Bioecology and movements of bull sharks, *Carcharhinus leucas*, caught in a long-term longline survey off northeastern Brazil

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A robust understanding of habitat usage by coastal shark species, and how it overlaps with human presence in densely-populated regions is needed to inform the development of efficient conservation strategies for these important top predators. An intensive longline survey conducted in nearshore waters off northeastern Brazil from 2004 through 2014 caught a total of 18 bull sharks (*Carcharhinus leucas*) (male-female ratio = 0.63:1), which can be dangerous to humans. Although most sharks were sexually mature, there was no evidence that this region could be used as a parturition or nursery area. Prey items identified in the guts of the sharks comprised teleosts, mollusks and elasmobranchs. Additionally, one satellite-tagged bull shark covered a great distance (> 3,000 km) in 75 days at liberty, making most use of shallow waters (< 20 m depth) and presumably also entering an estuarine area. Although bull sharks are not an important fishery resource in this region, such a reduced abundance coupled with its affinity for coastal and inshore habitats highlights the potential vulnerability of *C. leucas* to deleterious anthropic interferences off northeastern Brazil.

Keywords: Drumline, Longline, Maturity status, Pop-up satellite archival tag, Recife.

Um melhor entendimento sobre a utilização de hábitat das espécies de tubarões costeiros, e como ela se sobrepõe à presença humana em regiões altamente populosas, se faz necessário a fim de subsidiar o desenvolvimento de eficientes medidas de conservação para esses importantes predadores de topo. Um estudo intensivo utilizando espinhel, conduzido em águas costeiras do nordeste do Brasil entre os anos de 2004 e 2014, capturou um total de 18 tubarões cabeça-chata (*Carcharhinus leucas*) (proporção macho-fêmea = 0,63:1), os quais podem ser perigosos para humanos. Apesar da maioria dos tubarões estarem sexualmente maduros, não houve evidências de que essa região esteja sendo utilizada como uma área de parto ou berçário. Entre os itens alimentares identificados foram encontrados teleósteos, moluscos e elasmobrânquios. Além disso, um tubarão cabeça-chata marcado com um transmissor satélite percorreu uma grande distância (> 3.000 km) em 75 dias em liberdade, fazendo o uso de águas superficiais (< 20 m profundidade) e presumivelmente entrando em uma área estuarina. Apesar de os tubarões cabeça-chata não corresponderem a um recurso pesqueiro importante nessa região, tal reduzida abundância juntamente com a sua afinidade por hábitats costeiros reforçam a potencial vulnerabilidade de *C. leucas* às interferências antrópicas deletérias ao longo da costa nordeste do Brasil.

Palavras-chave: Espinhel, Linhas de espera, Recife, Status de maturação, Transmissor satélite.

Introduction

Increasing human populations have generally been responsible for negative influences such as overfishing, water pollution and climate change on coastal ecosystems (Jackson *et al.*, 2001), which correspond to important foraging and nursery grounds for several shark species (Heithaus *et al.*, 2002; Simpfendorfer *et al.*, 2005; Wiley, Simpfendorfer, 2007). Despite the high mobility of many sharks, some species exhibit considerable site fidelity in coastal regions (Simpfendorfer *et al.*, 2005; Conrath, Musick, 2007; Wiley, Simpfendorfer, 2007), making them more susceptible to

anthropogenic impacts. Indeed, some shark species may inclusively use artificial habitats created by large-scale urban development (Werry *et al.*, 2012). Therefore, a better understanding of their bioecology, *i.e.* the interrelationships between biological and ecological features of species, their environments, and movement patterns is necessary to promote effective conservation.

The bull shark, *Carcharhinus leuca*s (Müller & Henle, 1839), is a large carcharhinid, which can grow up to 4 m in total length (L_T) (McCord, Lamberth, 2009). It is circumglobal in tropical and warm temperate coastal waters (Compagno, 2001; Hueter *et al.*, 2005) and also in

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estuarine and freshwater habitats, which it tolerates due to an efficient osmoregulatory capability (Pillans *et al.*, 2005; Reilly *et al.*, 2011). Even though there is no evidence that this species copulates in freshwater, parturition likely occurs in warm-water estuaries and rivers (Montoya, Thorson, 1982; Compagno *et al.*, 2005; Pillans *et al.*, 2006). Adult *C. leucas* sharks make use of shallow nearshore habitats (Brunnschweiler *et al.*, 2010; Hammerschlag *et al.*, 2012; Heupel *et al.*, 2015; Graham *et al.*, 2016), particularly in areas of high freshwater inflow, associated with an elevated productivity, where they usually exhibit some level of site fidelity (Carlson *et al.*, 2010; Daly *et al.*, 2014). Nevertheless, this species also undertakes coastal migrations regulated by environmental, foraging and reproductive drivers (Daly *et al.*, 2014; Espinoza *et al.*, 2016). Open ocean migrations have also been observed, including one pregnant individual, which is known to have traversed the Indian Ocean from the Seychelles to Madagascar (Lea *et al.*, 2015). The occurrence of bull sharks has also been reported from the insular shelves of the northeastern and southwestern Atlantic Ocean (Gadig *et al.*, 2006; Bornatowski *et al.*, 2012).

In Brazil, *C. leucas* have been found up to 3,000 km away from the Atlantic Ocean in the Amazon river (Thorson, 1972), and its occurrence has been reported in industrial and artisanal coastal fisheries from the northernmost state south to the Santa Catarina State, 27° in latitude (Amorim *et al.*, 1998; Mazzoleni, Schwingel, 1999; Menezes *et al.*, 2005; Rodrigues-Filho *et al.*, 2009). Despite a considerable amount of published literature, little is yet known about the bioecology of *C. leucas* in the Southwestern Atlantic. The parturition period in Cananéia lagoon, in the São Paulo State, has been reported to occur from November to February (Sadowsky, 1971). Off Recife, in the Pernambuco State, the bull shark occurs occasionally but with much less frequency than other medium to large-bodied species such as the blacknose (*Carcharhinus acronotus*), the nurse (*Ginglymostoma cirratum*) and the tiger (*Galeocerdo cuvier*) sharks (Afonso *et al.*, 2014). Also, bull sharks have been implicated in a local spate of shark bites in this region (Hazin *et al.*, 2008), bringing additional concerns regarding the species.

This study aims at assessing the population structure of *C. leucas* off Recife and providing preliminary information on the bioecological traits of this species in a region poorly known to marine sciences, thus benefiting its conservation. Such information is also locally relevant for shark hazard mitigation purposes. Furthermore, the vertical and horizontal movements of one adult *C. leucas* assessed with a pop-up satellite archival tag are described for the first time in the western South Atlantic Ocean.

Material and Methods

Ethics statement. The capture and handling of *C. leucas* has been approved by the Instituto Chico Mendes de Conservação da Biodiversidade of the Brazilian Ministry of the Environment (permit no. 15083-8) and was carried out in full compliance with the recommendations of the regiment of the Commission of Ethics on the Usage of Animals from the Universidade Federal Rural de Pernambuco (license no. 041/2009; protocol no. 23082.009679/2009 D18).

Sampling procedure. Sharks were captured in nearshore waters off Recife, northeastern Brazil (8.17ºS, 34.88ºW). The fishing gear comprised two bottom longlines and 23 drumlines deployed in shallow water at mean (± SD) depths of 13.6 ± 1.0 m and 8.6 ± 2.2 m, respectively (Fig. 1). Both fishing gears were equipped with circle hooks (17/0) and baited with moray eel (*Gymnothorax* spp.). The longlines were deployed alongshore ca. 2-3 km from the coastline during the afternoon and retrieved early in the following morning (mean ± SD soak time = 15.55 ± 2.45 hours). Drumlines were deployed < 1 km from shore and were continuously in the water during each fishing trip, being retrieved in the morning for bait replacement.

The data were originated from a long-term shark survey in this region conducted from May 2004 to December 2014, and a thorough description of the fishing gear and fishing procedures can be found in Afonso *et al.* (2011) and Hazin, Afonso (2014). Further information regarding the abundance patterns of *C. leucas* in this region are detailed in Afonso *et al.* (2017).
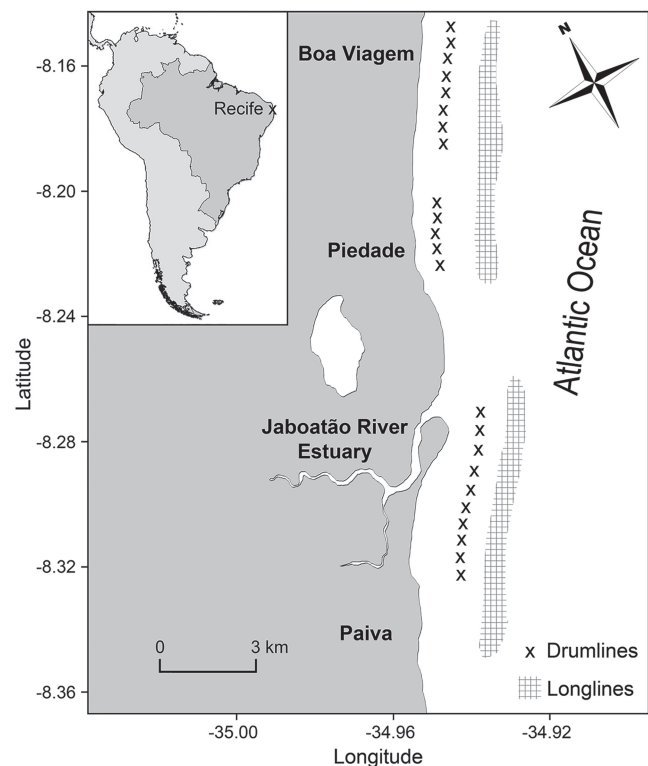

Fig. 1. Map of the study area with the locations of Recife in South America, and fishing sites, *i.e.* Boa Viagem, Piedade and Paiva beaches. The deployment locations of the respective fishing gears, *i.e.* each drumline (x) and the two longlines, are also represented.

Shark biology. Upon capture, bull sharks were sexed and measured for stretched L_T to the nearest centimeter (cm). The specimens which did not survive the fishing gear were taken to the laboratory where they were weighed and dissected. Their stomach contents, when present, were identified to the lowest possible *taxon* and their reproductive tracts were analyzed to assess maturity status. In males, clasper calcification and rotation were inspected, as well as the presence of seminal fluid in the ampullae of the *ductus deferens*. Sexual maturity in females was determined based on the developmental stage of the reproductive organs, *i.e.* oviducal gland, ovary and uterus. The width of these organs was taken to the nearest millimeter (mm), and the presence of vitellogenic follicles, uterine eggs and ova still in the ovary was determined.

Because the data were not normally-distributed, non-parametric statistics were used to inspect for significant patterns in the *C. leucas* biological traits pooled by year. Possible shifts in shark sex ratio between the austral summer, *i.e.* from September to February, and winter, *i.e.* from March to August, were inspected with a Fisher's test. Sex-related differences in shark size were analyzed with a Mann-Whitney test. Also, seasonality in bull shark L_T was assessed using a Kruskal-Wallis test considering month as a factorial variable. Statistical significance was set at $p < 0.05$.

Vertical and horizontal movements. A mature male *C. leucas* (210 cm L_T) was caught (8.14ºS, 34.54ºW) on 17 July 2012. The shark was tagged with a pop-up archival transmitter (mk-10; Wildlife Computers, USA) fitted to the first dorsal fin and set to detach after 75 days at liberty. Satellite-relayed data included maximum and minimum depths and temperatures and the proportion of time spent at 14 depth and temperature bins following a 3-hour time resolution. The 14 depth and temperature intervals were set at 0-1, 1-5, 5-10, 10-15, 15-20, 20-25, 25-30, 30-40, 40-50, 50-60, 60-80, 80-100, 100-150, and > 150 m, and at 12-15, 15-18, 18-20, 20-21, 21-22, 22-23, 23-24, 24-25, 25-26, 26-27, 27-28, 28-29, and > 29ºC, respectively.

Luminosity data were used to generate raw geolocation estimates with proprietary software (WC-GPE v. 1.02.005; Wildlife Computers). The unscented Kalman-Filter state-space model was then applied to estimate the horizontal movements of the shark using the UKFSST *R*-library (Nielsen *et al.*, 2012). An SST correction was carried out by comparing local SST recorded by the tag to satellite-measured SST data downloaded from the National Oceanic and Atmospheric Administration Earth System Research Laboratory (NOAA ESRL) database (ftp://ftp.cdc.noaa.gov). A bathymetric correction was also performed with the analyzepsat *R*-library (Galuardi, 2011) by screening the daily maximum depths achieved by the shark to avoid placing it either on land or in too shallow isobaths.

In order to inspect for possible behavioral shifts across the track, and considering the mostly latitudinal alignment of the movements performed, the movement rates were first calculated by dividing the latitude variation by the amount of time (number of days) elapsed between consecutive geolocations. The periods during which latitudinal movement rates were substantially lower than the overall mean movement rate were assigned to a resident mode, whereas movement rates higher than average were assigned to a transient mode. The distances between all locations were estimated to the nearest km with software GE-Path (v. 1.4.5) and used to calculate the corresponding swimming speeds between consecutive points, which were then averaged by movement mode, *i.e.* resident and transient.

The vertical movements were analyzed with generalized additive models (GAM) using the mgcv *R*-library (Wood, 2011). Models were built with the response variables *i)* time at surface (TAS), *i.e.* the percentage of time spent between the sea surface and the 5-m isobath, using a binomial distribution with logit link functions, and *ii)* maximum diving depth (MDD), using a Gaussian distribution with identity link functions, following Afonso, Hazin (2015). Candidate predictor variables included the diel cycle, *i.e.* day (from 6:00 a.m. to 5:59 p.m.) or night (from 6:00 p.m. to 5:59 a.m.), lunar phase, SST and movement mode. Additionally, a modified version of the split moving window gradient analysis (SMWGA) (Cornelius, Reynolds, 1991) was applied to the time at depth (TAD) and time at temperature (TAT) histograms to assess for shifts in shark vertical behavior as it adequately deals with ARGOS-relayed data with gaps in the dataset (Queiroz *et al.*, 2010).

Finally, a paired t-test was used to inspect for possible estuarine habitat usage in a specific period following a rapid decrease in SST in the last few days of the track. For such a purpose, the temperatures on the sea surface and at the 8-m isobath measured by the tag were compared during this particular event.

Results

Bioecology. A total of 18 *C. leucas* (male-female ratio = 0.63:1) were caught during the 11-year study span and no significant shifts in sex-ratio between austral summer and winter were observed (Fisher's test; odds ratio = 4.58; p-value = 0.315). Shark L_T ranged from 144 to 266 cm (mean = 206.44 ± 34.81 cm) and did not significantly differ between sexes (Mann-Whitney; W = 41.5; p-value = 0.820) neither throughout the year (Kruskal-Wallis; Chi-squared = 9.41; p-value = 0.308).

Mature *C. leucas* were more represented in the catch (61.1%) and were mostly caught during the austral summer (81.8%), when a higher abundance of bull sharks has been reported in this region (Afonso *et al.*, 2017). Among male sharks, 57.1% were mature with sizes ranging from 213 to 251 cm L_T (weight = 74.2-121.0 kg), whereas juvenile males measured between 157 and 186 cm L_T (30.6-50.5 kg).

In addition, two mature specimens measuring 213 (77.8 kg) and 249 (108.3 kg) cm L_T had a considerable amount of seminal volume. The great majority of females (72.7%) was also mature and measured between 205 and 266 cm L_T (72.0-148.5 kg), whereas immature females measured between 144 and 190 cm L_T (24.2-68.0 kg). Among females smaller than 201 cm L_T, the width of reproductive organs ranged from 1.3-2.5 cm (ovaries), 0.6-1.4 cm (oviducal glands) and 0.3-0.5 cm (uterus). In females larger than 206 cm L_T, the same measurements varied from 5.3-14.9 (ovaries), 3.0-7.7 cm (oviducal glands) and 2.2-11.3 cm (uterus). No pregnant females were sampled.

Among 16 dissected stomachs, nine (56.2%) were completely empty and one was everted (Tab. 1). The prey items identified in the stomachs of three juvenile sharks (< 190 cm L_T) comprised the vertebral columns of teleosts and a squid beak (Tab. 1). The stomachs of three mature individuals, measuring between 238-266 cm L_T, contained fragments of an unidentified species of crab, a squid beak, the head of a crucifix sea catfish (*Sciades proops* Valenciennes, 1840) and the remains of an unidentified species of stingray (Tab. 1).

Tab. 1. Stomach contents (Stomach) of the *Carcharhinus leucas* captured and their respective total length (L_T) and sexual development (Development). It was not possible to identify the stomach contents of the sharks typed in bold, *i.e.* S14 and S17, because they were tagged and released. (*) The tracking data from the recovered transmitter revealed that this shark has died a few hours after being released.

Year	Shark	Sex	L_T	Development	Stomach
2004	S1	Male	215	Mature	Empty
2004	S2	Female	207	Mature	Empty
2005	S3	Male	186	Imature	Empty
2006	S4	Female	212	Mature	Empty
2006	S5	Female	250	Mature	Everted
2006	S6	Female	190	Imature	Empty
2007	S7	Male	213	Mature	Empty
2008	S8	Female	170	Imature	Teleost vertebral column
2008	S9	Female	144	Imature	Teleost vertebral column
2011	S10	Male	157	Imature	Empty
2012	S11	Female	200	Imature	Empty
2012	S12	Male	150	Imature	Squid beak
2012	S13	Male	249	Mature	Crab and Squid beak
2012	**S14**	**Male**	**210**	**Mature**	
2013	S15	Female	266	Mature	Head of *Sciades proops*
2014	S16	Female	210	Mature	Empty
2014	**S17***	**Female**	**248**	**Mature**	
2014	S18	Female	238	Mature	Stingray

Movement patterns. The tagged shark (S14; Tab. 1) spent 97.4% of the time between the sea surface and the 20-m isobath, and reached a maximum depth of 64 (± 4) m (Fig. 2a). Accordingly, it was exposed only to a small thermal gradient and spent 96.9% of the time in

temperatures warmer than 24ºC (Fig. 2b), which correspond to the typical temperatures from the mixed surface layer in this region (Afonso, Hazin, 2015). The SMWGA output indicated two significant shifts in its vertical distribution. The first occurred on 22 July 2012, when the shark moved through relatively shallower waters (Fig. 2a) although experiencing lower temperatures (Fig. 2b). The second, more pronounced shift occurred on 29 August 2012, when the shark once again moved to shallower habitats (Fig. 2a) but with warmer waters (Fig. 2b). In the beginning of the track the shark experienced a progressive decrease in SST, whereas a second marked decrease occurred much faster in the end of the track and lasted for at least 3 days (Fig. 2c). During this period, the shark maintained a consistently shallow distribution (maximum depth = 8 ± 4 m) and the temperature at the 8-m isobath was significantly warmer than the temperatures at the surface (T-test; mean of the differences = 0.52ºC; t = -5.099; df = 4; p-value = 0.006), which is typical of salt-wedge estuaries (Newton, 1996). During September, the Maraú Estuary (ca. 30 km away from pop-off location) exhibits similar temperatures to those registered by the tag, and its maximum depth of 12 m (Santana, 2012) is compatible with the maximum depths reached by the shark. All these evidences indicate that the shark probably accessed this particular estuary on 26 September 2012.

This *C. leucas* traveled 3,389 km during the 75 days of the monitoring period. Although the geolocations estimated with the Kalman-filter algorithm suggested an extensive use of oceanic waters during most of the track, the Brazilian continental platform was included in nearly all the respective error ellipses (Fig. 3). The shark initially moved southwards through a minimum distance of 2,116 km away from the release location, reaching the coast of the Rio de Janeiro State (24.58ºS, 37.50ºW) after 38 days at-liberty. Then the shark traveled 1,273 km northwards until the tag detached in coastal waters off Bahia State (14.15ºS, 38.94ºW) (Fig. 3).

Although only 13 geolocations were used to classify the shark movement mode as transient or resident, this method is considered to be adequate because there is no evidence of movement rates being influenced by the amount of time elapsed (**S1** - Available only as online supplementary file accessed with the online version of the article at http://www.scielo.br/ni), which could translate into a sampling artifact rather than its actual movement rate. Three residency periods were identified, with minimum residency time varying from 5 to 17 days (Figs. 2a-b). In these periods the shark moved at a considerably lower mean rate (0.08 ± 0.04º latitude variation·day⁻¹) in comparison with transient periods (0.65 ± 0.26º latitude variation·day⁻¹). The overall mean swimming speed equaled 0.52 ± 0.31 m·s⁻¹. During transiency periods the shark moved at a mean speed of 0.77 ± 0.08 m·s⁻¹, whereas considerably slower swimming speeds were observed during residency periods (0.18 ± 0.09 m·s⁻¹).
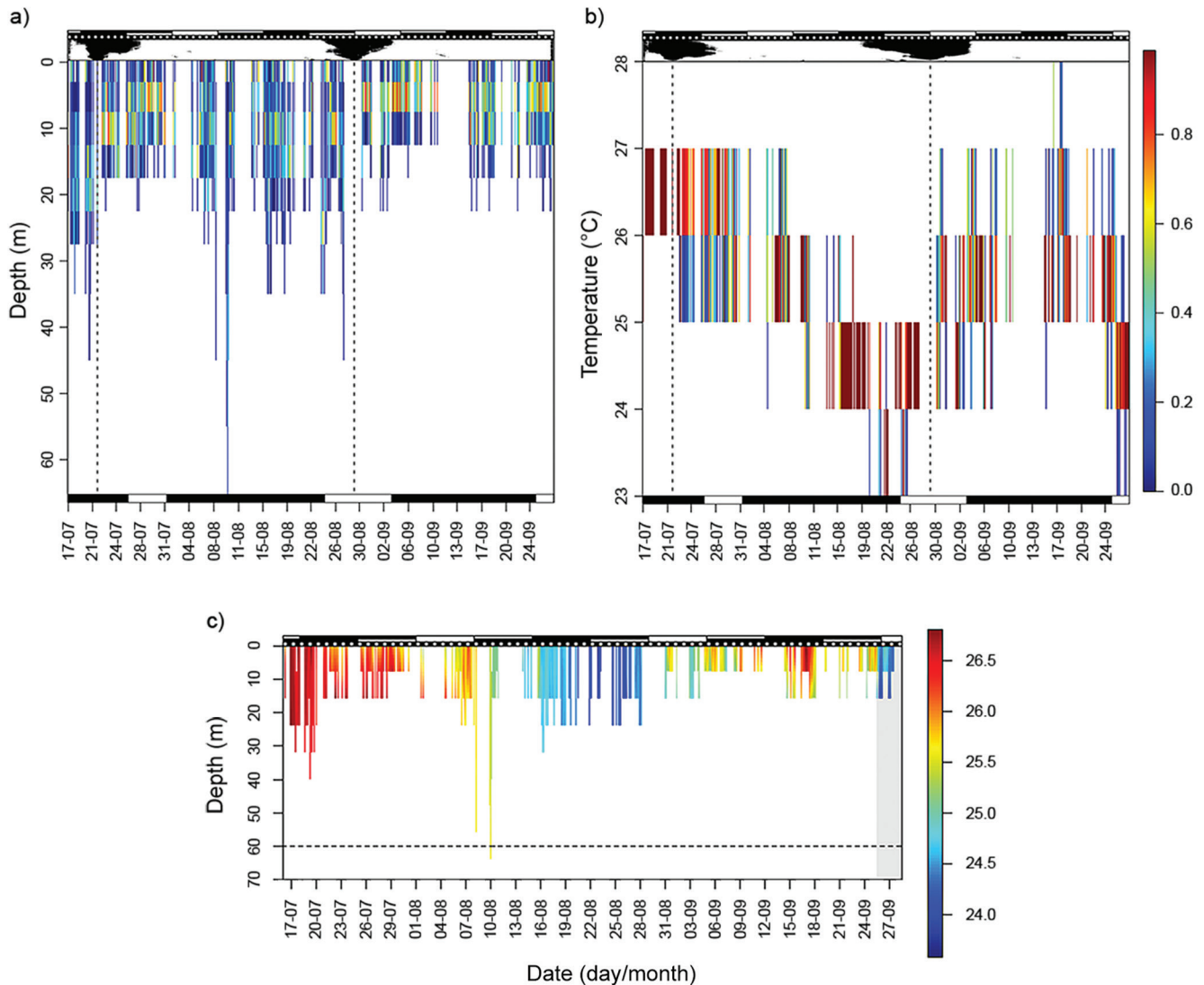
Fig. 2. Representative tracks depicting vertical usage by the *Carcharhinus leucas* during the track. The color scale in the upper panel inform the proportion of time spent at each depth/temperature stratum, whereas in the lower panel it represents the water temperature (°C). Above the plots, the first graduated horizontal bars with small divisions represents the diel cycle, *i.e.* daytime (white squares) and night time (black squares). The second graduated horizontal bar with wider divisions depicts the lunar cycle, where the all-black and allwhite rectangles depict the new and full moon phases, respectively. On the top of (a) and (b) a panel depicts the SMWGA output, and the vertical dotted lines represent statistically significant shifts in vertical behavior. Bellow (a) and (b) plots, the black and white rectangles represent transiency and residency behavior, respectively. The horizontal dashed line and shaded area in (c) represent the 60-m isobaths of the shelf break and the period when the temperatures rapidly decreased. a. depth; b. temperature; and c. temperature at depth.

The TAS model included the variables lunar phase and diel cycle (Tab. 2; **S2** - Available only as online supplementary file accessed with the online version of the article at http://www.scielo.br/ni). The shark spent a significantly lower proportion of time at depths shallower than 5 m during the new moon (Tab. 2). Regarding the diel cycle, a greater proportion of time was spent at depths < 5 m during the nighttime (Tab. 2). The MDD model included the variables SST and movement mode as the best predictors (Tab. 3; **S3** - Available only as online

supplementary file accessed with the online version of the article at http://www.scielo.br/ni). The shark tended to dive to greater depths (around the 30-m isobath) when the SST ranged from 23.5°C to 24.5°C (Fig. 4; Tab. 2, **S4** - Available only as online supplementary file accessed with the online version of the article at http://www.scielo. br/ni), corresponding to the region between the Rio de Janeiro and the Espírito Santo States (20°S-19°S). In addition, it also moved through deeper isobaths when exhibiting transient behavior (Tab. 2).
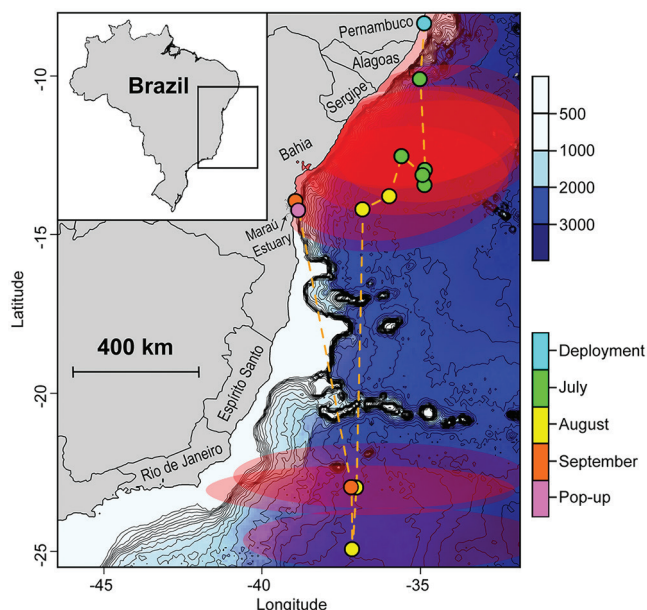
Fig. 3. UKFSST model of the *Carcharhinus leucas* movements along the Brazilian coast. The blue and pink points represent deployment and pop-up locations, respectively. The bathymetric profile and corresponding months of each geolocation are represented by the color scales. The dashed orange line represents the most probable track of the shark. The red shaded areas depict the confidence intervals of the model positions.

Tab. 2. Generalized additive model of the time spent at the sea surface. Included are the predictor variables lunar phase (LunPha) and diel cycle (Diel), the coefficient estimate (Est.), standard errors (SE), z-statistics (z) and corresponding *p*-values (p).

Model	Variable	Est.	SE	z	p
	Intercept	-0.08	0.25	-0.33	< 0.001
	(LunPha) full	0.43	0.33	1.31	0.189
LunPha + Diel	(LunPha) last	0.50	0.38	1.32	0.184
	(LunPha) new	-0.75	0.30	-2.46	0.013
	(Diel) night	0.51	0.24	2.12	0.033

Tab. 3. Generalized additive model of the maximum diving depth. Included are the predictor variables sea surface temperature (SST) and movement mode (MovMod), the coefficient estimate (Est.), standard errors (SE), z-statistics (z) of the categorical variable, effective (Edf.) and reference (Ref.df) degrees of freedom, and χ²-statistics (Chi.sq) of the continuous variable, and corresponding *p*-values (p). (*) Variable modeled with a continuous smooth function.

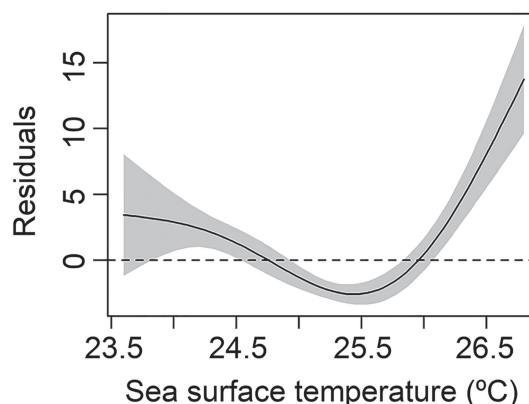| Model	Variable	Est.	SE	z	Edf.	Ref.df	Chi.sq	p
SST + MovMod	Intercept	13.07	0.71	18.32				< 0.001
	SST*				5.15	6.24	10.35	< 0.001
	(MovMod) transient	3.31	0.87	3.76				< 0.001

Fig. 4. Significant effect of the continuous variable sea surface temperature upon the maximum diving depth of the *Carcharhinus leucas* tagged, assessed with a generalized additive model (GAM). The horizontal dashed line and shaded area depict null effect and 95% confidence intervals, respectively.

Discussion

Despite the low number of sharks sampled (N = 18), this study provides important information about *C. leucas* from the western South Atlantic, where the demography of the species is uncertain and the few studies available suggest intense fishing exploitation (Karl *et al.*, 2010). Given the current Near Threatened status of *C. leucas* (Simpfendorfer, Burgess, 2009), the collection of bioecological data is essential for implementing future efficient conservation strategies in the Brazilian northeastern coast.

The low numbers of *C. leucas* caught off Recife, coupled with a substantial sampling effort (ca. 500,000 hooks) and time length (132 months) being employed in this study, all suggest that this region does not hold a sustained population of this species. Hence, the bull sharks caught during this survey probably correspond to transient individuals from subpopulations distributed more densely elsewhere in this region. However, the lack of fisheries data precludes the assessment of *C. leucas* distribution at a regional scale. Although bull sharks are caught by industrial and artisanal fisheries operating in Brazilian waters, they usually occur at considerably lower abundances in comparison with other carcharhinids, such as *C. porosus* and *C. acronotus* in the northern region (Menezes *et al.*, 2005; Rodrigues-Filho *et al.*, 2009), and *C. signatus* and *Prionace glauca* in the southern region (Amorim *et al.*, 1998; Mazzoleni, Schwingel, 1999). However, such a pattern could be related with the mostly offshore location of the longline fisheries in the southern region, consequently reducing the likelihood of capturing a bull shark. Such a combination of factors seems to be alarming for the conservation of *C. leucas* off the northeastern Brazilian coast, suggesting that management policies might be urgently needed. Considering that it is usually a non-targeted species, the prompt release of the bull sharks caught is strongly advised in this region, and further detailed studies on its demography should also be done.

Bull sharks have been implicated in hazardous shark-human interactions in South Africa (Cliff, Dudley, 1991), Australia (Dudley, 1997), Reunion Island (Lemahieu *et al.*, 2017) and Brazil (Hazin *et al.*, 2008). Although bull sharks are considerably less abundant than tiger sharks off Recife (Afonso *et al.*, 2017), six incidents were reportedly inflicted by a *C. leucas* (Hazin *et al.*, 2008) whereas only one incident was ascribed to *G. cuvier* (Gadig, Sazima, 2003). In addition, the generally large body sizes of the *C. leucas* caught in this study, together with a preferential use of shallow coastal waters including estuarine areas highlights the potential hazard that this species might pose to bathers off Recife, a densely-populated region encompassing several estuaries along its coast. The risk posed by *C. leucas* indicates that a better understanding of its spatial ecology should be achieved with such information being of utmost importance for eventual mitigation strategies of shark hazard.

The migratory patterns and drivers of *C. leucas* are yet to be thoroughly understood. Bull sharks have been reported to migrate towards warmer latitudes during the austral winter in the western Indian Ocean (Daly *et al.*, 2014), and evidence of partial migrations in *C. leucas* tagged at the Great Barrier Reef, Australia, suggests a reproductive response (*e.g.* females migrating potentially to give birth) as the main driver (Espinoza *et al.*, 2016). Although the shark tagged in this study has moved southwards during the austral winter, the temperature regime in this equatorial region might be sufficiently warm to inhibit a temperature-driven latitudinal migration. The tagged shark exhibited a clear preference for waters < 20 m in depth, similarly to conspecifics from the northern hemisphere (Carlson *et al.*, 2010). It seems thus unlikely that the shark had moved at superficial waters from the oceanic province for such a protracted period, as proposed by the location estimates of the UKFSST algorithm. Considering that *C. leucas* exhibit a clear preference for coastal habitats (Carlson *et al.*, 2010; Hammerschlag *et al.*, 2012; Heupel *et al.*, 2015; Graham *et al.*, 2016), the fact that the maximum depth registered by the transmitter (64 ± 4 m) matches the minimum depth of the continental shelf break (Martins, Coutinho, 1981) suggests that this shark moved mostly within the neritic province. Previous tracking studies on *C. leucas* across the oceanic realm reported movements through greater depths (122-164 m) and lower temperatures (16-21°C) (Carlson *et al.*, 2010; Lea *et al.*, 2015) than the shark tracked in this study, which sustain such a hypothesis. Since the error ellipses of geolocation estimates did comprise waters from the continental shelf, it is very plausible that the tagged shark remained closer to the coast than the track suggests. Notwithstanding, *C. leucas* have previously been reported to use oceanic regions (Gadig *et al.*, 2006; Bornatowsky *et al.*, 2012; Lea *et al.*, 2015), and therefore it is possible that the shark moved off the continental shelf for some time. Despite the speed of movements observed by the tracked shark during the study, previous research on *C. leucas* suggest comparable migratory and residential movement rates to individuals in other water bodies (Carlson *et al.*, 2010; Daly *et al.*, 2014; Lea *et al.*, 2015). Thus, the movement estimated, herein, was considered to be biologically plausible besides representing the most substantial movements ever reported for a male *C. leucas*.

The satellite track herein described suggest that *C. leucas* off Brazil might move through broad coastal areas, even though they tend to exhibit some level of residency in specific regions, as observed around highly productive areas from the North Atlantic (Carlson *et al.*, 2010). In accordance, the longest residency period (17 days) measured in this study occurred in a region influenced by the Cabo Frio upwelling system (Valentin *et al.*, 1985), suggesting that feeding responses might have influenced such a behavior. Besides, the shark dove to deeper isobaths of ca. 30-m while exhibiting transient behavior, similarly to that observed in an adult male *C. leucas* moving off the southeast coast of the United States (Carlson *et al.*, 2010). The use of deeper isobaths while moving off the southeastern Brazilian coast could be explained by the considerably wider shelf (90,210 km) and deeper shelf break (150-185 m) in this region (Martins, Coutinho, 1981). The continuous use of inshore habitats by *C. leucas* throughout its lifecycle increases the species' exposure to potentially harmful impacts resulting from anthropic interference, which is obviously higher in these habitats (Beatley *et al.*, 2002). Indeed, skeletal deformities observed in the caudal fins of bull sharks caught at the Brazilian northeastern region suggest a negative influence posed by anthropogenic impacts in the coastal zone (Afonso *et al.*, 2016).

The biological features of *C. leucas* herein reported generally agree with previously published studies on conspecifics from other regions, and contribute to the knowledge about this shark species in a region where little is yet known. The maturation size of the female *C. leucas* caught in this study agrees with the estimates of Cruz-Martínez *et al.* (2004), since all mature females were larger than 204 cm L_T. Although mature specimens were largely represented in *C. leucas* catch and were mostly sampled during the austral summer, which reportedly corresponds to the parturition period of the species at the Brazilian southeastern coast (Sadowsky, 1971), no pregnant females were noted and no signs of recent mating activity were detected either (Clark, Schmidt, 1965; Pratt, Carrier, 2001). Further research comprising a greater number of specimens sampled, probably adopting a different fishing strategy, is required to better understand several important aspects of *C. leucas* bioecology in the southwestern Atlantic Ocean, including reproduction, age and growth, diet and habitat use.

Acknowledgments

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