

# Individual variability in the settlement of juvenile green turtles in the western South Atlantic Ocean: relevance of currents and somatic growth rate

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**ABSTRACT:** The settlement of demersal animals is influenced both by physical processes ruling the distribution of pelagic juveniles in the open ocean and by their active selection of suitable benthic habitats. Green turtles *Chelonia mydas* inhabiting the coastal areas of the western South Atlantic Ocean derive primarily from the rookery at Ascension Island and settle over a huge area spanning from northern Brazil to Uruguay. Here, we analysed the stable C and N isotope ratios in 30  $\mu\text{m}$  of carapace layers from juvenile green turtles collected from 2 distinct areas of Brazil (Praia do Forte, 12° 38' S, 38° 05' W, and Ubatuba, 23° 26' S, 45° 05' W), with the goal of reconstructing their individual diets and habitat use patterns. Juvenile neritic green turtles from Praia do Forte usually had herbivorous diets, with limited individual variability and few temporal changes in diet or habitat. Conversely, most juvenile green turtles from Ubatuba had omnivorous diets, although they exhibited high levels of individual and temporal variability. These contrasting patterns could be linked to less abundant and predictable food availability in subtropical Ubatuba compared to tropical Praia do Forte. It is unknown why large numbers of juvenile green turtles bypass foraging grounds in north-eastern Brazil to settle in subtropical or warm temperate areas, although it may be related to individual differences in growth rate and their size being too small when reaching Brazil from Ascension Island.

**KEY WORDS:** Juvenile turtles · *Chelonia mydas* · Settlement · Developmental habitat · Stable isotopes

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## 1. INTRODUCTION

Demersal marine animals often use a diversity of habitats throughout their lives, with juveniles typically inhabiting the water column and adults residing near the sea bed (Rodríguez et al. 1993, Harmelin-Vivien et al. 1995, Juanes 2007). Settlement into benthic habitats is a critical process for these demersal animals, and this usually involves juveniles actively selecting suitable habitats (Harmelin-Vivien et al. 1995, Montgomery et al. 2001, Jenkins 2005). Currents may profoundly impact the dispersal of juvenile, pelagic stages because of their small body size and limited swimming skills. This, in turn, may result

in long-distance dispersal, thus connecting pelagic foraging grounds, settlement areas, developmental habitats of neritic juveniles and, finally, the foraging grounds for adults (Cowen & Sponaugle 2009).

Marine turtles offer a good example of these complex life cycles, which result largely in part from the broad dispersal of post-hatchlings and oceanic juveniles (Putman & Naro-Maciel 2013, Mansfield et al. 2014, Briscoe et al. 2016), and also from the fidelity of adults to foraging grounds and nesting beaches (Bowen & Karl 2007). Green turtles *Chelonia mydas* inhabit all the tropical regions of the planet (Wallace et al. 2010), and the dispersal of post-hatchlings and oceanic juveniles is strongly influenced by oceanic

currents (Naro-Maciel et al. 2017, Monzón-Argüello et al. 2018; but see Shamblin et al. 2018). Juvenile green turtles settle into neritic habitats when their curved carapace length (CCL) reaches 25–50 cm (Bjorndal 1985, 1997, Seminoff et al. 2002, Reich et al. 2007, Arthur et al. 2008, Cardona et al. 2009, Williams et al. 2014, Howell et al. 2016, Williard et al. 2017). At this point, they shift from a carnivorous diet based on gelatinous zooplankton to an herbivorous or omnivorous plant-based diet (Reich et al. 2007, Arthur et al. 2008, Cardona et al. 2009, 2010, Parker et al. 2011, Vélez-Rubio et al. 2016). Settlement may take place at the same feeding grounds used by adults (Chaloupka et al. 2004, Arthur et al. 2008) or, alternatively, at developmental habitats that are different from those used by adults, particularly in subtropical and warm temperate regions (Cardona et al. 2009, González Carman et al. 2012, Williams et al. 2014, Santos et al. 2015, Howell et al. 2016, Jardim et al. 2016). In the latter situation, green turtles will eventually move to the adult foraging grounds as they grow older. The benefits of settling in developmental habitats remain unknown (Meylan et al. 2011), but using neritic foraging grounds that are distinct from those of adults might simply be a result of oceanic juveniles drifting with the currents until they grow large enough to control their buoyancy (Scott et al. 2014).

According to tagging and genetic markers, the majority of the green turtles inhabiting the western South Atlantic derive from the rookery at Ascension Island (Carr et al. 1978, Caraccio Noriega 2008, Proietti et al. 2012, Prosdocimi et al. 2012, Putman & Naro-Maciel 2013, Scott et al. 2014). Virtual particle modelling indicates that most hatchlings leave Ascension Island and drift westward along the Atlantic South Equatorial Current (Fig. 1) before reaching the neritic habitats off the coast of north-eastern Brazil in less than 2 yr (Putman & Naro-Maciel 2013, Scott et al. 2014). Mixed adult/juvenile foraging grounds exist only at latitude 12° S and farther north (Gallo et al. 2006, Poli et al. 2014, Santos et al. 2015, Jardim et al. 2016) and, hence, most juvenile green turtles are expected to settle immediately after reaching north-western Brazil. However, large numbers of juvenile green turtles continue drifting southward along the Brazil Current before settling at developmental habitats off central and southern Brazil (Gallo et al. 2006, Poli et al. 2014, Santos et al. 2015, Jardim et al. 2016), Uruguay (Vélez-Rubio et al. 2018) and northern Argentina.

The climate is tropical in north-eastern Brazil, with increasing seasonality southwards and a warm temperate climate in Uruguay and northern Argentina.

In this scenario, green turtles inhabiting the western South Atlantic are expected to exhibit a diversity of life histories. Those settling in tropical mixed adult/juvenile foraging grounds will inhabit a rather constant and predictable environment; hence, they will experience little variability in diet and habitat throughout their lifetimes, with the exception of their periodical breeding migration to Ascension after adulthood. In contrast, individuals settling in subtropical and warm temperate developmental habitats will shift habitats frequently as a result of not only increasing seasonality but also the northward displacement towards the tropical adult foraging grounds off north-eastern Brazil.

Satellite tagging has offered some evidence of seasonal migration in juvenile green turtles from northern Argentina (González Carman et al. 2011, 2012) and Uruguay (Vélez-Rubio et al. 2018), but the tags remain attached to small green turtles for only a few months (Godley et al. 2003, González Carman et al.

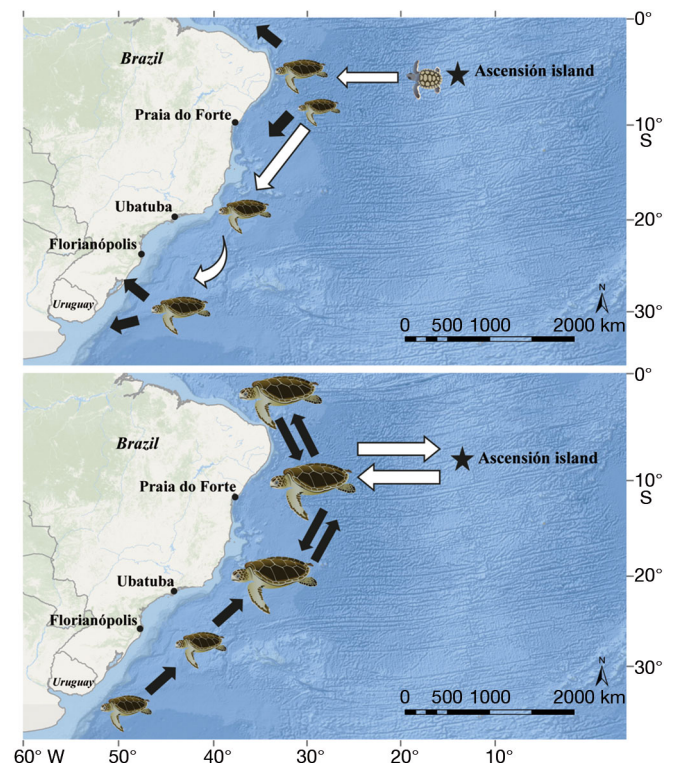


Fig. 1. Movements of green turtles from Ascension Island across the western South Atlantic. (a) Developmental dispersal from Ascension Island to neritic foraging grounds along South America. (b) Movements from developmental habitats in central Brazil, Uruguay and northern Argentina to adult foraging grounds in north-eastern Brazil and reproductive migration. White arrows denote oceanic (deeper than 200 m) pathways and black arrows denote neritic (shallower than 200 m) pathways. Turtle drawings (source: IAN image library) denote hatchlings, small and larger juveniles, and adults

2012, Putman & Mansfield 2015, Williard et al. 2017); thus, they do not serve as a viable alternative for long-term tracking. Furthermore, satellite tagging offers no information about diet. Analysing stable isotope ratios in the layers of carapace scutes is an alternative approach to reconstructing ontogenetic changes in the diets and habitats of juvenile green turtles, because this metabolically inert tissue records a timeline of the consumer's isotopic history spanning several years, even if the resolution is often coarse (Reich et al. 2007, Cardona et al. 2009, 2010, Vander Zanden et al. 2013, Vélez-Rubio et al. 2018).

The basic assumptions of the stable isotope analysis in scutes are: (1) that stable isotope ratios in animal tissues integrate those in their diet and the trophic discrimination factor is tissue specific; (2) that the stable isotope ratios of metabolically inert tissues do not change after deposition and hence integrate the diet during short periods (days to weeks); and (3) that variations of stable isotope ratios across habitats and prey are known. The first 2 assumptions are not redundant, because the stable isotope ratios of metabolically active tissues, such as skin or muscle, change over time and hence offer no timeline, whereas the opposite is true for layers of metabolically inert tissues.

We used the stable isotope ratios of N and C in the carapace scute layers of juvenile green turtles captured in neritic habitats of north-eastern and central Brazil to track their individual ontogenetic trajectories in diet and habitat use. Turtles from north-eastern Brazil are expected to have settled immediately after arriving from Ascension and hence exhibit rather constant stable isotope ratios across their carapace scutes after the drop associated with the settlement (Reich et al. 2007, Vander Zanden et al. 2013). Conversely, as a result of frequent shifts in both diet and habitat in a more seasonal environment, juvenile green turtles from central Brazil are expected to exhibit more variable stable isotope profiles across carapace scutes and higher individual variability.

## 2. MATERIALS AND METHODS

### 2.1. Study area

We collected samples from February to March 2016 in 2 different regions of the Brazilian coast: 16 were collected from tropical Praia do Forte (12° 38' S 38° 05' W), located 70 km from Salvador do Bahia, and 14 were collected from subtropical Ubatuba (23° 26' S, 45° 05' W), off the northern coast of the state of Sao Paulo (Fig. 1).

### 2.2. Sampling

At both sites, most turtles were captured alive through free diving or with a monofilament nylon net (30 cm mesh size) by members of Projeto Tamar ([www.tamar.org.br](http://www.tamar.org.br)), and this formed a part of their long-term study on the abundance and habitat use of green turtles along the Brazilian coast. Some of the juvenile green turtles from Ubatuba were captured alive in pound nets (Gallo et al. 2006). The mortality in pound nets is low because turtles are free to breathe, especially when the gear is open-roofed (Silva et al. 2017). Additional samples were collected at Praia do Forte during the necropsy of 5 recently dead turtles that had been caught incidentally by local fishermen.

Curved carapace length (CCL) was measured with flexible tape, and carapace scute samples were collected from the posterior medial region of the third left lateral scute of each individual, close to the posterior margin, using a 6 mm Miltex biopsy punch (Reich et al. 2007).

Previous research has shown that the macroalgae *Ulva* spp., *Chondracanthus* spp. and *Pterocladia capillacea* are the staple food of green turtles along the coast of Brazil (Santos et al. 2015, Jardim et al. 2016) and Uruguay (Vélez-Rubio et al. 2018), and that a steep latitudinal gradient exists for their  $\delta^{15}\text{N}$  values but not for  $\delta^{13}\text{C}$ . Furthermore, green turtles regularly consume gelatinous zooplankton in southern Brazil and Uruguay (Santos et al. 2015, Vélez-Rubio et al. 2018). According to this information, we collected *Ulva* sp., *Chondracanthus* sp., *P. capillacea* and other macroalgae for stable isotope analysis at Praia do Forte and Ubatuba (5 replicates each). The jellyfish *Velevella velevella* was also collected at Ubatuba. Prey samples were kept frozen ( $-20^{\circ}\text{C}$ ) prior to analysis.

### 2.3. Stable isotope analysis

All carapace scute samples were rinsed with deionized water in the laboratory prior to analysis. Each sample was embedded in an optimal cutting temperature (OCT) compound manufactured by Tissue-Teck<sup>®</sup>, with the dorsal side (oldest tissue) down and frozen. Scute samples were then subsampled in successive 30  $\mu\text{m}$  layers using a cryostat (Leica Cryostat CM 3050S). Each layer was rinsed with deionized water for 24 h and kept separately. Previous tests confirmed that this procedure removed OCT traces and did not modify the stable isotope ratios of C or N (Monzón-Argüello et al. 2018, Vélez-Rubio et al. 2018). Samples were dried in an oven at  $55^{\circ}\text{C}$  for 1 d.

The number of layers obtained was proportional to the scute thickness, which varied individually. As a scute grows outward, the oldest tissue remains in the outermost part of the scute and the most recent tissue forms in the innermost section (Alibardi 2005). According to previous studies (Reich et al. 2007, Cardona et al. 2010, Vander Zanden et al. 2013), each 30  $\mu\text{m}$  thick layer integrates approximately 54 d, although the associated variance is unknown and hence should be considered as a coarse estimate only. Each layer was analysed independently for the stable isotope ratios of carbon and nitrogen. Subsamples were weighed in tin cups with a microbalance (approximately 0.3 mg of sample), combusted at 1000°C and analysed with a continuous flow isotope ratio mass spectrometer (Flash 1112 IRMS Delta C Series EA; Thermo Finnigan) at the Centres Científics i Tecnològics de la Universitat de Barcelona (Spain).

Stable isotope abundances were expressed in  $\delta$  notation according to the following expression:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3 \quad (1)$$

where  $X$  is  $^{13}\text{C}$  or  $^{15}\text{N}$ ,  $R_{\text{sample}}$  is the heavy to light isotope ratio of the sample ( $^{13}\text{C}/^{12}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}$ , respectively), and  $R_{\text{standard}}$  is the heavy to light isotope ratio of the reference standards, which were Vienna Pee Dee belemnite calcium carbonate for  $^{13}\text{C}$  and atmospheric nitrogen (air) for  $^{15}\text{N}$ . For calibration at a precision of 0.2‰, we used international isotope secondary standards of known  $^{13}\text{C}/^{12}\text{C}$  ratios, as given by the International Atomic Energy Agency (IAEA), and these were namely polyethylene (IAEA CH<sub>7</sub>,  $\delta^{13}\text{C} = -31.8\text{‰}$ ), graphite (IAEA USGS24,  $\delta^{13}\text{C} = -16.1\text{‰}$ ) and sucrose (IAEA CH<sub>6</sub>,  $\delta^{13}\text{C} = -10.4\text{‰}$ ). For nitrogen, we obtained a precision of 0.3‰ using international isotope secondary standards of known  $^{15}\text{N}/^{14}\text{N}$  ratios, namely (NH<sub>4</sub>)<sub>2</sub>SO<sub>4</sub> (IAEA N1,  $\delta^{15}\text{N} = +0.4\text{‰}$  and IAEA N<sub>2</sub>,  $\delta^{15}\text{N} = +20.3\text{‰}$ ) and KNO<sub>3</sub> (IAEA NO<sub>3</sub>,  $\delta^{15}\text{N} = +4.7\text{‰}$ ).

## 2.4. Data analysis

The coefficient of variation was used as a measure of variability across carapace layers (Table 1). The Fisher test was used to compare the variability across individuals in the coefficient of variation for the 2 populations.

The prey-to-consumer trophic discrimination factor for carapace scutes of green turtles was assessed empirically by Shimada et al. (2014) as  $-1.4\text{‰}$  for  $\delta^{13}\text{C}$  and  $2.5\text{‰}$  for  $\delta^{15}\text{N}$ . The stable isotope ratios of local macroalgae from Praia do Forte and Ubatuba were corrected accordingly to define the polygon within the  $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$  isospace that is expected for enclosing the stable isotope ratios of carapace scute layers in a way that is compatible with herbivorous diets at each locality.

We used the Bayesian stable isotope mixing model in the Stable Isotope Analysis in R (SIAR) package (Parnell et al. 2010) to assess the feasible contribution

Table 1. Summary of stable isotope descriptors for 16 green turtles *Chelonia mydas* sampled from Praia do Forte, Bahia, and 14 from Ubatuba, São Paulo, Brazil. ID: identification number; CCL: curved carapace length; CV: coefficient of variability

Study area	ID	CCL (cm)	$\delta^{13}\text{C}$ range (‰)	$\delta^{13}\text{C}$ CV (%)	$\delta^{15}\text{N}$ range (‰)	$\delta^{15}\text{N}$ CV (%)	Time recorded (d)
Praia do Forte	PF1	45.6	-17.6/-21.7	7.0	7.7/7.9	1.0	378
Praia do Forte	PF2	85.9	-18.0/-18.7	1.7	8.7/9.0	1.4	270
Praia do Forte	PF3	104	-15.2/-16.6	3.7	8.0/8.6	2.6	270
Praia do Forte	PF4	70.2	-15.4/-15.7	6.7	8.0/8.1	1.7	486
Praia do Forte	PF5	53.7	-14.9/-16.2	3.8	8.1/9.1	4.9	216
Praia do Forte	PF6	56.4	-14.1/-14.2	0.3	7.7/4.8	0.7	162
Praia do Forte	PF7	60.5	-16.3/-18.0	4.1	9.4/10.7	4.6	270
Praia do Forte	PF8	66.0	-18.6/-19.6	3.9	6.7/10.4	2.5	216
Praia do Forte	PF9	49.3	-15.4/-15.7	0.7	8.0/8.1	0.7	378
Praia do Forte	PF10	57.8	-15.4/-17.4	4.7	8.1/8.5	1.6	432
Praia do Forte	PF11	49.6	-15.5/-15.9	1.0	8.2/8.5	1.3	216
Praia do Forte	PF12	38.8	-13.9/-14.5	4.7	11.3/11.6	1.1	270
Praia do Forte	PF13	44.0	-15.0/-21.1	11.1	6.6/10.0	6.2	162
Praia do Forte	PF14	31.1	-15.7/-17.6	4.2	5.7/7.5	12.5	216
Praia do Forte	PF15	35.0	-17.6/-18.8	2.5	8.9/10.1	4.8	270
Praia do Forte	PF16	40.0	-14.5/-16.2	3.4	8.4/9.0	2.7	486
Ubatuba	UB1	41.3	-14.9/-17.4	6.0	10.5/11.2	2.5	270
Ubatuba	UB2	45.0	-16.2/-16.6	1.0	9.8/10.0	1.1	162
Ubatuba	UB3	58.3	-15.8/-19.5	7.0	10.8/12.3	5.3	378
Ubatuba	UB4	53.3	-15.0/-17.3	5.2	10.1/11.7	5.0	324
Ubatuba	UB5	54.2	-19.8/-20.5	1.4	12.2/12.4	0.5	378
Ubatuba	UB6	61.4	-17.4/-18.3	5.7	10.4/13.4	21.0	324
Ubatuba	UB7	45.7	-18.6/-19.6	1.6	6.7/10.4	17.0	378
Ubatuba	UB8	39.7	-18.5/-20.1	3.7	5.3/6.6	10.3	216
Ubatuba	UB9	40.0	-18.1/-20.1	3.7	8.1/11.4	14.4	270
Ubatuba	UB10	44.7	-18.9/-19.8	44.3	6.9/11.8	48.1	378
Ubatuba	UB11	47.0	-19.6/-20.2	1.0	10.9/11.8	2.5	432
Ubatuba	UB12	37.0	-17.3/-19.3	3.6	5.6/6.0	2.0	324
Ubatuba	UB13	70.7	-17.2/-18.0	2.0	13.5/14.0	1.6	270
Ubatuba	UB14	34.0	-16.7/-19.7	4.6	8.4/9.8	4.7	486

of the jellyfish *V. velella* and several macroalgae to the diet of those green turtles with stable isotope ratios lying outside the mixing polygon. SIAR assumes that the variability associated with food sources and trophic enrichment is normally distributed (Parnell et al. 2010). To better restrict our model, we used elemental concentrations (%C and %N) in each prey (Claudino et al. 2013). Only the innermost layer from each turtle was included in SIAR, because older samples may correspond to foraging somewhere else and do not reveal local diet. Data are reported as means  $\pm$  SD, unless stated otherwise.

### 3. RESULTS

Turtles ranged from 31.1–104.0 cm CCL in Praia do Forte, and from 34.9–70.2 cm CCL in Ubatuba (Table 1).

Variability in  $\delta^{13}\text{C}$  values across carapace layers was similar in the juvenile green turtles from Praia do Forte and Ubatuba (Table 1;  $F = 2.255$ ,  $p = 0.144$ ). Conversely, variability in  $\delta^{15}\text{N}$  values across carapace layers was much greater in the green turtles from Ubatuba than in those from Praia do Forte (Table 1;  $F = 8,703$ ,  $p = 0.006$ ).

The stable isotope ratios of most of the turtles from Praia do Forte (14 out of 16) were highly consistent across carapace layers (Table 1) and were also compatible with a local herbivorous diet (Fig. 2). Only 2 of the smallest turtles (measuring 31.1 and 38.1 cm CCL) had stable isotope ratios incompatible with a local herbivorous diet in at least some carapace layers (Fig. 2, panels P6 and P16). The layers outside the mixing polygon were more enriched than expected in  $^{13}\text{C}$ , but not in  $^{15}\text{N}$ . This suggests that unusual stable isotope ratios resulted from foraging somewhere else and not because of local mixed diets that included animal prey.

Conversely, only 2 turtles from Ubatuba (measuring 34.0 and 45.0 cm CCL) had stable isotope ratios in their carapace scutes compatible with a local herbivorous diet (Fig. 3, panels P2 and P14). The remaining 12 turtles (ranging from 37.0–70.7 cm CCL; Table 1) had stable isotope ratios lying outside the local mixing polygon and they varied largely across layers in  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$  or both (Fig. 3). Two of them (Fig. 3, panels P8 and P12) had  $\delta^{15}\text{N}$  values lower than those expected for a local herbivorous diet; 7 had  $\delta^{15}\text{N}$  values higher than those expected for a local herbivorous diet (Fig. 3, panels P1 to P6); and 3 had values both above and below those expected for a green turtle with a local herbivorous diet (Fig. 3, panels P9, P10 and P7). SIAR revealed that the stable isotope ratios

above the mixing polygon were consistent with a mixed diet deriving approximately 20% of the nutrients from *Velella velella* and 80% from local macroalgae (Fig. 4). However, turtles from southern Brazil eating a plant-based diet were expected to have similar stable isotope ratios; thus, a recent arrival from more southern foraging grounds cannot be ruled out. On the other hand,  $\delta^{15}\text{N}$  values lower than those in the mixing polygon revealed foraging somewhere else, and these were observed in 2 of the smallest turtles from Ubatuba (measuring 37.0 and 39.7 cm CCL; Fig. 3, panels UB8 and UB12).

### 4. DISCUSSION

It is no straightforward task to interpret whether an isotope ratio within a given portion of a turtle's scute is due to local trophic status or to prior foraging location, particularly if residency times are unknown and individual diet preferences exist. Turtles from southern Brazil were particularly challenging, as the stable isotope ratios observed in their more recent carapace scute layers were consistent with either a local omnivorous diet or a plant-based diet from Uruguay that would thus represent a recent arrival to the sampling area.

Despite those challenges, juvenile neritic green turtles from Praia do Forte and Ubatuba clearly differed in their diets and patterns of habitat use, as revealed by stable isotope ratios across carapace layers. Those from Praia do Forte had relatively consistent isotope ratios, which were usually consistent with an herbivorous diet based on local seaweeds. This evidence suggests that most of the turtles settled in the area and shifted to an herbivorous diet more than 1 yr prior to sampling. They also exhibited limited individual variability and few temporal changes in diet or habitat. Conversely, most juvenile green turtles from Ubatuba had omnivorous diets, with high levels of individual and temporal variability in stable isotope ratios, particularly in  $\delta^{15}\text{N}$ . This evidence suggests a more complex life history, with frequent changes in diet and habitat.

Previous research has already reported not only a rapid dietary shift from a carnivorous to an herbivorous diet after the settlement of juvenile green turtles in tropical neritic habitats (Reich et al. 2007, Guebert-Bartholo et al. 2011, Santos et al. 2011, Nagaoka et al. 2012, Bezerra et al. 2015, Gama et al. 2016, Jardim et al. 2016), but also a remarkable temporal consistency in diet and habitat use thereafter (Vander Zanden et al. 2013). In contrast, juvenile green turtles settling in

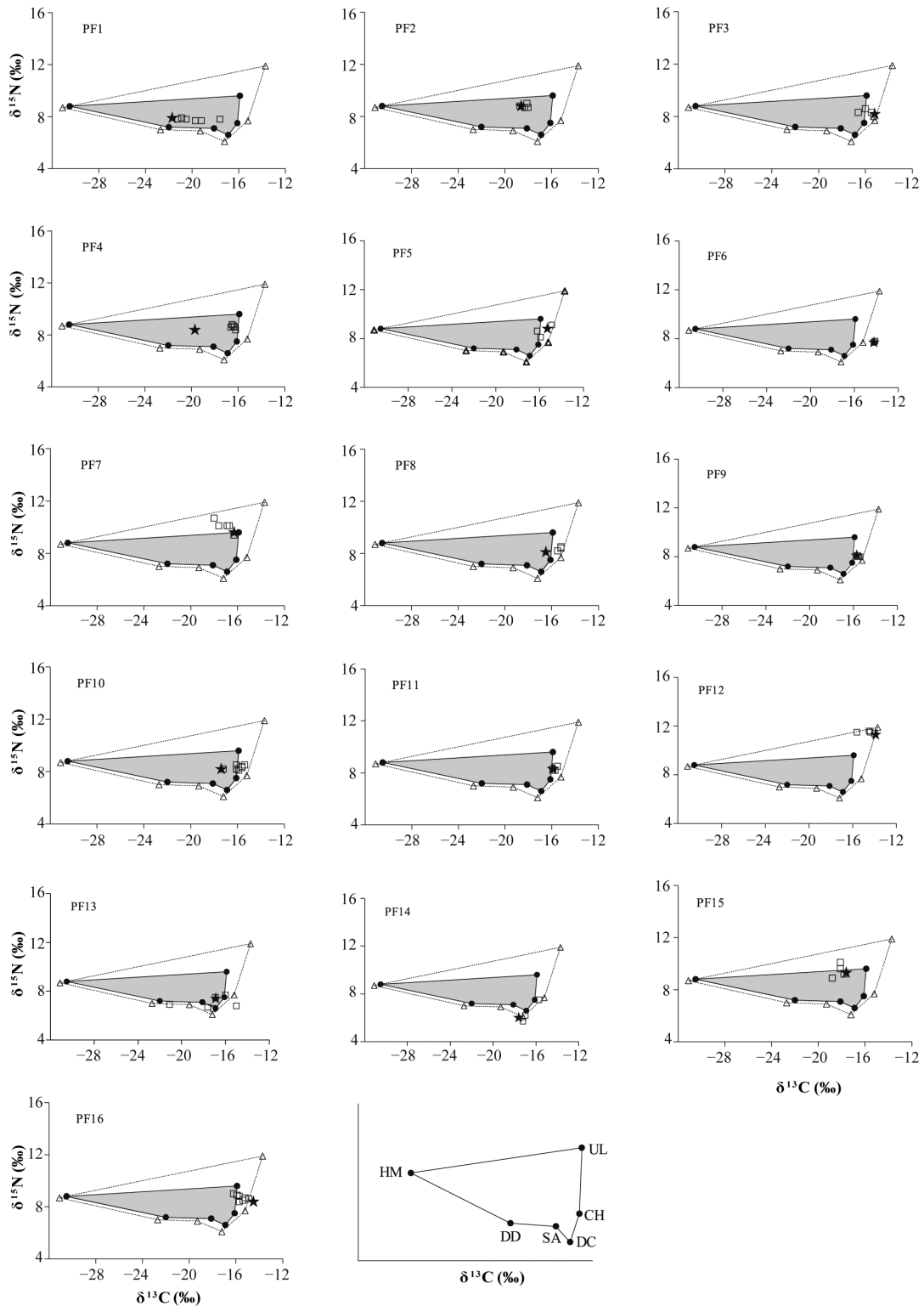


Fig. 2.  $\delta^{15}\text{N}$ – $\delta^{13}\text{C}$  biplot showing the position of 16 green turtles (PF1–PF16; see Table 1) in relation to the mixing polygon delimited by the macroalgae from Praia do Forte. The solid star denotes the innermost carapace layer and the open squares the older layers. The solid line connecting the solid circles shows the mixing polygon delimited by the average values of macroalgae, and the dashed line connecting the triangles shows the 95% confidence interval contour. The bottom right panel shows the position of each macroalgae in the mixing polygon (CH: *Chondracanthus* sp.; DD: *Dictyopterus delicatula*; DY: *Dictyota dichotoma*; HM: *Hypnea musciformis*; SA: *Sargassum* sp.; UL: *Ulva* sp.)

warm temperate or subtropical habitats usually consume plant-based omnivorous diets and exhibit frequent habitat and diet shifts (Cardona et al. 2009, 2010, González Carman et al. 2012, 2014, Morais et al. 2014, Vélez-Rubio et al. 2016, Williard et al. 2017).

Campos et al. (2018) revealed the fast acquisition of a carbohydrate-fermenting gut microbiota by neritic green turtles after settlement both in Praia do Forte and Ubatuba, with no major differences in the com-

position of the gut microbiota at the 2 localities. Accordingly, the hypothesis should be ruled out that green turtles in subtropical and warm temperate regions have more carnivorous diets because of a delayed acquisition of a carbohydrate-fermenting gut microbiota (Cardona et al. 2010). Alternatively, higher levels of omnivory and frequent diet and habitat shifts in subtropical and warm temperate regions might result from a lower and highly seasonal food

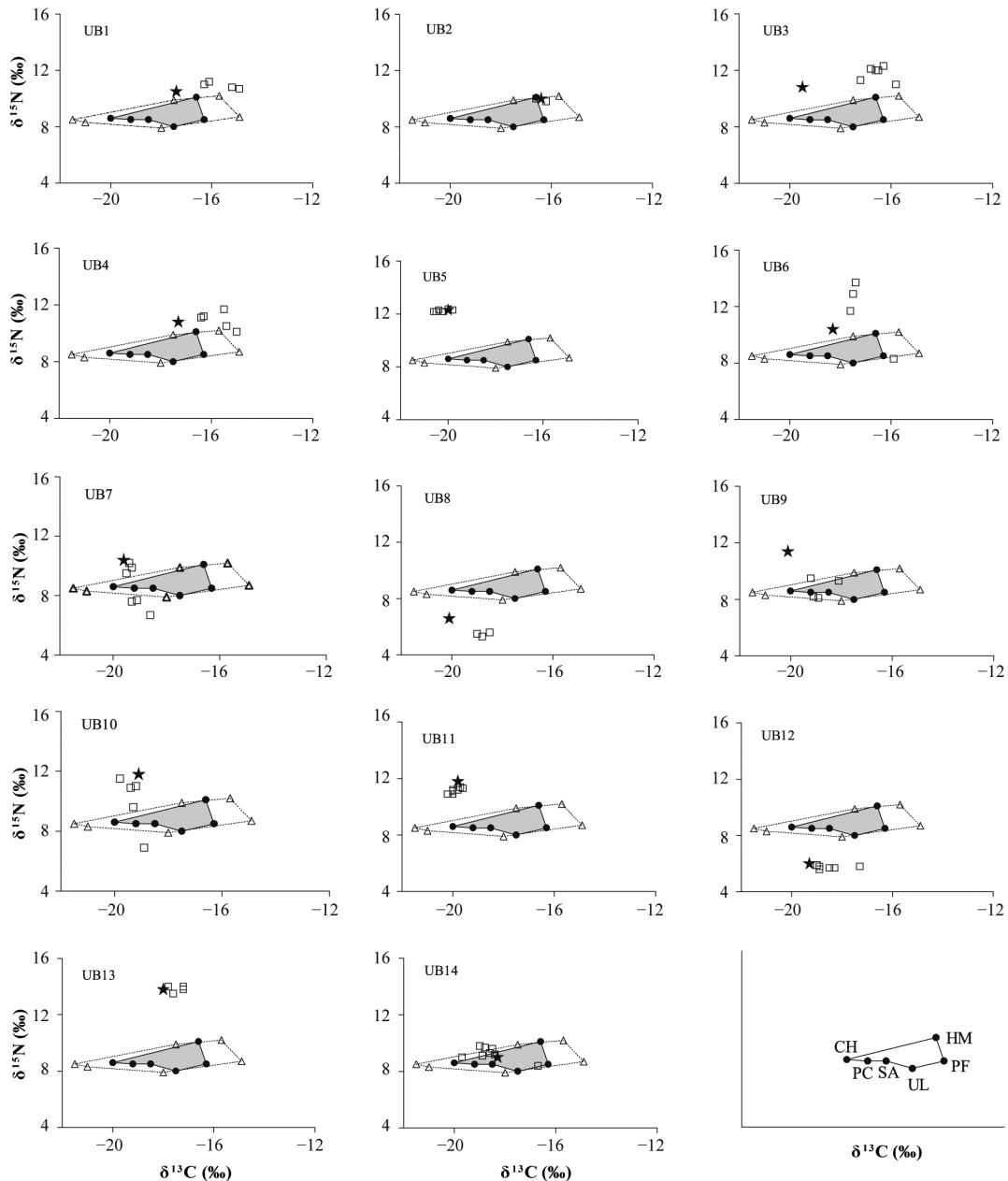


Fig. 3.  $\delta^{15}\text{N}$ - $\delta^{13}\text{C}$  biplot showing the position of 13 green turtles (UB1-UB13; see Table 1) in relation to the mixing polygon delimited by the macroalgae from Ubatuba. The bottom right panel shows the position of each macroalgae in the mixing polygon (CH: *Chondracanthus* sp.; HM: *Hypnea musciformis*; PC: *Pterocladia capillacea*; PF: *Palisada flagelifera*; SA: *Sargassum* sp.; UL: *Ulva* sp.). All other details as in Fig. 2

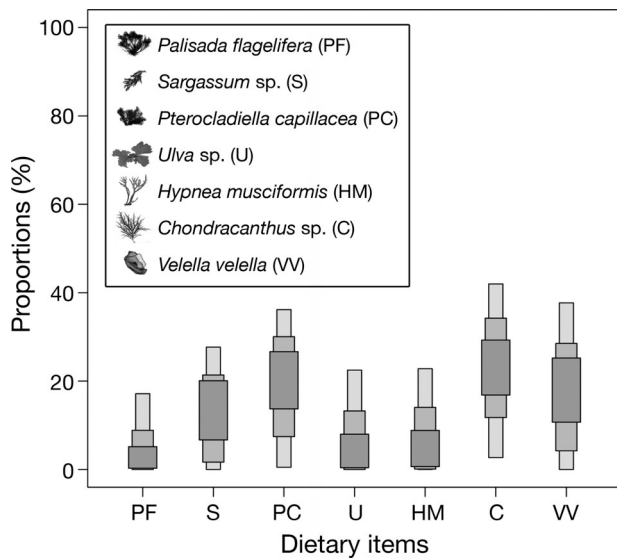


Fig. 4. Feasible contribution of prey to the diet of juvenile green turtles from Ubatuba ( $n = 12$ ), according to the Stable Isotope Analysis in R (SIAR), including 95, 75 and 50% credibility intervals (light, medium and dark grey shading, respectively)

availability. If so, subtropical and warm temperate developmental habitats are indeed suboptimal, and juvenile green turtles settle there only because they drift there with the currents.

This is particularly dramatic in the western South Atlantic, where most oceanic juveniles from Ascension Island drift to north-eastern Brazil (Putman & Naro-Maciel 2013) while skipping past the mixed juvenile/adult foraging grounds stretching north to latitude  $12^{\circ}\text{S}$ , and they instead settle in southern developmental habitats. As adults occur only north to latitude  $12^{\circ}\text{S}$ , they must move north as they grow older, thus returning to areas they bypassed as juveniles (Fig. 1).

Laboratory experiments, satellite telemetry and genetic markers have revealed that juvenile green turtles ranging from 14 to 30 cm are able to sustain short periods of directional swimming to avoid areas and conditions unfavourable for survival (Prange 1976, Reich et al. 2007, Putman & Mansfield 2015). However, they probably lack the necessarily tight control of their buoyancy for settling in neritic habitats (Hochscheid et al. 2003). Indeed, even larger juveniles (38–48 cm CCL) may follow prevailing currents (González Carman et al. 2011).

Most post-hatchlings from Ascension reach north-western Brazil in less than 2 yr (Putman & Naro-Maciel 2013). Juvenile green turtles that age in the western South Atlantic are  $<35$  cm CCL (Andrade et al. 2016, Lenz et al. 2017), although young green tur-

tles from other populations can grow much faster (Turner Tomaszewicz et al. 2018). This indicates that only the fastest-growing members of each cohort from Ascension Island are probably large enough to settle in the neritic habitats of north-eastern Brazil upon reaching them for the first time. The majority of each cohort will likely continue drifting southwards along the Brazil Current until they grow large enough to control buoyancy and settle in neritic habitats.

The meandering of the Brazil Current far away from the continental shelf south to Cape Sao Tomé (Longhurst 1998, da Silveira et al. 2008) may delay settlement even more, because most oceanic juveniles reaching latitude  $20^{\circ}\text{S}$  are probably averted offshore and reside in the ocean for an extended period before once again approaching the continental shelf off southern Brazil and Uruguay (Putman & Naro-Maciel 2013). They will then be 3–4 yr old (Putman & Naro-Maciel 2013) and 40 cm CCL (Andrade et al. 2016, Lenz et al. 2017), which corresponds to the size at settlement reported for Uruguay (Vélez-Rubio et al. 2018). The high level of individual variability observed in the  $\delta^{15}\text{N}$  values of juvenile green turtles from Ubatuba likely reveals the diversity of drifting trajectories during the pre-settlement and settlement phases of the life cycle.

In conclusion, this study demonstrates a diversity of ontogenetic trajectories for green turtles before and after settlement in the neritic habitats of the western South Atlantic, which likely results from broad variability in the rate of somatic growth of juvenile green turtles. This suggests that juvenile green turtles settle in developmental habitats south to latitude  $12^{\circ}\text{S}$  not because they are optimal, but merely because they serve as convenient end points in the oceanic dispersal phase once they grow large enough to become neritic.

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