



Olive ridley inter-nesting and post-nesting movements along the Brazilian coast and Atlantic Ocean

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ABSTRACT: The states of Sergipe and Bahia comprise the main nesting beaches for olive ridley sea turtles *Lepidochelys olivacea* in Brazil. Between February 2014 and March 2015, 40 *L. olivacea* were equipped with Argos platform transmitter terminal tags. A state-space model was applied to Argos location data to investigate the animals' spatial ecology and identify areas of restricted movements (ARMs) and directional movements. The inter-nesting ARMs included the continental shelf from the south of Alagoas state to the north of Bahia, totaling 7244 km² (kernel density estimation, 90% isopleth) and generally extended up to 22 km from the coast or to the 50 m isobath. The post-nesting directional movements were classified as either (1) neritic north/northeastern (N/NE) Brazil to French Guiana (n = 4 turtles), (2) neritic south/southeastern (S/SE) Brazil (n = 16), or (3) oceanic (n = 19) from Brazil to West Africa. ARMs consistent with foraging areas were identified for 24 olive ridleys: 15 along the continental shelf of SE Brazil, 2 adjacent to Ceará and Maranhão states (between the 25 and 75 m isobaths), and 7 off the African countries of Cape Verde, Senegal, Gambia, Guinea-Bissau, and Sierra Leone. The results demonstrated the complexity of olive ridley movements from northern Brazil, raised questions about connectivity, and highlighted threats such as fisheries, ports, and hydrocarbon exploration fields overlapping with, or near to, high-use areas. These results can be used as a basis for spatial management measures to protect this endangered species.

KEY WORDS: Satellite tracking · *Lepidochelys olivacea* · Inter-nesting area · Migratory corridors · Spatial ecology

1. INTRODUCTION

Olive ridley turtles *Lepidochelys olivacea* (Eschscholtz, 1829) are the most abundant marine turtle species (Abreu-Grobois & Plotkin 2008), with widespread distribution in tropical and subtropical oceans, except for the Gulf of Mexico. Despite their wide distribution and abundance, olive ridleys are among the least studied species in terms of satellite-tracking, with a total of 25 publications, a number higher only than that for Kemp's ridley *L. kempii* (n = 18) and that

for flatback turtles *Natator depressus* (n = 4), both of which have more restricted distributions (Jeffers & Godley 2016).

Globally, olive ridleys exhibit greater plasticity of behavior and habitats than other marine turtles. Their habitats may be mainly neritic, as recorded from breeding areas located in Australia (McMahon et al. 2007, Whiting et al. 2007, Hamel et al. 2008), Oman (Rees et al. 2012), French Guiana (Plot et al. 2015, Chambault et al. 2016), and Brazil (Silva et al. 2011), or oceanic, as seen in Costa Rica (Plotkin 2010), India

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(Ram et al. 2009), and Gabon/Angola (Maxwell et al. 2011, Pikesley et al. 2013).

This species is subject to threats such as dredging (Goldberg et al. 2015), vessel collision, and high bycatch rates by coastal fisheries within breeding and foraging areas (Gopi & Pandav 2006, Silva et al. 2010, Casale et al. 2017, Guimarães et al. 2018), or during oceanic movements (Sales et al. 2008). In Brazil, the main threat to olive ridleys is bycatch and mortality associated with shrimp trawling. This fishery occurs intensely along the continental shelf and adjacent to nesting beaches (Silva et al. 2010, 2011, Guimarães et al. 2018). Along these nesting beaches, a large number of olive ridley strandings have been recorded, and efforts are underway to reduce incidental mortality (Silva et al. 2010). The main olive ridley nesting area in Brazil is located in the NE of the country, on the coast of Sergipe state and to the north of Bahia state (between 10.5° and 12.5° S). Nesting activity has also been recorded on the beaches of Espírito Santo state, in the SE region of Brazil.

The nesting season occurs primarily during the austral summer, from September to March, although occasional nesting is observed in all months of the year (Silva et al. 2007). Despite the recorded strandings, the number of nests per year for this species in Brazil shows an increasing trend. This is attributed to the conservation strategy implemented over the last 3 decades (Silva et al. 2007). The Brazilian National Action Plan for the Conservation of Sea Turtles (Santos et al. 2011) establishes the identification and protection of high-use areas for sea turtles as a conservation priority. Among the available techniques to assess the spatial-temporal distribution of animals, including high-use areas and range of migration strategies, satellite telemetry tracking has become a standard tool (Godley et al. 2008, Wilmers et al. 2015). To date, only 1 study using satellite telemetry has been performed on olive ridleys in Brazil (Silva et al. 2011). The 10 females tracked by Silva et al. (2011) from nesting beaches in Sergipe highlighted post-reproductive migration to neritic foraging areas along the Brazilian coast, as well as oceanic movements for 2 animals. That study also showed the overlap between satellite tracks and fishing areas, mainly neritic shrimp trawling and oceanic longliners, highlighting the potential of satellite telemetry to identify threats and support management strategies (Silva et al. 2011).

The objectives of the present study were to (1) identify inter-nesting area(s), post-nesting migration strategies, and foraging areas for olive ridleys from the main breeding area in Brazil; (2) improve knowl-

edge on the ecology of this species; and (3) propose alternatives for conservation in the Atlantic Ocean.

2. MATERIALS AND METHODS

2.1. Study site

The Pirambu beaches, located in the northern portion of the state of Sergipe, Brazil, can be characterized as high energy, with a narrow continental shelf, in the tropical zone, with warm temperatures and a dry summer. These beaches comprise the main reproductive site of *Lepidochelys olivacea* in Brazil, with nesting of loggerheads *Caretta caretta* and hawksbills *Eretmochelys imbricata* occurring regularly as well. Sporadic nests of green turtles *Chelonia mydas* are also recorded (Silva et al. 2007).

The importance of this area for the reproduction of sea turtles led the Brazilian government to create the Santa Isabel Biological Reserve in 1988. This protected area has the objective of maintaining the natural characteristics of coastal environments and associated biological processes in the area and covers approximately 40 km of sea turtle nesting beaches (Fig. 1).

2.2. Tag deployment

We deployed 40 platform terminal transmitters (PTTs) on olive ridley sea turtles nesting along the Pirambu beach. Two PTT models were used: SPOT-293A (n = 18) and SPLASH10-F-296A (n = 22), both manufactured by Wildlife Computers®.

Night patrols to capture olive ridleys occurred over 31 km of beaches located between 36.847° W, 10.734° S and 36.605° W, 10.582° S. The deployments occurred between 14 January 2014 and 14 January 2015. Prior to PTT attachment, individuals were measured and classified into 3 size classes based on curved carapace length (CCL): small (CCL ≤ 68 cm), medium (CCL 69–73 cm), and large (CCL ≥ 74 cm). The PTT attachment took place at the Pirambu TAMAR base. The attachment protocol consists of cleaning the second and third medial scutes of the carapace and attaching the satellite tag with Tubolit® epoxy and fiberglass. The SPLASH tags were initially protected with a Prospeed anti-fouling coat. The full attachment was then coated with anti-fouling paint (International Yacht Paint) and allowed to dry for 60 min before turtles were released. Inconel tags (National Band and Tag) were attached to the trailing edge of each front flipper following Balazs (1999).

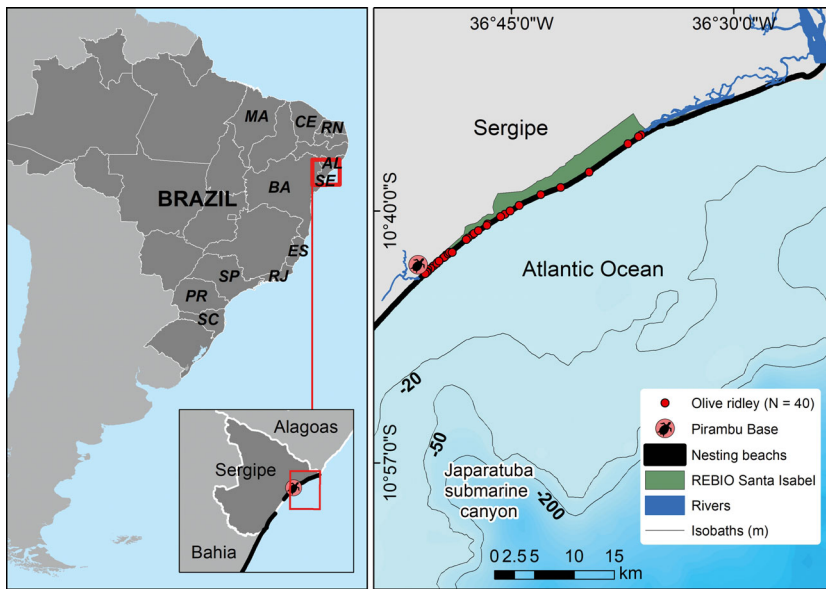


Fig. 1. Right: primary olive ridley nesting beaches in Brazil and locations of tagged sea turtles along the Pirambu beach and Santa Isabel Biological Reserve (REBIO). Left: the Brazilian coastal states of Maranhão (MA), Ceará (CE), Rio Grande do Norte (RN), Alagoas (AL), Sergipe (SE), Bahia (BA), Espírito Santos (ES), Rio de Janeiro (RJ), São Paulo (SP), Paraná (PR), Santa Catarina (SC)

The SPOT and SPLASH tags were configured for continuous collection of location data (no duty cycle). To acquire more accurate localization signals (Fastloc GPS), SPLASH tags were configured to obtain 1 GPS location per hour. All data were transmitted via the Argos system (www.argos-system.org), and the tracking information was automatically downloaded using the Satellite Tracking and Analysis Tool (STAT; Coyne & Godley 2005). The decoding of GPS locations collected by the SPLASH transmitters was accomplished using the Wildlife Computers® DAP-Processor software.

2.3. Switching state-space model (SSM)

An SSM was used to gain inference on animal behavior and smooth the satellite tracks into equal time intervals. Prior to the application of the SSM, all locations were filtered with the Douglas filter (Douglas et al. 2012) in Movebank (Wikelski & Kays 2015) to remove unrealistic Argos locations. GPS locations were treated as equivalent to Argos location class 3 for the purpose of the Douglas filter. Douglas filter parameters were selected based on criteria established by the Turtle Expert Working Group for hardshell turtles (TEWG 2009) and included filters for speed and turn angle. A best daily location was not selected, as the

subsequent SSM smoothed the tracks into even time intervals. In addition to the Douglas filter, both GPS and Argos locations were removed if they fell on land. The first 48 h of post-deployment locations were removed to account for any behavioral changes associated with tagging and release. Class Z Argos locations were also removed. Lastly, tracks were examined to determine if gaps greater than 1 wk occurred between subsequent points, in which case the 2 track segments were analyzed separately to avoid over interpolation of locations.

A modified version of the state-space switching model first introduced by Jonsen et al. (2005), and using code from Breed et al. (2009), was applied to all Argos and GPS locations. The code from Breed et al. (2009) was modified by creating additional error classes for GPS data based on circular error described by

Bryant (2007) and subsequently combining GPS and Argos locations in the SSM. The selected model was originally developed for seals but is also applicable to marine turtles (Hart et al. 2013).

The SSM was run using R (R Core Team 2015) and WinBugs (Thomas 1994). We used 6 h as the time interval to smooth the track, as a compromise between detecting meaningful changes in movement modes and model processing time. To reach convergence, 5000 burn-in iterations and 10 000 samples were used. SSM diagnostics were examined to ensure that Monte Carlo Markov chains were mixing and that model parameters were converging appropriately.

The model attempted to classify smoothed points into 2 states, an 'area-restricted movement' (ARM) mode, inferred to be either inter-nesting or foraging areas depending on timing and based on the known ecology of marine turtles (see Section 2.4), and a 'directional movement' mode, inferred to represent active migration.

The model produces 2 outputs for predicting behavioral state at each location: a mean and a mode of the total samples. Many studies use the mean values and cutoff thresholds to define one state or the other. Here we used the mode of the prediction to retain as many points as possible for analysis. In general, the turtles showed very distinctive behavioral switching, so we believe this decision to be justifiable.

2.4. Home range

Home ranges in the form of parametric utilization distributions (Worton 1989) for individuals were calculated using the R package 'adehabitat' (Calenge 2006). Home ranges were calculated for the SSM ARM locations using a kernel density estimation (KDE) method. The bandwidth, or smoothing parameter, of the KDE was calculated for each home range using the ad hoc (reference bandwidth, HREF) method (Worton 1989). Surface contours (isopleths) were created from the utilization distributions to measure core use areas, defined as the 50 % KDE, and the full home range, defined as the 90 % KDE.

Based on the available information about the ecology of the species, a distinction between the home ranges was made. The ARM locations near or associated with the reproductive beaches (deployment locations) were used to define inter-nesting area home ranges. ARM locations at the end of tracks, or between segments of migration, were defined as foraging areas. Turtles in this region enter a distinct migration phase after completion of nesting, allowing us to confidently assume that ARM prior to directional movement was in the inter-nesting area (similar to Maxwell et al. 2011), and subsequent ARM areas away from the nesting beaches were assumed to represent foraging activity.

Primary productivity and fishing effort were quantified within the inferred foraging ARM areas. Primary productivity was analyzed using a vertically generalized production model (VGPM; Behrenfeld & Falkowski 1997), and fishing effort was derived from the 'Daily fishing effort at 100th degree resolution' dataset (Kroodsmas et al. 2018). The data were downloaded for the years 2014 to 2016, which correspond to the duration of the present study. These data are available at www.science.oregonstate.edu/ocean.productivity/index.php and <https://globalfishingwatch.org>, respectively. A 3 yr average for primary productivity and the fishing effort sum was generated in the form of raster layers with a cell size of 32.210 m for VGPM and 5000 m for fishing effort that covered the entire study area.

An ANOVA was applied to identify significant variations between the mean values of productivity (VGPM) and fishing effort (fishing hours) within versus outside inferred foraging areas. The mean values of productivity and fishing effort within the combined inferred foraging areas were compared to 10 sets of randomly selected sample areas. Sample areas were generated from hexagons with a diameter of 160 km, or 17 000 km², corresponding to the aver-

age size of the foraging ARMs. The hexagons were placed in a regular grid bounded by the distribution of olive ridley tracks in the present study. Hexagons were added at random to the sample until the size of the sample area was approximately 498 584 km², the total area of the inferred foraging ARM home ranges. Heterogeneous mean groups were identified by the Tukey honestly significant difference test (Zar 1999).

2.5. Inter-nesting residence time and inferred inter-nesting interval

For the inter-nesting home range area, residence time was defined as the number of days spent in ARM mode (Barraquand & Benhamou 2008, Seidel et al. 2018). Inferred second nesting events were also evaluated following Maxwell et al. (2011). Given the low satellite coverage in equatorial areas and system limitations that prevent the transmission of all fastloc GPS data collected by the SPLASH PTTs (N = 22), secondary nesting events had to be primarily inferred from on-land or nearshore Fastloc GPS and Argos locations, taking into consideration their location classes. For 2 olive ridleys, second nesting events were confirmed by Fastloc GPS haul outs. The inferred second nesting events were compared to the known duration of the average inter-nesting interval for olive ridleys in Brazil (Matos et al. 2012).

2.6. Directional movement mode

In order to identify important migration corridors, a grid of hexagons with a 25 km diameter was overlaid with locations identified by the SSM as directional movement and inferred to represent migration. This diameter of 25 km was selected because it best captured the size of the continental shelf in the region (Dominguez et al. 2013), an important bathymetric feature for olive ridley migration. Tracks were aggregated by polygon, and points from individual tracks were weighted by track duration so that tracks with short durations biased the analysis less towards deployment locations. Hexagons with higher values are more important as migratory corridors. This analysis was performed using ArcGIS 10.3 (ESRI 2014).

3. RESULTS

Of the 40 olive ridleys, only 1 (PTT 135271) was excluded from analysis because of the premature

end of transmissions (after 13 d). Olive ridley CCLs varied from 64 to 79 cm, with a mean \pm SD of 71.5 ± 3.85 cm. The duration of the transmissions ranged from 44 to 431 d, with a mean of 165 ± 91.2 d. The average distance traveled per turtle, including ARM and directional movements, was 4577 ± 1918.3 km, with a minimum and maximum of 1286 and 8562 km.

Descriptive parameters for PTT deployments, including the capture and measurement of sea turtles, duration of transmissions, inferred inter-nesting interval, home range areas, duration in days for the different SSM modes (ARM and directional movements), and distances traveled during post-nesting migration are presented in Tables S1 to S4 in Supplement 1 at www.int-res.com/articles/suppl/n040p149_suppl/.

3.1. Inter-nesting period

Inter-nesting ARM was identified for 29 olive ridleys that stayed in the vicinity of the main nesting beaches. It was possible to infer second nesting events for 20 of those 29 turtles based on satellite locations.

For 10 olive ridleys, the post-nesting migration started immediately after attachment of PTTs and release. From the SSM it was clear when all animals

that had an inter-nesting period transitioned to directional movement at the end of nesting.

The sampled population's total inter-nesting area, estimated as the combined 90% KDE home range used by 29 turtles, comprised the north coast of Bahia, all of the continental shelf off Sergipe, and the southern coast of Alagoas. The size of the combined inter-nesting area was 7244 km². Although the inter-nesting area was relatively extensive, its core area (KDE 50%) totaled approximately 1400 km², which corresponds to 19% of the total inter-nesting home range area (Fig. 2).

The turtles' residence time in the inter-nesting area ranged from 7 to 34 d, with a mean of 20 ± 7.6 d. Inferred secondary nesting events occurred on an average of 18 ± 4.5 d (range: 9–23 d) from tagging release, with shorter durations possibly associated with a false crawl followed by a re-nesting event.

The combined inter-nesting area derived from ARM locations was adjacent to the main nesting beach for the species in Brazil, comprised depths up to 1000 m, and extended approximately 40 km from the coast, reaching the continental shelf slope. The greatest depths were associated with a submarine canyon feature, which was used by 11 of the turtles. The core area (KDE 50%) was mainly located in shallow waters, as deep as the 50 m isobath, reaching distances 22 km from the coast (Fig. S1 in Supplement 1).

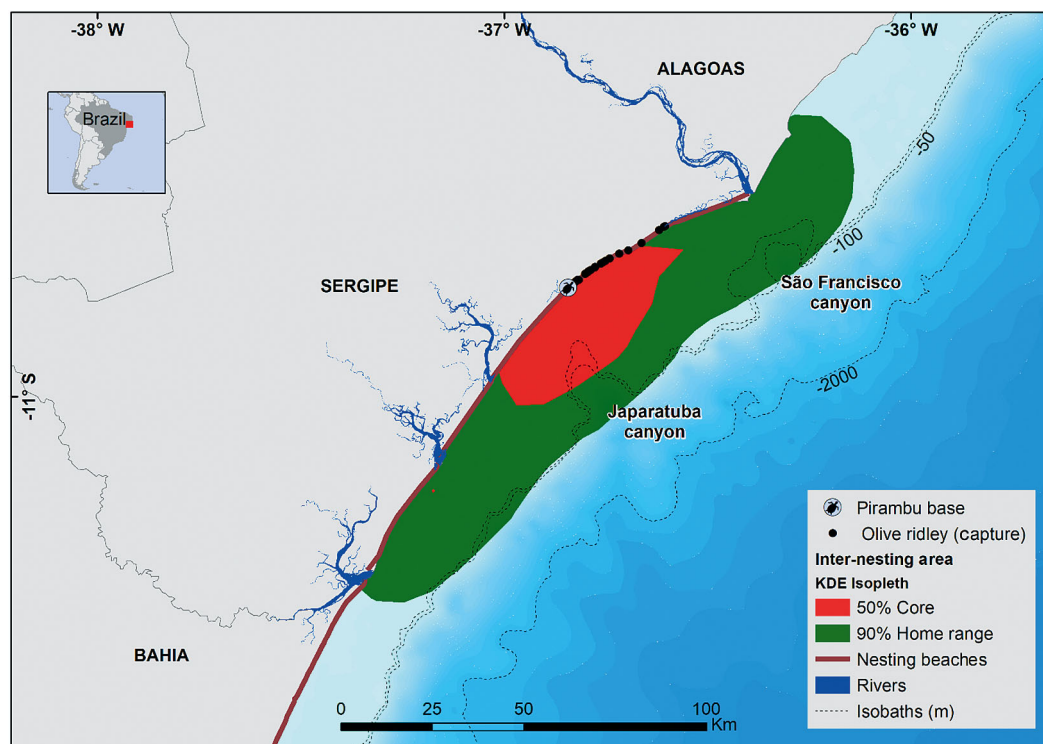


Fig. 2. Olive ridley combined kernel density estimation of the inter-nesting area used by 29 turtles and platform transmitter terminal tag deployment locations (•)

3.2. Post-nesting period

3.2.1. Directional movements

Olive ridleys from Brazil showed remarkable variation in their behavior, although classification into 2 main categories was possible: those who traveled and settled along the coast, both to the north ($n = 4$) and to the south ($n = 16$), and those with an oceanic migration strategy ($n = 19$). The oceanic migration strategy included individuals with initial coastal and subsequent oceanic movements ($n = 15$), and those that moved offshore immediately ($n = 4$).

For the 24 turtles that concluded their directional movements and began an ARM, which was inferred as foraging (coastal = 17 turtles and oceanic = 7 turtles), there was significant variation in the distance traveled and duration of the migration, which was longer for the animals with oceanic movements (Table 1).

The directional movement locations highlighted a migration corridor, which runs along the continental shelf of Brazil, totaling 3370 km length. The width of the migratory corridor was variable and was associated with the width of the continental shelf (Fig. 3).

The southern migratory corridor, defined by 16 olive ridleys' directional movements, had an average length of 2283 ± 281.69 km (range: 1507.18–2606.65 km). An average of 50 ± 7.1 d (range: 36–61 d) passed before animals completed their directional movements. Of the 16 olive ridleys with southern movements, only 1 (PTT 135248) ceased transmission before a switch to ARM.

Of the 23 post-nesting olive ridleys that moved north, 19 showed oceanic directional movements and 4 traveled along the northern coast of South America. The directional movements were concluded for 7 oceanic turtles after traveling an average of $4509 \pm$

984 km (range: 3442–6063 km) over 110 ± 24 d (range: 75–142 d), moving toward different parts of west Africa such as Cape Verde, Senegal, and Sierra Leone. The other 12 turtles ceased transmissions during directional movements with similar trajectories. Two of the 4 neritic turtles ceased directional movement off the Ceará and Maranhão state coasts in northern Brazil, after traveling 1338 and 2260 km in 33 and 51 d, respectively. The other 2 turtles ceased transmissions off the coast of Ceará, after traveling 1098 km in 30 d, and off French Guiana, after traveling 3260 km in 61 d (Fig. 3).

3.2.2. Olive ridley class sizes and post-nesting directional movements

The olive ridleys that migrated along the northern coast of Brazil had intermediate CCLs. Larger animals migrated south, and the smallest turtles traveled to oceanic waters (see the video in Supplement 2 at www.int-res.com/articles/suppl/n040p149_supp/). The relationship between CCL and migration strategy was significant (ANOVA, $F = 22.77$, $df = 36$, $p < 0.0001$) with a heterogeneous group formed by the largest olive ridleys that migrated to the south.

The distinct migration strategies also varied by the time period in which they were observed. Southward, coastal post-nesting migrations made by the largest turtles started only between the months of September and March. Turtles began migrating to coastal areas in the north and to oceanic waters throughout the year (Fig. 4).

3.2.3. Foraging ARMs

The SSM identified the transition from directional movement behavior to ARM in 24 of the 40 tagged turtles. The core sizes (50% KDE) of the coastal and oceanic inferred foraging areas did not show significant differences (Mann-Whitney U -test, median coastal: 3442.04 km², median oceanic: 3898.12 km², $p = 0.391$). However, high variability was observed among individuals (mean \pm SD: 5654 \pm 5903 km², range: 35–24 795 km²).

The combined ARM home range area identified in SE Brazil comprised almost the entire continental shelf adjacent to the states of Rio de Janeiro, São Paulo, Paraná, and the northern portion of Santa Catarina, totaling 114 527 km² (KDE 90%, $n = 15$ olive ridleys combined). The core of this area (KDE 50%) was 22 523 km² and comprised the middle portion of the

Table 1. Descriptive parameters for duration and distance traveled for the 3 olive ridley migration strategies, as well as statistical comparison using the Mann-Whitney U -test

Migratory strategy	Duration (d)				U -test $U = 0.00$
	N	Mean \pm SD	Min	Max	
Coastal	17	49 \pm 7.8	33	61	$p = 0.000006$
Oceanic	7	109 \pm 24	75	142	
	Distance (km)				U -test $U = 1.0$
	N	Mean \pm SD	Min	Max	
Coastal	17	2226 \pm 349	1338	2607	$p = 0.00015$
Oceanic	7	4509 \pm 984	3442	6063	

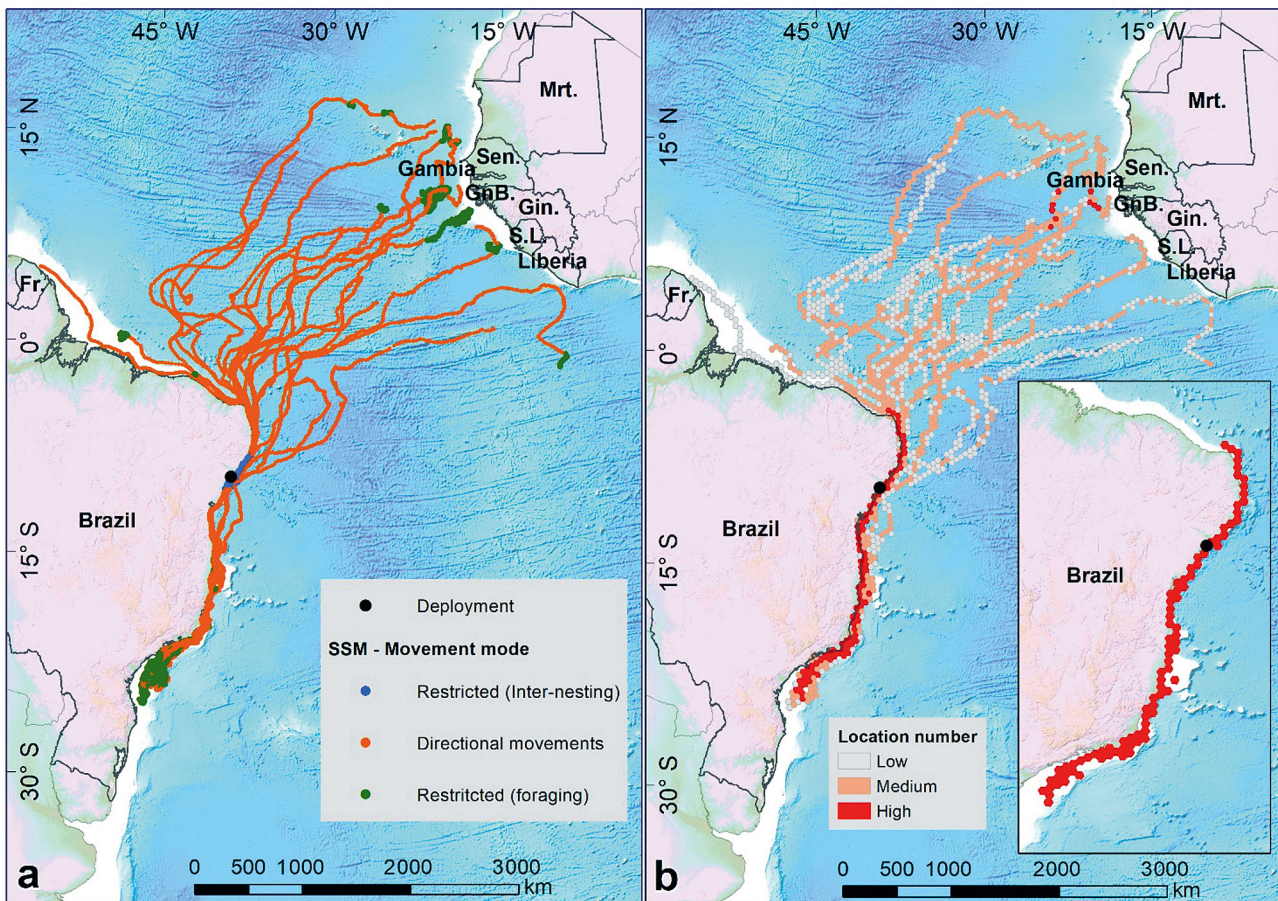


Fig. 3. Olive ridley post-reproductive displacement. (a) State-space model predicted behavior; (b) weighted point density per 25 km hexagon. Continuous high-density areas along the Brazilian continental shelf indicate a migratory corridor. Fr.: French Guiana, Mrt.: Mauritania, Sen.: Senegal, G.B.: Guinea-Bissau, Gin.: Guinea, S.L.: Sierra Leone

continental shelf off São Paulo, between the 25 and 150 m isobaths, ranging around 40 to 160 km from the coast (Fig. 5, and see Fig. S2 in Supplement 1).

The 2 neritic ARM areas identified in NE Brazil were situated off the coast of Ceará (core area 35 km²), about 35 to 40 km from the coast and between the 20 and 50 m isobaths, and off Maranhão state (core area 437 km²) about 130 to 155 km from the coast and between the 50 and 100 m isobaths (Fig. 6).

The 7 oceanic ARM areas showed a wide variation in size (core KDE range: 1370–24 794 km²) and location. One ARM was near the archipelago of Cape Verde, 5 were along the Cape Verde basin, off the coasts of Senegal, Gambia, Guinea-Bissau, Guinea, and Sierra Leone, and 1 ARM area was off Liberia and Ivory Coast. Of these olive ridleys, the area used by PTT 140731 was the largest identified in this study, located near the Sierra Leone Rise and overlapping the edge of the continental shelf of Guinea-Bissau (Fig. 7).

The southern and oceanic inferred foraging ARMs showed a partial overlap with significantly high pri-

mary productivity and fishing effort areas, when compared to the sets of randomly selected sample areas (fishing effort ANOVA, $F = 8.567$, $df = 10$, $p < 0.0001$; VGPM ANOVA, $F = 7.8186$, $df = 10$, $p < 0.0001$; see Figs. S3 & S4 in Supplement 1).

Similarly, the end point of the turtles' tracks, including the ones without ARM inferred foraging, overlapped with areas of high fishing effort. This was particularly evident within the equatorial Atlantic, along the turtles' displacements to west Africa and on the continental shelf of French Guiana (Figs. S5 & S6 in Supplement 1).

4. DISCUSSION

4.1. Inter-nesting period

Lepidochelys olivacea residence times within the inter-nesting area (mean 20 ± 7.6 d, range 7–34 d) and the inferred second nesting intervals (mean $18 \pm$

4.5 d, range 9–23 d) were similar to the inter-nesting intervals previously identified for this species in Brazil, with shorter intervals possibly associated with a false crawl followed by a re-nesting event (Matos et al. 2012).

The duration of the inter-nesting interval is also similar to observations for olive ridleys in other regions, such as Australia (12–23 d, Whiting et al. 2007; 18 and 27 d, Hamel et al. 2008), Gabon and Republic of the Congo (9–25 d, Maxwell et al. 2011), French Guiana (18–39.8 d, Plot et al. 2012), and Oman (17–30 d, Rees et al. 2012).

The core inter-nesting area, mainly out to the 50 m isobath, can be characterized as a complex ecosystem, in which the mud bottom (67 %) is permeated by sands (29 %), gravel, and reef environment. This area is the head of a submarine canyon (Neves et al. 2005, Fontes et al. 2017). During the summer, when olive ridley nesting occurs, cooler, nutrient-rich ocean water has been recorded moving on to the continental shelf through the canyon, which affects the demersal fauna in the area (Paes et al. 2007).

We posit that the concentration of olive ridleys in this area, including the submarine canyon, is associ-

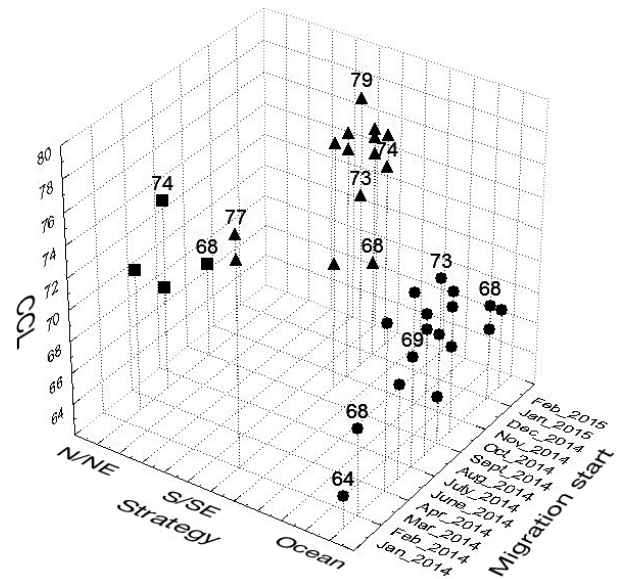


Fig. 4. Post-nesting migration strategies (square: coastal N/NE; triangle: coastal S/SE, circle: oceanic) by month when migration started, and curved carapace length (CCL, cm)

ated with the diversity of features, bottom types, and abundance of resources and refuge. This area contains potential hazards, such as a port terminal with

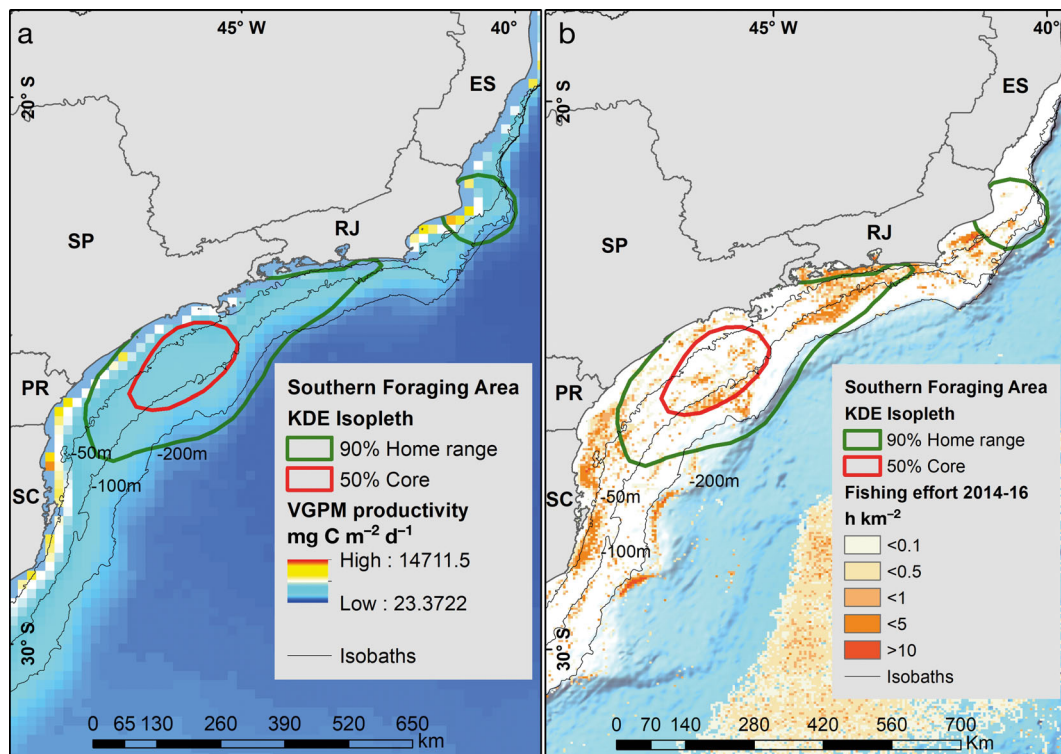


Fig. 5. Southeastern Brazil continental shelf olive ridley foraging area. The kernel density estimation (KDE) combines the state-space model (SSM) foraging behavior locations of 15 turtles that showed similar dispersal strategies. (a) Vertically generalized production model (VGPM) primary productivity mean (2014 to 2016). (b) Hours of fishing effort km^{-2} (2014 to 2016). Brazilian states: ES: Espírito Santo, RJ: Rio de Janeiro, SP: São Paulo, PR: Paraná, SC: Santa Catarina

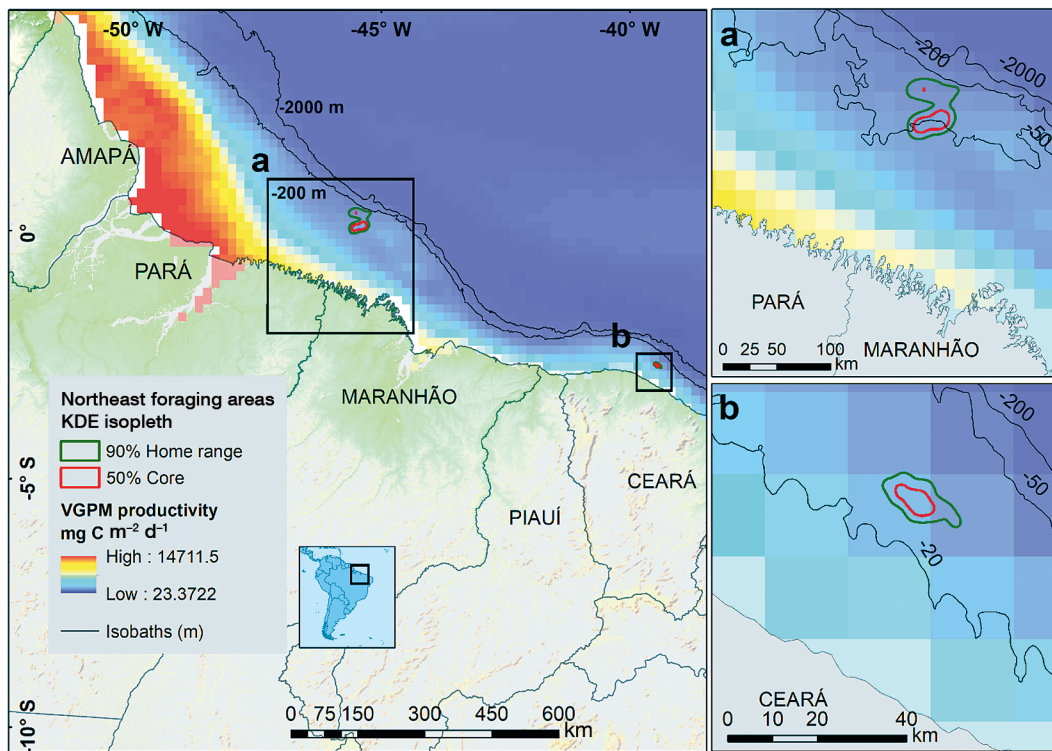


Fig. 6. Primary productivity off the coast of Brazil, with northeastern neritic foraging areas of olive ridley turtles indicated by squares: (a) off the coast of Maranhão state and (b) off Ceará state. KDE: kernel density estimation, VGPM: vertically generalized production model

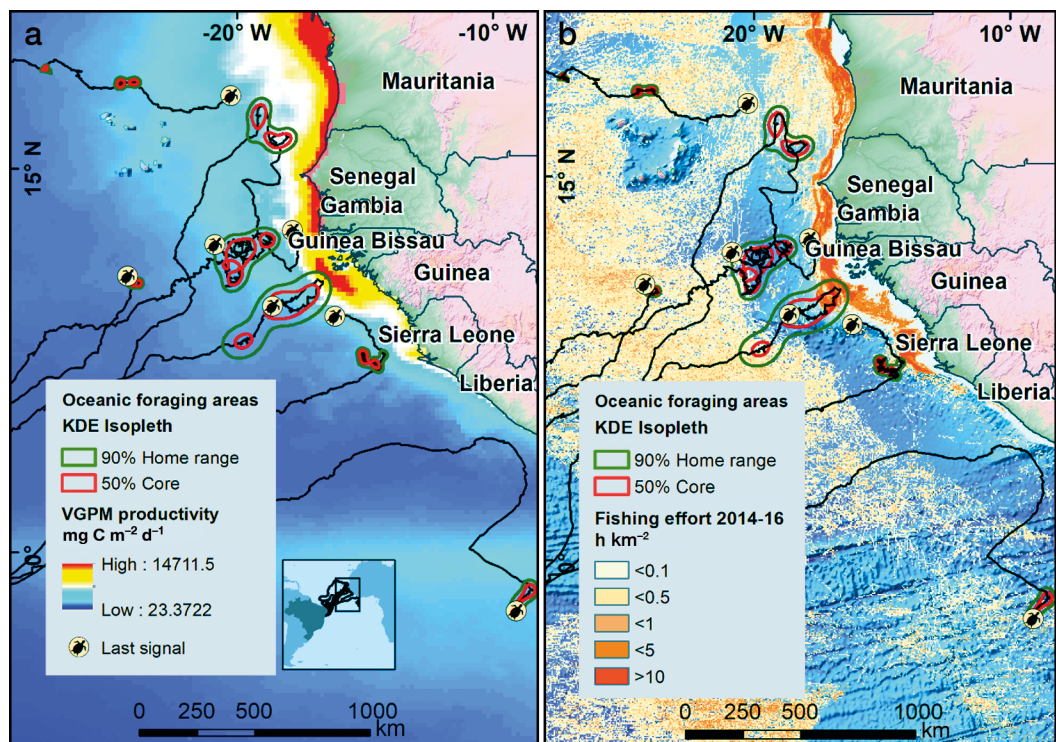


Fig. 7. Olive ridley oceanic foraging areas in west Africa and the overlap with (a) primary productivity (vertically generalized production model, VGPM) and (b) fishing effort in h km^{-2} . KDE: kernel density estimation

associated vessel traffic and dredging activities, as well as shrimp trawling, which is implicated in olive ridley strandings along the nesting beaches (Silva et al. 2011). Considering the impacts, a portion of the core area could be converted into a marine protected area, as suggested by Dawson et al. (2017) and Maxwell et al. (2011) for Gabon and the Republic of Congo. The marine protected area should have restrictions for the shrimp trawl fishery during the peak of the olive ridley nesting season (December to March), as well as for marine construction activities like drilling, pile-driving, and dredging.

4.2. Post-nesting directional movements

The results of the present study enhance the catalog of post-reproductive movements recorded by Silva et al. (2011) with new records of transoceanic migrations to West Africa and to the S/SE neritic waters of Brazil and suggest an overlap with the use area of olive ridleys nesting in French Guiana (Plot et al. 2015, Chambault et al. 2016). The movements show a remarkable overlap with areas of intense fishing effort, especially for the oceanic directional movements to west Africa, where 7 of 19 turtles stopped transmitting locations. This corroborates the concerns of Silva et al. (2011) regarding the impacts of fisheries bycatch. The region has also been characterized as a high fishing pressure area for leatherbacks (Fossette et al. 2014), including bycatch of juveniles, possibly coming from west African nesting beaches (Lopez-Mendilaharsu et al. 2019), which also supports the importance of bycatch reduction measures being implemented in this area.

The use of oceanic and coastal areas by Brazil's olive ridleys was also suggested by Petit et al. (2017), based on stable isotopes analyses, and is now confirmed by this study. The plasticity of olive ridleys' post-reproductive behaviors, when considering distinct breeding grounds around the globe, is remarkable. In the Eastern Tropical Pacific, olive ridleys display oceanic nomadic movements, without defined foraging areas (Swimmer et al. 2009, Plotkin 2010); similar patterns have been recorded in Africa, mainly along Angola's exclusive economic zone (Maxwell et al. 2011, Pikesley et al. 2013), and off India (Ram et al. 2009). In Australia, post-reproductive movements are mainly neritic, using distinct portions of the continental shelf, including the slope (McMahon et al. 2007, Whiting et al. 2007). Similar behavior has been recorded for turtles nesting in French Guiana (Plot et al. 2015, Chambault et al.

2016) and Oman (Rees et al. 2012). In Brazil, the drivers of a mixed strategy are unclear and merit further investigation. Among the available techniques, an evaluation of the movements recorded here against Lagrangian drifters or virtual particle trajectories models, is recommended (Scott et al. 2014, Hays 2017, van Sebille et al. 2018).

The olive ridley movements along the continental shelf of Brazil suggest a migratory corridor. This corridor is used by olive ridleys throughout the year after leaving or returning to the nesting beaches in Sergipe and northern Bahia, complicating conservation of this species along the several thousand-kilometer journey.

Remigration to the nesting area was partially recorded for 1 olive ridley (PTT 140732, see Fig. S2 in Supplement 1) that foraged in SE Brazil, with a total track duration close to 1 yr (337 d). The return track was similar to the post-nesting movement, which reinforces the hypothesis of a migratory corridor along the Brazilian continental shelf. The importance of Brazil's continental shelf as a migratory corridor has also been reported for loggerhead, hawksbill, and green turtles (Marcovaldi et al. 2010, 2012, Baudouin et al. 2015).

Hays & Scott (2013) proposed that for cheloniid turtles, breeding and feeding areas should be limited to distances of less than 3000 km apart based on physiological limitations. However, here we have recorded greater distances for the oceanic migrations for olive ridleys (averages of 4500 km in directional movement and 3100 km in straight line distance). Hays & Scott (2013) also stated that for leatherbacks and juvenile cheloniids, feeding during their movement limits dispersion to factors such as thermal niches or currents. Considering the distance and the duration of migrations recorded here (approximately 4500 km in 110 d), it is plausible that some foraging is occurring during oceanic movements for these olive ridleys.

Interestingly, our results showed that variation in post-nesting migration has a relationship with animal size and seasonality. The larger olive ridleys (mean CCL: 74.9 ± 2.7 cm) captured on the nesting beaches during summer migrated to neritic foraging grounds in the south and southeast of Brazil. Smaller olive ridleys (mean CCL: 68.9 ± 2.5 cm) with oceanic migration behavior were observed nesting throughout the year. An intermediate class size (mean CCL: 70.3 ± 2.7 cm) used neritic areas in the north and NE of Brazil. Similar behavioral dichotomy was also observed for loggerheads that nest in Japan (Hatase et al. 2002) and Cape Verde (Hawkes et al. 2006), with larger animals feeding in neritic areas, and smaller

animals in the open ocean. The authors proposed that the size variation may be related to dietary distinctions and nutritional characteristics of different food sources (Hawkes et al. 2006), the recruitment and settlement of the immature loggerheads (Hatase et al. 2002), and an increased probability over time for the turtle to find and re-settle in a more productive shelf area (Eder et al. 2012).

Another possible determining factor for the dichotomy of olive ridley behaviors in Brazil is the seasonality of the coastal/oceanic currents. The importance of currents for sea turtle dispersal and migratory routes was proposed by Hays et al. (2010) and Scott et al. (2014), and for early stages of sea turtle life by Putman & Mansfield (2015). Variations in the bifurcation of the South Equatorial Current (biSEC), and in the origin of the Western Boundary Brazil and North Brazil currents (Stramma & England 1999, Silveira et al. 2000, Amorim et al. 2011, Pereira et al. 2014) appear to be related to the north and south dispersion patterns recorded for loggerhead turtles in Brazil (Mansfield et al. 2017). As the biSEC generally occurs between 10° and 14° S (Rodrigues et al. 2007), olive ridley hatchlings leaving Sergipe nesting beaches are exposed to seasonally varying ocean current conditions.

4.3. Foraging ARMs

In general, the olive ridley post-nesting movements observed here ended in areas that can be characterized as high primary productivity, either due to the presence of either upwelling systems (oceanic and southeast coast of Brazil) or neritic mud bottoms (southeast Brazil). The association of olive ridley foraging areas with higher productivity zones was previously recorded for olive ridleys, either for those located on the continental shelf (Whiting et al. 2007, Plot et al. 2015, Chambault et al. 2016) or related to oceanographic fronts, eddies, and upwelling (Ram et al. 2009, Swimmer et al. 2009, Plotkin 2010, Pikesley et al. 2013). The oceanic foraging areas off west Africa showed high primary productivity values when close to the continental slope and are also used by loggerheads that nest in Cape Verde, which illustrates the importance of the area for different species and populations of sea turtles (Hawkes et al. 2006).

Many of the areas highlighted as important for olive ridley sea turtles in this study are heavily impacted by fisheries. The oceanic portions of migratory movements, as well the inferred foraging grounds in west Africa, are associated with high levels of pelagic long-lining (Sales et al. 2008, Fossette et al. 2014).

Foraging grounds in SE Brazil overlap with an industrial bottom trawl fishery that has the sixth highest rate (relative to effort) of incidental capture of sea turtles globally (Guimarães et al. 2018). If these areas remain poorly protected, it is possible that they could act as population sinks, negating positive initiatives being undertaken elsewhere in Brazil and the wider Atlantic.

5. FINAL CONSIDERATIONS

The dispersion patterns identified for *Lepidochelys olivacea* that nest in Brazil suggest that conservation actions must consider that significant variation in the ecology of a species can occur in the same nesting area, as well as at the national and international level.

Among the identified high-use areas, the SE foraging ground, as well as the inter-nesting area, may represent opportunities for the implementation or expansion of marine protected areas. The use of satellite telemetry data to confirm or reshape marine protected areas was reviewed by Hays et al. (2019), and some examples cited are Gabon (Maxwell et al. 2011, Casale et al. 2017, Dawson et al. 2017), Mexico (Méndez et al. 2013, Cuevas et al. 2018), and Indonesia (Hitipeuw et al. 2007). In Brazil, such a measure would effectively contribute to surpassing the Aichi Biodiversity Targets (Convention on Biological Diversity). Another action could be the update of the Joined Normative Instruction No. 1, of 27 May 2011, which established restrictive measures for activities such as pipeline construction, drilling, and seismic research. The act could be revised, and the protective measures extended for the new high use areas identified here and dredging activities added to its scope.

In SE Brazil, the suggested measures could benefit a set of threatened species in addition to olive ridleys, such as fish (*Epinephelus itajara*, *Lutjanus cyanopterus*, *Scarus trispinosus*), rays (*Manta birostris*, *Dasyatis centroura*), guitarfishes (*Zapteryx brevirostris*), the shark *Carcharhinus longimanus* (Luiz et al. 2008), and one of the main foraging areas in Brazil for Bryde's whale *Balaenoptera edeni* (Gonçalves 2006).

To counteract fisheries bycatch in the inter-nesting area, one possibility would be seasonal closures for shrimp trawling. The closures should include the months of December through March, which represent the peak of the olive ridley nesting season. Also, the use of turtle excluder devices should be encouraged through monitoring and training programs, and potentially made mandatory, wherever a high-use area overlaps with shrimp trawl effort.

In oceanic areas, despite the considerable complexity in implementing protection measures for the variety of fishery types and fleet nationalities, a viable alternative is the use of circular hooks, which have shown evidence of bycatch reduction, as well as reduction in the severity of the injuries caused (Sales et al. 2010), or restrictions on the use of surface longlines shallower than 100 m (Polovina et al. 2004). Another option is to create an app or website, similar to the TurtleWatch tool, that integrates bycatch data, turtle tracks, and sea surface monitoring, to inform fleets about fishing areas that must be avoided, based on sea turtle habitat characteristics (Howell et al. 2008).

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