploitation. Therefore, for the first year considered in the model, the stock was assumed to be at 80% of its pre-exploitation biomass. This value is based on the results from the South Atlantic blue shark stock assessment, using a Bayesian state–space surplus production model (SPM), presented in Carvalho *et al.* (2014). Their results indicated that in 2002 the South Atlantic blue shark stock had decreased 20% of its pre-exploitation biomass.

In the Bayesian framework, samples are generated from the posterior distribution of parameters, which can be implemented using Markov Chain Monte Carlo (MCMC) techniques (MacKay, 2003). The MCMC samples were calculated using the default algorithm in ADMB (Fournier *et al.*, 2012). Each simulation included three chains with 2 million cycles, discarding the first 200 000 iterations as a burn-in phase then thinning the chain by saving every 200th iteration to reduce autocorrelation. The final step in the SCAM was to compute the residuals between the observations and predictions for the relative abundance indices and the catch-at-age proportions used in the negative log-likelihoods during parameter estimation or numerical integration of posterior distribution (Table 4).

Model fit was evaluated by assessing whether the distribution of predicted catch rates, and proportions-at-age calculated using parameters sampled from the joint posterior distribution corresponding to MCMC simulations, included the corresponding observed value at the 95% credible level (posterior predictive check; Gelman *et al.*, 2004).

Results

Movement

Tracking results showed complex and remarkable movement patterns by blue sharks in the Southwest Atlantic Ocean. Most

individuals stayed in the area of the tagging location (Figures 4 and 5); however, one mature female (“Blue shark 2”) performed a trans-oceanic migration, spanning the entire equatorial Atlantic Ocean in 209 d from the northeast coast of Brazil to the Gulf of Guinea, Africa. From Area II, a mature female (“Blue shark 15”) arrived in Area I after travelling along a large portion of the Brazilian coast in 175 d, a distance of 3470 km. Time-at-depth box-plots show that patterns of segregation varied based on which area the blue sharks were tracked in (Figure 6). Within Area I, adults occupied shallower depths while juveniles spent most of their time in waters deeper than 100 m. The 4-year-old juvenile exhibited the

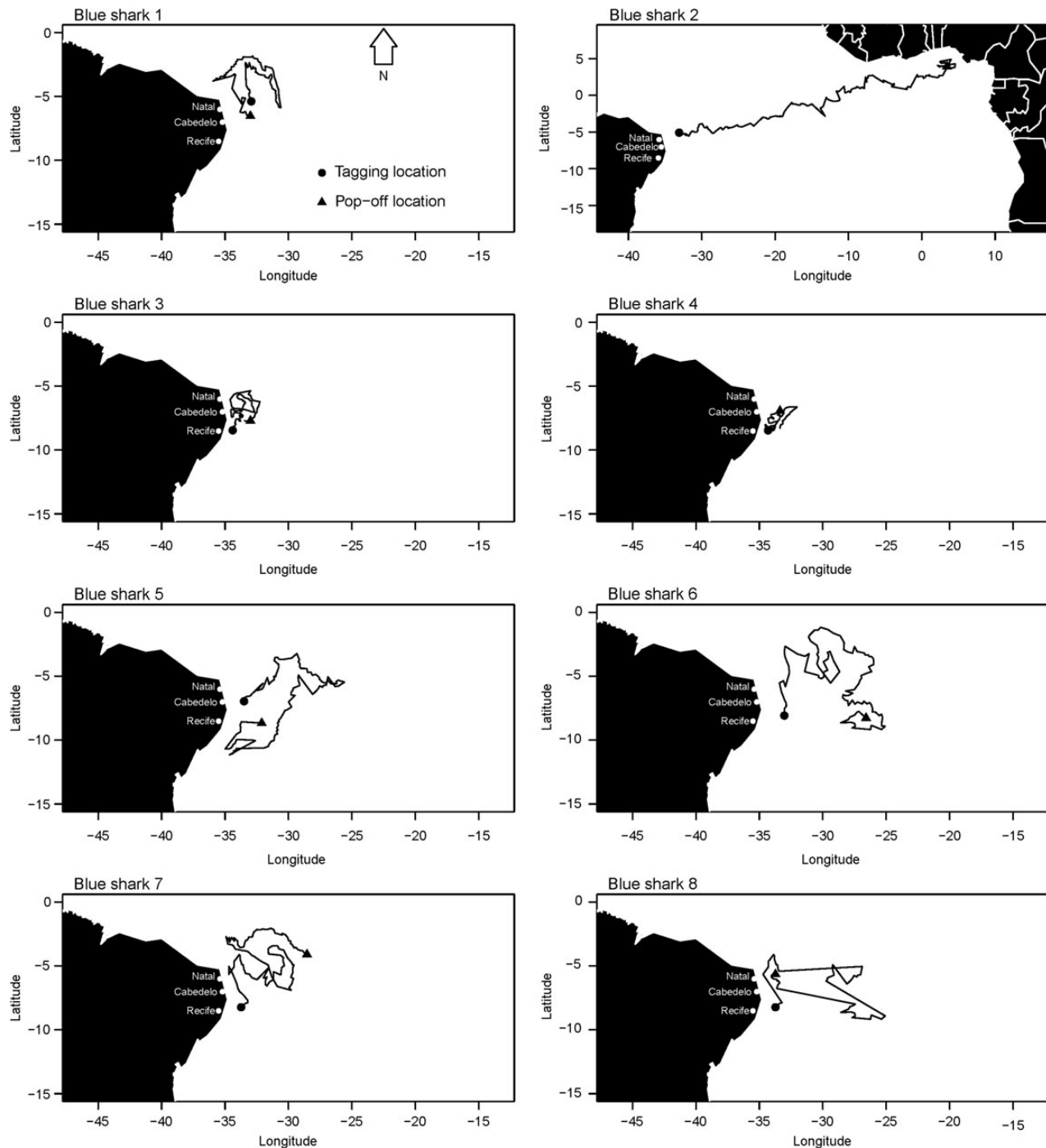


Figure 4. MPT for blue sharks across Area I, fit with Kalman Filter State – Space Model.

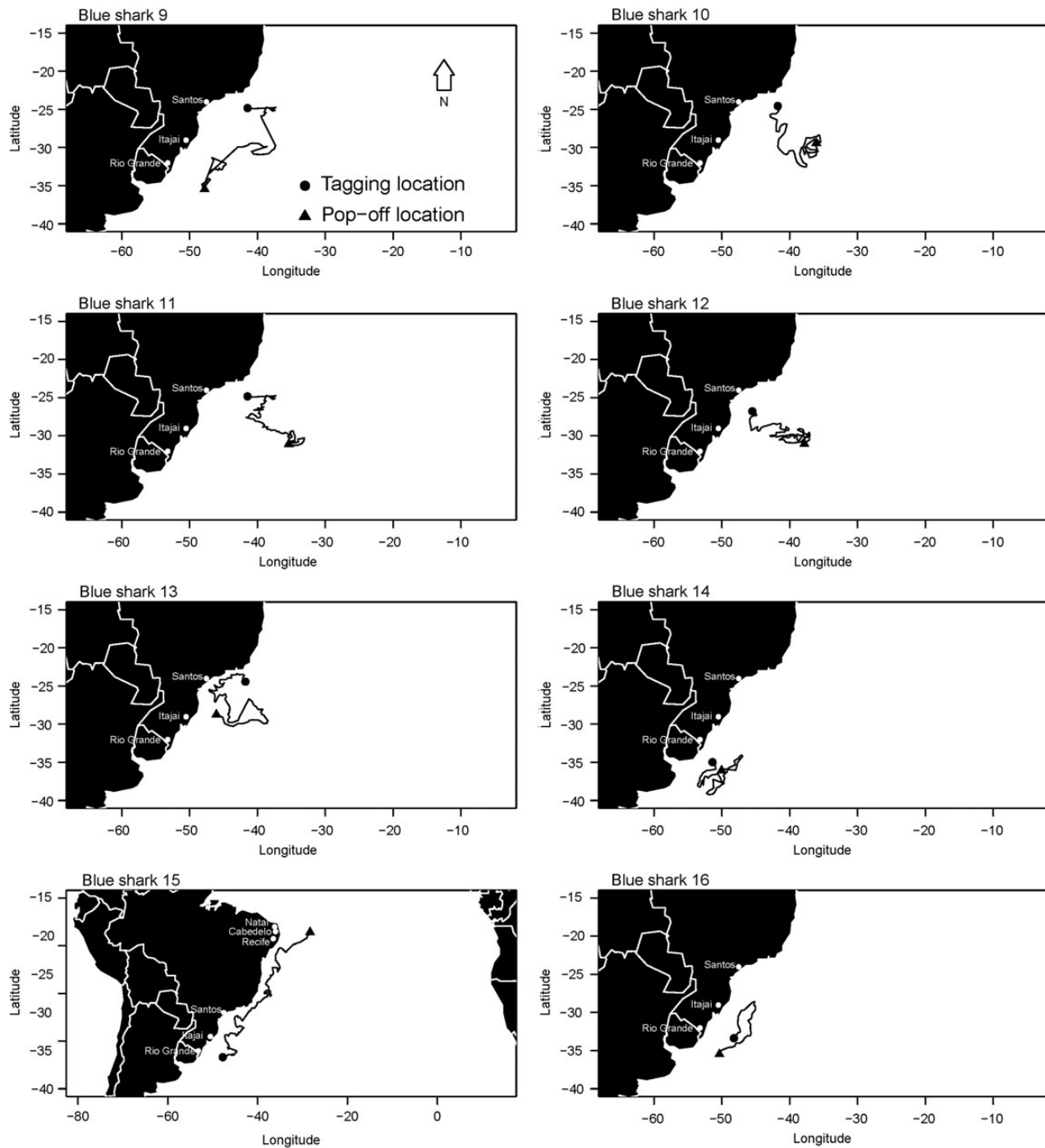


Figure 5. MPT for blue sharks across Area II, fit with UKFSST.

greatest depth range, occupying waters between 40 and 335 m. In Area II, it was the juveniles that mostly occupied shallower depths between 0 and 100 m.

Availability

The mean depth of the deepest hook of a set observed by the TDRs was 62.4 (\pm s.d. 18.7) m for Fleet A and 66.8 m (\pm s.d. 20.2 m) for Fleet B, and the maximum depth recorded was 97.1 and 98.6 m for Fleets A and B, respectively. The time-at-depth

distribution for the TDR dataset for the deepest hook and the time-at-depth distribution of blue sharks tagged show a high percentage of overlap with adults in Area I and juveniles in Area II (Figure 6).

Selectivity from tagging data

The selectivity patterns obtained using tagging data alone had an asymptotic selectivity for Fleet A and dome-shaped selectivity for Fleet B. Fishing mortality was higher for juvenile blue sharks (ages

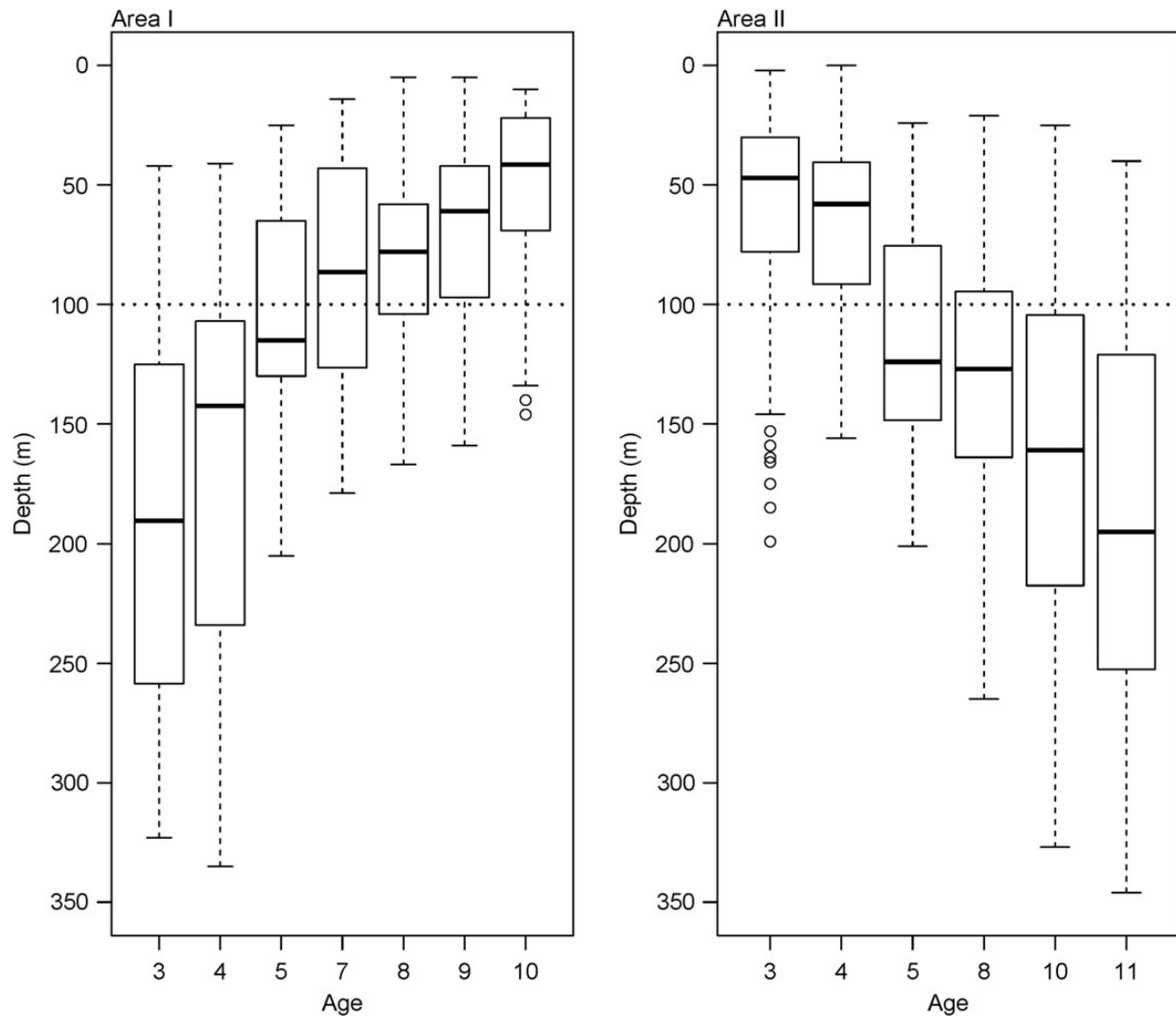


Figure 6. Boxplots of time-at-depth by age for tagged blue sharks in Areas I and II. Black horizontal dotted line indicates the maximum depth recorded for the observed hooks.

3 and 4) in Fleet B than in Fleet A. In Fleet B, there was a clear drop in selection patterns for blue sharks older than age 10, with age 7 being fully selected, whereas for Fleet A, blue sharks from age 9 to 16 were fully selected (Figure 7).

cpue standardization

The final model for the blue shark cpue standardization for both fleets consisted of four variables and explained 59 and 58% of the total deviance for Fleets A and B, respectively. The relative contribution from each variable to the total explained deviance for the model for Fleet A showed that target (42%) was the most important factor, followed by year (32%), quarter (19%), and depth (7%) (Table 5). For Fleet B, target (45%) and year (37%) were the most important factors, followed by quarter (15%) and depth (3%). Residual diagnostic plots and Q–Q plots showed that a good fit was obtained and that the assumed error structure was satisfactory for both models. In terms of nominal cpue for the blue shark, there was a relatively small variability in the time-series for both fleets (Figure 8). cpue values oscillated between 2 and 3 individuals per 1000 hooks for Fleet A;

and around 2 individuals per 1000 hooks for Fleet B. In general, the trend of standardized cpue time-series was stable and similar to that nominal cpue for both fleets. However, Fleet B showed lower values for nominal and predicted cpue during the entire time-series (Figure 8).

Stock assessment model

The SCAM produced a reasonable fit, with posterior median estimates of steepness for the stock–recruitment relationship very similar to the prior. This is expected, given the relatively low variability and short length of the cpue time-series, as well as the informative nature of the prior on h . For cpue, the model predicted the same stable trend as was observed, producing lower predictions of cpue for Fleet B than for Fleet A (Figure 8). Observed age for both fleets showed a stable trend during the study period, with Fleet A catching predominantly adult individuals and Fleet B catching mostly juveniles (Figure 9). Residual patterns in the age composition data from both fleets do not appear to show any significant

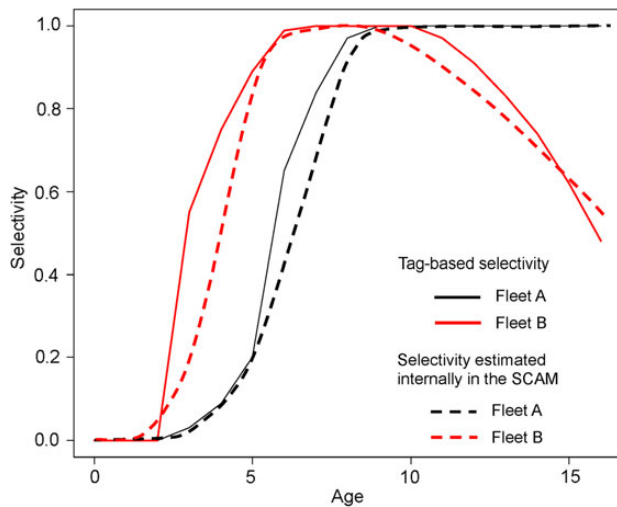


Figure 7. Selectivity curves for Fleets A and B constructed using regression models and tagging data alone; and estimated internally in the assessment model.

Table 5. Deviance analysis of explanatory variables in the Tweedie models for blue sharks caught by the Brazilian pelagic tuna longline fleet from 2002 to 2012

| | Deviance | Resid. d.f. | Resid. Dev | Significance (<i>p</i> -value) |
|-------------------|----------|-------------|------------|---------------------------------|
| Model for Fleet A | | | | |
| Null | | 3882 | 124 598 | |
| Quarter | 21 316 | 3874 | 103 282 | <0.001 |
| Year | 32 969 | 3873 | 70 313 | <0.001 |
| Depth | 8454 | 3871 | 61 859 | <0.001 |
| Target | 43 390 | 3863 | 18 469 | <0.001 |
| Model for Fleet B | | | | |
| Null | | 2271 | 3994 | |
| Quarter | 462 | 2265 | 3532 | <0.001 |
| Year | 784 | 2261 | 2748 | <0.001 |
| Depth | 276 | 2259 | 2472 | <0.001 |
| Target | 1839 | 2256 | 633 | <0.001 |

patterns that would indicate a major model misspecification (Figure 9).

Selectivities estimated by the SCAM show a clear difference between fleets, with age 9 being fully selected by Fleet A and age 7 by Fleet B (Figure 7). The shapes of the curves were very similar to the ones constructed using tagging data alone. In addition, these results clearly demonstrate that when fishing effort is concentrated in a shallower depth (0–100 m) and there is an ontogenetic shift toward deeper waters for older blue sharks, the result is a dome-shaped selectivity.

Changes in posterior median estimates of total biomass, vulnerable biomass, and SSB were relatively small throughout the time-series for both scenarios. The posterior median estimate for MSY was 879 490 metric tonnes ($\pm 108 637$ metric tonnes), with a corresponding estimate of SSB_{MSY} of 682 741 ($\pm 88 721$). The estimates of the current stock status suggest that total biomass in 2012 decreased by 4% of the initial total biomass, whereas SSB decreased by 5% (Figure 10). The posterior median estimate for SSB_{2012}/SSB_{MSY} was 1.49, whereas F_{2012}/F_{MSY} was 0.32. The current stock status relative to MSY (F_{2012}/F_{MSY} , SSB_{2012}/SSB_{MSY}) suggests that the stock is not overfished ($SSB_{2012} > SSB_{MSY}$), nor is overfishing occurring

($F_{2012} < F_{MSY}$), and the stock is therefore not in danger of overexploitation or collapse (Figure 11).

Discussion

Size and space segregation of blue shark

Our study is the largest spatially stratified satellite tagging study of South Atlantic blue shark to date. Most blue sharks showed relatively high levels of residency, staying near the release site. These results support a growing number of studies, indicating that oceanic sharks show site fidelity within core areas, although some individuals also undertake long range movements (Kohler *et al.*, 2002; Weng *et al.*, 2005).

Results also revealed variability in vertical habitat utilization between juveniles and adults. Fishing records have shown that juvenile sharks will vertically segregate from adults sharks (Papastamatiou *et al.*, 2006). Vertical size segregation is common in elasmobranchs and may be related to juveniles avoiding predation by the adults (Papastamatiou *et al.*, 2006) or physiologically optimal conditions for gestation or parturition (Hight and Lowe, 2007; Wearmouth and Sims, 2008). Pregnant female sharks are hypothesized to select warmer waters to reduce gestation and development time of embryos (Jirik and Lowe, 2012). On the other hand, adult female blue shark generally prefers relatively cold waters during outside of the ovulation–fertilization–parturition periods (Pratt, 1979).

Hazin and Lessa (2005) suggested that, in the South Atlantic, blue shark mating occurs off the Southeast coast of Brazil (Area II), and ovulation and fertilization occurs off the northeast coast of Brazil (Area I). In general, the sea surface temperature in Area II is much lower than in Area I throughout the year (Carvalho *et al.*, 2011). Area I is mainly under the influence of the warm South Equatorial Current, and Area II is characterized by the presence of the cold, north-flowing Malvinas (Falklands) Current (Garcia, 1997; Seeliger *et al.*, 1997). This variability in habitat preference of adult female blue shark and threat of predation during juvenile life stages might explain the size and spatial segregation observed here.

Incorporating PSATs data into stock assessment

One reason for the absence of PSATs data in selectivity models is that PSATs are much more expensive than conventional tags (one PSAT is \sim USD4000). This can be problematic as tag-based selectivity studies require recapture of enough tags in each spatial–temporal stratum from each age-cohort to estimate how the species interact with the fishing gear. We selected the entire Southwest Atlantic as a tagging site, which was an appropriate spatial scale to cover fishing grounds from Fleets A and B. However, most of the PSATs were deployed in 2009 and 2011 and stayed attached to the animal for no longer than 6 months. An appropriate temporal scale for tagging studies may need to cover multiple seasons and years, as individuals can modify their behaviour in response to long- or short-term changes in the environment (Vandeperre *et al.*, 2014). In the present study, for example, the mature female blue shark 15 changed significantly its preferred depths when it migrated from Areas II to I. We believe that a larger number than 16 tags would be needed to fully understand the migration patterns of juvenile and adult blue shark and its interaction with fishing gear across the South Atlantic Ocean. However, even under low sample sizes, the completely fishery-independent nature of the PSATs data and the detailed information about horizontal and vertical movements that these tags can provide are unique. It is our hope that by introducing this new application that integrates PSATs data into selectivity

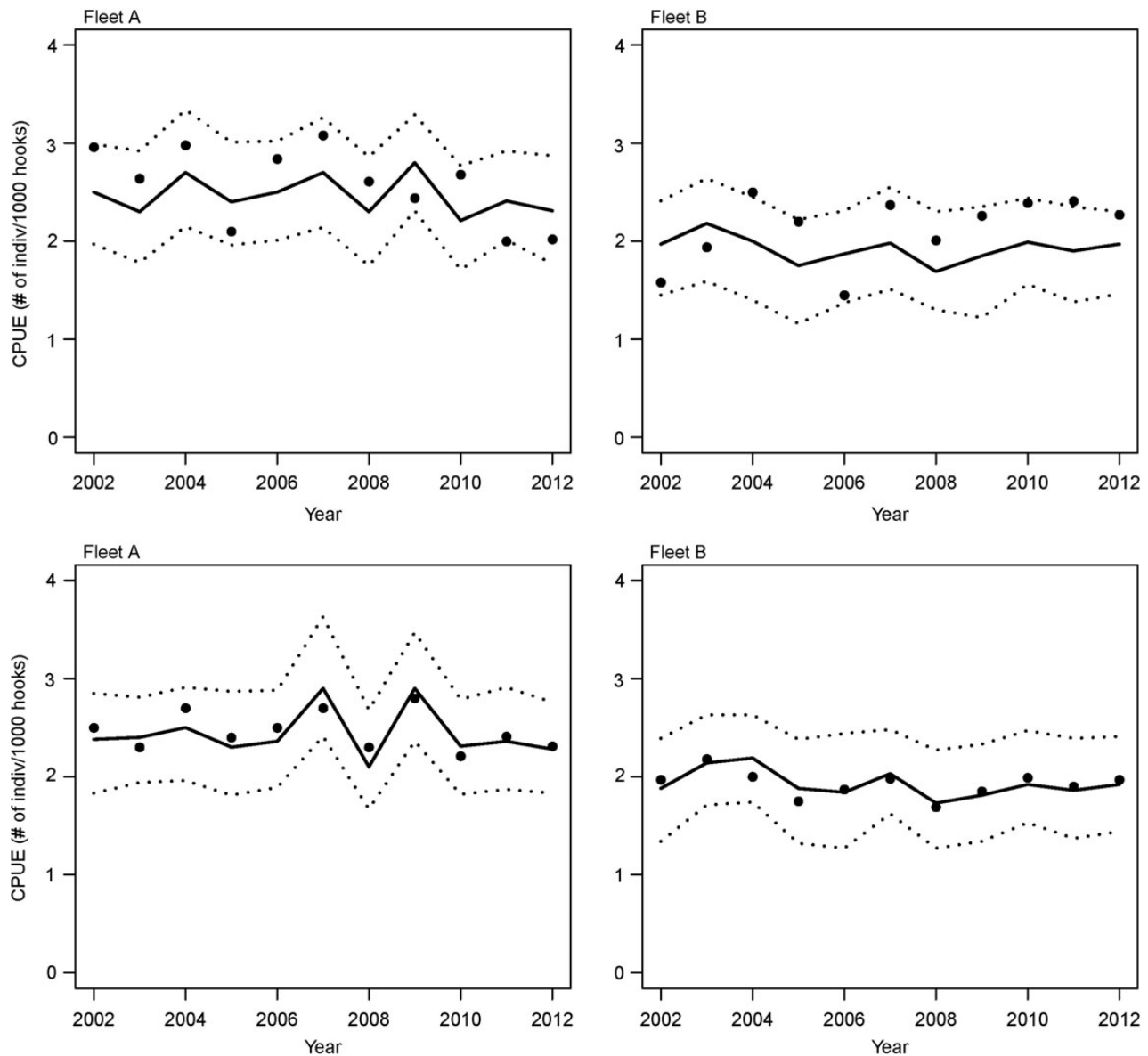


Figure 8. Nominal (circle) and standardized (line) cpue of blue sharks caught by the Brazilian pelagic tuna longline Fleets A and B from 2002 to 2012 (Top panel). Observed (circle) and predicted (line) cpue from the South Atlantic blue shark stock assessment using a SCAM (Bottom panel). Dotted lines represent the 95% confidence interval for predicted cpue values.

models, their popularity for assessment purposes will continue to increase despite the financial costs.

Here, we have shown that logistic regression models can be used to estimate selectivity based on PSATs data. However, while its asymptotic properties are recognized and can be demonstrated, it is concerning that maximum likelihood estimation of the logistic model suffers from small-sample bias. To reduce the bias and predict the selectivity for age-classes of fish with very few observations, we used the alternative penalized likelihood estimation method proposed by King and Zeng (2001).

Integrated assessment methods are capable of estimating selectivity within models when the data are sufficient. This typically requires that assumptions be made about the shape and temporal stability of the selectivity curve (Methot and Wetzel, 2013). Externally derived estimates of selectivity, such as those obtained

here using PSATs data, can assist in identifying which selectivity curve is the most appropriate for each fishery, especially in cases where there are not enough data to estimate selectivity within the model. However, given the increasing use of modern integrated stock assessment models (e.g. Stock Synthesis), future research should address the idea of integrating *a priori* information on selectivity directly into the assessment model. External analysis of selectivity might also help to understand overall estimates of other quantities, such as M . Estimating M , which is one of the most influential quantities in fisheries stock assessment and management, is notoriously difficult because of confounding from other model parameters estimates, including selectivity (Thompson, 1994). Good estimates of Z can be obtained from good catch composition by cohorts, including relative/absolute abundance and a way to deal with selectivity

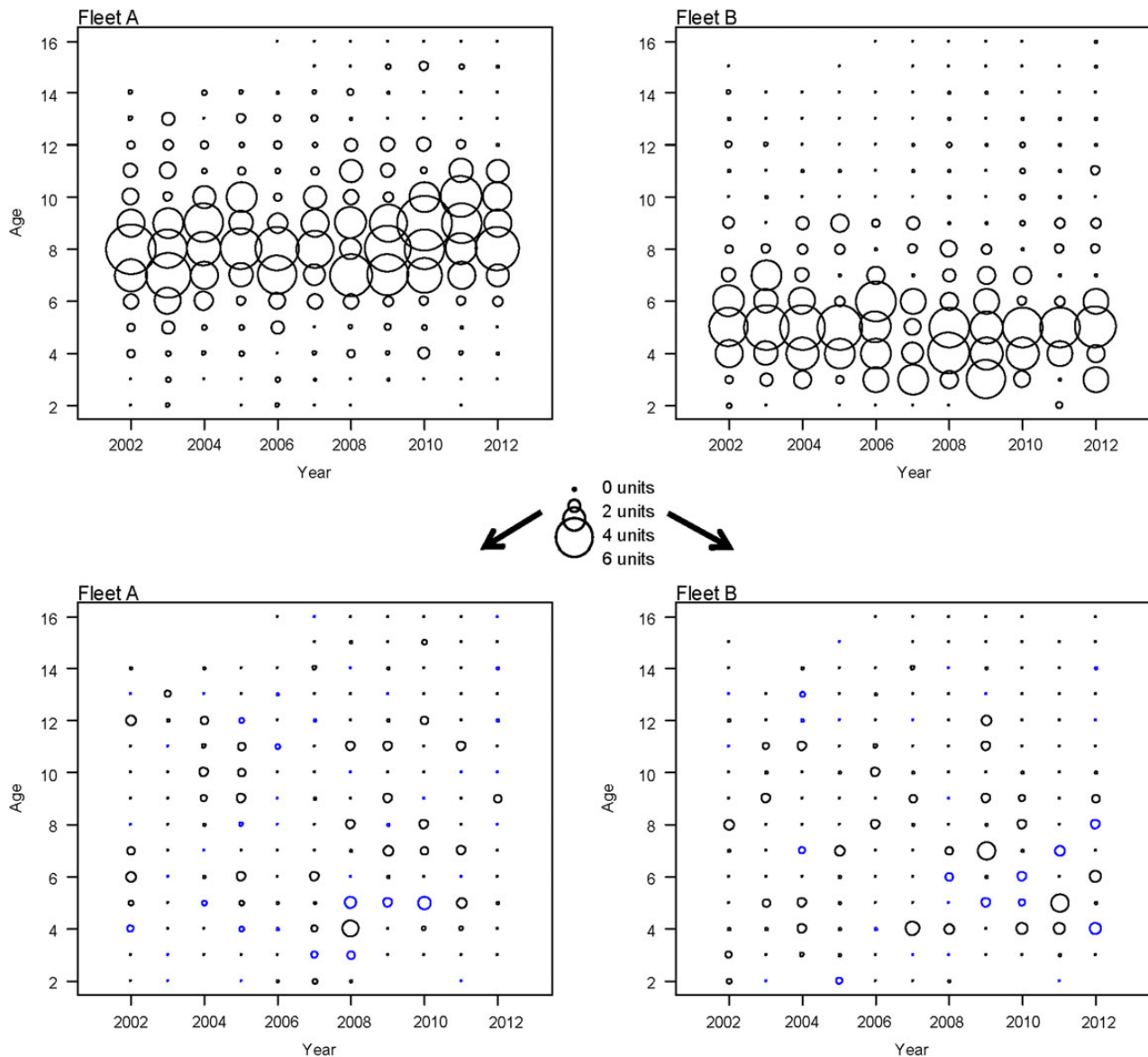


Figure 9. Observed age-composition (top panel) and Pearson residuals between observed and predicted proportions-at-age (bottom panel). Blue circles denote negative residuals.

externally leaves a good potential source of information on natural mortality.

The use of “areas-as-fleets” approach in stock assessment has been criticized. Some concerns are that it assumes that the stock is evenly distributed in a given area and fleets have complete access to it and that any difference in length and age structure is due to gear selectivity (Hurtado-Ferro *et al.*, 2014). In fact, in the present study, these assumptions did not hold true. The spatial segregation pattern between juvenile and adult blue shark observed in the PSATs data were also seen in the catch-at-age data. Interestingly, results from 63 fishery-independent deep longline survey sets (i.e. deepest hook depth between 200 and 250 m) conducted in Area I (36 sets) and Area II (27 sets) in 2012, showed that 78% (317 individuals) and 28% (219 individuals) of the blue sharks caught in Areas I and II, respectively, were juveniles (unpublished data). These findings, in conjunction with information presented here, lead us to conclude that Areas I and II are occupied by adult and

juvenile blue shark and that some level of vertical segregation is occurring. Thus, the differences in length and age structure of blue shark between Areas I and II found in the catch-at-age data used in the SCAM are due to the difference in population spatial structure, not selectivity. It is still not clear in what circumstances the “areas-as-fleets” method is sufficient to model spatial (depth) differences in age or length structure of the population.

Status of the South Atlantic blue shark stock

Regarding the overall stock status, the estimated biological reference points showed that the South Atlantic blue shark stock has been exploited below their maximum sustainable levels, similar to the conclusion reached by the ICCAT assessment (2008) and Carvalho *et al.* (2014), both using SPMs. It is important to highlight that SPMs treat stocks as an undifferentiated biomass, ignoring gender, size, and age-based differences among individuals. The minimal data requirements of SPMs lead many fisheries

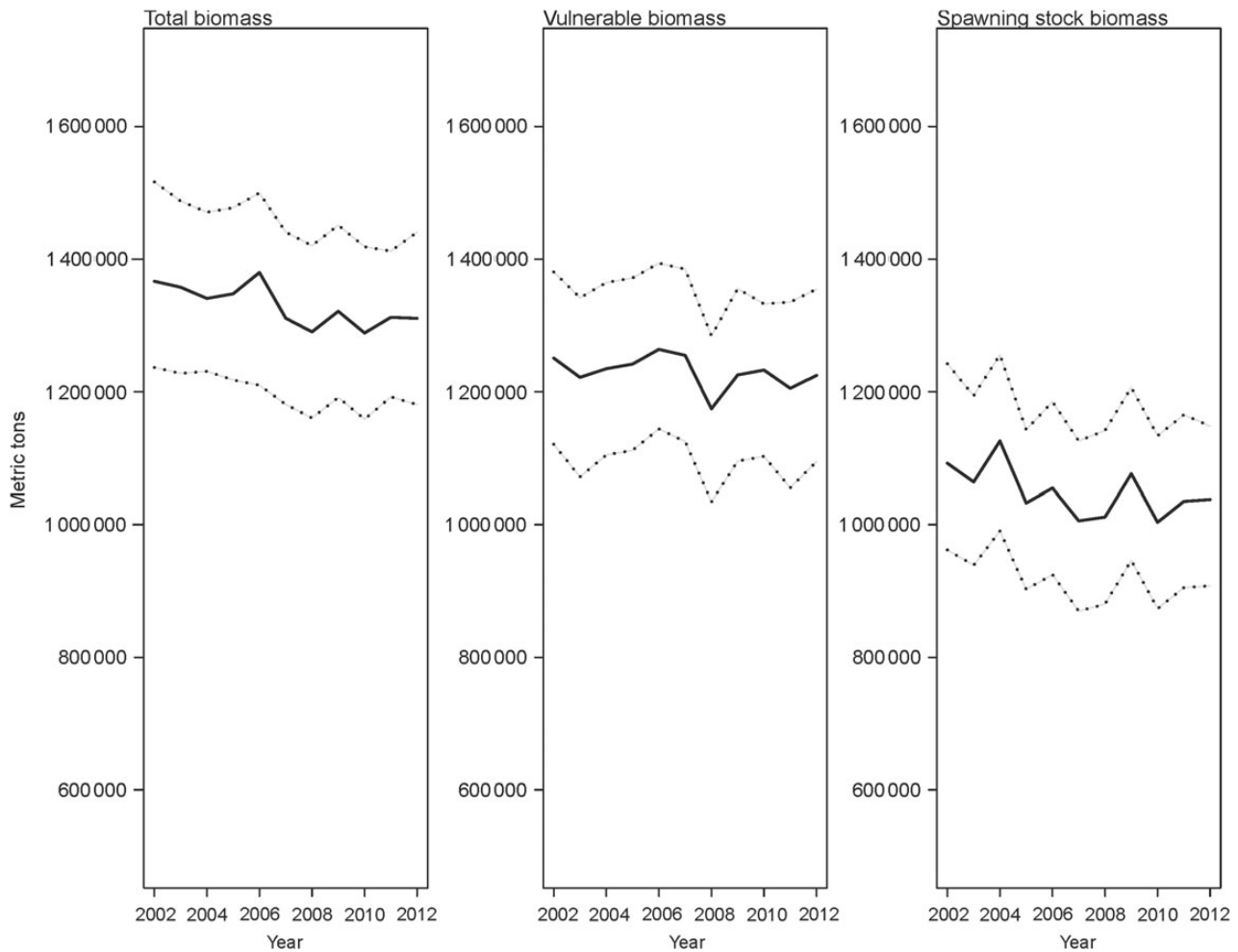


Figure 10. Total biomass, vulnerable biomass, and SSB estimated by the southern Atlantic blue shark stock assessment using a SCAM. Dotted lines represent the 95% confidence interval for predicted biomass values.

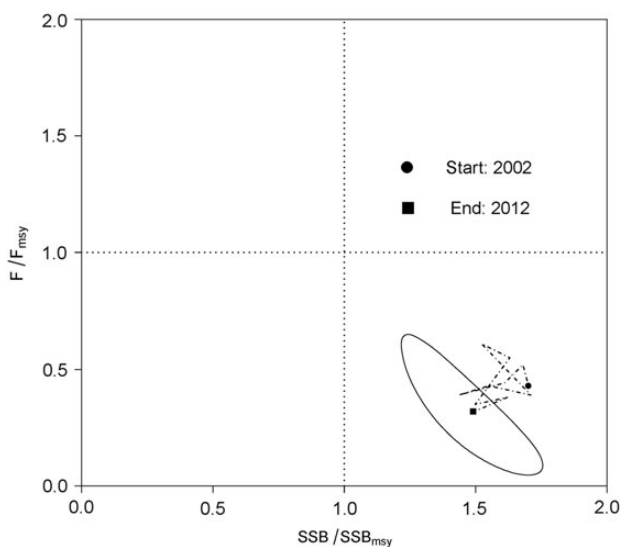


Figure 11. Estimated trajectories for the posterior median of SSB/SSB_{MSY} and F/F_{MSY} from the southern Atlantic blue shark stock assessment using a SCAM. Black solid line represents the 95% confidence interval for SSB_{2012}/SSB_{MSY} and F_{2012}/F_{MSY} values.

management agencies, including ICCAT, to use these SPMs, but ecological differences within and between members of a population suggest that this simple form of model may overlook important influences on population dynamics. SPMs also ignore the spatial structure of the population and assume that the stock is homogeneously distributed (i.e. fully mixed; Punt and Hilborn, 1997). It is clear that the blue shark stock in the Southwest Atlantic Ocean segregates spatially at a large scale, which violates the fully mixed assumption for this stock. Consequently, spatially explicit assessment models, as the one presented here, may lead to a better understanding of the spatial aspects of the population dynamics, as well as improve the quality of stock status information for fishery management decisions.

Acknowledgements

We thank the Brazilian Ministry of Fisheries and Aquaculture for providing the set-by-set catch and effort data from the Brazilian longline fishery. We are also grateful to the Program of Fisheries and Aquatic Science and the School of Forest Resources and Conservation of the University of Florida for the Alumni Scholarship Award provided to FC. Daryl Parkyn (UF Program of Fisheries and Aquatic Sciences), John Carlson (NOAA Fisheries, Panama City, FL), and the three anonymous reviewers are acknowledged for their constructive

comments, which helped to improve the manuscript. We gratefully acknowledge Steve Martell (International Pacific Halibut Commission) and Catarina Wor (University of British Columbia) for help coding the statistical catch-at-age model in ADMB. We also wish to acknowledge the contributions of all the people who have been involved in the Southwest Atlantic blue shark tagging project in particular George Burgess (Florida Program for Shark Research), Dimas Gianuca (Project Albatroz-Brazil), Paulo Travassos and Mariana Travassos (Universidade Federal Rural de Pernambuco), Diogo Martins and Humberto Hazin (Universidade Federal Rural do Semi-Árido), Santiago Montealegre-Quiano (Universidade Estadual Paulista), Alberto Ferreira de Amorim (Instituto de Pesca – Governo do Estado de São Paulo), Bruno Leite Mourato (Universidade Federal de São Paulo), and Pedro Afonso (Universidade dos Açores-Portugal).

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Handling editor: Caroline Durif