



## Foraging niche segregation between juvenile and adult hawksbill turtles (*Eretmochelys imbricata*) at Príncipe island, West Africa



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### ABSTRACT

Hawksbill sea turtles are the most tropical sea turtle species with one of the last remaining aggregations in West Africa found on Príncipe Island (1° 37' N; 7° 23' E). Here we present for the first time, data on the trophic and foraging ecology of both juvenile and adult hawksbill turtles found in the shallow waters of Príncipe, using stable isotope analyses of carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ), and assess any isotopic niche segregation between these two life-stages. Hawksbill turtles were sampled from December 2012 to June 2014, complementary to a snorkeling survey conducted around the entire coastline (ca. 100 km).  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values were measured in epidermal samples of 40 individuals and analyzed in the context of isotopic niche width and overlap (i.e. trophic and foraging niches). Juveniles hawksbills ( $n = 29$ ; < 60 cm curved carapace length (CCL)) occupy a significant smaller isotopic niche than adults ( $n = 11$ ; > 75 cm), especially in relation to  $\delta^{13}\text{C}$  values (i.e. habitat use) but also in  $\delta^{15}\text{N}$  values (i.e. trophic level). Variances between adults and juveniles were not homogenous for both isotopes and larger for adults, particularly for  $\delta^{13}\text{C}$  values. We found significant differences in  $\delta^{13}\text{C}$  values between the two groups, but not for  $\delta^{15}\text{N}$ , and a significant correlation between  $\delta^{13}\text{C}$  values and CCL for the pooled data. SIBER (stable isotopes Bayesian ellipses in R) outcomes support these results and, although niches are not completely segregated, it indicates spatial foraging segregation between juveniles and adults. The fact that Príncipe Island's shallow waters are constantly being patrolled by spearfishermen, together with the existence of a large insular platform and a superior dive capacity in larger hawksbills, might influence this segregation. Our results suggest that part of the adults may be originating from isotopically distinct areas. To have a better understanding on the distribution and abundance of the sea turtle populations in Príncipe, including their connectivity with other foraging and breeding areas, future in-water studies focused mainly on the entire insular platform of Príncipe, but also on the adjacent probable foraging areas of the Gulf of Guinea, are required.

### 1. Introduction

Hawksbill turtles (hereafter hawksbills) have a circumglobal distribution throughout tropical and some sub-tropical oceans and are of great importance for healthy reefs (e.g. by controlling sponges), but their numbers and habitat continue to decline worldwide (Mortimer and Donnelly, 2008). Like other cheloniid turtles, after emergence, post-hatchlings are found in major gyre systems, where they feed primarily on zooplankton near the ocean surface, followed by the recruitment (at 20 to 30 cm carapace length) to coastal inshore waters, where they feed primarily on benthic invertebrates (Bjorndal, 1997; Bolten, 2003; Mortimer and Donnelly, 2008). As juveniles grow and swimming capacity improves, they gradually migrate between a series of development habitats towards foraging grounds closer to their

rookery of origin, although some may first recruit to foraging grounds close to their natal beaches (Bowen et al., 2007; Proietti et al., 2014). These development habitats are usually related to coral reef areas (Pilcher et al., 2014) and, in most of the studied sites, do not seem to differ from that of the adults in terms of habitat characteristics (Broderick et al., 1994; Limpus, 1992; Velez-Zuazo et al., 2008). Nevertheless, and since larger turtles can dive longer and explore deeper ranges of the reef (Blumenthal et al., 2009a; Van Dam and Diez, 1996, 1997), a spatial segregation based on size appears to be the norm in certain areas (Blumenthal et al., 2009a; León and Diez, 1999; Meylan et al., 2011).

Once mature hawksbills began undertaking cyclical migrations between foraging and breeding areas every two-three years and, due to philopatry, each breeding population is a unique demographic entity

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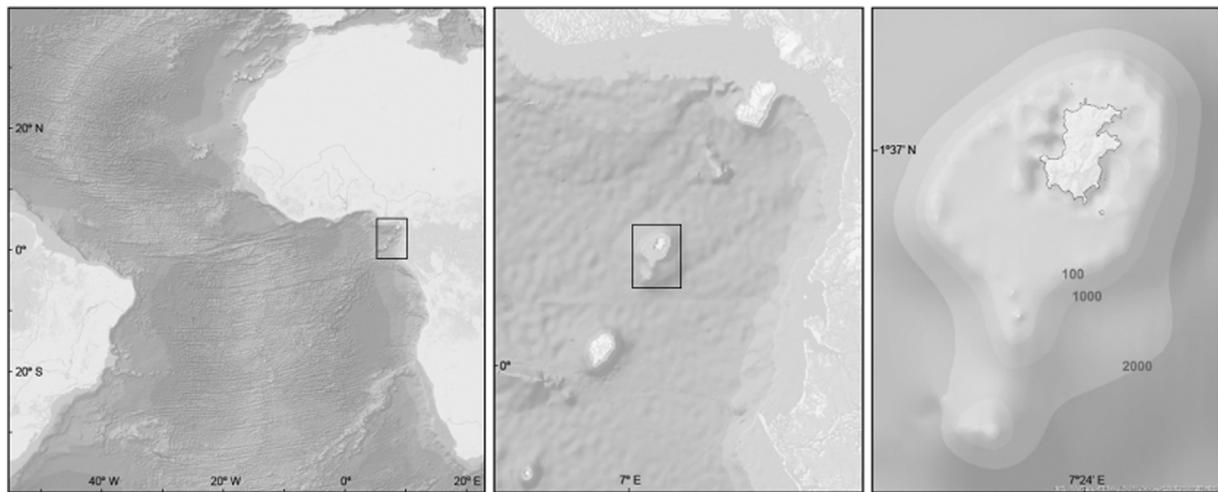


Fig. 1. Location of Príncipe Island and bathymetric contours within the Atlantic Ocean and Gulf of Guinea.

that might be comprised by several proximal nesting sites and rookeries within a region (Broderick et al., 1994; Bowen and Karl, 2007; Bowen et al., 2007). Adult migration distances vary greatly among and within populations, from a few kilometres to more than a thousand, but in average slightly over 300 km (see Hays and Scott, 2013). Hawksbill turtles of all life stages usually maintain limited foraging home ranges with small core areas, sometimes restricted to individual reefs, and appear to be resident for periods that can last several years (Blumenthal et al., 2009a; Limpus, 1992; Pilcher et al., 2014; Van Dam and Diez, 1998). Most often, differences in migrations and home-ranges of higher trophic level marine organisms in general and sea turtles in particular, are strongly connected to the relations between the proximity and magnitude of suitable foraging habitats, predation risk, intraspecific competition and local environmental and oceanographic conditions (see Ceia et al., 2015; Heithaus, 2013; Pilcher et al., 2014; Van Dam et al., 2008).

There is a lack of knowledge in the spatial distribution of hawksbill genetic stocks within West Africa. However, this region is considered one of the most threatened Regional Management Units for Marine Turtles (RMU's; Wallace et al., 2010). Hawksbill genetic studies performed in Príncipe and São Tomé Islands point to a unique and low variability genetic stock, which diverged from the Indo-Pacific phylogenetic clade (Monzón-Argüello et al., 2011; Proietti et al., 2014; Wallace et al., 2010). In all West and Central Africa it is estimated that < 100 hawksbills nest per year (Mortimer and Donnelly, 2008), and presumably the Islands of Príncipe and São Tomé harbor one of the last remaining hawksbill nesting aggregations in the region, with Príncipe accounting for > 20% of that total (Ferreira et al., 2012). In São Tomé and Príncipe, besides the recent law prohibiting all sea turtle use, hawksbill from all sizes are taken due to their high value for craftwork (Ferreira, 2015). Although Príncipe holds the larger insular platform of the region, little is known about hawksbills and the importance of these potential foraging grounds. However, near shore shallow waters (< 20 m) are occupied year round by juveniles and a small proportion of adult and sub-adults (Ferreira et al., 2015; Monzón-Argüello et al., 2011).

The distribution and movements across broad inaccessible areas make hawksbills, like many marine organisms, difficult to study with conventional methods and, therefore, not much effort has been directed in studying them at sea (Pilcher et al., 2014). Stable isotope analyses (SIA) are increasingly being used to better understand the spatial ecology and migratory connectivity of highly mobile and resident marine organisms, helping to develop effective conservation and management strategies (Ceia et al., 2015; Ceriani et al., 2014; Vander Zanden et al., 2015). While carbon stable isotope ratio ( $\delta^{13}\text{C}$ ) is an

effective tracer of the organism food source or habitat, the nitrogen stable isotope ratio ( $\delta^{15}\text{N}$ ) is generally used to assess the relative trophic position of species or individuals within a community or a population (Bearhop et al., 2004; Layman et al., 2007). Laboratory experiments with hard-shelled turtles (*Trachemys scripta* and *Chelonia mydas*) showed that epidermis isotopic values achieved equilibrium with diet (i.e. turnover rate) between 176 and 371 days (i.e. around 6 to 12 months) (Seminoff et al., 2006, 2007), meaning that isotopic ratios in the epidermis of individuals should reflect past locations and the food ingested there (Graham et al., 2010; Pajuelo et al., 2012).

Here we measured epidermis isotope values ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ) of hawksbill turtles, from near shore shallow waters of Príncipe Island, to estimate and compare isotopic niche widths (i.e. an area with  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values as axes) between juvenile and adult individuals while interpreting them in relation to their habitat use and trophic ecology as a proxy of foraging niche (Bearhop et al., 2004; Ceia et al., 2014; Layman et al., 2007; Newsome et al., 2012). Our goal is to assess differences in the habitat exploited and trophic ecology related with life-stages. While the juveniles found in the shallow water are assumed to be residents, adults found there can be either residents or migrants. Therefore, any habitat or trophic segregation between life stages should be reflected in the isotopic signatures. However, other sources of variation should be considered although these were not contemplated during this study. These include: 1) possible differences in turnover rate or discrimination factor between juveniles and adults, and 2) isotope ratios of hawksbills were not compared with those of potential prey to confidently infer their foraging ecology and habitat use due to the lack of isotopic data for potential prey (and diet itself) in this area; thus, baseline isotopic values which can vary spatiotemporally (Graham et al., 2010) may drive any possible intrinsic differences in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values between juveniles and adults.

## 2. Methods

### 2.1. Study area

Príncipe Island (1° 37' N; 7° 23' E) is the smallest (140 km<sup>2</sup>) of a two oceanic island nation, São Tomé and Príncipe, located in the Gulf of Guinea, West Africa (Fig. 1). This volcanic Island is also the oldest (ca. 30 m.yr.) of all the Gulf of Guinea Islands (see Burke, 2001), which can be seen by the extension of its eroded insular platform. It presents a warm and humid equatorial climate, with luxurious vegetation and a rich biodiversity with high number of endemic species, including marine (Jones, 1994). It has a valuable cultural heritage and around 7500 inhabitants (I.N.E., 2013) that live mainly in the northern half of

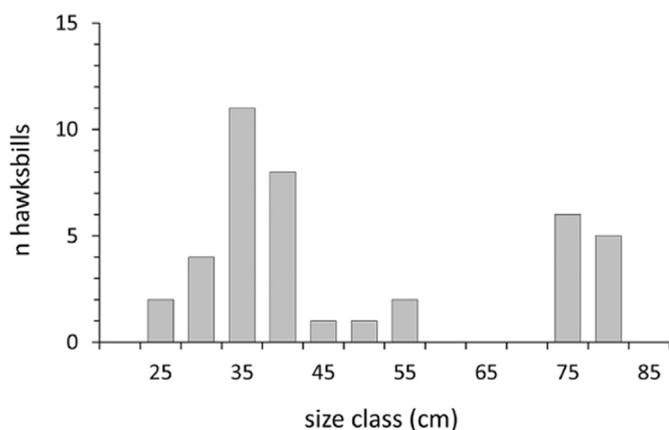


Fig. 2. Number of hawksbill turtles sampled ( $n = 40$ ) by 5 cm size classes (CCL).

the island, where the relief is lower and protected from the prevailing winds by the mountainous southern half of the island. The main currents and winds arrive from SW, which creates a division between the NE sheltered and sandy coast with the SW exposed rocky coast. As part of the Gulf of Guinea, Príncipe Island is a marine biodiversity hotspot of conservation concern (Roberts et al., 2002). Although large scale tourism investments are on the way, local authorities are committed to the sustainable development of the island and have so far avoided the implementation of negative anthropogenic activities (e.g. crude oil extraction support facilities and extensive palm oil farming); in 2009 a regional law on the protection of sea turtles was approved and recently it was nominated a Biosphere Reserve (recognized by UNESCO in 2012).

## 2.2. Turtle sampling

Forty hawksbill turtles were sampled from December 2012 to June 2014 during nesting (December/January) and post-nesting seasons (May/June). Individuals were captured in-water by hand, opportunistically, and hauled to the support boat during a snorkeling survey around the near shore shallow waters of Príncipe Island (Ferreira et al., 2015). Minimum curved carapace length (CCL) of each individual was obtained by a fiberglass tape measure and one Inconel tag was applied in each front flipper to avoid resampling. Body weight to the nearest 0.5 kg was obtained with a spring scale but, due to the high correlation with body size ( $F_{1,38} = 1289$ ,  $r = 0.99$ ,  $p < 0.001$ ), it was not analyzed in the scope of this work. Immediately before release, within 10 min from hauling, a small portion of skin was collected from the shoulder area with sterilized scalpel and tweezers, and then stored in 70% laboratory ethanol until isotopic analysis. Although preservation in ethanol can increase both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values in muscles of fish and squids (Kaehler and Pakhomov, 2001; Ruiz-Cooley et al., 2011), it was demonstrated that it has no significant effect on epidermal samples in three turtle species, two of them marine (Barrow et al., 2008). It was also found that preservation effects seems to be taxa-specific and not dependent on storage duration, at least for fish muscle and cetacean epidermis (Kiszka et al., 2014; Xu et al., 2011). Nevertheless, all samples were equally treated and any bias resulting from preservation in ethanol will be consistent, thus comparisons among the samples can be done with confidence.

## 2.3. Stable Isotope Analysis (SIA)

Prior to SIA, the epidermis of the hawksbill skin samples were dried for 24 h at 60 °C, cleaned of surface contaminants, minced and homogenized. Successive rinses in a 2:1 chloroform-methanol solution were used to remove lipids (Cherel et al., 2005). After this process, the means  $\pm$  SDs in C:N mass ratio of the skin samples were  $2.86 \pm 0.15$

( $n = 40$  individuals). The values are thus below the 3.50 threshold which correspond to a low lipid concentration in tissue (Post et al., 2007). Carbon and nitrogen isotope ratios were determined by a continuous-flow isotope ratio mass spectrometer (Delta V Advantage, Thermo Scientific, Bremen, Germany) coupled to an elemental analyser (Flash EA1112, Thermo Scientific). Approximately 0.4 mg of each sample was combusted and isotope values expressed as:  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$ , where  $R = {}^{13}\text{C}/{}^{12}\text{C}$  and  ${}^{15}\text{N}/{}^{14}\text{N}$ , respectively. The standards for carbon and nitrogen isotope values were Vienna PeeDee Belemnite (V-PDB) and atmospheric  $\text{N}_2$  (air), respectively. Replicate measurements of internal laboratory standards (acetanilide STD: Thermo scientific—PN 338 36700) indicate precision  $< 0.2\text{‰}$  for both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values.

## 2.4. Data analysis

Juvenile ( $J < 60$  cm CCL;  $n = 29$ ) and adult ( $A > 75$  cm CCL;  $n = 11$ ; one male and 10 females) hawksbills were grouped based on their size. The division in two size groups was clear owing to the absence of individuals between 60 and 75 cm (Fig. 2), the size range when individuals become reproductively mature (Witzell, 1983). Each group presented normalized data in their isotope values (both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) and CCL distributions. However, for the pooled sample ( $n = 40$ ),  $\delta^{13}\text{C}$  values and CCL did not follow a normal distribution. Due to the larger number and size range of the juveniles they were further subdivided by the median (39.2 cm) in two size groups and by geographic areas ( $1^\circ 37' \text{N}$ ;  $7^\circ 24' \text{E}$ ) into four groups. This enabled us to explore possible isotopic differences between sizes and capture locations within the juveniles. However, and since no significant differences were found in any of the isotopes (all  $p$  values  $> 0.3$ ) all juveniles were combined into a single group.

Statistical analyses were performed with Statistica software (StatSoft, Inc.) although, when specified, R 2.15.0 (R Core Team 2015) was used. Levene's test was used to test the homogeneity of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  variances between the groups, which provide a measure of niche width (see Bearhop et al., 2004 for more details). Pearson's  $r$  and Spearman  $r$  were employed to evaluate the relationships among the collected variables (CCL,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ), within the groups and in the pooled sample respectively. Because the sample sizes differed considerably between the groups (i.e.  $J = 29$  and  $A = 11$ ), SIA results were compared using a Mann-Whitney  $U$  test. Means  $\pm$  standard deviations were employed in the presentation of the results. Alpha = 0.05 was used to determine statistical significance.

To analyze stable isotope data in the context of isotopic niche width, comparing juveniles and adults, we adopted the metrics based in a Bayesian framework (Stable Isotope Bayesian Ellipses in R: SIBER; Jackson et al., 2011 but see also Syväranta et al., 2013). To test the SIBER assumption of a multivariate normal distribution for each group the R package 'mvnormtest' was used (Jarek, 2015). The area of the standard ellipse ( $\text{SEA}_C$ , an ellipse obtained by Bayesian inference that contains 40% of the data regardless of sample size and corrected for small sample sizes) was adopted to compare niche width between groups, and a Bayesian estimate of the standard ellipse and its area ( $\text{SEA}_B$ ) to test whether a group ellipse is smaller or larger than the other (i.e., the proportion of estimated ellipses, ten thousand, in adults group that were lower than the juveniles group; see Jackson et al., 2011 for more details). The convex hull area (TA) (Layman et al., 2007), although much more sensitive to sample size, was also employed to compare among groups and their overlap. All metrics were calculated using the functions implemented in the R package 'siar' (Parnell and Jackson, 2015). To further explore the data we pooled the groups and identified multivariate outliers with the R package 'mvoutlier' (Filzmoser and Gschwandtner, 2015). SIBER analyses were also performed removing outliers and the three larger juveniles from the sample (from 50 to 60 cm, Fig. 2). Isotopic spatial metrics (IsoSpace) can be used to evaluate variations in diet, trophic structure and habitat

use and do not need to be trophic-corrected prior to the calculations (Newsome et al., 2012).

### 3. Results

Minimum curved carapace length (CCL) of juveniles (captured throughout the year) varied from 26.5 to 59.8 cm ( $39.6 \pm 7.6$ ) and CCL of adults (captured only during the nesting season) ranged between 75.5 and 83.8 cm ( $79.3 \pm 2.4$ ) (Fig. 2).  $\delta^{13}\text{C}$  values ranged from  $-16.9$  to  $-14.9\text{‰}$  ( $-16.1 \pm 0.6$ ) for juveniles and from

$-20.5$  to  $-16.1\text{‰}$  ( $-17.9 \pm 1.5$ ) for adults. Overlap between adults and juveniles in  $\delta^{13}\text{C}$  values was narrow and highly significant differences were found between the two groups (Mann-Whitney Test:  $Z = -3.71$ ,  $p < 0.001$ ). In relation to  $\delta^{15}\text{N}$  values there was a clear overlap between groups, ranging from 8.8 to 11.2‰ (mean  $\pm$  SD;  $9.9 \pm 0.6$ ) for juveniles and from 8.9 to 11.7‰ ( $10.5 \pm 1.0$ ) for adults. Although near significance, no differences between the two groups were found in  $\delta^{15}\text{N}$  values (Mann-Whitney Test:  $Z = 1.94$ ,  $p = 0.053$ ).

There were significant differences in variances for both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values between the two groups (Levene's Test:  $\delta^{13}\text{C}$ :  $F_{1,38} = 14.1$ ,  $p < 0.001$ ;  $\delta^{15}\text{N}$ :  $F_{1,38} = 6.0$ ,  $p = 0.019$ ), with adults presenting much larger variances than juveniles, especially for  $\delta^{13}\text{C}$ . No significant relationships were found between  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$  and CCL within both juveniles and adults (Pearson correlation, all  $p > 0.05$ ). However, for the pooled data, there was a significant negative relationship between  $\delta^{13}\text{C}$  values and CCL (Spearman correlation:  $r = -0.46$ ,  $p = 0.003$ ) (Fig. 3), but not between  $\delta^{15}\text{N}$  and CCL or  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  (Spearman correlation: all  $p > 0.05$ ).

SIBER analyses (Fig. 4) indicate that the Bayesian probability of adults occupying a smaller isotopic niche than juveniles approaches zero (i.e.  $p < 0.001$ ). The area metrics revealed that the  $\text{SEA}_C$  and TA of the juveniles were, respectively, 4.5 and 2.8 times smaller than the isotopic niche area of the adults. Almost no overlap was detected in the isotopic niche, with 40% credible intervals, between juveniles and adults ( $\text{SEA}_C$ : juveniles, 0.27%; adults, 0.06%), and a small overlap was found in the convex hull area (TA: juveniles, 31.58%; adults, 11.32%) (Table 1). Variation from the juveniles to adult  $\text{SEA}_C$  was higher in both isotopic axes, towards a higher  $\delta^{15}\text{N}$  and lower  $\delta^{13}\text{C}$  values, with more expression for  $\delta^{13}\text{C}$  (Fig. 4).

Multivariate outlier detection of the pooled sample identified three adults with the adjusted quantile method (four with the 97.5% quantile), which were the three heaviest females in the sample (although not the largest ones). The removal of those three outliers from the adult  $\text{SEA}_C$  analyses (Fig. 4 and Table 1) decreased its area by 1.9,

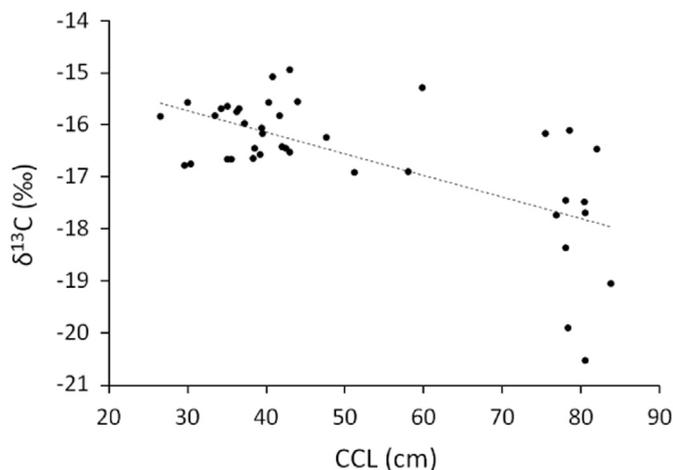


Fig. 3. Relationship between  $\delta^{13}\text{C}$  values (‰) and minimum curved carapace length (CCL, cm).

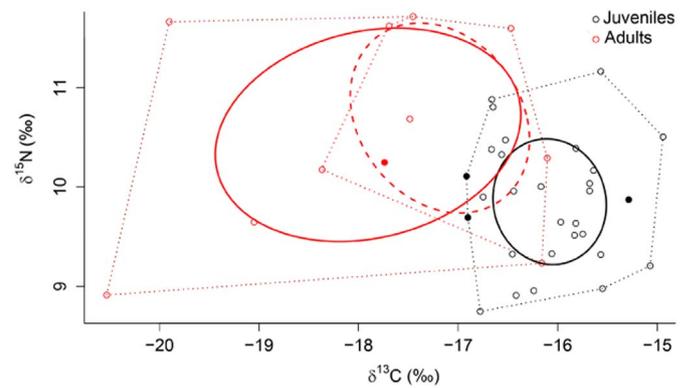


Fig. 4. Epidermal stable isotope values ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ) of hawksbill turtles captured in Príncipe shallow waters. Juveniles ( $n = 29$ ) are represented in black and adults ( $n = 11$ ) in red. The area of the standard ellipses ( $\text{SEA}_C$ , 40% credible interval) were represented by the solid bold lines and the convex hull area (TA) by dotted lines. Dashed ellipse represents adult  $\text{SEA}_C$  without outliers (the 3 dots on the left). The adult males and the three larger juveniles ( $> 50$  cm) are shown by filled dots. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1

Standard ellipse area ( $\text{SEA}_C$ , 40% credible interval) and convex hull area (TA) for juveniles and adults stable isotopes and respective overlap between them. Adults are presented with (a) and without (b) the three outliers.

	$\text{SEA}_C$	TA
Juveniles ( $n = 29$ )	1.127	3.708
Adults (a; $n = 11$ )	5.081	10.342
Adults (b; $n = 8$ )	2.629	3.643
Overlap (a)	0.003	1.171
Overlap (b)	0.111	1.05

nevertheless it was still 2.3 times larger than the juvenile  $\text{SEA}_C$  area. In relation to TA, the adult area decreased by 2.8 and become similar to the area for juveniles. As expected, overlap increased for  $\text{SEA}_C$  (juveniles, 9.85%; adults, 4.22%) and TA of adults (28.82%) while it slightly decreases for juvenile TA (28.3%). Removing the three larger juveniles (between 50 and 60 cm) from the analysis did not considerably affect the  $\text{SEA}_C$  or TA, in both area and location, thus the interpretation of the results remained similar.

### 4. Discussion

Carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotope ratio data show a foraging niche partition between adult and juvenile hawksbill turtles occurring in Príncipe Island's shallow coastal waters. This difference was most evident for  $\delta^{13}\text{C}$  values, suggesting a spatial segregation between these life-stages. Moreover, adults were distributed by a much wider range of isotopic values (both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) than juveniles, suggesting higher plasticity in their foraging and trophic niches. Niche metric comparisons underscore these differences by showing a clear segregation of isotopic niche area ( $\text{SEA}_C$ ) between life-stages, although ellipses partially overlapped, with adults occupying a highly significant larger isotopic niche than juveniles.

Although there are no studies on the hawksbill diet throughout the region, in other areas hawksbills are predominantly spongivorous but they feed on a variety of items (e.g. tunicates, algae, soft corals) depending on the habitat type, prey abundance and feeding selectivity (Bjorndal, 1997; León and Bjorndal, 2002; Mortimer and Donnelly, 2008). The lack of these types of studies for the region, also on hawksbill and prey stable isotopes analysis at a global scale, limits our ability to make inferences on their foraging ecology. However, it is likely that the diet among the hawksbills found at a given foraging ground is similar, even across size classes (Bjorndal, 1997; Mortimer

and Donnelly, 2008; Stringell et al., 2016). Thus, the highly significant differences in  $\delta^{13}\text{C}$  values between the two hawksbill life-stages, primarily indicative of the location and habitat use of the consumers (Layman et al., 2007; Michener and Kaufman, 2007), suggests spatial foraging segregation although not far apart due to the proximity of both isotopic niches. Since  $\delta^{13}\text{C}$  values often decrease from inshore to offshore, well as from shallow to deeper waters (Hill et al., 2006; Michener and Kaufman, 2007; Nerot et al., 2012), the significantly higher  $\delta^{13}\text{C}$  values of juveniles, together with the fact that adults are rare in the shallow coastal waters of Príncipe during the post-nesting season (Ferreira et al., 2015; Monzón-Argüello et al., 2011), supports the spatial segregation between life stages at Príncipe foraging habitat. Although  $\delta^{13}\text{C}$  values can increase with trophic level and have an effect in the observed differences, it does to a much less degree than  $\delta^{15}\text{N}$  (Bearhop et al., 2004; Michener and Kaufman, 2007) and, on happening, it would mean that adults were foraging on lower trophic level prey than juveniles. In fact, results showed the opposite with adults presenting slightly higher  $\delta^{15}\text{N}$  values than juveniles. Though differences were not significant they were near significance and thus we cannot ignore the possibility of ingestion of higher trophic level prey by adults, and further research is necessary. However, a recent study with hawksbills harvested at a legal turtle fishery in the Caribbean did not find differences in the taxonomic distinctness of diet related to body size (Stringell et al., 2016), reinforcing the similar foraging strategies between adults and juveniles. Although the movement of nitrogen in the marine ecosystems is mainly dictated by biological processes, baseline  $\delta^{15}\text{N}$  values also vary laterally and vertically within the water column and may differ among consumers even if they are foraging at the same trophic position (Montoya, 2007; Vander-Zanden et al., 2013). In this way, if adults are foraging away from the shallow waters, as might be the case, the difference in  $\delta^{15}\text{N}$  values is probably reflecting the abrupt decline of the influence of run offs away from the coast, in which organic matter is usually depleted in  $\delta^{15}\text{N}$  values (Montoya, 2007). The partial overlap of the isotopic niches makes it plausible that the adult foraging areas might be geographically close, however our data does not allow to correctly infer it. This is because the entire Gulf of Guinea area is characterized by a uniformity in the baseline isoscapes, of both carbon and nitrogen (Graham et al., 2010), and the upper ceiling on hawksbill migration (1630 km, Hays and Scott, 2013) allows them to potentially occupy foraging areas throughout that region.

Juvenile and adult hawksbills displayed considerable differences in the homogeneity of variances for both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ . This is noted by the larger standard deviations of both isotopes (especially in  $\delta^{13}\text{C}$ ) in the adult group. According to Bearhop et al. (2004) and Ceia et al. (2014), it is expected that populations where individuals explore wider geographic areas show higher variations in isotope ratios, than populations foraging in more restricted areas. This suggests that adults exploited extensive and isotopically distinct areas, and presumably different habitats. In addition, for the pooled data, we found a negative significant relationship between  $\delta^{13}\text{C}$  and CCL. We associated this result with the increase in dive capacity as turtles grow, which enables larger animals to explore a greater variety of depths and consequently a wider geographic area (Blumenthal et al., 2009b; Van Dam and Diez, 1996, 1997). Available in-water studies report the simultaneous presence of juveniles and adults hawksbills in foraging areas (Broderick et al., 1994; Limpus, 1992; Velez-Zuazo et al., 2008), thus being accepted that juvenile development habitat does not seem to differ from that of the adult (Musick and Limpus, 1997). However, this fact does not preclude the observations, similar to this study, of the almost complete absence of adult animals in some locations (see Meylan et al., 2011, for a review). León and Diez (1999) proposed that this might be a result from past captures. However, evidence of movements of the larger juveniles out of the studied areas, probably to adult foraging grounds, suggests developmental migration (Blumenthal et al., 2009a; Meylan et al., 2011; Whiting et al., 2014). We are confident that these differences

between study areas might be related to the differences in the extension and depth range of the available habitats (i.e. reef topography). In some locations the available foraging habitats are narrow with abrupt slopes, where the deeper reef or cliffs walls are still available for larger turtles, and thus juveniles and adults are observed together. In other locations, however, reefs are scattered in a large geographic area and hence more prone to a segregation by size. At Príncipe waters, segregation by size is supported by a strong near shore fishing pressure and a large insular platform above the 100 m isobath ( $> 1000 \text{ km}^2$ ), where potentially suitable foraging habitat for larger hawksbills might exist. Although a 192 m dive was reported for an adult hawksbill, bottom foraging is normally limited to depths above 100 m (Van Dam and Diez unpublished data, in Van Dam et al., 2008). The absence in our sample of adult hawksbills during the post-nesting season, well as the low occurrence of larger juveniles throughout the year, is supported by the observations from other studies that also focused on Príncipe shallow waters (Ferreira et al., 2015; Monzón-Argüello et al., 2011), indicating that these larger turtles inhabit areas out of reach from the great majority of the spearfishermen ( $> 20 \text{ m}$ ). Most likely they are avoiding favorable and productive feeding coastal areas in order to be safe from capture, as the relation between green turtles (*Chelonia mydas*) and tiger sharks (*Galeocerdo cuvier*) where turtles moved to less favorable foraging locations when sharks arrive (see Heithaus et al., 2008, but also Heithaus, 2013 for more examples on the influences of predators on adult sea turtles).

The removal of three females identified as outliers (in the pooled sample) from the SIBER analyses greatly decreased the isotopic niche width of adults, although it still continues to be larger than juveniles. Overlap between groups increased but the data still endorses a clear foraging segregation between adults and juveniles, even though adult sample size were relatively small to make robust interpretations (Jackson et al., 2011; Syväranta et al., 2013). Although Jackson et al. (2011) recommended a minimum of 10 samples per group, as the smallest reliable sample size for SIBER analyses, Syväranta et al. (2013) found it to be too low and both agree that an  $n > 20$  (preferably  $n > 30$ ) should be targeted. This suggests that the adult's niche width might be underestimated. Thus, if sample sizes were similar between the groups, the observed differences have the potential to be higher, especially for Layman metrics (i.e. TA) as they are much more sensitive to sample size (Jackson et al., 2011; Syväranta et al., 2013). As mentioned before, the migration limit of hawksbills makes them capable to be distributed by the large Gulf of Guinea region, where baseline isoscapes are expected to be uniform, therefore it is likely that those three females arrived from areas with distinct prey varieties and abundances, that may or may not be far away from the rest of the adults in our sample. These turtles were also the heaviest, being important to note that Hays and Scott (2013) found a weak linear relationship between migration distance and body mass. Moreover, the range of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values without those females (presumably migrants) was analogous to the observed for a resident hawksbill population in a Caribbean foraging habitat (Bjorndal and Bolten, 2010). Nevertheless, with the available data, the possibility of these females to share the same foraging areas with the rest of the adults but present distinct foraging strategies cannot be discarded, although unlikely due to the similarity in diets at a specific foraging area (Bjorndal, 1997; Stringell et al., 2016).

The only male sampled during this study falls within the local females' isotope signatures. Contrary to females, males might breed every year and thus are more prone to stay closer to the nesting area. On the other hand, for a post-nesting female it might be better to go back to a foraging area where they know safe and abundant food exists, than to stay close by and compete with territories already occupied by other adults (Van Dam et al., 2008). Although a couple recorded hawksbill breeding migrations (straight line) reached  $> 1500 \text{ km}$ , overall they do not surpass 500 km and they might be connected to the closeness of proper foraging habitats (Hays and Scott, 2013; Van Dam et al., 2008).

In this way, it is plausible that the large insular platform is also a very important foraging habitat for the hawksbills that breed at Príncipe, as its likely that hawksbill take up residency at foraging habitats closest to their beaches of origin (Bowen et al., 2007; Proietti et al., 2014). However, the formulation of a thorough picture is hindered by the absence of studies on their diet, prey isotopic signatures and of comparable data from other areas. Thus further studies are needed, whether in deeper and offshore Príncipe waters well as at the wider Gulf of Guinea region. In addition, the urgency to identify the habitats used by hawksbills and other marine areas of the Gulf of Guinea islands, to conserve the most significant diversity of marine species, has been noted by researchers for decades (Jones, 1994; Roberts et al., 2002). Hawksbills can play a major role in this process as flagship and umbrella species, in the meantime the entire island platform of Príncipe should be targeted for research and management purposes.

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