

High-use areas, seasonal movements and dive patterns of juvenile loggerhead sea turtles in the Southwestern Atlantic Ocean

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ABSTRACT: Characterizing the behaviors of sea turtles and identifying high-use areas as they vary in time and space is important for conservation planning, particularly when turtles overlap with fisheries that may unintentionally harm them. Between July 2006 and March 2010, 27 satellite transmitters were deployed at sea on juvenile loggerheads *Caretta caretta* captured as bycatch in the Uruguayan and Brazilian pelagic longline fisheries operating in the Southwestern Atlantic Ocean. Tracking duration ranged from 3 to 639 d (mean \pm SD: 259 \pm 159 d; n = 27), during which turtles moved between latitudes of 25 to 45° S and longitudes 35 to 54° W. High-use areas for the tracked turtles were over the continental shelf and slope within the Uruguayan, Argentinian, and Brazilian exclusive economic zones and in adjacent international waters. Diving information was available for 5 turtles. The maximum dive depth recorded varied between 100 and 300 m. Two turtles demonstrated potential bottom-feeding behaviors by diving to depths that corresponded closely with the depth of the seafloor (<200 m) at their given location. The sea surface temperature encountered by tagged turtles was on average 19.8 \pm 2.3°C (range: 10.2 to 28.4°C), and turtles showed an affinity for waters supporting moderate to high primary productivity levels (0.43 \pm 0.89 mg m⁻³ chlorophyll *a*). Latitudinal movements varied by season and sea surface temperature. These findings, along with those of other studies conducted in the region, demonstrate the need to strengthen ongoing collaborative efforts between neighboring countries and other international partnerships to further the research and management of sea turtles in this area.

KEY WORDS: Satellite tracking · Juvenile · High-use areas · Seasonal variations · Pelagic longline fishery · Remote sensing

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INTRODUCTION

The loggerhead sea turtle *Caretta caretta* (Linnaeus, 1758) is distributed widely in the tropical, subtropical, and warm-temperate waters of the world's

oceans and occupies a range of habitat types (Dodd 1988). This species has a prolonged and complicated developmental life history and is listed by IUCN as endangered over its entire distribution (IUCN 2012). The study of loggerhead sea turtles is extensive, but

there are still significant gaps in our knowledge about their ecology and behavior at sea, particularly in the southern hemisphere.

The presence of loggerhead sea turtles in the Southwestern Atlantic (SWA) has been reported for close to 90 yr (Murphy 1914, Freiberg 1945) due to their occurrence in fishing gear, strandings, and nesting events. In the South Atlantic, the primary nesting beaches are located along the mainland coast of Brazil (Marcovaldi & Chaloupka 2007). The majority of the nesting occurs in the state of Bahia, followed by nesting in Espírito Santo, Rio de Janeiro, and Sergipe. From almost 3 decades of tag-recapture data, the reproductive biology and adult female movements are well defined for Brazilian loggerheads (Marcovaldi et al. 2000, 2010). Adult female *C. caretta* are known to reach southern foraging regions along the Uruguayan coast and Rio de la Plata estuary as well as over to the Azores Islands in the North Atlantic (Marcovaldi et al. 2000, Laporta & Lopez 2003). Recently, satellite telemetry has provided insight into the inter- or post- nesting migratory routes, habitat use, and high-use areas of adult female loggerheads from the state of Bahia along the northern coast of Brazil (Marcovaldi et al. 2010). While adults have been extensively studied in this region, much less is known about the ecology of juveniles in this part of the world.

The life history and behaviors of loggerhead sea turtles are considerably more complex than previously thought. The classic life-history model proposes that after swimming away from nesting beaches as hatchlings, small juveniles spend more than a decade in the oceanic environment, actively swimming as well as passively drifting (Bolten 2003). This conceptual model also presumes that immature oceanic loggerheads at a certain size undergo an ontogenetic shift and move from the oceanic to neritic habitats to maximize growth potential (Musick & Limpus 1997, Bjørndal et al. 2000). In contrast, there are numerous examples of both adult and juvenile stage loggerheads exhibiting a diversity of foraging and migratory strategies. For example, juveniles in the North Pacific forage both in the central North Pacific and in neritic habitats off the coast of the Baja California Peninsula, Mexico (Peckham et al. 2007, 2011, Howell et al. 2010). Also, those in the North Atlantic Ocean have been found to return to oceanic habitats after spending time in the coastal neritic region, which suggests that the ontogenetic shift in this region is actually facultative and reversible (McClellan & Read 2007, Mansfield et al. 2009, McClellan et al. 2010). Until now, there has been no

available data describing the movements and behaviors of juvenile loggerheads in the SWA, which has unique physical features that likely influence patterns of behavior and habitat use through the turtles' development.

The ability to answer questions regarding the behavior of marine vertebrates in the open ocean has greatly increased with the latest advancements in technology, as is evidenced by a vast array of satellite telemetry and other tools for research (Hart & Hyrenbach 2009). Satellite tags have been used to track the movements of sea turtles since the 1980s, with an exponential increase in the number of studies and turtles tagged in recent years (Godley et al. 2008). Satellite telemetry and remote sensing have assisted in identifying and characterizing some oceanic regions used by juvenile loggerheads in the North Pacific Ocean (Peckham et al. 2007, 2011, Kobayashi et al. 2008, 2011), in the Northwestern and mid-Atlantic (Bolten 2003, McClellan & Read 2007, Mansfield et al. 2009), and in the Mediterranean (Bentivegna et al. 2007, Revelles et al. 2007, Cardona et al. 2009). Oceanographic variables such as sea surface temperature (SST), chlorophyll *a* (chl *a*), meso-scale eddies and frontal regions have been found to be key variables that characterize the pelagic habitat of loggerhead sea turtles in the North and equatorial Atlantic Ocean as well as the North Pacific Ocean (Kobayashi et al. 2008, Mansfield et al. 2009).

While most satellite-tracking studies have focused on adult female turtle movement, due to the ease of satellite deployment on nesting beaches, there are a growing number of studies on the underrepresented majority of the population, specifically adult males and juveniles (Godley et al. 2008). Recent findings suggest some similarities between the major life stages: both adults and juveniles demonstrate dichotomous migratory vs. resident behavior, clearly differentiated neritic vs. oceanic habitat use, and seasonal movement patterns (reviewed by Godley et al. 2008). Foraging area use and site fidelity is a critical element of sea turtle biology that needs to be described to maximize conservation efforts (Wallace et al. 2010). Within some populations of adult female loggerheads, dichotomous foraging habitat utilization has been identified and linked to body size (Hawkes et al. 2006, Hatase et al. 2010; however, see Rees et al. 2010), with small females utilizing oceanic habitats and larger females utilizing neritic habitats (Hatase et al. 2002, 2007, Hawkes et al. 2006). The neritic vs. oceanic foraging habitat fidelity has also been identified in juvenile loggerheads. For example, Peckham et al. (2007, 2011) found movement

patterns of juvenile loggerheads that were restricted to the neritic habitat of the Baja California Peninsula, Mexico, whereas juveniles are also known to inhabit a broad swath of the oceanic Central North Pacific (Howell et al. 2008, Kobayashi et al. 2008). In the Mediterranean Sea, there may also be a duality in the foraging habitats (oceanic or neritic) preferred by juvenile loggerheads. Some satellite tracking studies of loggerheads in oceanic waters of the southwestern Mediterranean have found that juveniles infrequently approach the eastern coast of mainland Spain (Cardona et al. 2005, Revelles et al. 2007), whereas other studies have revealed that some juveniles avoid the oceanic realm and instead make extensive use of the neritic habitat (Cardona et al. 2009). Peckham et al. (2011) compared 2 foraging strategies in juvenile loggerheads in the Pacific using a demographic model and hypothesized that the neritic strategy offers the potential for faster growth and ultimately higher fecundity, whereas the oceanic strategy may be a slower but safer life-history strategy. The mechanisms that produce and uphold this diversity in movement patterns of both adults and juveniles are presently unknown (Hatase et al. 2010) yet may be guided by various ecological trade-offs.

Using a variety of research methods, such as aerial and shipboard surveys, flipper tag returns, and satellite-telemetry, seasonal movement patterns have been described for both adult and juvenile loggerhead turtles in the North Atlantic (Plotkin & Spotila 2002, Dodd & Byles 2003, Hopkins-Murphy et al. 2003, Hawkes et al. 2006, 2007, Mansfield et al. 2009), for subadult loggerhead turtles in the North Pacific (Polovina et al. 2004, 2006), and for adults in the Mediterranean (e.g. Bentivegna 2002). Thermal conditions are likely cues for seasonal movement, along with other environmental features (e.g. primary productivity and prey availability) (Godley et al. 2008).

Understanding the relationship between sea turtle movements and habitat is important for the conservation of these endangered species as efforts are underway for dynamic management of species in response to ecosystem variables. Multiple studies have implicated pelagic longline fisheries as an important threat to immature loggerhead sea turtle populations in various regions of the world (Lewison & Crowder 2007, Howell et al. 2008, Pons et al. 2010, Alfaro-Shigueto et al. 2011). Impacts to this age class is of particular conservation concern given that population models for loggerhead turtles indicate that the survival rate of large juvenile loggerheads has a large effect on the population growth rate of the species (Crouse et al. 1987, Heppell 1998, Heppell et al. 2005).

The Brazilian and Uruguayan pelagic longline fisheries operate in an extended portion of the SWA, and their principal target species are swordfish *Xiphias gladius*, tunas *Thunnus obesus*, *T. alalunga*, and *T. albacares*, and blue shark *Prionace glauca* (Mora & Domingo 2006). These fisheries also have high sea turtle bycatch rates, principally of immature loggerhead turtles with a mean curved carapace length (CCL) of 58.9 cm (range: 32 to 109 cm) (Giffoni et al. 2008, Sales et al. 2010).

In order to effectively reduce the impact of fisheries bycatch, we need to improve our understanding of how turtles utilize their dynamic marine habitats (Godley et al. 2008), specifically by providing an oceanographic characterization of the distribution patterns of juvenile loggerhead turtles during different seasons, when temperatures and water conditions vary. The aims of the present study were to characterize the broad scale behavioral patterns, inter-seasonal variability, and general high-use areas for immature loggerhead turtles in the SWA by using satellite telemetry of turtle movements and remotely sensed oceanographic data.

MATERIALS AND METHODS

Turtle, transmitter, and satellite data

Onboard scientific observers of PNOFA-DINARA (the National Program of Scientific Observers Onboard the Tuna Fleet) (Mora & Domingo 2006) and Projeto TAMAR-ICMBio (the national Brazilian sea turtle conservation program) (Marcovaldi & Marcovaldi 1999) deployed a total of 27 satellite transmitters on loggerhead sea turtles incidentally captured in Brazilian and Uruguayan pelagic longline fisheries operating in the SWA between July 2006 and November 2009. For a characterization of the Brazilian and Uruguayan longline fisheries, see Sales et al. (2008), Jimenez et al. (2009), Pons et al. (2010). Baits most often used are squid *Illex argentinus* and different species of mackerel (mainly *Scomber* spp. but also *Trachurus* spp.) (Mora & Domingo et al. 2006, Sales et al. 2008).

The protocol was to bring captured sea turtles on to the vessel for measurements and attachment of a transmitter. The CCL of turtles was measured following Bolten (1999). Turtles were evaluated pre-release, and the body condition was noted. Sex was not determined as it was not externally evident due to the small size of the turtles. To prepare turtles for satellite tag attachment, the second central carapa-

cial scute mount region was cleaned of epibiota, wiped down with ethanol, lightly sanded, and allowed to air dry. Satellite tags were adhered to the turtles using quick drying 2-part epoxies, Poxipol™ (Uruguay) and Durepoxi™ (Brazil), and allowed to dry for 30 min to 1 h on deck before release of the turtle. ARGOS-linked Telonics platform transmitter terminals (PTTs), models ST-18 and ST-20, were attached to 5 and 6 turtles, respectively, on Brazilian vessels. ARGOS-linked Wildlife Computers PTTs, models SPLASH and SPOT 5, were attached to 6 and 10 turtles, respectively, on Uruguayan vessels. Transmitters had 3 different duty cycles: (1) no duty cycle, continuous transmissions with daily transmit allowance set to 300 transmissions d^{-1} , (2) 24 h on, 24 h off, with the daily transmit allowance set to 250 transmissions d^{-1} , and (3) 12 h on, 2.5 d off with the daily transmit allowance set to 200 transmissions d^{-1} . Differences in duty cycle were accommodated in the analysis by daily interpolation of location fixes (described below).

Horizontal movements

ARGOS assigns location accuracy estimates (location class [LC]) to each reported location that are classified as 1–3, 0, A, B, or Z, where locations with LC between 1 and 3 have estimated associated errors of <1500 m of the tag's actual position (CLS 2007, Witt et al. 2010). Tracking (transmitted locations up to 24 March 2010) and remote sensing data were downloaded and filtered using the Satellite Tracking and Analysis Tool (STAT) (Coyne & Godley 2005) program available from <http://seaturtle.org>. For the present study, we included the first location received during a 24 h period in order to reduce spatial autocorrelation (De Solla et al. 1999, James et al. 2005, Mansfield et al. 2009). We chose to include only LC classes 1 to 3 in the analysis, and to reduce potential inaccurate locations, we excluded points that were indicative of transit speeds $>5 \text{ km h}^{-1}$ (following standard filtering techniques, e.g. Luschi et al. 1998, James et al. 2005, Hawkes et al. 2007, Mansfield et al. 2009). Filtering removed 1.14 % of the locations.

We excluded the first 10 d (3% of the total points) of tracking data from each turtle to avoid including immediate potential post-release behavior that may have been affected by the capture event. This resulted in a total of 26 turtles utilized in the present study (for summary information, refer to Table 1), as Turtle 79832 transmitted for only 3 d. We do not draw conclusions in relation to the nature of transmission

cessation or the effects of injury on tracked individuals in the present study. Of the total LC filtered positions for the remaining 26 turtles ($n = 3435$ good quality locations), net displacements between consecutive daily locations for each individual turtle were calculated using Hawth's Geospatial Analysis tools (www.spatialecology.com/htools) summing over the entire track length to obtain the minimum distance traveled by each turtle. We divided the distance between 2 observed locations separated by >24 h by the number of missing days (James et al. 2005, Mansfield et al. 2009). Average travel rate (km h^{-1}) for individual turtles were calculated using the ratio of net displacement between each consecutive location and the time elapsed between each location.

Seasons and bathymetric domains were defined as follows: summer (January to March), autumn (April to June), winter (July to September), spring (October to December), continental shelf (0 to 200 m), continental shelf break (>200 to 1000 m), slope (>1000 to 3000 m), and oceanic (>3000 m). Bathymetry data (1' latitude/longitude resolution) were obtained from the General Bathymetric Chart of the Oceans (GEBCO, British Oceanographic Data Centre, www.bodc.ac.uk). World exclusive economic zone (EEZ) boundaries were acquired from Flanders Marine Institute's Maritime Boundaries Geodatabase v.6.1 (VLIZ 2012). Weekly averaged SST and surface chl *a* data were obtained from STAT and used to obtain SST and chl *a* values for each daily turtle location to characterize turtle and habitat associations. In STAT, SST data were derived from a weekly average of Advanced Very High Resolution Radiometer (AVHRR) sensors onboard NOAA satellites, and average weekly surface chl *a* was estimated from MODIS satellite sensors at 4 km resolution (Coyne & Godley 2005).

Vertical movements

Maximum dive-depth histograms (described as the number of dives whose maximum depth was within the specified depth ranges or 'bins' for each 6 h period) were collected by each of the 5 functioning SPLASH satellite tags (see Table 1) and relayed through the ARGOS system. Turtles with tag numbers 79830, 79831, and 79835 were programmed with depth ranges distributed as follows: 0, 10, 20, 50, 100, 150, 200, 300, 400, 500, 600, 700, 800, and >800 m. Turtles with tag numbers 79833 and 79834 were programmed as follows: 0, 10, 15, 25, 35, 45, 55,

70, 100, 150, 200, 300, 400, and >400 m. To compare dive depth data among all diving turtles, we consolidated depth bins that ranged between 10 and 100 m. Dive data were collected for every 6 h period throughout the day, starting at midnight GMT time. For the 5 turtles equipped with SPLASH tags, a total of 1798 dive depth histograms (6 h bins) were reported during the tracking duration.

High-use areas

To examine habitat use, the number of filtered daily locations was tallied within hexagonal area bins. In the present study and similar to grids used by James et al. (2005) and Mansfield et al. (2009), hexagonal area bins were chosen over square bins to more accurately capture the orthogonality of movement paths between adjacent cells. The diagonal and edge length of each hexagonal cell were 64.3 km and 32.2 km, respectively, and each hexagonal cell had an area of 2686 km² (which is greater than the estimated location error associated with the least precise position estimate; LC 1: 350 to 1000 m error) (CLS 2007, Mansfield et al. 2009). Each 1° of latitude in the study region was represented by ~1.5 hexagons (~90 km). For defining high-use areas, we created 50 and 75 % utilization distribution (UD) contours of turtle tracking days using the Spatial Analyst extension of ArcGIS (ESRI), using a smoothing factor of 120 km and a grid size of 10 km.

Independently of the high-use area analysis, we also simply classified turtles in regard to their distributions within bathymetric zones using a threshold of ≥75 % of each turtle's daily locations as being contained within either the neritic/shelf-break region (0 to 1000 m), the slope region (>1000 to 3000 m), the oceanic region (>3000 m), or in mixed regions (turtles having < 75 % of locations in any 1 region).

Statistical analyses

All track analyses were carried out in ArcMap 9.2 (ESRI) in a projected Universal Transverse Mercator 22S coordinate system to avoid distortion associated with geographic coordinate systems. All statistical analyses were conducted in the program R v.2.9.2 (R Development Core Team 2009). We used 1-way analysis of variance (ANOVA) with a post-hoc Tukey test to test for seasonal differences in oceanographic conditions experienced by tracked turtles. Additionally, as travel rate data did not meet the assumption

of normality, we used the Kruskal-Wallis test (Zar 1996) with a post-hoc Wilcoxon rank sum test to evaluate differences in median speed among seasonal groups as well as bathymetric zone turtle classification groupings. As the strength of inference on the importance of turtle size (CCL) for turtle behavior or habitat use was low due to small sample size and unequal size distribution of tracked turtles (see Table 1), we did not include CCL in statistical analyses. The statistical significance level for all analyses was set to $\alpha = 0.05$. All descriptive statistics are presented as mean \pm SD.

RESULTS

Turtles

The overall CCL was 61.8 ± 6.9 cm (range: 49 to 83 cm, $n = 27$, Table 1). All turtles were captured and released within Uruguayan or Brazilian EEZ over the continental shelf or slope ($n = 24$; approximately along 53° W, in waters >200 m in depth) or in international waters ($n = 3$) (Table 1, Fig. 1).

General movements

The overall mean turtle tracking duration for the study period was 259 ± 159 d (range: 3 to 639 d, $n = 27$), and the minimum distance from release location for all turtles transmitting >10 d was 6050 ± 3630 km (range: 153 to 14 665 km, $n = 26$) (Table 1). During the entire monitoring period, 5 turtles were tracked for >1 yr, 20 were tracked for 100 to 365 d, and 2 turtles were monitored for <100 d before their transmissions ceased in March 2010. All turtle movements were contained within a relatively small region of the SWA, including part of the Uruguayan, Brazilian, and Argentinean EEZs and adjacent international waters. The movements spanned a minimum convex polygon area of 2 244 685 km² (Fig. 1). Horizontal tracks were distributed between 25 and 45° S latitude and between 35 and 54° W longitude (Fig. 1). Of the turtles tracked, Turtle 79820 traveled the farthest north, reaching 25° 49' S, 40° 30' W in December 2008. Turtle 79821 traveled the farthest south, reaching 45° 40' S and 50° 58' W in October 2008. Two turtles (12096 and 79830) were classified as predominantly within the neritic/shelf-break region (>75 % of their movements), and both spent >50 % of their time within the 200 m isobath (Turtle 12096: 86 %, Turtle 79830: 56 %). The remaining turtles were classified

Table 1. Summary table with information from 27 satellite tracked immature loggerhead turtles in the SW Atlantic Ocean between 2006 and 2010. Turtle 79832, indicated with an asterisk (*), transmitted for <10 d and was excluded from all subsequent analysis. Dates given as mm/dd/yy. CCL: curved carapace length, Year: year of turtle release, BR: Brazil, UY: Uruguay, IW: international waters, ST: still transmitting as of 24 March 2010, NA: not available

Year	PTT	Type of tag	CCL (cm)	Deploy date	Release location	End date	Last location	Track classification	Tracking duration (d)	Minimum distance traveled (km)	Average daily rate of travel (km h ⁻¹)
2006	12499	ST-20	62	07/01/06	BR	01/27/08	IW	Oceanic	575	14664.72	1.29
	12580	ST-20	63	07/06/06	BR	01/29/07	IW	Oceanic	207	5164.07	1.23
2007	12415	ST-20	62	04/24/07	BR	03/16/08	BR	Mixed	327	6357.38	0.94
	12690	ST-20	61	04/29/07	BR	03/07/08	IW	Mixed	313	5062.91	0.85
	12682	ST-20	63	05/31/07	BR	05/18/09	BR	Oceanic	639	10013.04	0.92
	12826	ST-20	83	06/05/07	BR	11/15/07	BR	Mixed	163	3248.54	1.11
	12258	ST-18	59	06/26/07	IW	07/25/07	IW	Oceanic	29	153.47	0.46
	12376	ST-18	51.5	06/29/07	IW	10/12/08	IW	Oceanic	471	7454.06	0.77
	12372	ST-18	73.5	09/16/07	BR	06/07/08	BR	Mixed	265	5602.97	0.93
2008	12284	ST-18	72	06/27/08	BR	12/13/08	BR	Oceanic	169	3569.42	1.15
	12096	ST-18	69	08/18/08	IW	05/18/09	BR	Neritic	273	3979.12	0.58
	79820	SPOT 5	60	04/02/08	UY	01/29/09	UY	Mixed	305	7406.56	0.89
	79821	SPOT 5	56	04/03/08	UY	03/20/09	IW	Oceanic	351	13202.68	1.59
	79822	SPOT 5	63	04/02/08	UY	06/02/09	IW	Oceanic	426	11444.75	1.11
	79823	SPOT 5	60	05/26/08	UY	11/01/09	BR	Mixed	524	11063.76	0.95
	79830	SPLASH	68	04/02/08	UY	09/20/08	BR	Neritic	174	3889.40	0.90
	79831	SPLASH	56	04/05/08	UY	11/06/08	IW	Mixed	215	9832.29	1.89
	79832*	SPLASH	49	05/26/08	UY	05/28/08	UY	NA	3	81.97	2.17
	79833	SPLASH	64	05/26/08	UY	11/03/08	IW	Oceanic	161	3006.35	0.77
	79834	SPLASH	64	05/26/08	UY	10/18/08	IW	Oceanic	145	4096.76	1.21
79835	SPLASH	63	03/30/08	UY	10/08/08	BR	Mixed	192	5026.93	1.13	
2009	95591	SPOT 5	57	11/11/09	UY	ST	IW	Oceanic	136	3648.10	1.08
	95592	SPOT 5	58	11/11/09	UY	ST	BR	Mixed	135	3955.60	1.33
	95593	SPOT 5	59	11/11/09	UY	ST	IW	Oceanic	135	4080.60	1.32
	95594	SPOT 5	55	08/26/09	UY	ST	IW	Oceanic	212	6928.19	1.34
	95595	SPOT 5	58	08/26/09	UY	03/10/09	BR	Mixed	196	3981.23	0.84
	95596	SPOT 5	62	08/25/09	UY	03/16/10	UY	Mixed	202	6423.73	2.98

as either primarily oceanic ($n = 13$) or within the mixed group ($n = 11$). No turtles were classified into the slope group.

The mean rate of travel for all successfully tracked turtles was 1.13 ± 0.86 km h⁻¹ ($n = 26$ turtles) and 1.04 ± 0.78 km h⁻¹ ($n = 24$ turtles) when the 2 fastest turtles were excluded. Turtles 79831 and 95596 had considerably higher mean rates of travel than the other tracked turtles (1.83 ± 0.94 and 1.75 ± 1.07 km h⁻¹, respectively). Approximately 55% of the recorded daily rates of travel were between 0 and 1.5 km h⁻¹. Mean rate of travel varied among turtles (Kruskal-Wallis, $\chi^2 = 462.04$, $df = 25$, $p < 0.0001$), and there were significant rate of travel differences among the bathymetric zone classification groups (Kruskal-Wallis, $\chi^2 = 61.08$, $df = 2$, $p < 0.0001$), specifically, between neritic/shelf-break vs. oceanic ($p < 0.001$) and neritic/shelf-break vs. mixed group ($p < 0.0001$). The rate of travel of neritic/shelf-break tur-

tles was significantly slower (0.77 ± 0.63 km h⁻¹) than turtles in the other 2 categories (mixed group: 1.17 ± 0.87 km h⁻¹, oceanic group: 1.12 ± 0.85 km h⁻¹). No significant differences in travel rates were found between the oceanic vs. mixed group turtles ($p = 0.63$).

High-use areas

Hexagonal binning of tracking data (Fig. 2) and kernel utilization distributions (50 and 75%) (Fig. 3) indicated that the areas of highest use for the 26 tracked turtles were mainly concentrated over the continental shelf and slope within the northern portion of the Argentinean, Uruguayan, and southern portion of the Brazilian EEZs and in oceanic international waters between the Rio Grande Rise and the continental slope off of Brazil. Over the continental

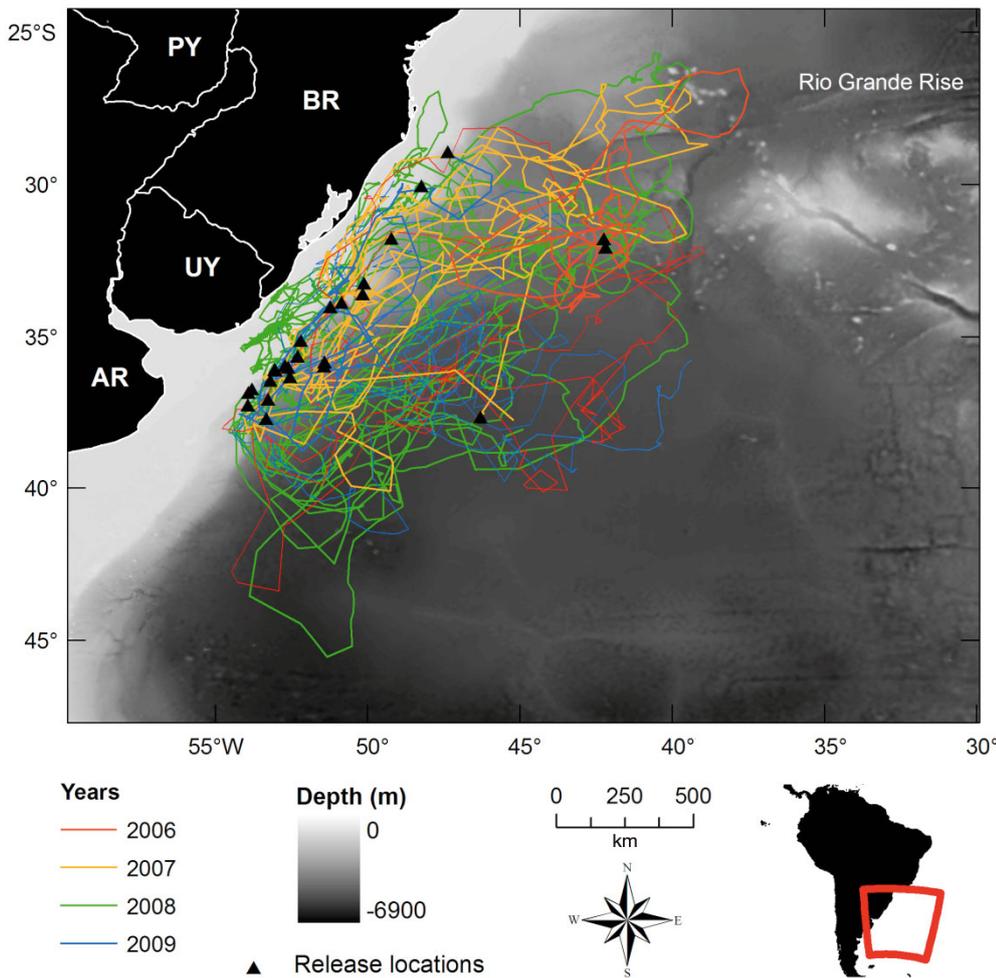


Fig. 1. Movement paths of 26 immature loggerheads in the SW Atlantic Ocean between 2006 and 2010. Release locations for each turtle indicated by black triangles. Minimum convex polygon indicates the total area (~2 250 000 km²) utilized by all tracked turtles. PY: Paraguay, BR: Brazil, UY: Uruguay, AR: Argentina

shelf in northern Uruguayan and southern Brazilian EEZ, 5 individual hexagonal bins contained between 25 and 36 turtle days, which reflect the cumulative use of 4 and 5 turtles each, ~15 % of all studied turtles (Fig. 2).

Diving behavior

On average, for the 5 SPLASH tagged turtles, 15 % percent of dives were to depths less than 10 m, 84 % of dives were between 10 and 100 m, and 1 % of dives were to depths greater than 100 m. Maximum dive depth ranges for each of the 5 turtles that collected dive data are reported in Table 2. Percentages of dives reaching each depth bin did not vary noticeably by season. The maximum dive depth range was achieved by Turtles 79830 and 79835, which reached the 200 to 300 m bin in 2008. The neritic/shelf-break turtle, Turtle 79830, had dives that reached the 200 to

300 m bin in regions where, according to bathymetric data, the water column was <200 m deep (Table 2). This indicates that this turtle may have been foraging close or at the seafloor in ~200 m of water, but the discrepancy between the depth reached in dives and the bathymetry suggests a possible measurement error in either the turtle’s exact location and/or bathymetric data. For the turtles classified into the mixed group (Turtles 79831 and 79835), maximum dive-depth bins reached in the 3 different bathymetric regions was 200 to 300 m. Both oceanic turtles dove to depths greater than 70 m in the water column; Turtle 79833 reached a maximum depth bin range of 100 to 150 m.

Seasonality

The quarterly latitude frequency plot (Fig. 4) illustrates seasonal variations in north to south turtle

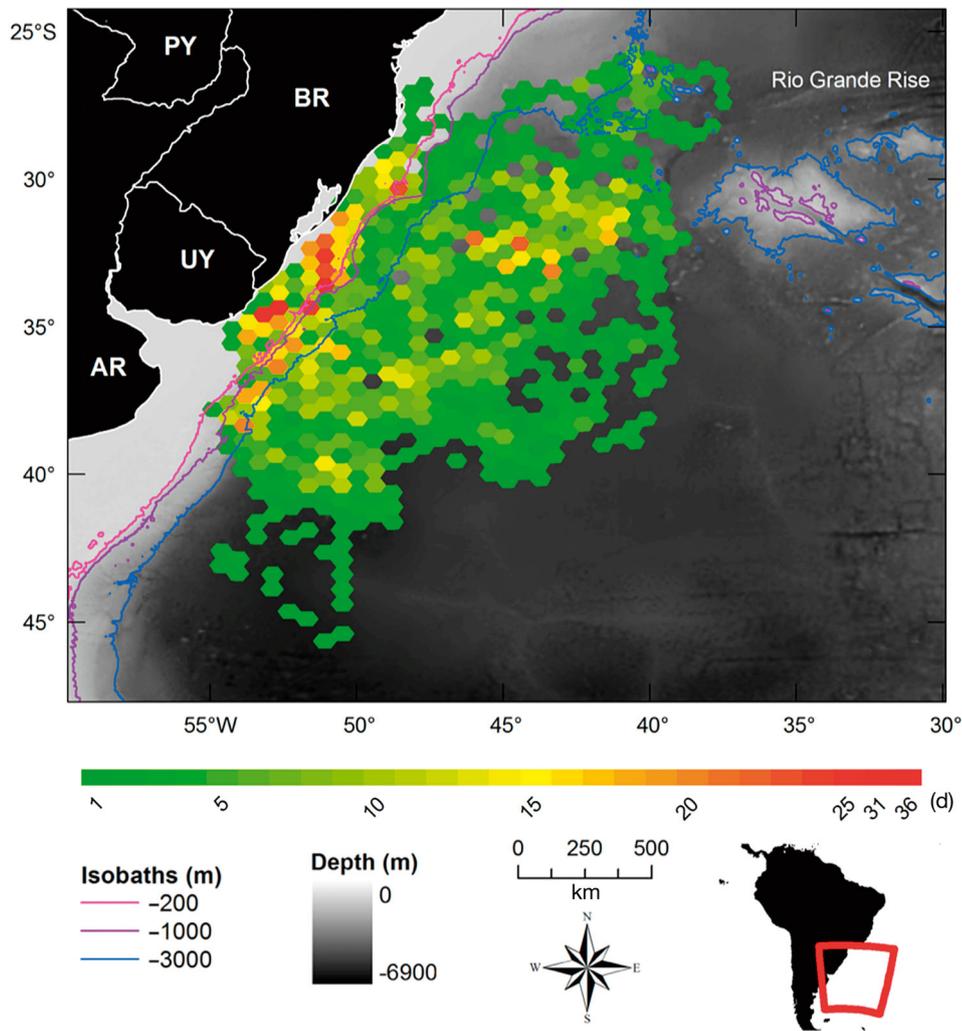


Fig. 2. Spatial use of 26 immature loggerheads tracked in the SW Atlantic between 2006 and 2010. Color denotes the number of days a turtle spent within each hexagonal bin with 200, 1000, and 3000 m isobaths

movement in the SWA study region. There were significant differences in mean latitude between seasons (ANOVA, $F_{3,58} = 7.45$, $p = 0.0013$), and a post-hoc Tukey test showed that the mean latitude was significantly different between summer and winter, summer and spring, and spring and winter ($p < 0.0001$). During winter, turtles were distributed between 26 and 41° S, and they spent a high percentage of their time between 31 and 32° S ($32.4 \pm 3.1^\circ$ S) (Fig. 4). During autumn, turtle movements ranged between 27 and 42° S, occurring 55% of the time in latitudes between 34 and 38° S ($34.7 \pm 3.1^\circ$ S). In the spring, turtles moved between 26 and 46° S, where >75% of all locations were between 31 and 37° S ($33.2 \pm 3.36^\circ$ S), and in summer, turtles moved between 30 and slightly more than 44° S, spending ~64% of their time between latitudes of 35 and 39° S ($36.1 \pm 2.6^\circ$ S).

There were also differences in mean speed by season (Kruskal-Wallis, $\chi^2 = 122.14$, $df = 3$, $p < 0.0001$), and pairwise comparisons indicated that summer rates of travel ($1.3 \pm 0.99 \text{ km h}^{-1}$) were not significantly different than those in autumn ($1.2 \pm 0.77 \text{ km h}^{-1}$) ($p = 0.97$) but were significantly faster than those in winter ($0.9 \pm 0.72 \text{ km h}^{-1}$) ($p = 0.021$) and those in spring ($1.16 \pm 0.88 \text{ km h}^{-1}$) ($p = 0.021$). Autumn rates of travel were significantly faster than those in winter ($p < 0.0001$) and those in spring ($p = 0.024$). Winter rates of travel were significantly slower than those in spring ($p < 0.0001$).

The turtles' movements in relation to SST were also observed to vary between different seasons of the study years. The overall mean SST encountered by the tracked turtles was $20 \pm 2.3^\circ\text{C}$ (range: 10.2 to 28.4°C). More than 98% of the turtle tracks

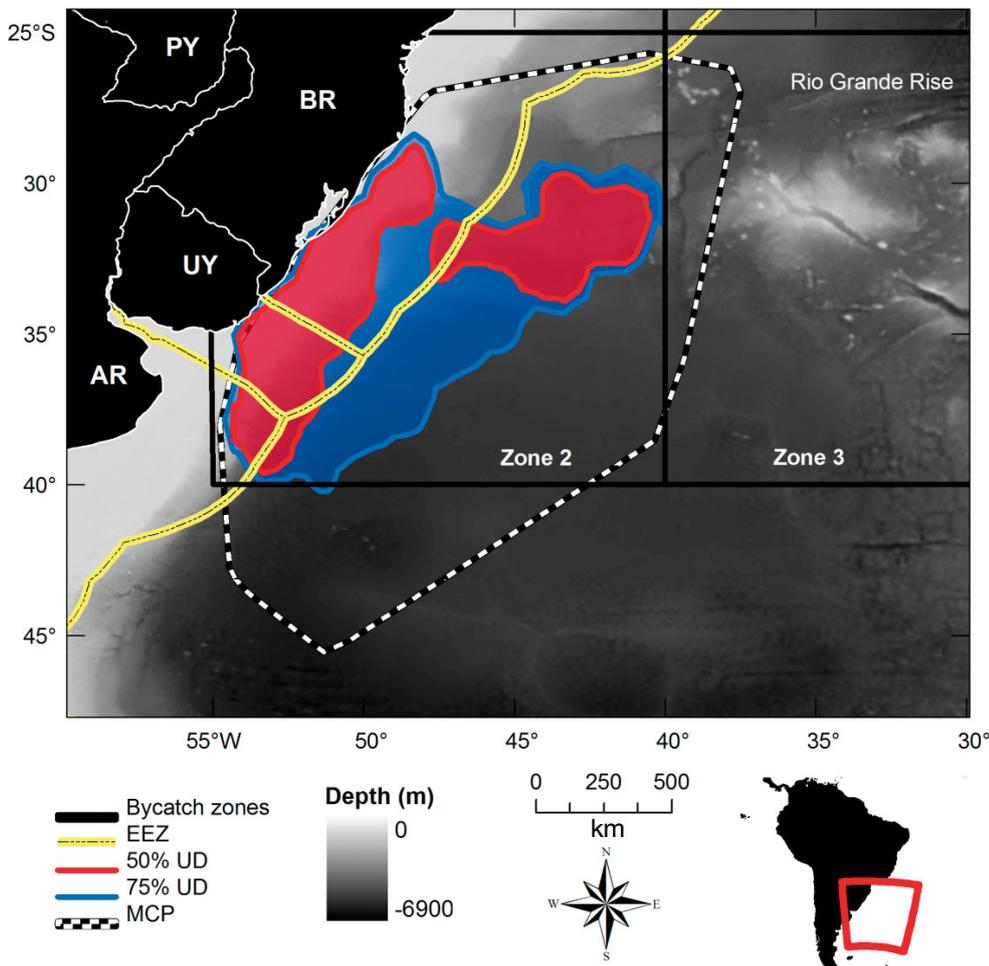


Fig. 3. High-use areas defined by 50 and 75% utilization distributions (UD) plotted with exclusive economic zones (EEZ) of adjacent countries, the minimum convex polygon (MCP), and bycatch zones specified by Giffoni et al. (2008)

Table 2. Maximum dive-depth bin reached in different bathymetric regions by each turtle equipped with a SPLASH tag. ND: no data. Groupings refer to which bathymetric region the turtle spent the most time (>75% of tracked days) over the tracking duration

PTT	Grouping	Bathymetric regions (m)			
		Shelf (0–200)	Break (>200–1000)	Slope (>1000–3000)	Oceanic (>3000)
79830	Neritic	150–200	200–300	100–150	200–300
79831	Mixed	100–150	100–150	100–150	100–150
79833	Oceanic	ND	ND	ND	100–150
79834	Oceanic	ND	ND	25–35	70–100
79835	Mixed	200–300	200–300	150–200	100–150

were in surface waters of temperatures greater than 15°C. There were significant differences in mean SST between seasons (ANOVA, $F_{3,58} = 56.52$, $p < 0.001$), and similar to latitude, mean SST differed significantly between summer and winter, summer and spring, and spring and winter seasons

(post-hoc Tukey test, $p < 0.05$). Turtles experienced cooler surface temperatures during the winter (mean SST: $18 \pm 1.8^\circ\text{C}$) and spring ($19 \pm 2^\circ\text{C}$) than during the summer ($22 \pm 2^\circ\text{C}$) and autumn ($20 \pm 2^\circ\text{C}$) seasons (Fig. 4).

There were no significant seasonal trends in relation to chl *a* (ANOVA, $F_{3,58} = 1.76$, $p = 0.18$). Turtles showed an affinity for chl *a* density values between 0.1 and 1 mg m^{-3} ($0.43 \pm 0.89 \text{ mg m}^{-3}$). During the autumn, winter, spring, and summer seasons,

turtles spent 77.7, 75.1, 65.1, and 67.8% of their time, respectively, in areas where surface chl *a* concentration ranged between 0.2 and 0.4 mg m^{-3} . There was no evident seasonality in the turtle's use of different bathymetric regions (ANOVA, $F_{3,58} = 0.28$, $p = 0.75$).

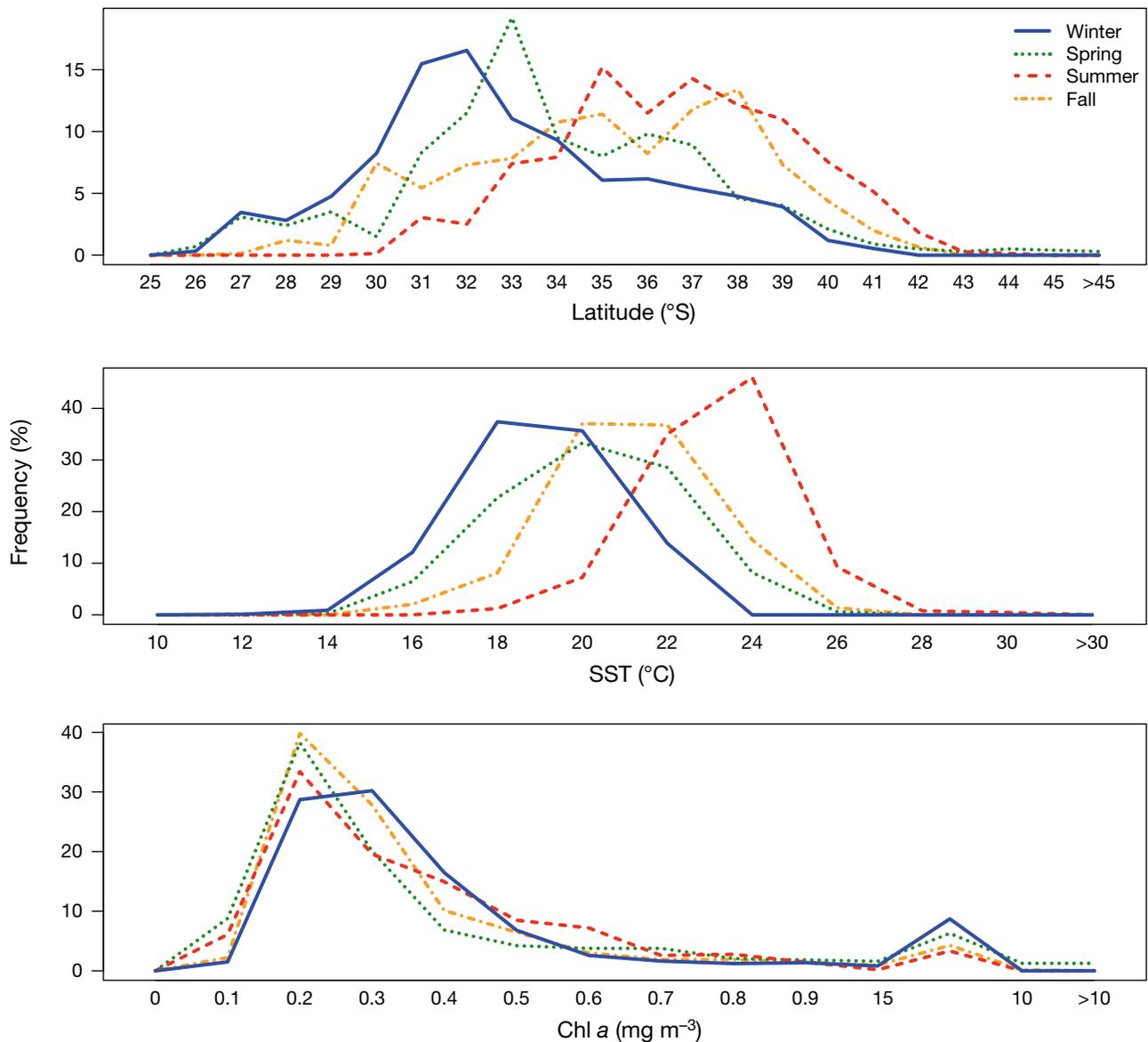


Fig. 4. Quarterly frequency distribution plots of (a) latitude, (b) sea surface temperature (SST) and (c) chl *a*. Seasons specified as follows: winter (July to September, $n = 924$), spring (October to December, $n = 1337$), summer (January to March, $n = 757$), autumn (April to June, $n = 754$). STAT-derived SST and chl *a* weekly averages identified for each first daily location point for all turtles

DISCUSSION

The present study is the first to present satellite-tracking data of juvenile loggerheads in the SWA. A key result from the present study is the identification of the SWA as a juvenile loggerhead high-use area. All tracked turtles remained within a relatively small area ($\sim 2\,250\,000\text{ km}^2$) during the entire 5 yr of tracking; this is restricted compared to areas used by oceanic juveniles tracked in other major ocean basins (e.g. Kobayashi et al. 2008, Mansfield et al. 2009).

The minimum convex polygon represents only a portion of the known distribution of this species in the SWA, as tracked turtles did not move into areas such as the Rio Grande Rise and the Rio de la Plata estuary where juvenile loggerhead turtles are known to be incidentally captured by the Brazilian longline fleet (Sales et al. 2008) and Uruguayan and Argentinean coastal bottom trawl fisheries (P. Miller unpubl. data). The residence of turtles within the restricted area observed in our study is likely a result of the high prevalence of pelagic and benthic prey

stemming from high primary production occurring along the Uruguayan, Argentinean, and Brazilian shelf and offshore regions. Similar residence patterns have been observed in the Mediterranean but mainly restricted to neritic areas (Casale et al. 2012).

The results indicate a strong seasonality in turtle movements in the SWA, a seasonality driven mainly by SST variability. In addition to seasonal shifts in latitude, turtles tracked in the present study also display seasonal patterns in their mean rates of travel that are consistent with the seasonal pattern in SST encountered by turtles in each season, where highest and lowest temperatures and speeds are in the summer and winter, respectively. The variability in temperatures in the SWA are evidenced by satellite images demonstrating that the warm Brazil current reaches its southernmost latitude during the austral summer (January, February, and March), whereas in the austral winter (June, July, and August), colder waters dominate as the Malvinas current reaches northernmost latitudes (Garzoli 1993). This seasonality in the turtle movements is similar that of tracked loggerheads in the North Pacific (Polovina et al. 2004, Kobayashi et al. 2008), as well as that of juvenile loggerheads tracked in the North Atlantic (Mansfield et al. 2009) and along the Italian coast (Bentivegna 2002, Bentivegna et al. 2007). In contrast, juvenile loggerheads in the western Mediterranean (Algerian Basin) do not demonstrate seasonality in their movements, which Revelles et al. (2007) explain by the fact that the Algerian Basin is largely thermally homogenous. Other studies on adult loggerheads, as well as leatherback turtles, also indicate the presence of a seasonal north-south trend in migration patterns (Plotkin & Spotila 2002, Hopkins-Murphy et al. 2003, Hawkes et al. 2007, 2011). This seasonality is possibly driven by the species' thermal preference (Howell et al. 2010) or limit (McMahon & Hays 2006). Our results are consistent with findings from other studies on juvenile loggerheads, as we also find that ~98% of the turtle movements were in water temperatures greater than the 15°C isotherm.

Seasonality in movements may also be influenced by a combination of both thermal preference and prey availability in certain seasons. High prey availability is generally known to be associated with productive blooms during the spring and summer seasons corresponding with turtles being distributed more polewards, whereas during colder seasons, turtles will tend to be distributed more equatorward with warmer waters to rely more heavily upon prey concentrations at frontal regions/mesoscale eddies (Mansfield et al. 2009). Kobayashi et al. (2008) have

found that latitudinal movements of loggerheads in the Pacific Ocean also correspond to variations in chl *a*; however, the tracked turtles in the present study do not seem to track chl *a*. It is important to note that there may also be lags between turtle movement and biological features, as turtles do not directly consume primary producers.

The SWA, characterized by the Brazil-Malvinas confluence, is a highly energetic and productive region (Chelton et al. 1990, Saraceno et al. 2005). From surface drifter data, mean surface currents in the study region range in mean speeds from 0.01 to ~2.5 km h⁻¹; however, this region (particularly around the Brazil-Malvinas Confluence) is highly variable (standard deviations as high as 1.44 km h⁻¹), and maximum current speeds are reported to be up to ~5 km h⁻¹ (Vivier et al. 2000). Given this, turtle rates of travel in the present study area are well within those theoretically possible. A mean rate of travel of 1.04 or 1.1 km h⁻¹ described for the turtles in the present study is comparable to mean rates of travel reported by Kobayashi et al. (2008) (0.913 km h⁻¹), Polovina et al. (2000) (1.08 km h⁻¹), Cejudo et al. (2006) (~1.3 km h⁻¹), and Nichols et al. (2000) (1.05 km h⁻¹), among others. The tortuous tracks as well as the rates of travel exhibited by the SWA juvenile turtles could possibly be the result (to some degree) of passive transport by local currents in the region in addition to their own station-holding abilities, diving behavior, and directed active movements. While clearly demonstrated for leatherbacks (Gaspar et al. 2006), further research is necessary to differentiate between active and passive movement for loggerhead turtles of all life stages and in all ocean basins.

Tracking studies of juvenile loggerhead sea turtles have begun to describe their movements in relation to mesoscale features, such as fronts and eddies (Polovina et al. 2000, 2004, Bentivegna et al. 2007, Revelles et al. 2007, Kobayashi et al. 2008, Howell et al. 2010). The SWA is a region with high presence of warm and cold core eddies (Chelton et al. 1990) and a diversity of fronts (Acha et al. 2004), which are linked to the high primary productivity of the region (Saraceno et al. 2005) and have differing effects on fish biodiversity and abundance (Alemany et al. 2009). Although the present study does not address the fine-scale habitat associations of tracked turtles, further studies on these turtles could determine if they exhibit distinct scales of movement and whether those scales of movement are associated with mesoscale environmental features, such as eddies and fronts. Furthermore, with recent advances in

detection and monitoring of remotely sensed oceanic frontal features (Belkin et al. 2009), a finer spatial and temporal scale identification of frontal regions may be possible, which may lead to a better understanding of the environments encountered by turtles (e.g. Kobayashi et al. 2011).

While there is recent evidence for a reversible ontogenetic shift in the North Atlantic population of loggerheads (McClellan & Read 2007) and alternative foraging strategies in the North Pacific (Peckham et al. 2011), movement data from juvenile loggerheads in the SWA is suggestive of individuals in the 'juvenile transitional stage' (Bolten 2003). Bolten (2003) suggests that this transitional stage is likely to vary in duration and probably occurs in geographic regions where major currents near or enter into the neritic zone (Bolten 2003); the Brazil-Malvinas confluence is such a region. Most of the turtles tracked in the present study (15 individuals of 26 total) remained largely in the oceanic region (depths > 200 m) for the entire tracking duration; however, 8 turtles moved from oceanic regions to neritic regions (<200 m depth) and remained in neritic regions until tracking cessation. Moreover, 2 turtles moved from oceanic regions to neritic regions and then back out to depths >200 m. Interestingly, 1 turtle (79823) moved from the oceanic to neritic, back out to the oceanic, and then back in to the neritic, spending multiple months in each habitat. The mean CCL for the tracked turtles in the present study is ~61 cm, which is larger than that reported for the transitional stage in other regions, e.g. ~53 cm CCL reported by Tiwari et al. (2002) off the coast of Morocco; however, it falls within the overlapping neritic and oceanic turtle sizes (from 45 to 68 cm) reported by Bolten (2003). In comparison, for immature loggerheads tracked in the NW Atlantic, it was found that those individuals that exhibited a preference for neritic habitats were not significantly larger than those that spent more time in the oceanic habitat (Mansfield et al. 2009). Regardless, our data are consistent with the hypothesis that immature loggerheads in the SWA do not recruit to the benthic phase in one step from a strict oceanic pelagic phase.

Further support for the 'transitional stage' hypothesis is given by the diving behavior presented in the present study as well as the diets of stranded loggerheads along the coast of Uruguay. Results from the present study demonstrate that 1 individual actively dove to depths close to the seafloor in regions within the 200 m isobath. Although this is not conclusive evidence of bottom feeding, it does suggest at least exploratory and possibly foraging dives.

Evidence also suggests that juveniles in this region may be foraging on the seafloor in neritic regions, based on a diet study of stranded juvenile loggerheads (Martinez-Souza 2009) along the Uruguayan coastline, where items such as crustaceans (*Libinia spinosa* and *Dardanus arrosor insignis*) and mollusks (*Buccinanops cochlidium* and *Pachycymbiola brasiliiana*) were found in turtle stomachs. While we were not able to compare the sizes of turtles that spent a significant amount of time on the continental shelf to those tracked primarily in deeper depths in the present study (due to the small sample size), it is possible that larger juveniles in this region may display more dives to bottom depths than smaller individuals. Further investigation into the variation in diving patterns of juvenile loggerheads present in the SWA neritic region will help to further elucidate this facultative habitat shift.

A large proportion of the turtle movements presented in the present study fall within a high juvenile loggerhead turtle bycatch zone as identified by Giffoni et al. (2008) (Zone 2, from latitudes 25 to 39° S) and by Sales et al. 2008 (Zone 3). Both the 50% and 75% utilization distributions are almost entirely contained within Zone 2 (Fig. 3). According to Giffoni et al. (2008), between January 2005 and July 2007, Zone 2 had the highest loggerhead catch-per-unit-of-fishing-effort (CPUE, number of turtles caught) values (0.939 turtles per 1000 hooks) and 78% (n = 1532 turtles) of the total observed loggerhead captures for both the Brazilian and Uruguayan pelagic longline fleets. Similarly, Sales et al. (2008) also reported high CPUE values (up to 2.17 turtles per 1000 hooks) in this region using Brazilian pelagic longline data from 2003 to 2005. Additionally, bycatch data from Uruguayan and Brazilian pelagic longline fisheries operating in the SWA (Domingo et al. 2006, Giffoni et al. 2008, Sales et al. 2008) indicate that juvenile loggerheads are also distributed in oceanic waters to the north of the region that was utilized by tracked turtles in the present study. Associations between turtle bycatch positions, tracking locations, and physical and biological oceanographic features may lead to a more complete understanding of the possible environmental indicators for turtle interactions with pelagic longline sets (similar to that of the Hawaii-based pelagic longline Turtlewatch program) (Howell et al. 2008), which in turn may allow for more efficient future management.

The results of the present study clearly define the waters off southern Brazil and Uruguay as the first identified juvenile loggerhead developmental high-use area in the South Atlantic; however, much still

remains to be understood about their environmental niche and vulnerability to anthropogenic threats in the region. We suggest that further research in this geographic region is needed to provide a more comprehensive view of the ecology of juvenile loggerheads in the SWA. For example, additional satellite telemetry studies and subsequent analysis of the horizontal and vertical behavior of juvenile-stage loggerheads along the SWA continental shelf will lend further insight into the prevalence of the 'transitional stage' or presence of the ontogenetic shift (be it reversible or discrete) as well as their 3-dimensional behavior in relation to regionally operating fisheries (Howell et al. 2010).

Recent research has also indicated the SWA to be an important area for other species of sea turtles (e.g. Lopez-Mendilaharsu et al. 2009) as well as seabirds (e.g. Jiménez et al. 2011), marine mammals (e.g. Pasadore et al. 2013), and sharks (e.g. Hazin et al. 2008), which is likely due to the region's unique physiographic (i.e. extensive Patagonian shelf and steep slope) features and oceanographic conditions (i.e. Brazil-Malvinas Confluence). As the issue of bycatch is a regionally understood issue in pelagic longline fisheries as well as in other commercial and artisanal fisheries along the coasts of Uruguay, Brazil, and Argentina, further collaborative research with the fishing sector is required to quantify the proportion of overlap of fisheries with independent data on the distributions of sea turtles and other marine mega-vertebrates in the region. Fortunately, bycatch monitoring and mitigation has been operating at a high level for more than a decade due to the efforts of multiple regional fisheries management organizations since the late 1990s (Domingo et al. 2006), and researchers have performed pertinent research aiming to understand the spatio-temporal patterns in bycatch (Giffoni et al. 2008, Pons et al. 2010), the efficacy of mitigation measures (i.e. circle hooks; see Sales et al. 2008, Domingo et al. 2012), and the general ecological patterns of different life stages (e.g. Marcovaldi et al. 2010, González Carman et al. 2012) in the region.

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LITERATURE CITED

- Acha EM, Mianzan HW, Guerrero RA, Favero M, Bava J (2004) Marine fronts at the continental shelves of austral South America: physical and ecological processes. *J Mar Syst* 44:83–105
- Aleman D, Acha EM, Iribarne O (2009) The relationship between marine fronts and fish diversity in the Patagonian Shelf Large Marine Ecosystem. *J Biogeogr* 36: 2111–2124
- Alfaro-Shigueto J, Mangel JC, Bernedo F, Dutton PH, Seminoff JA, Godley BJ (2011) Small-scale fisheries of Peru: a major sink for marine turtles in the Pacific. *J Appl Ecol* 48:1432–1440
- Belkin IM, Cornillon PC, Sherman K (2009) Fronts in Large Marine Ecosystems. *Prog Oceanogr* 81:223–236
- Bentivegna F (2002) Intra-Mediterranean migrations of loggerhead sea turtles (*Caretta caretta*) monitored by satellite telemetry. *Mar Biol* 141:795–800
- Bentivegna F, Valentino F, Falco P, Zambianchi E, Hochscheid S (2007) The relationship between loggerhead turtle (*Caretta caretta*) movement patterns and Mediterranean currents. *Mar Biol* 151:1605–1614
- Bjorndal KA, Bolten AB, Martins HR (2000) Somatic growth model of juvenile loggerhead sea turtles *Caretta caretta*: duration of pelagic stage. *Mar Ecol Prog Ser* 202:265–272
- Bolten AB (1999) Techniques for measuring sea turtles. In: Eckert KL, Bjorndal KA, Abreu-Grobois FA, Donnelly M (eds) Research and management techniques for the conservation of sea turtles. SSC/IUCN Marine Turtle Specialist Group, p 110–115
- Bolten AB (2003) Active swimmers—passive drifters: the oceanic juvenile stage of loggerheads in the Atlantic system. In: Bolten AB, Witherington BE (eds) Loggerhead sea turtles. Smithsonian Institution Press, Washington, DC, p 63–78
- Cardona L, Revelles M, Carreras C, San Felix M, Gazo M, Aguilar A (2005) Western Mediterranean immature loggerhead turtles: habitat use in spring and summer assessed through satellite tracking and aerial surveys. *Mar Biol* 147:583–591
- Cardona L, Revelles M, Parga ML, Tomás J and others (2009) Habitat use by loggerhead sea turtles *Caretta caretta* off the coast of eastern Spain results in a high vulnerability to neritic fishing gear. *Mar Biol* 156:2621–2630
- Casale P, Broderick AC, Freggi D, Mencacci R, Fuller WJ, Godley BJ, Luschi P (2012) Long-term residence of juvenile loggerhead turtles to foraging grounds: a potential conservation hotspot in the Mediterranean. *Aquatic Conserv* 22:144–154
- Cejudo D, Varo-Cruz N, Liria A, Castillo JJ, Bellido JJ,

- López-Jurado L (2006) Transatlantic migration of juvenile loggerhead turtles (*Caretta caretta* L.) from the Strait of Gibraltar. *Mar Turtle Newsl* 114:9–11
- Chelton DB, Schlax MG, Witter DL, Richman JG (1990) Geosat altimeter observations of the surface circulation of the Southern Ocean. *J Geophys Res* 95:17877–17903
- CLS (2007) ARGOS user's manual: worldwide tracking and environmental monitoring by satellite. 14 October 2008 update. Argos/CLS, Toulouse, available at www.argos-system.org/manual
- Coyne MS, Godley BJ (2005) Satellite Tracking and Analysis Tool (STAT): an integrated system for archiving, analyzing and mapping animal tracking data. *Mar Ecol Prog Ser* 301:1–7
- Crouse DT, Crowder LB, Caswell H (1987) A stage-based population model for loggerhead sea turtles and implications for conservation. *Ecology* 68:1412–1423
- De Solla SR, Bonduriansky R, Brooks RJ (1999) Eliminating autocorrelation reduces biological relevance of home range estimates. *J Anim Ecol* 68:221–234
- Dodd CK (1988) Synopsis of the biological data on the loggerhead sea turtle *Caretta caretta* (Linnaeus 1758): biological report. US Fish Wildl Serv, Washington, DC, p 1–110
- Dodd CK, Byles R (2003) Post-nesting movements and behavior of loggerhead sea turtles (*Caretta caretta*) departing from East-Central Florida nesting beaches. *Chelonian Conserv Biol* 4:530–536
- Domingo A, Bugoni L, Prosdocimi L, Miller P and others (2006) The impact generated by fisheries on sea turtles in the Southwestern Atlantic. WWF Marine Program for Latin America and the Caribbean, San José
- Domingo A, Pons M, Jiménez S, Miller P, Barceló C, Swimmer Y (2012) Circle hook performance in the Uruguayan pelagic longline fishery. *Bull Mar Sci* 88:499–511
- Friberg MA (1945) Observaciones sobre las tortugas de mar que se encuentran frente a las costas Argentinas. *Physis* 20:50–53
- Garzoli SL (1993) Geostrophic velocity and transport variability in the Brazil-Malvinas Confluence. *Deep-Sea Res I* 40:1379–1403
- Gaspar P, Georges JY, Fossette S, Lenoble A, Ferraroli S, Le Maho Y (2006) Marine animal behaviour: neglecting ocean currents can lead us up the wrong track. *Proc Biol Sci* 273:2697–2702
- Giffoni B, Domingo A, Sales G, Niemyer-Fiedler F, Miller P (2008) Iteración de tortugas marinas (*Caretta caretta* y *Dermochelys coriacea*) con la pesca de palangre pelágico en el Atlántico Sudoccidental: una perspectiva regional para la conservación. *Collect Vol Sci Pap-Int Comm Conserv Atl Tunas* 62:1861–1870
- Godley B, Blumenthal JM, Broderick AC, Coyne MS, Godfrey MH, Hawkes LA, Witt MJ (2008) Satellite tracking of sea turtles: Where have we been and where do we go next? *Endang Species Res* 4:3–22
- González Carman V, Falabella V, Maxwell S, Albareda D, Campagna C, Mianzan H (2012) Revisiting the ontogenetic shift paradigm: the case of juvenile green turtles in the SW Atlantic. *J Exp Mar Biol Ecol* 440:141–148
- Hart KM, Hyrenbach K (2009) Satellite telemetry of marine megavertebrates: the coming of age of an experimental science. *Endang Species Res* 10:9–20
- Hatase H, Takai N, Matsuzawa Y, Sakamoto W and others (2002) Size-related differences in feeding habitat use of female adult loggerhead turtles *Caretta caretta* around Japan determined by stable isotope analyses and satellite telemetry. *Mar Ecol Prog Ser* 233:273–281
- Hatase H, Omuta K, Tsukamoto K (2007) Bottom or midwater: alternative foraging behaviours in adult female loggerhead sea turtles. *J Zool (Lond)* 273:46–55
- Hatase H, Omuta K, Tsukamoto K (2010) Oceanic residents, neritic migrants: a possible mechanism underlying foraging dichotomy in adult female loggerhead turtles (*Caretta caretta*). *Mar Biol* 157:1337–1342
- Hawkes LA, Broderick AC, Coyne MS, Godfrey MH and others (2006) Phenotypically linked dichotomy in sea turtle foraging requires multiple conservation approaches. *Curr Biol* 16:990–995
- Hawkes LA, Broderick AC, Coyne MS, Godfrey MH, Godley BJ (2007) Only some like it hot—quantifying the environmental niche of the loggerhead sea turtles. *Divers Distrib* 13:447–457
- Hawkes LA, Witt MJ, Broderick AC, Coker JW and others (2011) Home on the range: spatial ecology of loggerhead turtles in Atlantic waters of the USA. *Divers Distrib* 17:624–640
- Hazin F, Broadhurst M, Amorin A, Arfelli C, Domingo A (2008) Catches of pelagic sharks by subsurface longline fisheries in the South Atlantic Ocean: a review of available data with emphasis on Uruguay and Brazil. In: Camhi MD, Pikitch EK, Babcock EA (eds) *Sharks of the open ocean*. Blackwell Scientific, New York, NY
- Heppell SS (1998) Application of life-history theory and population model analysis to turtle conservation. *Copeia* 1998:367–375
- Heppell SS, Heppell SA, Read AJ, Crowder LB (2005) Effects of fishing on long lived marine organisms. In: Norse E, Crowder L (eds) *Marine conservation biology: the science of maintaining the sea's biodiversity*. Island Press, Washington, DC, p 211–231
- Hopkins-Murphy SR, Owens DW, Murphy TM (2003) Ecology of immature loggerheads on foraging grounds and adults in interesting habitat in the eastern United States. In: Bolten AB, Witherington BE (eds) *Loggerhead sea turtles*. Smithsonian Institution Press, Washington, DC, p 79–92
- Howell EA, Kobayashi DR, Parker DM, Balazs GH, Polovina JJ (2008) TurtleWatch: a tool to aid in the bycatch reduction of loggerhead turtles *Caretta caretta* in the Hawaii-based pelagic longline fishery. *Endang Species Res* 5:267–278
- Howell E, Dutton P, Polovina JJ, Bailey H, Parker DM, Balazs GH (2010) Oceanographic influences on the dive behavior of juvenile loggerhead turtles (*Caretta caretta*) in the North Pacific Ocean. *Mar Biol* 157:1011–1026
- IUCN (2012) IUCN Red List of Threatened Species, Vers 2012.2. www.iucnredlist.org
- James MC, Ottensmeyer CA, Myers RA (2005) Identification of high-use habitat and threats to leatherback sea turtles in northern waters: new directions for conservation. *Ecol Lett* 8:195–201
- Jiménez S, Domingo A, Brazeiro A (2009) Seabird bycatch in the Southwest Atlantic: interaction with the Uruguayan pelagic longline fishery. *Polar Biol* 32:187–196
- Jiménez S, Domingo A, Abreu M, Brazeiro A (2011) Structure of the seabird assemblage associated with pelagic longline vessels in the southwestern Atlantic: implications for bycatch. *Endang Species Res* 15:241–254
- Kobayashi DR, Polovina JJ, Parker DM, Kamezaki N and others (2008) Pelagic habitat characterization of logger-

- head sea turtles, *Caretta caretta*, in the North Pacific Ocean (1997-2006): insights from satellite tag tracking and remotely sensed data. *J Exp Mar Biol Ecol* 356: 96–114
- Kobayashi DR, Cheng IJ, Parker DM, Polovina JJ, Kamezaki N, Balazs GH (2011) Loggerhead turtle (*Caretta caretta*) movement off the coast of Taiwan: characterization of a hotspot in the East China Sea and investigation of mesoscale eddies. *ICES J Mar Sci* 68:707–718
- Laporta M, Lopez G (2003) Loggerhead sea turtle tagged in Brazil caught by a trawler in waters of the common Argentinian-Uruguayan fishing area. *Mar Turtle Newsl* 102:14
- Lewison RL, Crowder LB (2007) Putting longline bycatch of sea turtles into perspective. *Conserv Biol* 21:79–86
- Lopez-Mendilaharsu M, Rocha CFD, Miller P, Domingo A, Prosdociami L (2009) Insights on leatherback turtle movements and high use areas in the Southwest Atlantic Ocean. *J Exp Mar Biol Ecol* 378:31–39
- Luschi P, Hays GC, Del Seppia C, Marsh R, Papi F (1998) The navigational feats of green sea turtles migrating from Ascension Island investigated by satellite telemetry. *Proc R Soc Lond B* 265:2279–2284
- Mansfield K, Saba V, Keinath JA, Musick JA (2009) Satellite tracking reveals a dichotomy in migration strategies among juvenile loggerhead turtles in the Northwest Atlantic. *Mar Biol* 156:2555–2570
- Marcovaldi M, Chaloupka M (2007) Conservation status of the loggerhead sea turtle in Brazil: an encouraging outlook. *Endang Species Res* 3:133–143
- Marcovaldi MÁ, Marcovaldi GG (1999) Marine turtles of Brazil: the history and structure of Projeto TAMAR-IBAMA. *Biol Conserv* 91:35–41
- Marcovaldi MA, Silva ACCD, Gallo BMG, Baptistotte C and others (2000) Recaptures of tagged turtles from nesting and feeding grounds protected by Projeto TAMAR-IBAMA, Brasil. In: Kalb HJ, Wibbels T (eds) *Proc 19th Annu Symp Sea Turtle Biol Conser*, 2–6 March 1999, South Padre Island, TX, USA. NOAA Tech Memo 443: 164–166
- Marcovaldi M, Lopez GG, Soares LS, Lima EHSM, Thomé JCA, Almeida AP (2010) Satellite-tracking of female loggerhead turtles highlights fidelity behavior in northeastern Brazil. *Endang Species Res* 12:263–272
- Martinez-Souza G (2009) *Ecologia alimentar da tartaruga marinha cabeçuda (Caretta caretta) no oceano Atlantico sul Ocidental, Uruguai*. MS thesis. Universidade Federal do Rio Grande, Rio Grande do Sul, Brazil
- McClellan CM, Read AJ (2007) Complexity and variation in loggerhead sea turtle life history. *Biol Lett* 3:592–594
- McClellan CM, Braun-McNeill J, Avens L, Wallace BP, Read AJ (2010) Stable isotopes confirm a foraging dichotomy in juvenile loggerhead sea turtles. *J Exp Mar Biol Ecol* 387:44–51
- McMahon C, Hays G (2006) Thermal niche, large-scale movements and implications of climate change for a critically endangered marine vertebrate. *Glob Change Biol* 12:1330–1338
- Mora O, Domingo A (2006) Informe sobre el Programa de Observadores a bordo de la flota atunera uruguaya (1998-2004). *Collect Vol Sci Pap ICCAT* 59:599–607
- Morreale SJ, Standora EA (1998) Early life stage ecology of sea turtles in northeastern US waters. NOAA Tech Memo NMFS-SEFSC 413:1–49
- Murphy RC (1914) *Thalassochelys caretta* in the South Atlantic. *Copeia* 2:4
- Musick J, Limpus CJ (1997) Habitat utilization and migration in juvenile sea turtles. In: Lutz P, Musick JA (eds) *Biology of sea turtles*. CRC Press, Boca Raton, FL, p 137–163
- Nichols WJ, Resendiz A, Seminoff JA, Resendiz B (2000) Transpacific migration of a loggerhead turtle monitored by satellite telemetry. *Bull Mar Sci* 67:937–947
- Passadore C, Domingo A, Szephegyi M, Secchi ER (2013) Influence of environmental and longline fishing operational variables on the presence of killer whales (*Orcinus orca*) in south-western Atlantic. *J Mar Biol Assoc UK* CJO2012 (in press) doi:10.1017/S002531541200166X
- Peckham SH, Maldonado-Diaz D, Walli A, Ruiz G, Crowder LB, Nichols WJ (2007) Small-scale fisheries bycatch jeopardizes endangered Pacific loggerhead turtles. *PLoS ONE* 2:e1041
- Peckham SH, Maldonado-Diaz D, Tremblay Y, Ochoa R and others (2011) Demographic implications of alternative foraging strategies in juvenile loggerhead turtles *Caretta caretta* of the North Pacific Ocean. *Mar Ecol Prog Ser* 425:269–280
- Plotkin PT, Spotila JR (2002) Post-nesting migrations of loggerhead turtles *Caretta caretta* from Georgia, USA: conservation implications for a genetically distinct subpopulation. *Oryx* 36:396–399
- Polovina JJ, Kobayashi DR, Parker DM, Seki MP, Balazs GH (2000) Turtles on the edge: movement of loggerhead turtles (*Caretta caretta*) along oceanic fronts, spanning longline fishing grounds in the central North Pacific, 1997–1998. *Fish Oceanogr* 9:71–82
- Polovina JJ, Balazs GH, Howell EA, Parker DM, Seki MP, Dutton PH (2004) Forage and migration habitat of loggerhead (*Caretta caretta*) and olive ridley (*Lepidochelys olivacea*) sea turtles in the central North Pacific Ocean. *Fish Oceanogr* 13:36–51
- Polovina JJ, Uchida I, Balazs G, Howell EA, Parker D, Dutton P (2006) The Kuroshio Extension Bifurcation Region: a pelagic hotspot for juvenile loggerhead sea turtles. *Deep-Sea Res II* 53:326–339
- Pons M, Domingo A, Sales G, Fiedler FN, Miller P, Giffoni B, Ortiz M (2010) Standardization of CPUE of loggerhead sea turtle (*Caretta caretta*) caught by pelagic longliners in the Southwestern Atlantic Ocean. *Aquat Living Resour* 23:65–75
- R Development Core Team (2009) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Rees AF, Saady SA, Broderick AC, Coyne MS, Papathanasopoulou N, Godley BJ (2010) Behavioural polymorphism in one of the world's largest populations of loggerhead sea turtles *Caretta caretta*. *Mar Ecol Prog Ser* 418: 201–212
- Revelles M, Isern-Fontanet J, Cardona L, San Félix M, Carreras C, Aguilar A (2007) Mesoscale eddies, surface circulation and the scale of habitat selection by immature loggerhead sea turtles. *J Exp Mar Biol Ecol* 347:41–57
- Sales G, Giffoni BB, Barata PCR (2008) Incidental catch of sea turtles by the Brazilian pelagic longline fishery. *J Mar Biol Assoc UK* 88:853–864
- Sales G, Giffoni BB, Fiedler FN, Azevedo VG, Kotas JE, Swimmer Y, Bugoni L (2010) Circle hook effectiveness for the mitigation of sea turtle bycatch and capture of target species in a Brazilian pelagic longline fishery. *Aquat Conserv* 20:428–436

- Saraceno M, Provost C, Piola AR (2005) On the relationship of satellite retrieved surface temperature fronts and chlorophyll *a* in the Western South Atlantic. *J Geophys Res* 110:C11016, doi:10.1029/2004JC002736
- Tiwari M, Bjorndal KA, Bolten A, Moumi A (2002) Morocco and Western Sahara: sites of an early neritic stage in the life history of loggerheads. In: Moiser A, Folley A, Brost B (eds) Proc 20th Annu Symp on sea turtle biology and conservation. NOAA Tech Memo NMFS-SEFSC 477:9
- Vigan X, Provost C, Podesta G (2000) Sea surface velocities from sea surface temperature image sequences: 2. Application to the Brazil-Malvinas Confluence area. *J Geophys Res* 105(C8):19515–19534, doi:10.1029/2000JC900028
- VLIZ (2012) Maritime Boundaries Geodatabase, v6.1, available at www.vliz.be/vmdcdata/marbound
- Wallace BP, DiMatteo AD, Hurley BJ, Finkbeiner EM and others (2010) Regional management units for marine turtles: a novel framework for prioritizing conservation and research across multiple scales. *PLoS ONE* 5:e15465
- Witt MJ, Akesson S, Broderick AC, Coyne MS and others (2010) Assessing accuracy and utility of satellite-tracking data using Argos-linked Fastloc-GPS. *Anim Behav* 80: 571–581
- Zar JH (1996) *Biostatistical analysis*, 3rd edn. Prentice-Hall, Upper Saddle River, NJ

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