

AN ABSTRACT OF THE THESIS OF

Caren Barceló for the degree of Master of Science in Fisheries Science presented on June 16, 2011.

Title: Movement Patterns and Marine Habitat Associations of Juvenile Loggerhead Sea Turtles (*Caretta caretta*) in the Southwestern Atlantic Ocean

Abstract approved:

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Bycatch, or the incidental capture of non-target species, has been implicated as one of the main factors leading to population declines of many large marine vertebrates, including sea turtles. To effectively manage and conserve these long-lived species, their marine distribution, high use areas, foraging habitats, and regions of highest likelihood of interaction with fisheries must be understood. I analyzed the movements and habitat use of satellite tracked juvenile loggerhead sea turtles (*Caretta caretta*) in the Southwestern Atlantic Ocean, a poorly studied region with high turtle-fisheries interactions. Between July 2006 and March 2010, 27 satellite transmitters were deployed at sea on juvenile loggerheads captured as bycatch in the Uruguayan and Brazilian pelagic longline fishing vessels. I characterized the broad-scale behavioral patterns, inter-seasonal variability, and general high use areas for 26 juvenile turtles, which were tracked for 259 ± 159 days between latitudes of 25-45°S and longitudes 35-54°W. The high use areas for the tracked turtles were over the continental shelf and slope within the Uruguayan and Brazilian Economic Exclusive

Zones, and in oceanic international waters between the Rio Grande Rise and the continental slope off of southern Brazil. Diving information was available for 5 of the tagged turtles; the maximum dive depth recorded varied between 100-300m depths, and two turtles demonstrated potential bottom-feeding behaviors by diving to depths that corresponded with the bathymetry at their location. The mean sea surface temperature encountered by turtles was $19.8 \pm 2.3^{\circ}\text{C}$ (10.21°C - 28.4°C) and turtles showed an affinity for mesotrophic waters ($0.458 \pm 1.012 \text{ mg/m}^3$ chlorophyll-a). Overall, broad scale latitudinal movements of juvenile loggerheads varied by season and sea surface temperature.

Because recent studies on marine megafauna movements have highlighted that ocean currents can have an important effect on movement paths, I decoupled active foraging behavior from likely passive movement of tracked juvenile loggerheads in ocean currents. Using First Passage Time analysis; a method to measure changes in movement patterns along a pathway through the environment, and generalized additive mixed models, I quantified similarities in the movement patterns and habitat “affinities” of the turtles and surface drifters in the ocean. Turtles and drifters both exhibited movement patterns that could be classified as likely “foraging behavior” at a spatial scale of 80km. This corresponds to the identified scale of eddies in the Southwestern Atlantic Ocean, which may suggest that passive movement of turtles in ocean currents largely drives their scale of search. Current velocity and sea floor depth were the most important variables correlated with both turtle and drifter movement patterns at that scale. Both turtles and drifters generally showed a negative relationship between first passage time and current velocities. Some differences

between turtle and drifter behavior were evident, particularly on the continental shelf; deviations in turtle behavior from the patterns of drifters is likely indicative of active movement on the turtles part. There were no seasonal or annual effects on the fine scale movements of turtles or drifters. Interestingly, turtle search behavior was not correlated with temperature or chlorophyll *a* in this scale of analysis. I suggest that evaluation of drifter movements in the area of study is an important addition to satellite tracking work that attempts to identify foraging behavior in sea turtles or other large marine vertebrates that may take advantage of ocean currents for transport and feeding.

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Movement Patterns and Marine Habitat Associations of Juvenile Loggerhead Sea
Turtles (*Caretta caretta*) in the Southwestern Atlantic Ocean

by

Caren Barceló

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

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CHAPTER ONE

MOVEMENTS OF JUVENILE LOGGERHEAD 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 successfully deployed at sea on juvenile loggerheads captured as bycatch in the Uruguayan and Brazilian pelagic longline fisheries operating in the Southwestern Atlantic Ocean. The mean turtle tracking duration for the study period was 259 ± 159 days (range: 3 - 639 days), during which turtles moved between latitudes of 25-45°S and longitudes 35-54°W. The high use areas for the tracked turtles were over the continental shelf and slope within the Uruguayan and Brazilian EEZs, and in oceanic international waters between the Rio Grande Rise and the continental slope off of southern Brazil. Diving information was available for 5 of the tagged turtles; the maximum dive depth recorded varied between 100-300m depths, and two turtles demonstrated potential bottom-feeding behaviors by diving to depths that corresponded with the bathymetry of their predicted location. The mean SST encountered by turtles was $19.8 \pm 2.3^{\circ}\text{C}$ (10.21°C - 28.4°C) and turtles showed an affinity for mesotrophic waters ($0.458 \pm 1.012 \text{ mg/m}^3$ 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 focus further tri-national and international collaborative efforts in research and management of sea turtles in this area.

INTRODUCTION

While the study of loggerhead sea turtles is extensive, there are still significant gaps in our knowledge of their ecology at sea, particularly in the Southern Hemisphere. The loggerhead sea turtle (*Caretta caretta*) is distributed widely in the tropical, subtropical and warm-temperate waters of the world's oceans, and occupies range of habitat types (Dodd 1988, Pritchard 1997). This species is listed by IUCN as endangered over its entire distribution range (IUCN 2010). Migratory paths and habitat affinities have been primarily identified for juvenile loggerhead turtles in the North Atlantic Ocean, Mediterranean Sea and North Pacific Ocean through the use of satellite telemetry (Polovina et al. 2000, 2004, Kobayashi et al. 2008, McClellan et al. 2009, Mansfield et al. 2009, Eckert et al. 2008, Bentivegna et al. 2002, McCarthy et al. 2010), while those in the South Atlantic Ocean remain largely unknown. The classic life history model proposes that after swimming away from nesting beaches as hatchlings, small juveniles spend approximately 7-10 years in the oceanic environment, both swimming actively as well as passively drifting (Bolten 2003). This model also presumes that immature oceanic loggerheads at a certain size undergo an ontogenetic shift and move from the oceanic to neritic habitats (Carr 1987, Musick and Limpus 1997, Bjorndal et al. 2000, Snover 2002). However, recent studies in the North Atlantic Ocean have indicated that this ontogenetic shift may be flexible in nature, where juvenile turtles exhibit plasticity in their habitat use (Witzell 2002, McClellan & Read 2007, Mansfield 2009).

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 types of research (Costa et al. 1993, Gillespie et al. 2001). Satellite tags have been used to track the movement 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, in the Northwestern and mid-Atlantic and in the Mediterranean (Polovina et al. 2000, 2004, Koboyashi et al. 2008, 2011, Peckham et al. 2007, 2011, McClellan et al. 2007, Mansfield et al. 2009, Bolten 2003, McCarthy et al. 2010, Cardona et al. 2009, Revelles et al. 2007, Betivenga et al. 2007). Oceanographic variables such as sea surface temperature (SST), chlorophyll *a* (Chl *a*), mesoscale eddies and frontal regions have been found to be key variables that characterize the pelagic habitat of loggerhead sea turtles in the North and Central Atlantic Ocean as well as Pacific oceans (Polovina et al. 2000, 2004, Koboyashi et al. 2008, Mansfield et al. 2009, McCarthy et al. 2010).

Understanding the relationship between sea turtle movements and habitat use is important for the conservation of these endangered species. Multiple studies have pointed to pelagic longline fisheries as an important threat to immature loggerhead sea turtle populations in various regions of the world (Domingo et al. 2006 ICCAT, Petersen et al. 2009, Lewison & Crowder 2007, Sales et al. 2008, Pons et al. 2009, Alfaro-Shigueto et al. 2004, 2008, Donoso & Dutton 2010, Howell et al. 2008). The loss of 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 proportional effect on the population growth rate of the

species (Crouse et al. 1987, Heppell et al. 1998). The Brazilian and Uruguayan pelagic longline fisheries operate in an extended portion of the Southwestern Atlantic Ocean (SWA) and their principal target species are swordfish (*Xiphias gladius*), tunas (*Thunnus obesus*, *T. alalunga* and *T. albacares*), and blue shark (*Prionace glauca*) (Domingo et al. 2002, Mora & Domingo 2006, Sales et al. 2010). These fisheries also have high sea turtle bycatch rates (Domingo et al 2006 ICCAT, Lopez-Mendilaharsu et al. 2007, Giffoni et al. 2008, Pons et al 2009, Sales et al. 2010), principally immature loggerhead turtles (mean curved carapace length = 58.9 cm, see Giffoni et al. 2008, Sales et al. 2010).

While the distribution of juvenile loggerheads and the spatio-temporal variability of their captures in Uruguayan and Brazilian longline fisheries has been recorded (see Lopez-Mendilaharsu et al. 2007, Giffoni et al. 2008), there is no information about the movements and behaviors of these turtles in the South Atlantic Ocean. 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 this study are to characterize the broad scale behavioral patterns, inter-seasonal variability and general high use areas for immature loggerhead turtles in the Southwestern Atlantic Ocean 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 southwestern Atlantic Ocean between July of 2006 and November of 2009. For a characterization of the Brazilian and Uruguayan longline fisheries, see Domingo et al. 2008, Jimenez et al. 2009, Pons et al. 2010, and Sales et al. 2008. Baits are most often squid (*Illex argentinus*.) as well as different types of mackerel (mainly *Scomber* spp. but also *Trachurus* spp.) (Domingo et al. (2002), Mora and Domingo et al. (2006), Sales et al. (2008)).

Protocol on board was to bring captured sea turtles on to the vessel for measurements and attachment of the transmitter. As the strength of inference on the importance of CCL for turtle behavior or habitat use is low due to the narrow range of turtle sizes tracked in this study, we do not include CCL in statistical analyses. Turtles were evaluated pre-release and body condition was noted. Sex was not determined as it was not externally evident due to the small size of the turtle. All turtles were released within Uruguayan (UY) or Brazilian (BR) Exclusive Economic Zones (EEZ) over the continental shelf or slope (n=23; approximately along 53°W, in waters

between 100 and 3000m in depth), or in international waters/high seas (HS) (n=3) (Figure 1).

ARGOS-linked *Telonics* (Mesa, AZ, USA) 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* (Redmond, WA, USA) PTTs, models SPLASH and SPOT 5, were attached to 6 and 10 turtles, respectively, on Uruguayan vessels. Tags were adhered to the turtles on the second central carapacial scute using quick drying two-part epoxies, PoxipolTM (Uruguay) and DurepoxiTM (Brazil), and allowed to dry for 30min to one hour on deck before release. Transmitters had three different duty cycles; i) no duty cycle, continuous transmissions with daily transmit allowance set to 300 transmissions per day, ii) 24h on, 24h off, with the daily transmit allowance set to 250 transmissions per day, iii) 12 hrs on, 2.5 days off with the daily transmit allowance set to 200 transmissions per day.

Horizontal Movements

ARGOS assigns location accuracy estimates (LC, location class) to each reported location which are classified as 1-3, 0, A, B, Z, where locations with LC between 1-3 have estimated associated errors of <1500m of the tag's actual position (ARGOS 2008). Tracking and remote sensing data was downloaded and filtered using the Satellite Tracking and Analyst Tool (STAT; Coyne & Godley 2005) and data includes transmitted locations up to March 24, 2010. At the time of analysis five turtles were still transmitting (see Table 1.1). For this study we used single daily locations in order to reduce spatial autocorrelation (De Solla et al. 1999, James et al.

2005a, Mansfield et al. 2009). We chose to include only LC 1, 2 and 3 in the analysis, and to reduce potential inaccurate locations we used a speed filter of $<5\text{ km h}^{-1}$ (Mansfield et al. 2009, James et al. 2005) that removed 1.14% of the locations.

We excluded the first ten days (3% of total points, and one turtle - 79832) of tracking data from each turtle in order to avoid including immediate post release behavior that may have been affected by the capture event. We do not draw conclusions in relation to the nature of transmission cessation in this study. As one turtle (79832, SPLASH model) transmitted data for only three days, it was not included in further analysis or interpretation, resulting in a total of 26 turtles utilized in this study (for summary information on this turtle refer to Table 1). 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 (Beyer et al. 2004), summing over the entire track length to obtain the minimum distance traveled by each turtle. We divided the distance between two observed locations separated by more than 24 h by the number of missing days (James et al. 2005a, TEWG 2007, Mansfield et al. 2009). Average speeds (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, respectively: summer (Jan-Mar), fall (Apr-Jun), winter (Jul-Sep), spring (Oct-Dec), and continental shelf (0-200m), continental shelf break ($>200\text{-}1000\text{m}$), slope ($>1000\text{-}3000\text{m}$) and oceanic ($>3000\text{m}$). Bathymetry data (1 minute latitude/longitude resolution) were

obtained from the General Bathymetric Chart of the Oceans (British Oceanographic Data Centre, www.bodc.ac.uk). Weekly averaged sea surface temperature (SST) and surface chlorophyll *a* (Chl *a*) data were obtained from STAT and used to obtain SST and Chl *a* values for each daily turtle location to characterize broad turtle - habitat associations. In STAT, SST data is derived from a weekly average of AVHRR (Advanced Very High Resolution Radiometer) sensors onboard NOAA satellites, and average weekly surface chlorophyll-*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 six hour period) was collected by each of the five functioning SPLASH satellite tags and relayed through the ARGOS system. Turtles with tag numbers 79830, 79831, 79835, were programmed with depth ranges distributed as follows: 0; 10; 20; 50; 100; 150; 200; 300; 400; 500; 600; 700; 800; >800 m, and turtles with tag #s 79833 and 79834, programmed as follows: 0; 10; 15; 25; 35; 45; 55; 70; 100; 150; 200; 300; 400; >400 m. To compare dive depth data among all diving turtles we consolidated depth bins that ranged between 10 and 100m. Dive data were collected for every 6-hour period throughout the day, starting at midnight GMT time. For the 5 turtles equipped with SPLASH tags, a total of 1,798 6-hr dive depth histograms were reported during the tracking duration.

High-use areas

In order to examine habitat use, the number of filtered daily locations was

tallied within hexagonal area bins. In this study, and similar to grids used in James et al. 2005 and Mansfield et al. 2009, hexagonal area bins were chosen over square bins in order to more accurately capture the orthogonality of movement paths between adjacent cells. The diagonal and edge length of each hexagonal cell are 64.3km and 32.2km, respectively, and each hexagonal cell has an area of 2,686 km² (which is greater than the estimated location error associated with least precise position estimate (LC 1 >1000m error) (ARGOS Manual 2008/10, Mansfield et al. 2009). Each degree latitude in the study region is represented by approximately 1.5 hexagons (~90km). For defining a high use area, we created a 50% utilization distribution (UD) contour of turtle tracking days using Spatial Analyst extension of ArcGIS (ESRI, Redlands, CA, USA), using a smoothing factor of 120km and a grid size of 10km. In addition, we defined individual turtle predominant spatial distributions, where 75% or more of their daily locations were contained within the shelf-break region, the slope region, the oceanic region, or in a mix of regions; in which turtles did not present more than 75% of their daily positions in any of the three categories.

Statistical analyses and figures

All track analyses were carried out in ArcGIS 9.2 (ESRI, 2005) in a projected Universal Transverse Mercator 22S coordinate system so as to avoid distortion associated with geographic coordinate systems. All statistical analyses were conducted in R v.2.9.2 (R Development Core Team 2007). Parametric and non-parametric statistical tests were used to analyze seasonal trends and large-scale environmental associations. The statistical significance level was set to $\alpha=0.05$ for all analyses.

RESULTS

General Movements

The overall mean turtle tracking duration for the study period was 259 ± 159 days (mean \pm SD) (range: 29-639 days, $n=26$) and the mean minimum distance from release location was $6,050 \pm 3,630$ km (mean \pm SD) (range: 153-14,664,72 km, $n=26$) (Table 1.1). Curved carapace length (CCL) of turtles was measured following Bolten (1999), and the overall CCL mean was 61.8 ± 6.9 cm (range: 49-83 cm, $n=27$, Figure 1.1, Table 1.1). During the entire monitoring period, 5 turtles were tracked for more than one year, 20 were tracked for 100-365 days, and only 2 turtles were monitored for less than 100 days before their transmissions ceased in March 2010. All turtle movements were contained within a relatively small region of the southwestern Atlantic Ocean, including part of the Uruguayan, Brazilian, and Argentinean EEZs, and also adjacent international waters. The movements spanned a minimum convex polygon area of $2,244,685 \text{ km}^2$ (Fig. 1.1). Horizontal tracks were distributed between 25° and 45°S latitude and between 35° and 54°W longitude (Fig. 1.1). Of the turtles tracked, turtle 79820 traveled the farthest north, reaching $25^\circ 49'\text{S}$, $40^\circ 30'\text{W}$ in the month of December 2008. Turtle 79821 traveled the farthest south reaching $45^\circ 40'\text{S}$ and $50^\circ 58'\text{W}$ in October of 2008.

Across all 26 turtles the mean speed was $1.13 \pm 0.86 \text{ km h}^{-1}$. Individual average speeds ranged between 0.46 ± 0.12 and $1.83 \pm 0.94 \text{ km h}^{-1}$ (Table 1.1). Turtles 79831 and 95596 mean speeds were considerably higher than the other tracked turtles (1.83 ± 0.94 and $1.75 \pm 1.07 \text{ km h}^{-1}$, respectively). Approximately 55% of the recorded

daily speeds were between 0 and 1.5 km h⁻¹. Mean speed varied among turtles (Kruskal-Wallis, $\chi^2=462.04$, df=25, $p<0.05$) and there were significant speed differences among the shelf area classification groups (Kruskal-Wallis, $\chi^2=61.08$, df=2, $p<0.05$), specifically, between shelf-break-oceanic and shelf-break-mix group turtle classifications (Wilcoxon-Rank Sum test, Bonferroni adjusted $p<0.05$).

High-Use Areas

The areas of highest use for the collective 26 tracked turtles were located mainly over the continental shelf and slope within the northern portion of the Argentinean, the Uruguayan and the southern portion of the Brazilian EEZs, and also in oceanic international waters between the Rio Grande Rise and the continental slope off of Brazil, approximately 600 km straight-line distance from shore (as identified by the 50 UD contour, see Figure 1.2). Over the continental shelf in northern Uruguayan and southern Brazilian jurisdictional waters, five individual hexagonal bins contained between 25 and 36 turtle days, which reflect the cumulative use of 4 and 5 turtles each, approximately 15% of all studied turtles (Fig. 1.2). Two turtles (12096 & 79830) were classified as predominantly within the shelf/break region (more than 75% of their movements) (See Methods: *High-use areas*), and both spent more than 50% of their time within the 200m isobath (12096: 86%, 79830: 56%). The remaining turtles were classified as either primarily oceanic (n=13), or within the mixed group (n=11), no turtles were classified into the slope group. Curved carapace length of the shelf-break, oceanic, mixed categories had means of 68.5 ± 0.7 , 60.7 ± 5.2 cm, and 63.3 ± 8 cm, respectively.

Diving Behavior

On average, for all diving turtles, 15% percent of dives were to depths less than 10m, 84% of dives were between 10 and 100m, and 1% of dives were in depths greater than 100m. Maximum dive depths ranges for each of the 5 turtles that collected dive data are reported in Table 1.1. Maximum dive depths varied by turtle, and are contained within the 100-150m, 150-200m and 200-300m bins. The maximum dive depth range was achieved by turtle 79835, which reached the 200-300 m bin during fall of 2008. Diving was different among shelf/break, oceanic and mix grouped turtles. Shelf/break turtle, 79830, had dives that reached the 200-300m bin in regions where the water column was less than 200m deep; this indicates a possible measurement error (location or depth or both), but it may also be that this turtle was foraging on the bottom in approximately 200m of water. While this turtle was in both the slope and in the oceanic regions, the maximum dive depths were in the 100-150 m and 200-300m depth bins respectively (Table 1.1). For the turtles classified as having less than 75% of their movement in all depth categories (i.e. mix group 79831 and 79835) maximum dive depth bins reached in the 3 different bathymetric regions was 200-300m. One of the mix group turtles, 79835, also had dives that reached the 200-300m depth bin over the continental shelf with less than 200m water column depth. For the oceanic group turtles (79833 and 79834), neither turtle had any dives on the continental shelf region, and only turtle 79834 presented dives within the slope region reaching a maximum depth in the bin range of 25-35m. Both oceanic turtles dove to depth bins greater than 70m in the oceanic water column, turtle 79833 reached a maximum depth bin range of 100-150m. This suggests that turtles that spent most of their time in deep oceanic

waters were moving and possibly feeding in the upper water column.

Seasonality

The quarterly latitude frequency plot (Fig. 1.3) illustrates the seasonal variations in N-S turtle 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 ($p<0.05$). During the winter season turtles were distributed between 26-41°S, and they spent a high percentage of their time between 31 and 32°S (mean: $32.4\pm3.1^\circ\text{S}$). During the fall, turtles movements ranged between 27 and 42°S, occurring 55% of the time in latitudes between 34 to 38°S (mean: $34.7\pm3.1^\circ\text{S}$). In the spring, turtles moved between 26-46°S, where more than 75% of all locations fell between 31 and 37°S (mean: $33.2\pm3.36^\circ\text{S}$), and in the summer, turtles moved between 30 and slightly more than 44°S, spending approximately 64% of their time between latitudes of 35 and 39°S (mean: $36.1\pm2.6^\circ\text{S}$). There were also differences in mean speed by season (Kruskal-Wallis, $\chi^2=122.14$, $df=3$, $p<0.05$), and pairwise comparisons indicated that summer-winter, fall-winter and spring-winter pairs were significantly different from one another (Wilcoxon-rank-sum test, Bonferroni adjusted $p<0.05$).

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 tracked turtles was $19.8\pm2.3^\circ\text{C}$, and they experienced a minimum SST of 10.21°C and a maximum SST of 28.4°C . There were significant differences in mean SST between

seasons (ANOVA, $F_{3,58}=56.52$ $p<0.01$) 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: $18\pm1.8^{\circ}\text{C}$) and spring (mean: $19\pm2^{\circ}\text{C}$) than during the summer (mean: $22\pm2^{\circ}\text{C}$) and fall (mean: $20\pm2^{\circ}\text{C}$) seasons (Fig. 1.3).

There was no significant seasonal trend in relation to Chl-a (ANOVA, $F_{3,58}=1.76$, $p=0.18$). Turtles showed an affinity for primarily mesotrophic/eutrophic (chl *a* density between 0.1 and 1 mg m^{-3}) values (mean: 0.458 ± 1.012 mg m^{-3}); during the fall, winter, spring and summer seasons, turtles spent 77.7, 75.1, 65.1, and 67.8% of their total locations, respectively, at 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, $F_{3,58}=0.28$, $p=0.75$).

DISCUSSION

This study is the first to present satellite-tracking data of juvenile loggerheads released by scientific observers from pelagic longline fishing vessels in the southwestern Atlantic. A key result from this study is the identification of the SWA as a juvenile loggerhead developmental high-use area. Remarkably, all tracked turtles remained within a relatively small area ($\sim 2,250,000$ km^2) during the entire 5 years of tracking; this is restricted compared to areas used by oceanic juveniles tracked in the major ocean basins (Polovina et al, 2000, 2004, McClellan et al, 2007, Kobayashi et al 2008, Mansfield et al. 2009). The minimum convex polygon (Fig. 1.1) 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 the Uruguayan and Argentinean coastal bottom trawl fisheries (Miller et al 2006, P. Miller *unpublished data*). While individuals included in this study were released in different years and from different locations, their paths remained within the minimum convex polygon (Fig. 1.1). The permanence of turtles within this restricted area indicates the prevalence of optimal foraging conditions and as such, the subsequent development of these turtles in this region.

Similar to tracked loggerheads in the North Pacific (detailed in Koboyashi et al. 2008 and Polovina et al. 2004), our results indicate that turtle movements, when summarized for latitude by season, correspond closely with the seasonal variability in SST. Satellite images from the southwestern Atlantic demonstrate that the warm Brazil current reaches its' southernmost latitude during the austral summer (January, February, March) whereas in the austral winter (June, July, August) Malvinas waters dominate and the Malvinas current reaches northernmost latitudes (Olson et al. 1988, Garzoli et al. 1992, 1993). There is also evidence for seasonal variability in latitudinal movements of loggerheads in the Pacific Ocean corresponding to variations in chlorophyll *a* (Koboyashi et al. 2008), however this pattern was not apparent from data collected in this study. Other studies on loggerheads, as well as leatherback turtles, also indicate the presence of a seasonal North-South trend in migration patterns (Hopkins-Murphy et al. 2003, Plotkin and Spotila 2002). This seasonality is possibly driven by thermal constraints experienced by the turtles, as well as high prey abundance generally known to be associated with productive blooms during the spring

and summer seasons corresponding with turtles being distributed further north, whereas, during colder seasons, turtles will tend to move south with warmer waters and rely more heavily upon prey concentrations at frontal regions/mesoscale eddies (Mansfield et al. 2009). It is also important to note that there may be lags between turtle movement and biological features as turtles do not directly consume primary producers. It is also possible that trends in ocean temperature, for example events triggered by climatic oscillations such as the El Niño Southern Oscillation, as well as global climate change, may lead to gradual relocations of foraging or migratory regions due to the importance of SST in juvenile loggerhead distribution (Koboyashi et al 2008).

The Southwestern Atlantic, characterized by the Malvinas/Brazil confluence, is a highly energetic (Gordon et al. 1989) and productive region (Bisbal, 1995). Currents in the region are often extremely fast; speeds as high as 5.4 km/h have been reported (Vidal et al. 2000). Given this, turtle speeds in this study are well within those theoretically possible, even if turtles were drifting passively with currents (Table 1.1). A mean speed of 1.13 km h^{-1} described for the turtles in this study is comparable to mean speeds reported in Koboyashi et al. 2008 (0.913 km h^{-1}), Polovina et al. 2000 (1.08 km h^{-1}), Cejudo et al. 2006 ($\sim 1.3 \text{ km h}^{-1}$), and Nichols et al. 2000 (1.05 km h^{-1}), among others. Additionally, 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, Revelles et al. 2007, Bentivenga et al. 2007, Koboyashi et al. 2008, Howell et al. 2010, McCarthy et al. 2010). The SWA is a region with high diversity of fronts and eddy formations (Acha et al. 2004), which are

linked to the high primary productivity of the region (Rivas, 2006, Romero et al. 2006) and have differing effects on fish biodiversity and abundance (Alemany et al. 2009). Although this 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 different movement behaviors are associated with mesoscale environmental features. Furthermore, with recent advancements in detection and monitoring of remotely sensed frontal oceanic features (Belkin et al. 2009, Miller et al. 2009) a finer spatial and temporal scale identification of frontal regions may be possible, which may lead to a broadening in our understanding of the environments encountered by large mega-vertebrates.

A large proportion of the range of turtle movements presented in this study fall almost entirely within regions of high loggerhead turtle bycatch identified in Giffoni et al. 2008 (Zone 2), and Sales et al. 2008 (Zone 3). When considering only the 50% utilization distribution (Fig. 2), the zone utilized most by the turtles tracked in this study is restricted between latitudes 30°S to 39°S. According to Giffoni et al. 2008, Zone 2 has the highest loggerhead CPUE values (0.939 Cc/1000 hooks) and 78% (n=1,532 turtles) of the total observed loggerhead captures for both the Brazilian and Uruguayan pelagic longline fleets between January 2005 and July 2007. Sales et al. (2008) also report relatively high CPUE values (0.419 turtles/1000 hooks) in this region. 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 this 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 (Howell et al. 2008), which may allow for more efficient future management.

This tracking study contributes to a growing body of literature (Morreale and Standora 1988; Witzell 2002; McClellan & Read 2007, Snover 2008, TEWG 2009, Mansfield 2009) that point towards the presence of a flexible ontogenetic shift between oceanic and neritic habitats for juvenile loggerheads, which differs from the classical life history model (Carr 1987; Musick and Limpus 1997; Bjorndal et al. 2000; Snover 2002). Results from this study demonstrate that tracked juveniles in the SWA actively dive to depths close to the bottom in regions within the 200 isobath. Although this is not conclusive evidence of bottom feeding, it does suggest at least exploratory, and possibly foraging dives. Further evidence suggesting that juveniles in this region may be foraging at depths in the neritic regions has arisen from a recent diet study of stranded juvenile loggerheads (Souza et al. in prep), where items such as crustaceans (*Libinia spinosa*, *Dardanus arrosor insignis*) and mollusks (*Buccinanops cochlidium*, *Pachycymbiola brasiliana*) were found in turtles stomachs. While in this study 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, it is possible that larger juveniles in this region may display more dives to bottom depths than those that are smaller. Further investigation into the variation in diving patterns of juvenile loggerheads present in the SWA neritic region will help to further understand this ontogenetic habitat shift.

Finally, when tracked movements are considered with the distribution and elevated bycatch levels of juvenile loggerheads in the SW Atlantic Ocean as reported by previous studies, the results of this study clearly define the waters off southern Brazil and Uruguay as the first identified juvenile loggerhead developmental high use area in the South Atlantic. This demonstrates the need to focus further tri-national and international collaborative efforts in research and management of sea turtles in this region of the world. The ability to identify features with which sea turtles associate will increase our predictive ability of essential turtle habitat and probability of fishery interactions, which will hopefully, ultimately, lead to a reduction in fisheries bycatch (Howell et al. 2008, Howell et al. 2010).

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Table 1.1 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 less than 10 days and was excluded from all subsequent analysis. ST: Still transmitting as of March 24, 2010, CCL: curved carapace length, Yr: year of turtle release.

Yr	PTT	Type of tag	CCL (cm)	Deploy date	Release location	End date	Last location	Tracking duration (Days)	Minimum distance traveled (km)	Average daily speed (km/h)
2006	12499	ST-20	62	7/1/06	BR (33.62°S, 50.51°W)	1/27/08	HS (34.56°S, 46.26°W)	575	14664.72	1.29
	12580	ST-20	63	7/6/06	BR (33.59°S, 50.16°W)	1/29/07	HS (35.70°S, 40.68°W)	207	5164.07	1.23
2007	12415	ST-20	62	4/24/07	BR (31.77°S, 49.21°W)	3/16/08	BR (32.37°S, 51.07°W)	327	6357.38	0.94
	12690	ST-20	61	4/29/07	BR (33.87°S, 50.84°W)	3/7/08	HS (37.86°S, 42.02°W)	313	5062.91	0.85
	12682	ST-20	63	5/31/07	BR (30.04°S, 48.22°W)	5/18/09	BR (28.39°S, 46.38°W)	639	10013.04	0.92
	12826	ST-20	83	6/5/07	BR (33.24°S, 50.11°W)	11/15/07	BR (31.74°S, 50.23°W)	163	3248.54	1.11
	12258*	ST-18	59	6/26/07	HS (31.78°S, 42.23°W)	7/25/07	HS (30.78°S, 40.39°W)	29	153.47	0.46
	12376	ST-18	51.5	6/29/07	HS (32.05°S, 42.18°W)	10/12/08	HS (28.90°S, 41.60°W)	471	7454.06	0.77
	12372	ST-18	73.5	9/16/07	BR (28.92°S, 47.36°W)	6/7/08	BR (31.13°S, 49.50°W)	265	5602.97	0.93
2008	12284	ST-18	72	6/27/08	BR (37.67°S, 46.28°W)	12/13/08	BR (34.82°S, 50.92°W)	169	3569.42	1.15
	12096	ST-18	69	8/18/08	HS (34.02°S, 51.21°W)	5/18/09	BR (33.79°S, 51.58°W)	273	3979.12	0.58
	79820	SPOT 5	60	4/2/08	UY (36.23°S, 52.97°W)	1/29/09	UY (34.65°S, 52.77°W)	305	7406.56	0.89
	79821	SPOT 5	56	4/3/08	UY (36.34°S, 52.53°W)	3/20/09	HS (38.11°S, 44.76°W)	351	13202.68	1.59
	79822	SPOT 5	63	4/2/08	UY (35.13°S, 52.18°W)	6/2/09	HS (33.84°S, 45.04°W)	426	11444.75	1.11
	79823	SPOT 5	60	5/26/08	UY (36.87°S, 53.93°W)	11/1/09	BR (34.50°S, 52.05°W)	524	11063.76	0.95
	79830	SPLASH	68	4/2/08	UY (36.13°S, 52.93°W)	9/20/08	BR (31.09°S, 49.90°W)	174	3889.40	0.90
	79831	SPLASH	56	4/5/08	UY (36.78°S, 52.06°W)	11/6/08	HS (34.15°S, 46.00°W)	215	9832.29	1.89
	79832*	SPLASH	49	5/26/08	UY (36.07°S, 52.03°W)	5/28/08	UY (36.71°S, 53.35°W)	3	81.97	2.17
	79833	SPLASH	64	5/26/08	UY (36.72°S, 52.73°W)	11/3/08	HS (30.50°S, 43.82°W)	161	3006.35	0.77
	79834	SPLASH	64	5/26/08	UY (36.09°S, 52.04°W)	10/18/08	HS (31.29°S, 41.70°W)	145	4096.76	1.21
2009	79835	SPLASH	63	3/30/08	UY (36.46°S, 52.19°W)	10/8/08	BR (33.36°S, 39.58°W)	192	5026.93	1.13
	95591	SPOT 5	57	11/11/09	UY (35.85°S, 51.24°W)	ST	HS (35.78°S, 39.36°W)	136	3648.10	1.08
	95592	SPOT 5	58	11/11/09	UY (35.98°S, 51.41°W)	ST	BR (29.67°S, 49.05°W)	135	3955.60	1.33
	95593	SPOT 5	59	11/11/09	UY (36.00°S, 51.38°W)	ST	HS (32.34°S, 48.96°W)	135	4080.60	1.32
	95594	SPOT 5	55	8/26/09	UY (35.96°S, 52.70°W)	ST	HS (34.69°S, 46.03°W)	212	6928.19	1.34
	95595	SPOT 5	58	8/26/09	UY (36.03°S, 52.60°W)	3/10/09	BR (32.48°S, 51.10°W)	196	3981.23	0.84
	95596	SPOT 5	62	8/25/09	UY (35.66°S, 52.28°W)	ST	UY (35.76°S, 51.82°W)	202	6423.73	2.98

Table 1.2 Maximum dive depth bin reached in different bathymetric regions by each turtle equipped with a SPLASH tag. NA: No Account.

PTT	Bathymetric regions (m)			Oceanic (>3000)
	Shelf (0-200)	Break (>200-1000)	Slope (>1000-3000)	
79830	150-200	200-300	100-150	200-300
79831	100-150	100-150	100-150	100-150
79833	NA	NA	NA	100-150
79834	NA	NA	25-35	70-100
79835	200-300	200-300	150-200	100-150

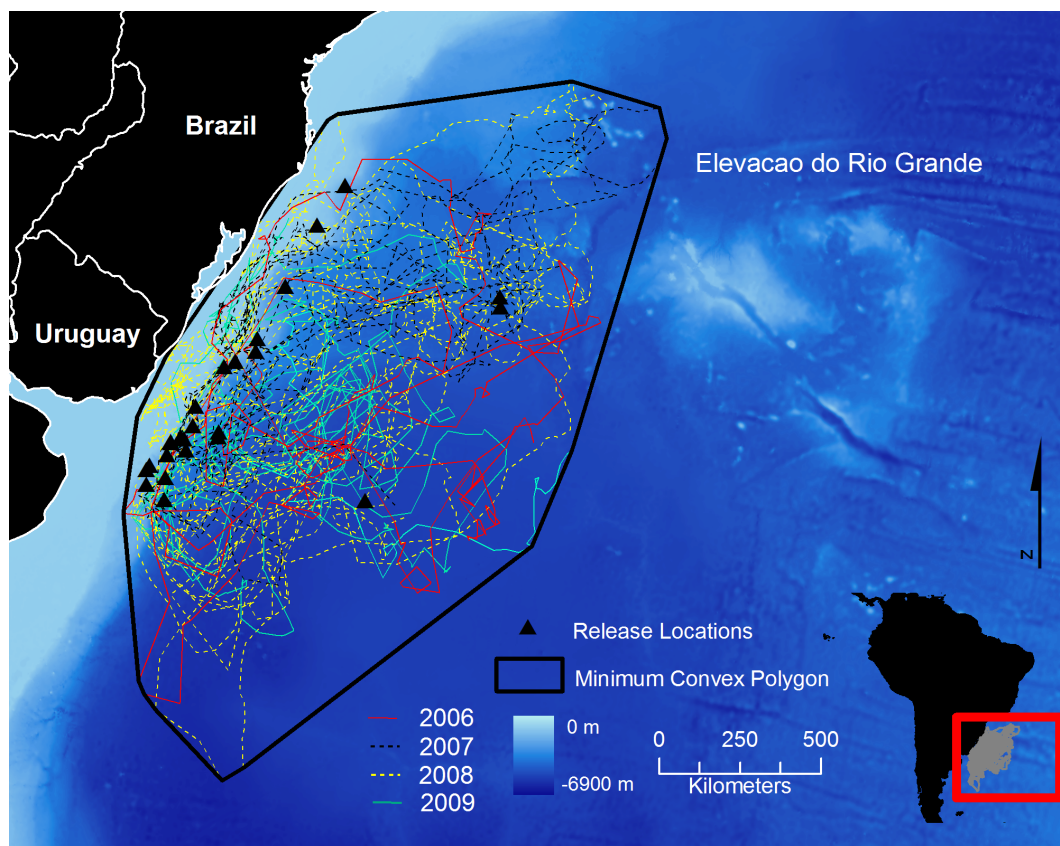


Figure 1.1. Movement paths of 26 immature loggerheads in the SW Atlantic between 2006 and 2010. Release locations for each turtle indicated by black triangles. Minimum convex polygon indicates the total area ($\sim 2,250,000 \text{ km}^2$) utilized by all tracked turtles. The first ten days (3% of total points) of tracking data from each turtle were removed in order to avoid including immediate post release behavior that may have been affected by the capture event.

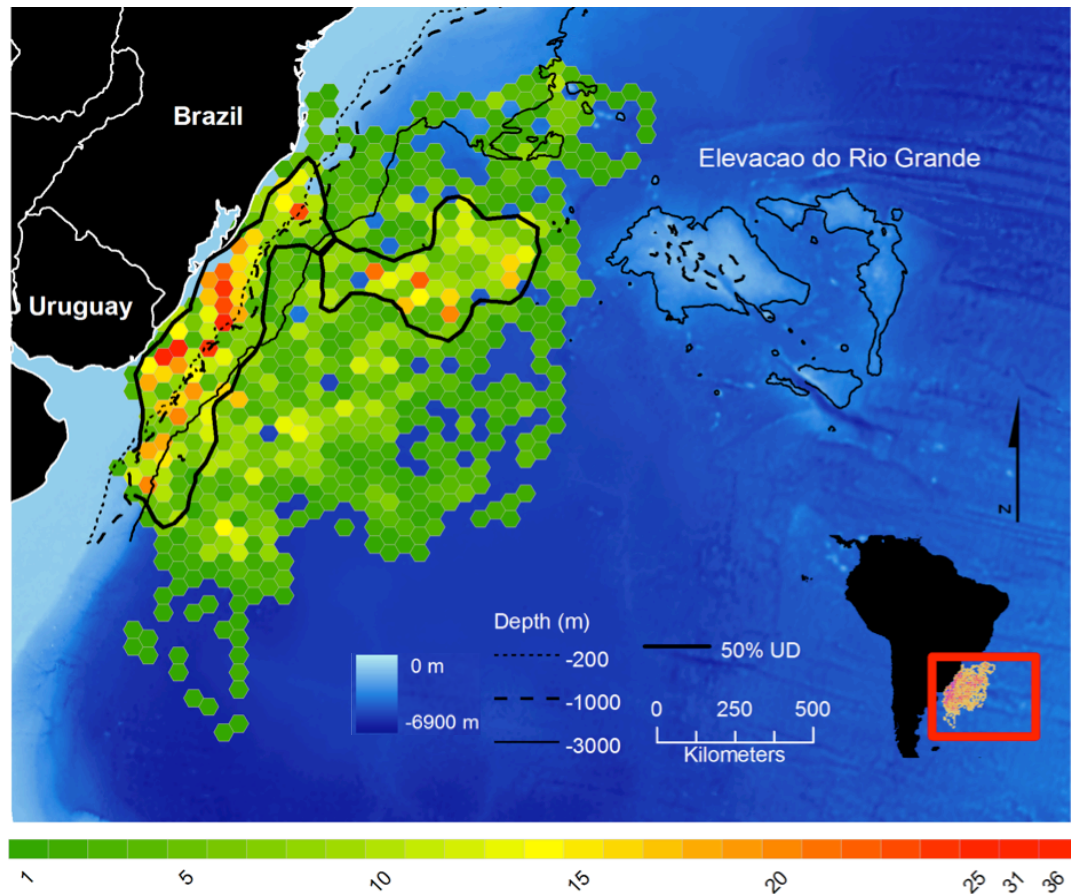


Figure 1.2. Spatial use of 26 immature loggerheads in the SW Atlantic between 2006 and 2010. Color denotes the number of days a turtle spent within each hexagonal bin. The 50% utilization distribution contour is presented as a dark black line. The first ten days (3% of total points) of tracking data from each turtle were removed in order to avoid including immediate post release behavior that may have been affected by the capture event.

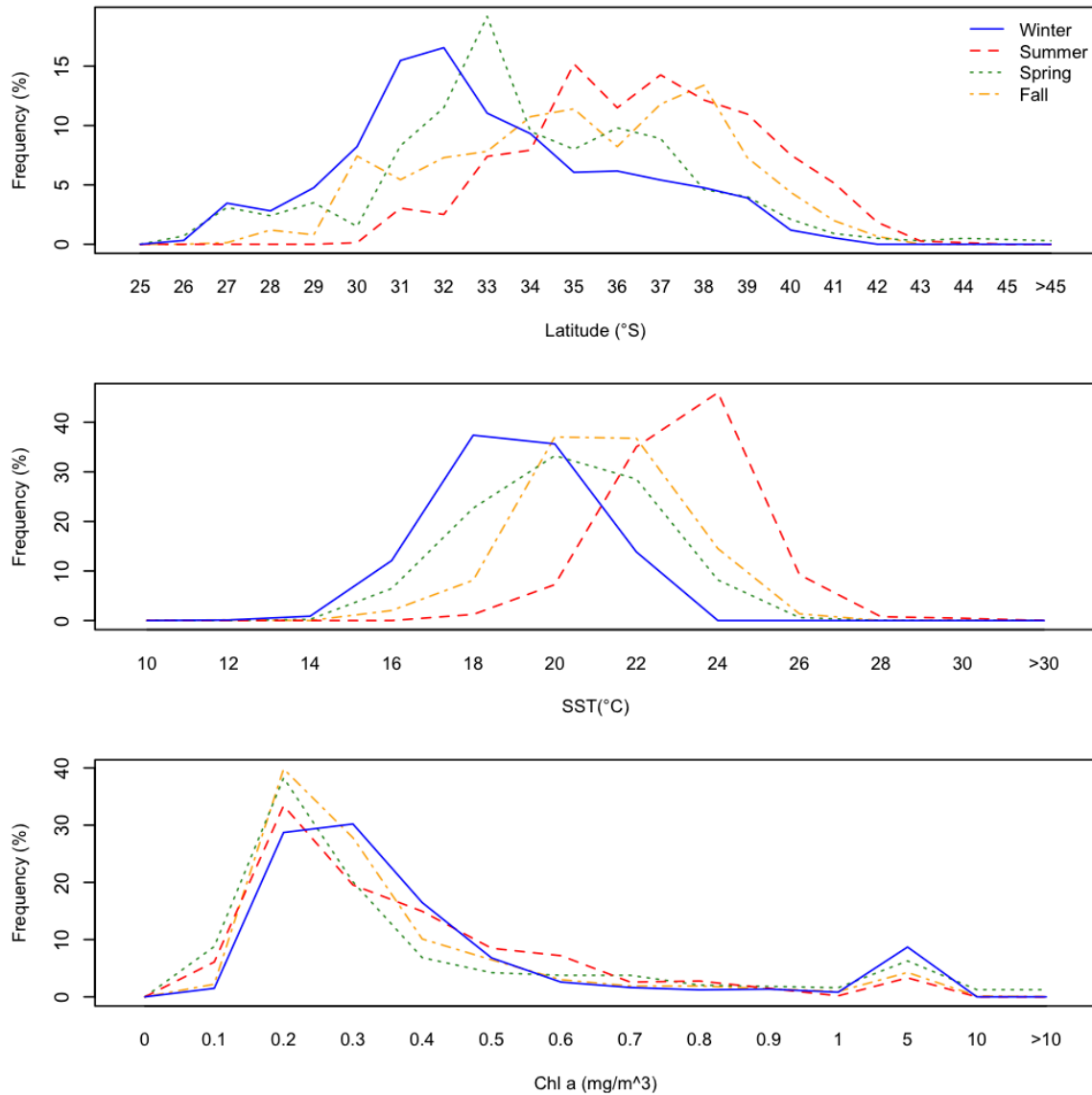


Figure 1.3. Quarterly frequency distribution plots of a) latitude, b) SST (°C), c) bathymetry region, d) chlorophyll a (mg m⁻³). Seasons specified as follows: Summer (Jan-Mar, N=757), fall (April-Jun, N=754), winter (Jul-Sep, N=924), spring (Oct-Dec, N=1337). STAT-derived SST and Chl a weekly averages identified for each first daily location point for all turtles.

CHAPTER TWO

DISTINGUISHING BETWEEN ACTIVE AND PASSIVE MOVEMENT IN PELAGIC MEGAFaUNA – ARE JUVENILE LOGGERHEAD SEA TURTLES JUST GOING WITH THE FLOW?

Caren Barceló

KEY WORDS: Loggerhead sea turtle · *Caretta caretta* · First-passage time · Area-restricted search · Active and Passive Movement

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ABSTRACT

Locomotion and feeding in marine animals are intimately linked to the flow dynamics created by their fluid environments, and factors that affect movement through a fluid medium are not the same as those in largely static terrestrial ecosystems. Recently, studies of marine predator movements have highlighted the effect of ocean currents on movement paths and our subsequent classification of active behaviors such as foraging. Here I quantitatively compare the behavior of 26 juvenile loggerhead sea turtles inferred from satellite tag tracks with the behavior of drifting surface buoys (hereafter “drifters”) in the Southwestern Atlantic Ocean. Using First Passage Time (FPT) analysis; a method to measure changes in movement patterns along a pathway through the environment, I determined that turtles and drifters exhibited Area Restricted Search (ARS) behaviors at the same spatial scale of 80km, suggesting that passive movement of turtles in ocean currents largely drives the scale of ARS behaviors. Current and sea floor depth were the most important correlates with turtle and drifter increased and decreased ARS. Both turtles and drifters generally showed a negative relationship between first passage time and current velocities. Time spent for turtles and drifters within an 80 km FPT radius indicated some similarities and differences between turtle and drifter behaviors. Main differences between both datasets were primarily observed on the continental shelf and shelf break, whereas offshore, time spent in 80 km radii showed no difference in behavior of turtles from drifters. The deviations in turtle behavior from the patterns of drifters are likely indicative of areas of increased active movement by the turtles. Also, turtle search

behavior did not exhibit strong relationships with sea surface temperature or chlorophyll *a*. There were no seasonal or yearly effects on ARS. I suggest that evaluation of drifter movements in the area of study is an important addition to satellite tracking work that attempts to identify foraging behavior in sea turtles or other marine nekton, including large marine vertebrates that may take advantage of ocean currents for transport and/or feeding.

INTRODUCTION

In order to more accurately describe the foraging ecology of marine megafauna, there is a need to account for both active and passive movements in the ocean when classifying behaviors. From a purely physical perspective, organisms living in fluid or gaseous habitats (such as birds, turtles, and fish) often take advantage of the existing kinetic energies of the environment to minimize energy expenditure while moving (Alerstam 1976, Klaassen et al. 2011). However, while the effect of wind and currents are known to impact movement in terrestrial environments, very few studies have quantitatively addressed the effect of ocean currents on tracks of marine mega-vertebrates (Gaspar et al. 2006). For animals tracked using satellite telemetry there also exists the challenge of distinguishing between different behavioral states (e.g. transiting or foraging) along paths. When active and passive movements are unraveled from the observed track, insights may be gained into the foraging habitat and the time budget of individuals (Gaspar et al. 2006, Weimerskirch et al. 2007). Identification of activities such as foraging is important for critical habitat designation,

and is an issue for fisheries management and marine reserve planning as many threats to marine megafauna are likely to take place during foraging (Hooker & Gerber 2004).

Rarely are we able to directly observe specific behaviors associated with successful foraging (Tinker et al. 2007). Most often we are limited to either specific technology developed to directly measure foraging success, such as stomach temperature sensors (Hooker et al. 2007, Kuhn & Costa, 2006), or by inferring behavior from indirect behavioral indices (Robinson et al. 2007). While the extensive use of direct measurement devices is currently not feasible due to the difficulty of deployment in large sample sizes, limited battery size/duration, and challenges of use in certain species (Myers & Hays 2006, Fossette et al. 2008), the use of indirect foraging metrics have been widely applied in terrestrial and marine ecosystems to decompose the movement path of an animal; defining track segments as one potential behavior or another. These analyses have often been used on wide ranging species such as oceanic predators where other behavioral information is not available.

There is a need to better understand how large marine vertebrates, such as pinnipeds, seabirds, sharks or marine turtles, make adjustments in their movements in response to food source patchiness in the ocean (Pinaud et al. 2005). Generally, predators searching for patchily distributed prey are expected to move in more twisted paths in areas rich with prey, and move in a more directed fashion in areas of low prey availability (Curio 1976, Kareiva & Odell 1987, Benhamou and Bovet 1989). Furthermore, the interactions between predators and prey are often known to take place at many, occasionally nested, spatial scales both in space and time (e.g., Kotliar and Wiens 1990, Fauchald & Tveraa, 2003) resulting in nested scales of predator

search behavior. Accordingly, two main types of movement behavior along trajectories of marine mega-vertebrates are generally of interest: a) movement that is usually synonymous with foraging, slower surface speeds and increasing turning rates, (a behavior termed Area Restricted Search (ARS)), and b) movement usually representative of transit while not foraging, characterized by more directed movement with faster speeds and lower turning rates (e.g. Benhamou 2004; Newlands et al. 2004). Multiple indirect behavioral indices have been employed to identify these different behavioral states including space-use metrics such as fractal dimension (Nams 1996, Laidre et al., 2004, Tremblay et al. 2007), first passage time (FPT) (Fauchald & Tverra, 2003, Pinaud & Weimerskirch 2007, Suryan et al. 2006), straightness and sinuosity indices (Erlandsson & Kostylev 1995, Benhamou 2004, McCarthy et al. 2010), and inferential modeling approaches such as switching state space models (SSSM) (Jonsen et al. 2007, Bailey et al. 2008).

However, like with all proxies, these indices are not perfect. Organisms may move or stay in one location for reasons other than foraging (Dingle 1996) therefore ARS behavior might be due to foraging, mating, parturition or a result of environmental constraints on behavior. For example, foraging time in seabirds or pinnipeds may be positively biased when individuals are forced to remain on the ocean surface due to strong wind conditions or while resting and/or digesting prey (Robinson et al. 2007, 2010, Gentry and Kooyman, 1986). Deciphering the elements of a movement path that derive from the environment or from the intention of tracked organism itself is essential if correct identification of the motivation for that behavior is important (Gaspar 2006, Dalziel et al. 2008).

The oceans are characterized by major currents and related features, such as eddies, meanders and fronts that influence the movements and distribution of large marine vertebrates (Lombardi et al. 2008, Polovina et al. 2004). Eddies and fronts have also been suggested to be aggregation zones for planktonic prey items (Witt et al. 2007). While not mutually exclusive, there are two important ways in which currents can affect the movement routes of animals in the ocean: the magnitude and direction of currents can modify the shape of the animal's trajectory (e.g. Gaspar et al. 2006), and currents can modify the distributions of planktonic prey resources (such as gelatinous organisms; salps and jellyfish), thereby indirectly affecting the foraging locations of predators such as sea turtles (Lombardi et al. 2008). As optimal foraging theory predicts, organisms will generally maximize energy intake while minimizing their energy expenditure when searching for, capturing, and consuming prey (MacArthur & Pianka 1966, Charnov 1976). Hence, marine vertebrates may be utilizing the currents to search for profitable prey patches or riding the current to move among habitats of varying quality. These scenarios need to be taken into account when attempting to differentiate between behaviors of animals living in fluid environments.

In this study I use 5 years of satellite tracking data from juvenile loggerhead sea turtles and Lagrangian surface drifters in the Southwestern Atlantic Ocean to compare the scales at which juvenile turtles and surface drifters conduct ARS-like movements using FPT analysis. I also compare ARS-like movements and transitory movements of turtles and drifters with environmental variables to assess whether habitat affected turtle ARS behavior is any different than that of passive drifters. Specifically, I set out to answer three key questions:

- 1) Are the spatial scales of “intensive searching behaviors” of satellite tagged sea turtles and passive drifters different?
- 2) Given that turtles are likely moving passively as well as actively, can a comparison of turtle and drifter median and maximum FPT be used to identify more active turtle ARS behavior from passive turtle ARS behavior?
- 3) Is active turtle behavior more likely to be associated with regions of high chlorophyll over the continental shelf and passive transitory movements with low chlorophyll, off the shelf?

MATERIALS AND METHODS

Study Region – Southwestern Atlantic Ocean

The SWA Ocean is one of the most energetic regions of the world's oceans (Gordon 1981, Chelton et al. 1990) as it is characterized by the Brazil-Malvinas Confluence formed by the collision of the Brazil Current (BC) and the Malvinas Current (MC) at approximately 38°S. The BC flows southwards along the continental margin of eastern side of South America forming part of the western boundary current of the South Atlantic subtropical gyre. The MC corresponds to a portion of the Antarctic Circumpolar Current (Piola and Gordon 1989) that carries cold, moderately fresh water towards the equator along the western edge of the Argentine Basin. After meeting with the MC, the BC continues to flow southwards until about 44°S where it changes direction and flows northeastwards (Saraceno et al. 2005). The SWA is a highly dynamic zone also influenced by the discharge of the Rio de la Plata estuary.

This region also has high spatio-temporal variability with great variations in water temperature, salinity, and primary productivity throughout the year. This complex environment may explain SWA's high biodiversity (Acha et al. 2004, Alemany et al. 2009). These characteristics contribute to the presence of abundant frontal areas, which have an important role in ecological processes (Carr 1986, Acha et al. 2004).

Tracking Data

I utilized satellite tracks obtained from 26 of 27 juvenile loggerhead sea turtles released by scientific observers from Uruguayan and Brazilian commercial longline vessels between 2006 and 2009 (see CHAPTER 1 & Table 1.1 for specific turtle details), and from 50 AOML-NOAA surface drifters used as Lagrangian tracers of the ocean currents in the SWA. All turtle transmitters were tracked by the ARGOS system (CLS, Toulouse, France); 1 turtle track from the original study was removed because the data record was for less than 10 days. Position fixes are divided into different Location Classes (LC) categories (A, B, and 0–3), corresponding to different location accuracies (see www.argos-system.org/manual). Turtle positions were filtered in STAT (Coyne & Godley 2005, seaturtle.org), using a 5km/h speed filter (Mansfield et al. 2009, James et al. 2005) excluding points on-land and including only those with lowest associated spatial errors, LC ranging from 3-1, corresponding to spatial errors between 150m to <1km (ARGOS 2008). All data were downloaded from STAT on November 17th, 2010. All locations were then linearly interpolated at 5km intervals retaining the original locations. The surface drifter data set was acquired from a pre-existing dataset compiled by NOAA's Atlantic Oceanographic and Meteorological

Laboratory (AOML, <http://www.aoml.noaa.gov/phod/index.php>) and extracted within the SWA bounded by the maximum and minimum latitude and longitudes reached by tracked turtles (26-45°S and 30-60°W) (see CHAPTER 1, Figure 2.1a) and for the tracking period (2006-2010). Drifters, drogued at 15m depth, were designed to follow the upper layer currents (see Niiler et al. 2005). Drifter locations were pre-processed and poor ARGOS locations were removed from the dataset and the trajectory of the drifter was created by optimal interpolation at uniform 6-h interval trajectories following custom AOML procedures for drifter track processing (Hansen and Poulain, 1996). I processed the dataset further by scaling back to one location per day and then spatially interpolating at 5km intervals to more closely resemble the processing of that of the turtles with equal 5km spatial intervals between points (see Figure 2.1b).

Oceanographic Data

I selected seven variables to describe the marine environment encountered by turtles and drifters between 2006 and 2010: sea surface temperature (SST), chlorophyll pigment concentrations (Chl *a*), bathymetry (depth), gradients of these three variables (depth_grad, sst_grad, & chl_grad), and mean geostrophic current velocity (curvel). Bathymetry data (1 minute latitude/longitude resolution) were obtained from the General Bathymetric Chart of the Oceans (British Oceanographic Data Centre, www.bodc.ac.uk). Due to intense year-round cloudiness in the SWA, the use of high spatial and temporal resolution remotely sensed variables was not possible. As such, 8-day composite images at 4km spatial resolution of satellite-derived SST and chlorophyll *a* concentrations were gathered from the Moderate Resolution

Imaging Spectro-radiometer (MODIS) (acquired from <http://oceancolor.gsfc.nasa.gov>), the key instrument aboard the Aqua satellite. Using the Sobel Gradient Operator (Russ, 1995), I calculated approximate front strength and locations of SST, Chl *a* and depth gradients over distance (3 x 3 pixel) (Suryan et al. 2006). I also utilized satellite-derived sea surface height (SSH) data of weekly (7 day) delayed-time merged Mean Absolute Dynamic Topography (MADT) product mapped at a global 0.3° by 0.3° from Ssalto-DUACS distributed by Archiving Validation and Interpretation of Satellite and Oceanographic data (AVISO, available from ftp.aviso.oceanobs.com), from which geostrophic current velocity (cm/s) was calculated. To ease interpretation I pooled currents into 40 cm/s bins, from 0-40 cm/s through >80 cm/s. Also for purposes of this study I labeled the bathymetric domains as shelf, shelf-break, slope, and oceanic bounded by the 200m, 1000m, and 3000m, >3000m isobaths, respectively.

First Passage Time Analysis

First passage time (FPT) analysis identifies the scale at which varying degrees of search effort take place along an animal's track, with elevated values of FPT (or search effort) referred to as Area Restricted Search (Fauchald 1999) and lower FPT values as extensive-mode or transitory movements. It is a valuable tool for analysis of remotely tracked animals because it provides an objective method to determine a scale for evaluation of animal behavior (Fauchald & Tveraa 2003). In animal tracking, FPT is defined as the “the time between the first passage of the circle backward and forward along the path” (Fauchald & Tveraa 2003) for a group of animal paths as a

scale-dependent measure of search effort. I calculated the FPT as the time spent within a circle of a given radius centered on each interpolated and original location of each track. This calculation was repeated for all positions along a track with radius varying from 10 to 500km at 10 km radii increments. The first part of the path was excluded, as the first-passage time backwards is unknown. The FPT values were natural log transformed so that times were independent of the magnitude of the mean FPT (Fauchald & Tveraa 2003).

It is expected that track regions with higher search efforts will have a higher first passage time at a given scale, and conversely, in regions where the animal moved with less intensive search, there will be lower FPT. To identify the mean spatial scale at which best to differentiate between high (ARS) and low (transitory) passage times for both turtle and drifter data sets, I plotted the mean variance of the log-transformed FPT for tracked individuals against the size of the radii), and calculated the peak in variance (following Fauchald & Tveraa 2003, Pinaud et al. 2005, Suryan et al. 2006). Additionally, to identify regions of more active movement from regions of more passive movement, I plotted FPT of turtles as a function of days since deployment (date), and superimposed a line representing the maximum FPT attained by drifters. This allowed us to conservatively identify regions along the track that were more likely representative of active behavior if the turtle FPT exceeded the drifter maximum FPT threshold.

Marine habitat characteristics associated with different levels of search effort was permitted using FPT using the following two-stage approach (as described in

Suryan et al. 2006). To minimize exaggeration of potential position errors while interpolating, I first only utilized the original (non-interpolated) position fixes. Secondly, from the original set of locations and their first passage times, I identified the position along the track having the highest FPT for the peak FPT radius identified with the mean variance peak plot. Retaining this location, I excluded all others that had radii overlapping in part with the radius pertaining to the identified maximum location. I then continued to search for the next maximum FPT (highest ARS) location for the remaining locations and iteratively repeated the exclusion process (Suryan et al. 2006) along each track until the entire path had been sub-sampled leaving only locations with no overlapping radii. The result of this sub-sampling procedure resulted in multiple location fixes along each track with corresponding FPT circles of the optimal scale (determined by the peak in variance described above). I then created an elliptical buffer of 10km surrounding the movement path the individual within each sub-sampled FPT circle. Within this buffer I extracted the median value (to reduce the influence of outliers) of each environmental variable of interest. When FPT was more than ~ 1.5 the temporal resolution of the environmental data (for SST and Chl *a* 8 day averaged data: > 12 days), I temporally averaged multiple successive files of each habitat variable within the given FPT radius defined buffer. All FPT processing and analysis and associated remote sensing data extraction was conducted in MATLAB Student Version 7.10.0 The MathWorks, Inc.) using custom programs developed by RS (Suryan et al. 2006).

Statistical Analysis

I used generalized additive mixed models (GAMM) to examine the effect of environmental variables (covariates or fixed effects hereafter) on the log-transformed FPT (a continuous response variable) at the peak radius scale (80km, see Fig. 2.3) for both tracked turtle and drifter datasets. Exploratory scatter plots indicated that the relationships between the dependent variable and covariates had clear non-linear relationships for most variables. As such, I regarded an additive model framework as appropriate for analysis rather than more common linear regression techniques. A Generalized Additive Model is a non-linear regression procedure that does not require *a priori* specification of the relationship between the dependent and independent variables (Hastie and Tibshirani, 1990, Wood, 2006); thus, GAMs have the possibility of fitting nonlinear relationships between the response variable and independent variables, which is often the case in ecological data (Ciannelli et al. 2008). Covariates in the model included all environmental variables described in the *Oceanographic Data* section. As there were multiple measures of FPT for each individual, each tracked individual (turtle or drifter) was included in the models as a random effect to account for correlation in FPT within each observed track. GAMM models were run for every combination of covariates and the response variable using Akaike's Information Criteria (AIC) to find the most parsimonious model (Burnham and Anderson, 1998). The variables of the single variable models with the lowest AIC scores were combined to construct multivariate models. Other variables were added until the lowest overall AIC score was achieved, and covariates were retained so long as they were significant ($p < 0.05$), resulting in the best-fit model. I assessed collinearity

among the oceanographic variables using scatterplots and calculating the pairwise Pearson correlations. Most correlations between variables were ≤ 0.4 indicating no significant correlations between our explanatory variables (Zuur et al. 2009), with the exception of Chl *a* and Chl *a* gradient, which were highly correlated (0.8). I excluded models containing both Chl *a* and Chl *a* gradient from the candidate model set. All inspected models presented no evidence of heteroscedasticity or departures from normality.

Preliminary explorations of the data to verify the assumption of independence indicated that the dependent variable was not spatially or temporally auto-correlated, verifying the usefulness of sub-sampling technique applied to the FPT data set. I determined that the dependent variable was not spatially autocorrelated by constructing spatial bubble plots of the standardized residuals from a linear model with depth as the independent variable versus the spatial coordinates, in this case, latitude and longitude (Zuur et al. 2009). I also determined a lack of temporal autocorrelation by plotting the standardized residuals versus time in autocorrelation function (ACF) plots. All GAMM and other statistical analysis were conducted in the software package R version 2.11.1 (R Development Core Team, 2008) and models were constructed using the R contributed *mgcv* and *nmle* packages (Wood et al. 2006, Pinheiro & Bates et al. 2007).

RESULTS

Spatial scale of turtle and drifter movements

A quantitative assessment of the turtle and drifter first passage times indicated that the area restricted search behaviors of the turtle movements were remarkably similar to the movements of surface drifters tracked in the region. A total of 302 and 633 FPT values were obtained for turtles and drifters, respectively. Both the turtles and drifters exhibited a peak in the variance of lnFPT at a spatial scale of 80km (Figure 2.2). The mean lnFPT at the optimal ARS scale (80km) was 0.58 ± 0.04 and 0.39 ± 0.024 for turtles and drifters, respectively. There was some variability in the FPT variance among tracked turtle individuals, as evidenced by the dispersion (standard error bars) around the mean lnFPT (Figure 2.2). The dispersion around the mean lnFPT for drifters was slightly less, indicative of less variability among individual drifters than turtles. Furthermore, the overall mean variance was higher in turtles than for drifters, suggesting that turtles switched between ARS and transitory behaviors more dramatically than what would be expected if solely a passive drifter.

A comparison of two turtle and two drifter tracks with their associated FPT radii ranging from 10-500km further demonstrates a similarity between the movement paths of turtles and drifters (Figure 2.3). For some individuals, different ARS scales were encountered at different locations along the track while others occurred nested within one another, where small scale ARS were contained within larger scales of ARS.

Indications of Active and Passive Behavior and Environmental Correlates

Areas of likely active and passive movements for juvenile loggerhead turtles were identified using a highly conservative method of classification of more active movements from more passive movements. Three of the 26 tracked turtles (12096, 95592, 12415) showed regions of more active movement compared to drifters (Figure 2.4). The location of active ARS for these three turtles occurred over the continental shelf. The remaining 23 turtles had no instance of FPT falling above the overall recorded maximum FPT of drifters.

Significant environmental variables associated with high or low FPT were strikingly similar between turtles and drifters. Model selection results indicated that the best fit models for turtles and drifters that described the effect of various environmental variables on lnFPT contained current velocity and sea floor depth as highly significant covariates (Turtles: $R^2 = 0.402$; Drifters: $R^2 = 0.506$, Tables 2.1 and 2.2). The turtle model also included depth gradient as a significant term. The inclusion of SST gradients in the turtle model and Chl *a* in the drifter model improved the variance explained by the models slightly (Tables 2.1, 2.2); however, as there was no significant improvement to the AIC, I chose the most parsimonious models for drifters and turtles as the best fit models, thereby excluding these variables from the final models. I also investigated the relationship of turtle and drifter lnFPT with Chl *a*, SST, gradients of each at lags of 7, 4, 21, 30, 60, and 90 days, but no association was identified. I additionally included Julian day, month and year factors into all models, however there was no significant association of FPT with seasonality and no yearly

effect. Furthermore, no interaction terms were significant and were not included in models.

Current and sea floor depth were the most important correlates with turtle and drifter FPT (Figure 2.6, 2.7, Table 2.3), but the model fits indicated some differences in turtle and drifter behavior. Current velocity was highly significant and nonlinearly related to lnFPT for the turtles and the drifters, with both generally showing a decreasing trend in lnFPT at high velocity currents (Turtle model: $p\text{-value} = 6.15\text{E-}11$, Figure 2.6, Drifter model: $p\text{-value} = <2\text{E-}16$, Table 2.3, Figure 2.7). While there was a general negative relationship of depth with FPT, the turtle model fit indicates the presence of some values closer to the mean FPT than evidenced by the drifters (Figure 2.6, 2.7). This is further supported by visual inspection of lnFPT color-coded turtle and drifter tracks (Figure 2.4); higher lnFPTs for turtles than drifters are evident along the continental shelf of South America than offshore. While the model fit to the behavior of turtles was remarkably similar to that of the drifters at low and fast currents (0-25, and 55-80 cm/s velocity currents, respectively) turtles showed some degree of active movement indicated by a plateau in the GAMM response curve of lnFPT with current velocities between ~25–55 cm/s that was not evident in the response curve of the surface drifters (Figure 2.6).

The effect of depth was non-linear in the turtle model and linear in the drifter model (Turtles: $p\text{-value} = 2.53\text{E-}09$, Drifters: $p\text{-value} = 0.00318$). Turtles had higher than average lnFPT in shelf and slope waters (up to ~4000m depth) and slightly below average lnFPT in waters deeper than 4000m (Figure 2.6). In contrast, drifters had less

of an effect of depth, with slightly below average lnFPT on regions over the shelf and slope (up to ~4000m depth) and slightly higher than average lnFPT in deeper waters (Figure 2.7). This difference in associations of turtle and drifter FPT with depth is further indicative of active ARS behaviors occurring in depths pertaining to the shelf and slope (Figure 2.8, Appendix B). Depth gradient had the least significant non-linear effect on turtle lnFPT, with slightly higher than average lnFPT with less depth gradient and decreasing lnFPT with increasing depth gradient.

All other variables examined such as temperature and chlorophyll in both simple exploratory statistics showed no correlation with lnFPT. This suggests that neither transit nor intensive search behavior (for turtles or drifters) were strongly correlated with these environmental variables. As this was also the case for drifters, the turtles tracked in this study may not be performing ARS in areas of higher or lower chlorophyll a as previously suggested, however further investigation is warranted.

DISCUSSION

Behavioral indices, such as straightness, sinuosity, first passage time, and switching state space models are commonly used to distinguish between foraging and transit in marine vertebrates with no simultaneous comparison to what passively moving objects (such as surface drifters) are capable of in the study region (e.g. Eckert et al. 2008, Weng et al. 2008). While the method described here does not remove the effect of currents on the track directly, it still accounts for currents by comparing the index of behavior of passive drifters to that of turtles. This may be more informative

way to identify active habitat selection than utilizing purely random movement (such as correlated random walks) to compare to marine animal movement.

While previous studies utilize first passage time as a behavioral metric, assuming that elevated values indicate elevated potential for foraging and straighter paths with higher movement speeds are indicative of more transitory movements, I demonstrate that FPT may also be useful to gain further insight into the active and passive behaviors of turtles when complemented with data from passively moving objects. In this study I provide evidence that for juvenile loggerhead turtles the identified scale at which area restricted search takes place, as well as the overall general relationship with current velocities, is remarkably similar to that of drifters. As the scale (overall mean peak in variance in FPT) is the same for our set of turtles and drifters (80km), the open ocean apparent ‘foraging behavior’ (or ARS) of juvenile loggerheads may be almost entirely due to passive advection by currents (see Appendix C). Additionally, as the scale of drifter and turtle ARS matches the scale of eddies in the study region, (Chelton et al. 2011), this lends further support to previous observations that turtles may be taking advantage of currents and foraging in eddies (Polovina et al, 2006, Mansfield et al. 2009). However, this apparent ‘use’ of eddies may be a largely the result of passive advection. This hinders our ability to infer a causal relationship between foraging and passive movements, such as those that might result in a loggerhead turtle’s path looping around an eddy (Polovina et al. 2004, Mansfield et al. 2009, Van-Houghtan et al. 2010). However, while the dominant behaviors of turtles identified with this analysis at this scale is largely driven by

current flow, juvenile loggerheads are likely foraging while passively moving through the ocean; identification of specific foraging maneuvering requires a finer scale analysis coupled with more precise movement tracking equipment.

Our results also suggest that while juvenile loggerhead turtles are largely passive in fast currents and oceanic habitats (currents greater than 80cm/s (Figures 2.5a 2.6a, 2.8a) and at depths greater than ~3500m (Figures 2.5b, 2.6b, 2.8b)), more active behavior (i.e. higher turtle lnFPT than drifters) generally occurred over the continental shelf and at medium current speeds than calculated for drifters (what is expected if entirely passive) (Figures 2.4 & 2.5). In general, turtles utilized more transitory movements when over oceanic waters, which are typically low in prey density, and more localized foraging movements when over continental shelf waters, which are typically higher in prey availability. While with this analysis I did not assess the directionality of movement when compared to the directionality of the current I infer that turtles are moving slower and more sinuously than exclusively passively moving drifters in regions over the continental shelf and in medium current velocities. I propose that turtles are able to compensate for currents between 25-55 cm/s while at currents of greater speeds (>55 cm/s) their behavior is more similar to exclusively passive movement. Medium currents over the slope are where the most differences are observed between turtles and drifters (Appendix B). This difference between turtles and drifters may be explained if the turtles are actively orienting towards the continental shelf an area that is very productive (Longhurst et al. 1998).

The apparent association of active behavior in relatively shallow depths and passive behavior in the open ocean is relevant when considering the life stage and body condition of the turtles in this study. As larger juveniles, these turtles are known to undergo a flexible ontogenetic shift into the neritic environment where they remain as adults (McClellan et al. 2007, Snover et al. 2008). During this transition period, individuals continue to use oceanic habitat as they grow (McClellan et al. 2007, Snover et al. 2008, Peckham et al. 2007, Mansfield et al. 2009), however the use of the oceanic environment may be largely passive in nature, resulting from turtles failing to retain themselves within the more productive neritic environment and being advected offshore. Furthermore, as the turtles tracked in this study may behave differently from each other respective of the type of injury suffered during incidental capture in pelagic longline fisheries, the prevalence of passive movement may be proportional to the severity of the injury. The three turtles (12096, 95592, 12415) observed to have more active foraging movements than drifters were hooked in the mouth and released without hooks, potentially indicative of light to moderate hooking, and the ability to successfully overcome drift by currents. Further study is needed to assess the differences of passive vs. active movement in post release turtles with differing levels of hooking injury; utilizing drifter data to characterize passive movement characteristics would greatly enhance such an evaluation.

To my knowledge there exists only one study that attempts to quantitatively separate voluntary motion (active movement) of a marine vertebrate from ocean current-driven motion (passive movement) (Gaspar et al. 2006). While the results

presented by Gaspar et al. clearly identify regions where the leatherback turtle's track is significantly modified by currents and where the track is largely due to the independent movement of the individual, the authors suggest that to properly identify active foraging along a track of this species one must completely subtract the contribution of currents from the trajectory. One crucial biological omission to this assertion is the fact that any given organism may, in fact, be using the flow of the currents to be carried and maintained within profitable food locations and away from poor quality habitat (e.g. very cold waters) all while minimizing energy expenditure on the part of the animal. A second important consideration is whether the accuracy of the device is sufficient to depict foraging movements of turtles.

In conclusion, the conservative approach I describe to distinguish active and passive movements and potential foraging behaviors may be a better way to identify where a sea turtle is actively compensating for current drift to remain in a profitable foraging location. This method does not remove the effect of currents on the track directly but still accounts for them by comparing the index of behavior of passive drifters to that of the turtles. Identification of foraging behavior of species and life stages that have mean traveling speeds of the same order of magnitude as current velocities, such as turtles (Luschi et al. 1998; Polovina et al. 2004; Ferraroli et al. 2004, 2006; Girard et al. 2006), tuna (Block et al. 1998) and non-breeding pinnipeds (Ream et al. 2005; Austin et al. 2006, Campagna et al. 2006)), remains to be clearly elucidated and previous results should be interpreted with caution. More direct measures of foraging, such as beak movement sensors or stomach temperature change

sensors, should be used in complement with satellite tracking when identification of foraging is essential, as proxies for foraging obtained from changes in tracks will always be uncertain.

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Table 2.1. Results from all turtle generalized additive mixed models (Gaussian error, identity link function) with lnFPT as the dependent term, various environmental variables as fixed effects (see text for details), all models contained individual turtles as the random effect. Best fit models highlighted in yellow and bold face and competing models indicated by boldface with no highlight.

<i>TURTLE MODELS</i>	<i>R²(%)</i>	<i>AIC</i>
curvel_med	0.321	649.46
depth_med	0.245	687.37
sstgrad_med	0.048	738.1
depthgrad_med	0.01	748.1
sst_med	0.011	750.75
chl_med	0.006	752.44
chlgrad_med	-0.003	753.78
jday	0.027	751.74
monthfac	0.0389	751.99
yearfac	0.002	753.81
curvel_med+depth_med	0.39	628.11
curvel_med+depth_med+sstgrad_med	0.403	616.89
curvel_med+depth_med+depthgrad_med	0.406	614.76
curvel_med + depth_med + sst_med	0.4	629.55
curvel_med + depth_med + chlgrad_med	0.416	628.24
curvel_med + depth_med + chl_med	0.402	629.69
curvel_med+depth_med+depthgrad_med+sstgrad_med	0.436	615.67
curvel_med+depth_med+depthgrad_med+chlgrad_med	0.412	620.59
curvel_med+depth_med+depthgrad_med+sst_med	0.405	616.37
curvel_med+depth_med+depthgrad_med+chl_med	0.406	615.93

Table 2.2. Results from all drifter generalized additive mixed models (Gaussian error, identity link function) with lnFPT as the dependent term, various environmental variables as fixed effects (see text for details), all models contained individual drifters as the random effect. Best fit models highlighted in yellow and bold face and competing models indicated by boldface with no highlight.

<i>DRIFTER MODELS</i>	<i>R²(%)</i>	<i>AIC</i>
curvel_med	0.495	1048.64
depth_med	0.09	1404.73
sstgrad_med	0.068	1406.04
chlgrad_med	0.044	1427.72
chl_med	0.019	1440.48
depthgrad_med	0.001	1445.55
sst_med	-0.0007	1446.48
jday	0.0309	1432.63
monthfac	0.0015	1447.2
yearfac	0.007	1442.8
curvel_med + depth_med	0.504	1042.3
curvel_med + depth_med + sstgrad_med	0.505	1045.38
curvel_med + depth_med + chlgrad_med	0.513	1044.7
curvel_med + depth_med + chl_med	0.51	1042.33
curvel_med + depth_med + depthgrad_med	0.504	1048.32
curvel_med + depth_med + sst_med	0.509	1048.57
curvel_med + depth_med + chl_med + sstgrad_med	0.505	1043.38
curvel_med + depth_med + chl_med + chlgrad_med	0.506	1044.47
curvel_med + depth_med + chl_med + depthgrad_med	0.504	1046.31

Table 2.3. Detailed results of best fit generalized additive mixed effects models for both turtle and drifter natural log-transformed first passage time for both linear and non-linear relationships of environmental variables (median depth, median change in bathymetry and median current velocity. Overall variance explained by turtle and drifter models were 41 and 50%, respectively. edf: estimated degrees of freedom.

TURTLES

Non-linear terms

Smoother term	edf	F	p-value	Signif. codes
s(curvel_med)	5.267	1.20E+01	6.15E-11	***
s(depth)	2.118	2.02E+01	2.53E-09	***
s(depthgrad_med)	2.661	5.013	0.00318	**

DRIFTERS

Non-linear terms

Smoother term	edf	F	p-value	Signif. codes
s(curvel_med)	3.416	181.666	< 2e-16	***

Linear term	Estimate	Std. Error	t value	Pr(> t)	Signif. codes
depth_med	-4.69E-05	1.58E-05	-2.962	0.00318	**

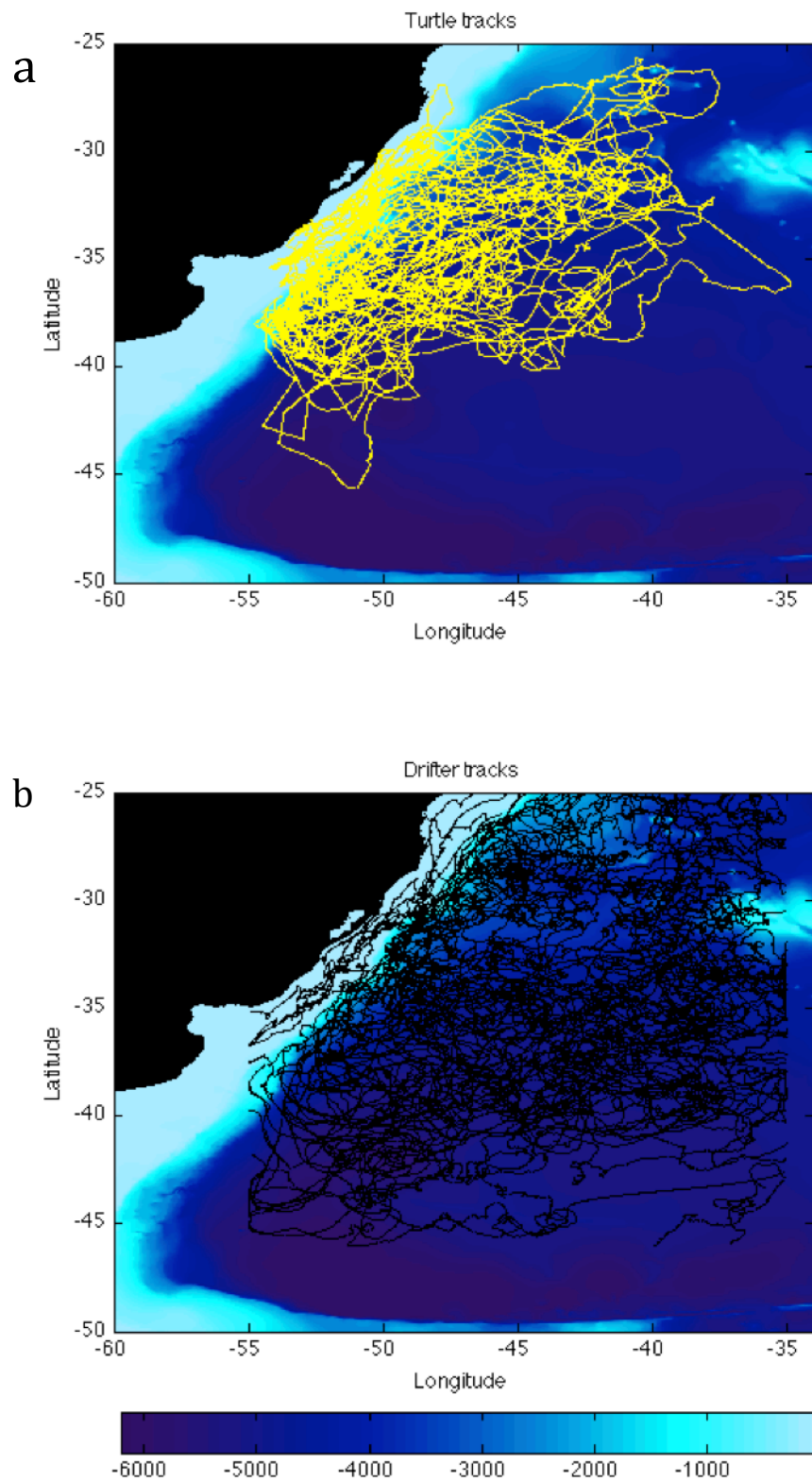


Figure 2.1. Tracks of all turtles (a) and all drifters (b) during the study period (all months between 2006 and 2010) overlaid on the bathymetry of in the Southwestern Atlantic.

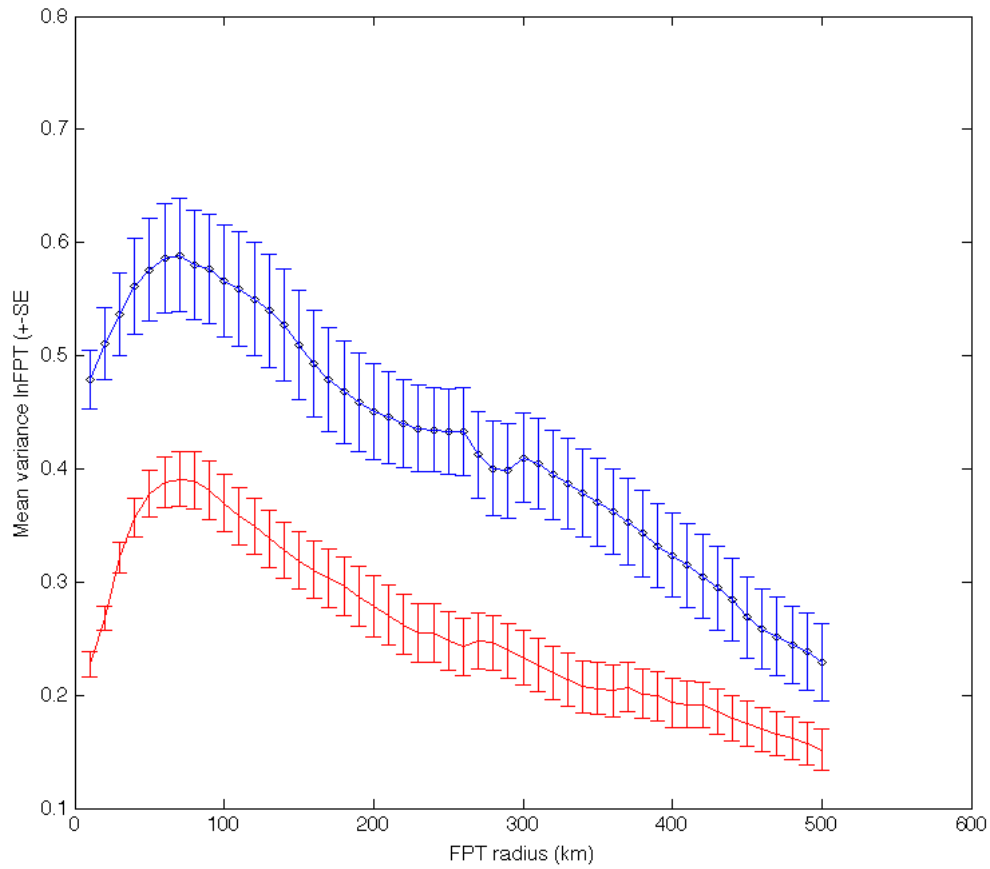


Figure 2.2. Plot of the mean variance (\pm standard error) in log-transformed first-passage time (FPT) vs. FPT radius size (km) ranging from 10-500km for 25 satellite-tracked juvenile loggerhead sea turtles (blue) and 50 langrangian AOML-NOAA surface drifters (red) in the SW Atlantic. For both turtles and drifters the variance peaked at a radius of 80km, the scale at which to best differentiate area restricted search from transitory movements.

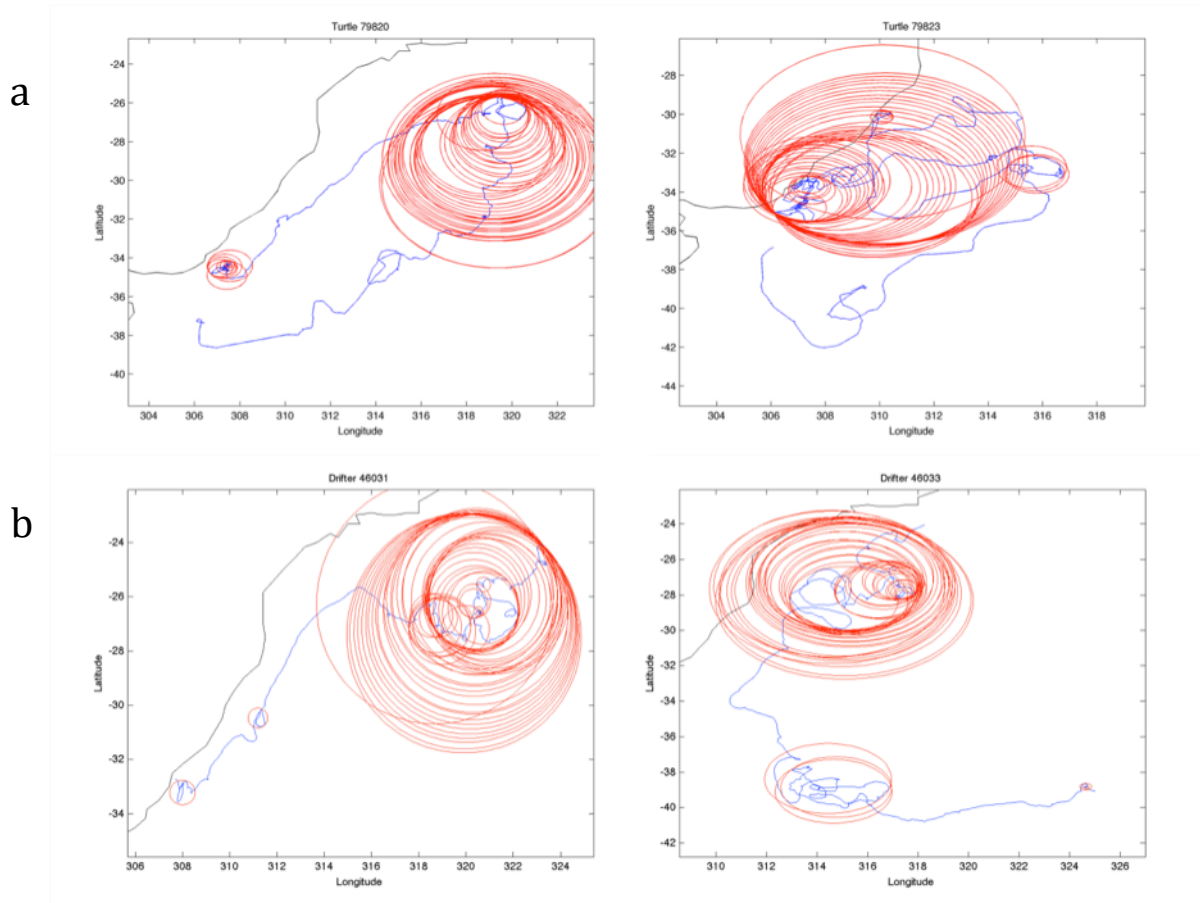


Figure 2.3. First passage circles ranging in scale from 10-500km centered on positions of maximum first passage time (FPT) for two turtles (a) (PTT #s: 79820,79823) and two drifters (b) (PTT #s: 46031,46033). The overlapping radii indicate that there are nested scales of “searching” occurring in both turtle tracks and that of drifters suggestive that currents play a major role in structuring the scale at which turtles conduct area restricted search.

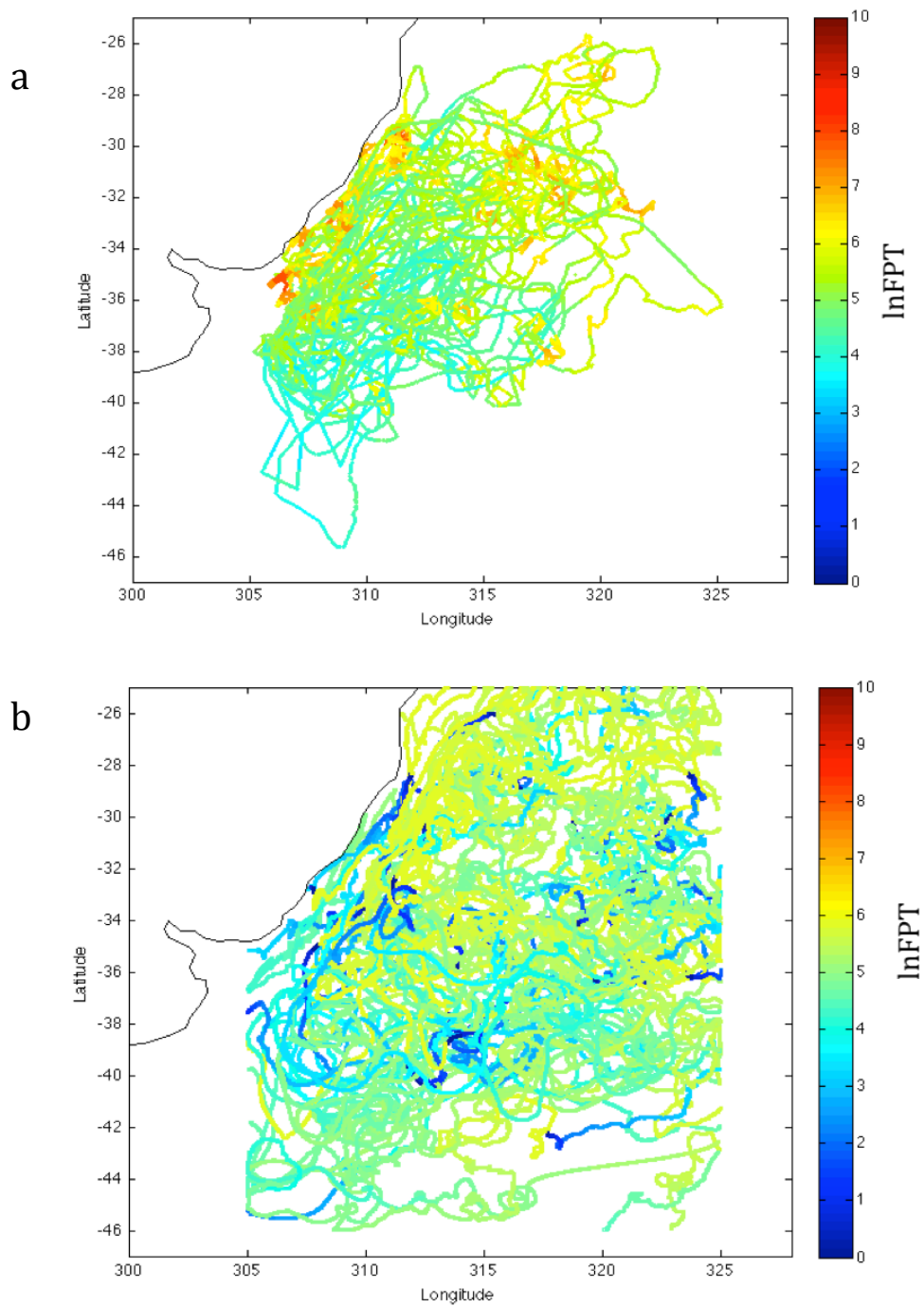


Figure 2.4. Tracks from all 25 tracked turtles (a) and from all 50 tracked drifters (b) with color-coding indicating values of first passage time metric (higher first passage time (lnFPT) indicative of area restricted search movements, lower lnFPT indicative of transitory movements).

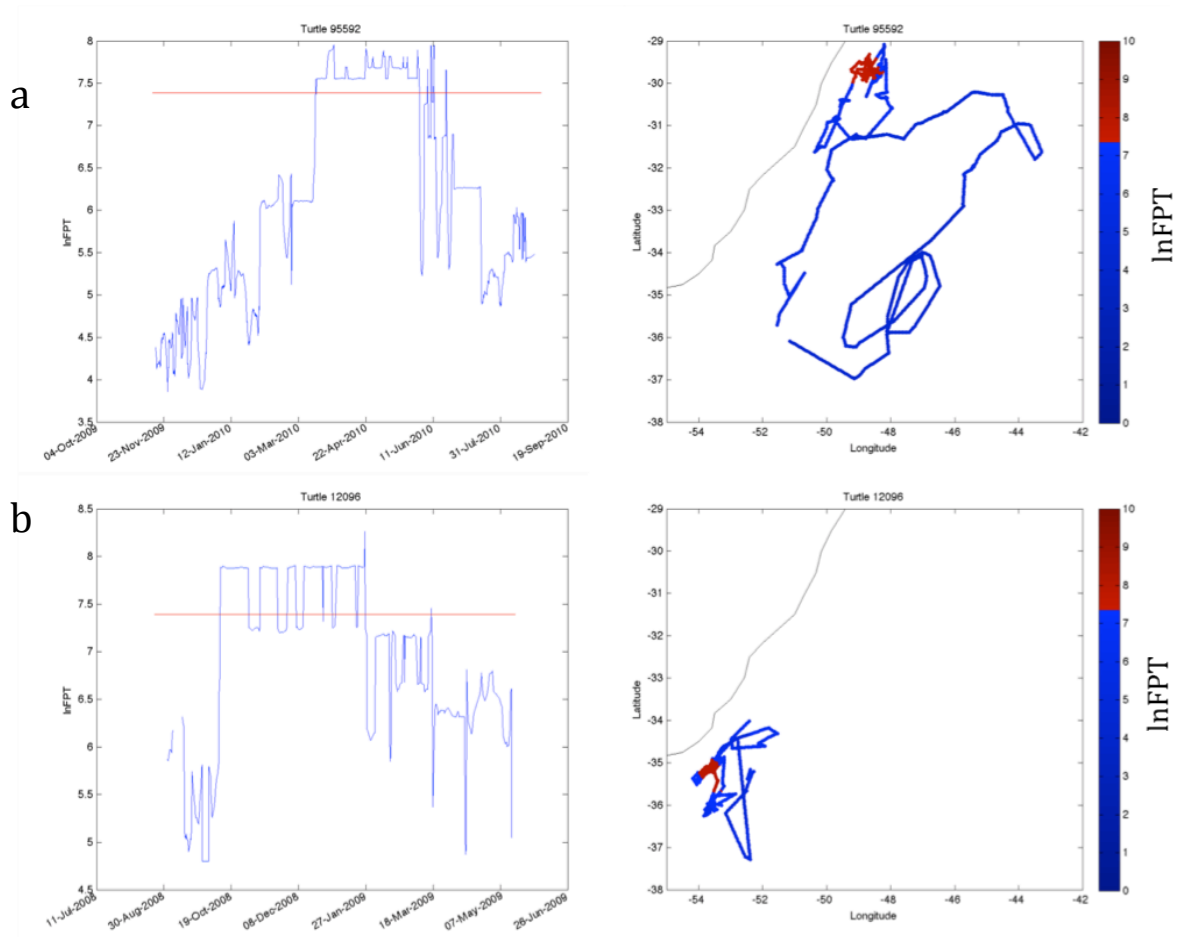


Figure 2.5. Time series of lnFPT for radius equal to 80 km for two turtles, 95592 and 12096, a and b, respectively, throughout tracking duration. On left, red line indicates maximum lnFPT (7.39) of drifters for entire study duration. On the right are the movement paths of the same two turtles with color-coding indicating values of first passage time along tracks. Higher (blue) than drifter maximum lnFPT indicative of active (red) area restricted search movements, lower than drifter maximum indicative of area restricted search or transitory movements containing some degree of passiveness.

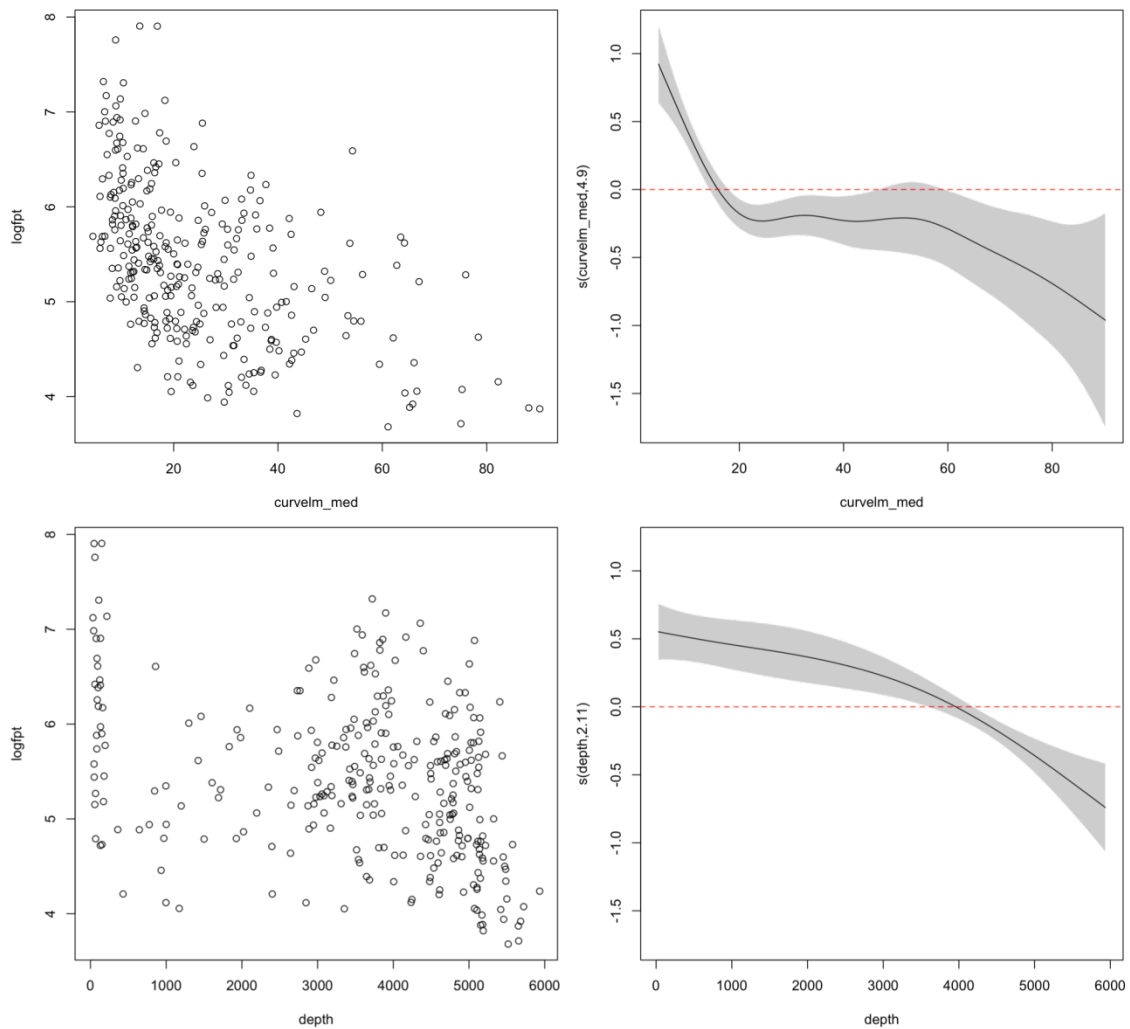


Figure 2.6. Results of the best fit generalized additive mixed model for the turtle data set showing the generalized additive model smoothing curves describing the effect of the predictor variables on lnFPT. Dotted lines represent mean lnFPT values scaled to zero, shaded areas indicate 95% confidence intervals around the main effects (continuous lines). The best fit model for the turtles is represented as a function of current velocity (cm/s), seafloor depth (m), and the median change in bathymetry (depth_grad). The effect of current velocity on lnFPT of turtles is higher than average FPT in slow currents (0-20cm/s) and lower than average FPT in fast currents (80-100cm/s). The effect medium current velocities on turtle lnFPT flattens out at slightly below average lnFPT values. Higher than average lnFPT were found in waters shallower than ~4000m and lower than average in waters deeper than 4000m.

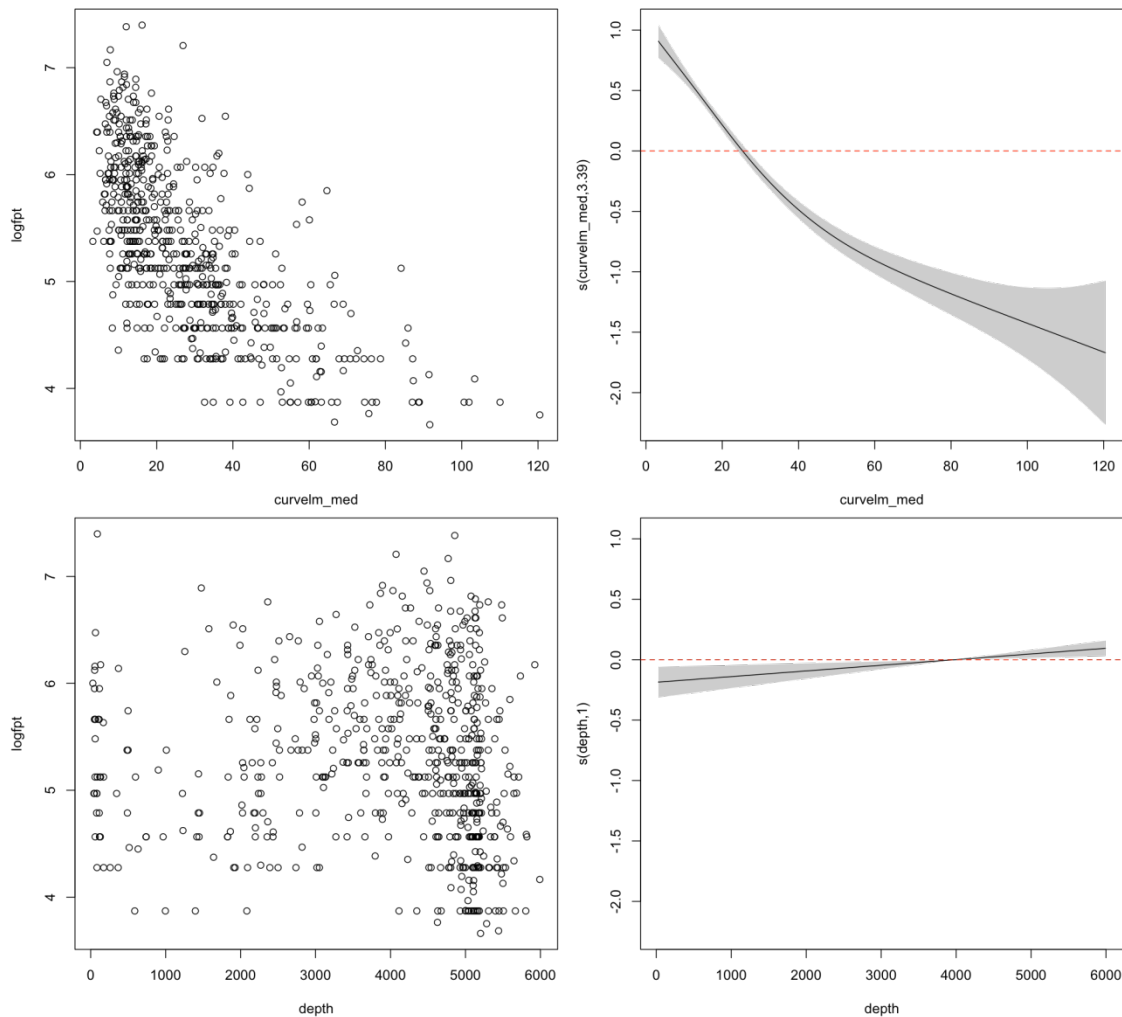


Figure 2.7. Results of the best fit generalized additive mixed model for the drifter data set showing the generalized additive model smoothing curves describing the effect of the current velocity and depth on lnFPT. Dotted lines represent mean lnFPT values scaled to zero, shaded areas indicate 95% confidence intervals around the main effects (continuous lines). The best fit model for the drifters is represented as a function of current velocity (cm/s), seafloor depth (m), and the median change in bathymetry (depth_grad). The effect of current velocity on lnFPT of turtles is higher than average FPT in slow currents (0-20cm/s) and lower than average FPT in fast currents (80-100cm/s). The effect medium current velocities on turtle lnFPT flattens out at slightly below average lnFPT values. Higher than average lnFPT were found in waters shallower than ~4000m and lower than average in waters deeper than 4000m.

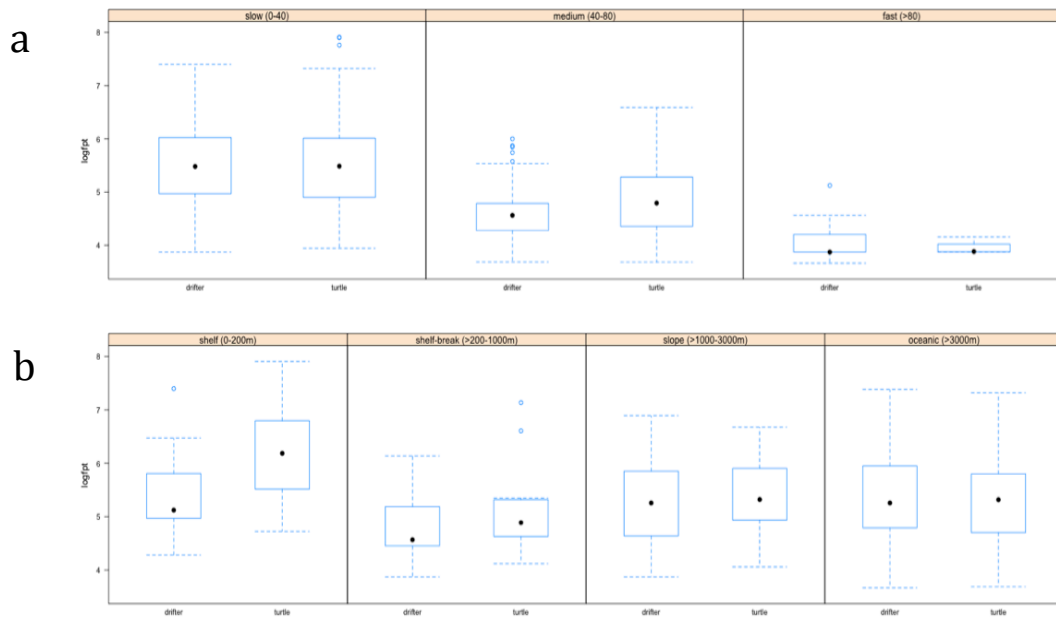
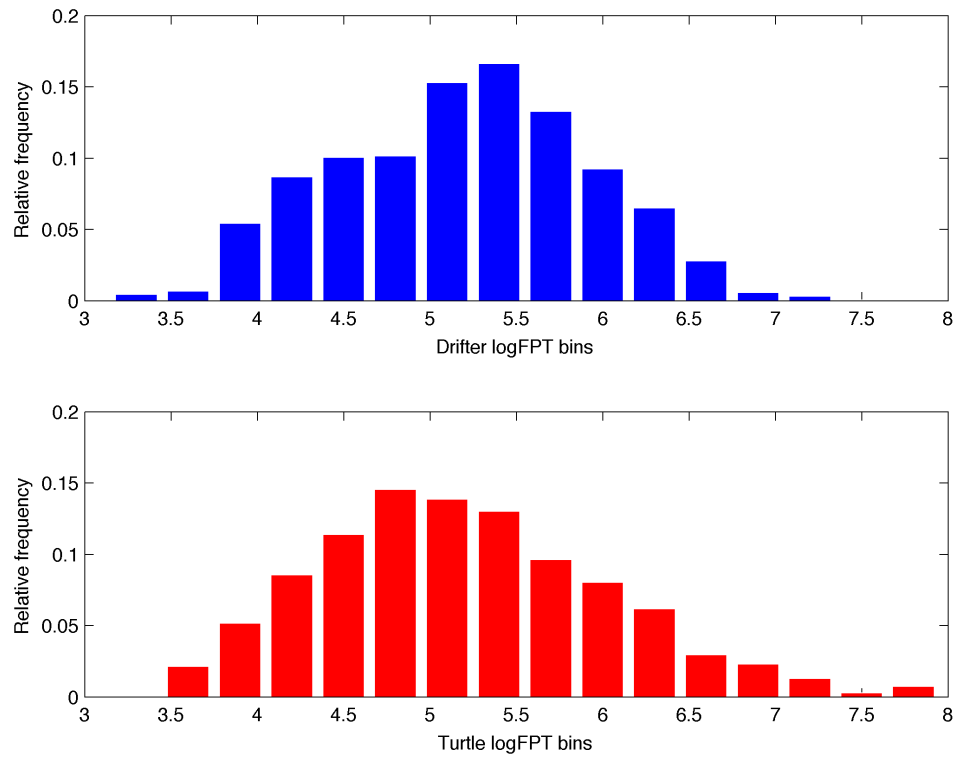
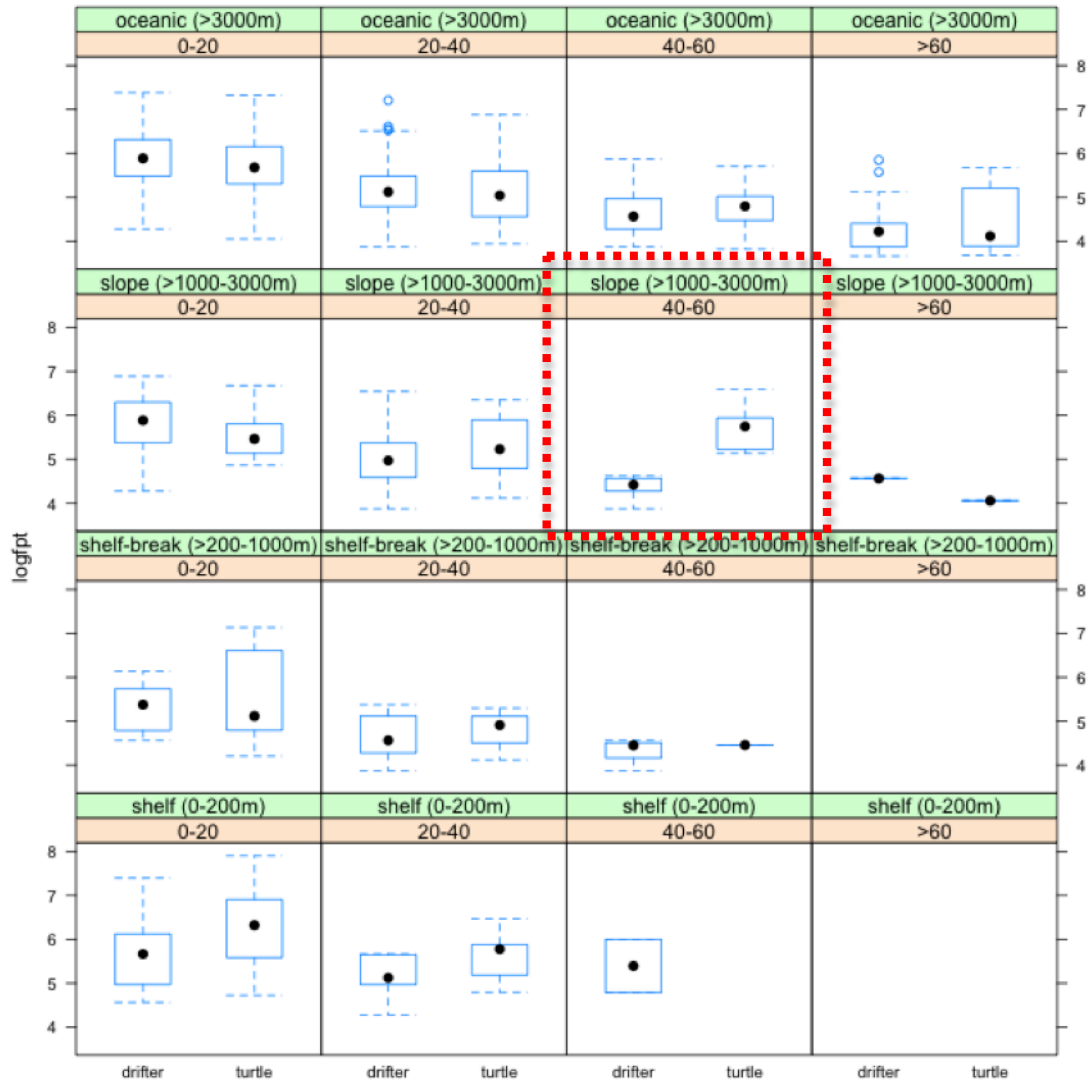


Figure 2.8. Boxplot comparison two main environmental variables of turtle (a) and drifter (b) log-transformed FPT in different depths and current categories. The shelf region (0-200) is the region where there is the most difference between turtle and drifter lnFPT.

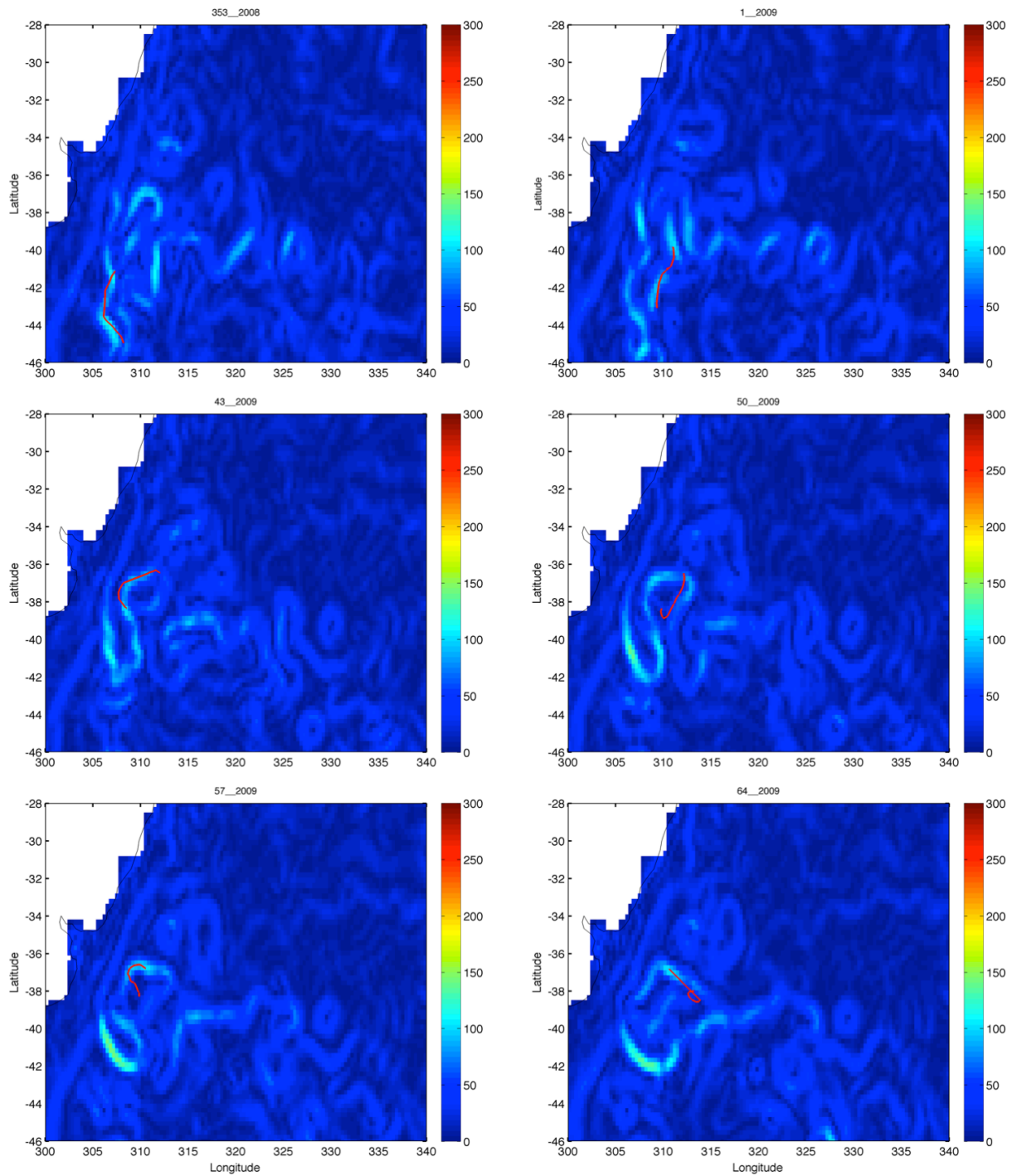
APPENDICES



Appendix A. Histograms of lnFPT for turtles (bottom, red) and drifters (top, blue). Mean lnFPTs (\pm SD) for turtles and drifters were 5.2 ± 0.8 and 5.2 ± 0.7 , respectively. In contrast to the relatively normal distribution of the drifter lnFPT, the turtle lnFPT histogram is slightly skewed to the left with a longer tail to the right at higher lnFPT.



Appendix B. Boxplot of lnFPT at each depth and current velocity category. Dashed red box surrounds depth (slope: >1000-3000m) and current velocities (40-60cm/s) where the most differences between turtle and drifter first passage time were observed.



Appendix C. Geostrophic current velocities from AVISO merged delayed time 7-day Mean Absolute Dynamic Topography product with loggerhead track line (red) from December 29th 2008 to February 19th, 2009, left to right & top to bottom, respectively.

