



Revisiting the ontogenetic shift paradigm: The case of juvenile green turtles in the SW Atlantic

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ABSTRACT

The green turtle (*Chelonia mydas*) is a subcosmopolitan species found in tropical and temperate latitudes. The best knowledge on its behavior described an abrupt and irreversible ontogenetic shift that takes place early in life in some areas such as the Greater Caribbean and Australia. Young turtles move from oceanic to neritic habitats, from pelagic to benthic feeding and from an omnivorous to an herbivorous diet. However, whether this pattern applies elsewhere in the range of the species is not known. In the temperate waters of the South West (SW) Atlantic, preliminary evidence suggests that these juveniles would not comply with the tenets of an abrupt and irreversible ontogenetic shift as in tropical waters. We satellite tracked 9 neritic juveniles moving along the coast of Argentina, and applied a switching state-space model combined with kernel density estimation to identify preferential putative foraging areas and migratory routes. Results indicate that immature green turtles are not strictly herbivores or neritic in the temperate SW Atlantic. In summer and fall, juveniles foraged most of the time in estuarine areas without submerged macrophytes. In winter and spring, the turtles migrated north to warm coastal areas where macroalgae and seagrass are available. Concomitant to pelagic feeding, some turtles reached deep water areas where macrophytes are unlikely to occur. Adaptation to local conditions explains behavior better for the SW Atlantic than the abrupt and irreversible ontogenetic shift described for warmer waters.

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1. Introduction

The green turtle (*Chelonia mydas*; Linnaeus, 1758) is a threatened species with a broad geographic distribution that includes the Mediterranean Sea and the Atlantic, Pacific and Indian Oceans (Pritchard, 1997; Seminoff, 2004). Its life history encompasses a diversity of ecosystems, from oceanic to neritic habitats, in tropical as well as temperate latitudes (González Carman et al., 2011; Hirth, 1997; Prosdocimi et al., 2012). The species is known to undergo an abrupt and irreversible ontogenetic shift in foraging habits early in life (Arthur et al., 2008; Bolten, 2003; Reich et al., 2007). However,

whether this pattern applies elsewhere in the range of the species is unknown.

In some areas such as the Greater Caribbean and eastern Australia, young individuals in oceanic environments feed on neustonic organisms (e.g. ctenophores, snails, siphonophores, hydroids, and sargasso; Bjorndal, 1997; Boyle and Limpus, 2008; Frick, 1976). This diet changes when juveniles recruit into neritic environments, where they remain in seagrass and macroalgae meadows upon which they feed for the rest of their lives, making it the only herbivorous sea turtle species (Bjorndal, 1997; Brand-Gardner et al., 1999; Mendonça, 1983).

In recent years, the ontogenetic shift pattern described for the Greater Caribbean and eastern Australia has been challenged in other locations of the green turtle's range. In populations from Japan, Mauritania, Western Australia and the Mediterranean Sea, neritic juveniles and adults have a considerable carnivorous component in their diets thus not supporting obliged herbivory for advanced stages of development (e.g. Burkholder et al., 2011; Cardona et al.,

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2009, 2010; Hatase et al., 2006). Are these results exceptions to the rule, or taken together, do they suggest that previous insights from Australia and the Greater Caribbean are in fact the exception?

In the SW Atlantic, immature green turtles occur widely along the coast, inhabiting shallow, sheltered habitats (Fig. 1). Largely accepted to be herbivores consuming either macroalgae or seagrass (Godley et al., 2003; Guebert-Bartholo et al., 2011; López-Mendilaharsu et al., 2006; Santos et al., 2011; Sazima and Sazima, 1983), sometimes they can also feed on animal matter like mollusks among other invertebrates (e.g. Bugoni et al., 2003; Nagaoka et al., 2012). The species reaches as south as the temperate waters of Argentina, where they occur in coastal systems (e.g. Río de la Plata, El Rincón, Fig. 1, González Carman et al., 2011) void of macroalgae and seagrass meadows (Boraso and Zaixso, 2008; Boschi, 1988; Mianzan et al., 2001; Parodi, 2004). In addition to this, relatively large juveniles (34–75 cm CCL) are accidentally captured by pelagic longline fleets operating in oceanic waters (Sales et al., 2008) where macrophytes do not grow. These preliminary observations do not support the pattern of an abrupt and irreversible ontogenetic shift in the SW Atlantic. Since previous knowledge suggests that environmental conditions and resource availability determines the selection of habitats and prey by the turtles (Casale et al., 2008; Hatase et al., 2006; Schofield et al., 2009; Southwood and Avens, 2010), we hypothesize that the behavior of juveniles in the temperate SW Atlantic is adaptable to local conditions, and therefore, it may be different from behavior observed in Australia and the Greater Caribbean.

Most evidence against the abrupt and irreversible ontogenetic shift of juvenile green turtles comes from diet studies (e.g. Burkholder et al., 2011; Cardona et al., 2009, 2010). Evidence on the habitat use is, however, scarce. Satellite tracking is the most practical tool to gain quick insight into the behavior of marine turtles, as the migratory routes and foraging habitats can be estimated with accuracy (Godley et al., 2008; Hart and Fujisaki, 2010; Makowski et al., 2006; McClellan and Read, 2009). The method also allows tracking animals across entire ocean basins (e.g. Luschi et al., 1998; Polovina et al., 2000). Yet, few studies to date have used to date satellite telemetry to study habitat use in immature green turtles (e.g. Godley et al., 2003; Hart and Fujisaki, 2010; McClellan and Read, 2009). In this study, we therefore describe the behavior and distribution of juvenile green turtles and explore potential implications of the ontogenetic shift. To accomplish this, we satellite tracked juveniles recovered from entanglement on the coast of Argentina and used two analytical techniques to identify the migratory routes and foraging areas: (a) state-space models (SSM), to estimate the probability of an animal being engaged in a certain behavioral mode such as foraging or transiting (Bailey et al., 2008; Breed et al., 2009; Jonsen et al., 2007; Patterson et al., 2008), and (b) the kernel density estimation (KDE), to identify areas of disproportionately heavy use, core areas, within a distribution range (Seaman and Powell, 1996; Worton, 1989). KDE is a methodology widely used to assess marine turtle habitat use (e.g. Hart and Fujisaki, 2010; Makowski et al., 2006; Seminoff et al., 2002). SSM is a relatively novel methodology successfully used to

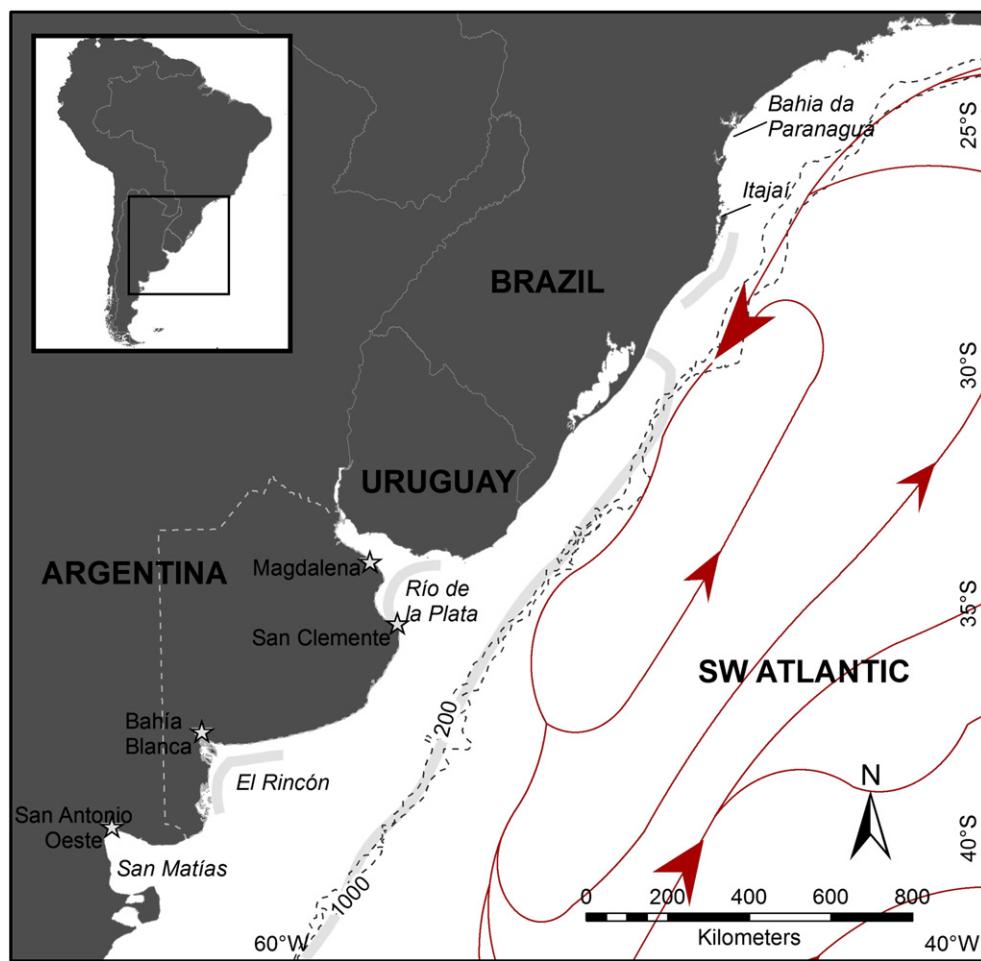


Fig. 1. Study area of juvenile green turtles in the SW Atlantic. Stars indicate localities on the Argentine coast where the turtles were captured. Black dashed lines show positions of 200 and 1000 m isobaths. Gray dashed lines show limits of the Buenos Aires province. Gray full lines show frontal areas. Red full line illustrates the Brazil Current adapted from Piola and Matano (2001).

infer behavior of adult leatherbacks (*Dermochelys coriacea*), olive ridleys (*Lepidochelys olivacea*) and loggerheads (*Caretta caretta*) (Bailey et al., 2008; Hart et al., 2011; Jonsen et al., 2007; Maxwell et al., 2011), but never applied to immature green turtles.

2. Materials and methods

2.1. Turtle recovery and measurement

From February 2008 to March 2011, nine green turtles in good body condition (i.e. not emaciated) and without symptoms of drowning were instrumented with satellite tracking devices. Animals originated from those entangled and rescued by the Regional Program for Sea Turtle Conservation and Research of Argentina (PRICTMA). The turtles were moved to a research center or an aquarium to evaluate health status and attach the tag. Animals were kept in captivity for no more than 3 to 5 days during which they were fed and responded to stimuli positively. Curved carapace length (CCL) was measured from the nuchal notch to the posterior notch at midline between supracaudal scutes (Bolten, 2000). All turtles were tagged with Inconel tags provided by the Cooperative Marine Turtle Tagging Program (National Marine Fisheries Service) in the first large proximal scale of each rear flipper.

2.2. Satellite tag deployment

Turtles were instrumented with Wildlife Computers SPOT5 platform terminal transmitters (PPT). The tags, 2 × AA and 1 × C-cell models, measured 71.5 × 34.0 × 24.4 mm and 83.5 × 41.5 × 37.7 mm (length × width × height) and weighed 80 g and 110 g, respectively. We ensured that the total weight of PPT plus the epoxy used to attach the instrument to the carapace did not exceed 5% of the turtle's body weight; therefore all tagged turtles weighed at least 6 kg. Prior to attaching the transmitter with epoxy Tubolit® (Duque de Caxias-RJ, Brazil), we removed epibionts and sanded and cleaned the carapace with acetone. We streamlined attachment materials to reduce effects of drag on the turtle's swimming ability (Watson and Granger, 1998). The anticipated battery life of each PPT was 8 months, and we set the tags with variable duty cycles (Table 1). All tagged turtles were released at or near the place where they were caught.

2.3. Data filtering and analysis

We used the Satellite Tracking and Analysis Tool (STAT; Coyne and Godley, 2005) to archive and filter location data. All location classes (0–3, A and B but not Z) were used in the analysis. We also filtered out those that required straight-line travel speeds over 5 km h^{−1}, or a turning angle of <10° (Semino et al., 2008). Using ArcGis 9.3® (Copyright© ESRI), we manually removed erroneous points

(e.g. those that "zig-zagged" land) and implausible locations that remained after the STAT filtering process.

After filtering, tracking data were analyzed following two complementary methodologies: a switching state-space models (SSM) and fixed kernel density estimation (KDE), following Hart et al. (2011). A behaviorally switching SSM was fitted to Argos tracks to infer animal behavioral state from the movement pattern (Breed et al., 2009). Using the free software packages R and WinBUGS, we fit the behaviorally switching SSMs initially developed by Jonsen et al. (2005) and refined by Breed et al. (2009) to each turtle track. We estimated locations and associated credible limits at five-hour intervals. This time interval reflects the average number of Argos locations per day for these animals. Following Bailey et al. (2008), behavior was discriminated into three states that were nominally referred as: "foraging" (state 1), "transiting" (state 2) and "uncertain" (state 0). Behavioral modes were based on two parameters: mean turning angle and autocorrelation in speed and direction. When animals encounter areas of sufficiently abundant prey or sufficient resources for forage, they often engage in area-restricted searches by decreasing their travel rate and/or increasing their turning frequency and angle. Conversely, animals encountering unsuitable habitat often have fast travel rates and infrequent and small turning angles (Hart and Fujisaki, 2010; Turchin, 1991). In this study, a lack of overlap between the parameters representing the opposing behavioral states indicated a true differentiation in movement patterns, with slow speeds and high rates of change in direction and turning angle indicative of foraging, and the opposite patterns indicative of transiting.

Once the tracks were fitted using SSM, we used Hawth's Analysis Tools extension (Beyer, 2004) for ArcGis 9.3® (Copyright© ESRI) and a smoothing parameter (*h*) of 40 km for each kernel density estimation. We used all locations regardless of state to construct seasonal density distribution maps. We then differentiated between foraging and transiting locations to construct maps of foraging areas and migratory routes, respectively. Density distributions were represented on the maps by the 50, 75, 95 and 100% utilization distribution (UD) contours, indicating areas within which tracked turtles spent 50, 75, 95 and 100% of their at-sea time. The 100% and 50% UD represent overall distribution range and core activity areas of turtles in the SW Atlantic during the tracking period, respectively.

To classify nearshore and offshore habitat use, we determined water depth along the tracks. Bathymetric data was obtained from the GEBCO Digital Atlas andETOPO2 Global 2' Elevations datasets distributed by the British Oceanographic Data Centre and NOAA's National Geophysical Data Center. To test if there were any seasonal differences between the habitat use (characterized by water depth and distance to shore) we applied a General Lineal Model (McCullagh and Nelder, 1989) with "season" as fixed factor (two levels: summer/fall and winter/spring) and "individual" as a random factor (nine levels: turtle A to I). Furthermore, we calculated the time that turtles spent in areas void of abundant macrophytes such as the Río de la Plata, El Rincón and areas

Table 1
Summary of tracking data for 9 juvenile green turtles studied from 2008 to 2011 in the SW Atlantic. CCL: curved carapace length. Duty cycle: hours on/off. SB: southern Brazil, RDP: Río de la Plata, URU: Uruguay Atlantic coast, BA: Buenos Aires coast.

Turtle ID	CCL (cm)	Mass (kg)	Origin	Recovered from	Date of deployment	Duty cycle	No. of days tracked	No. of received locations	Distance traveled (km)	Destination
A	38.5	7.3	Bahía Blanca	Shrimp net	15 Feb 2008	10/14	215	123	1525	SB
B	40.5	9.5	Bahía Blanca	Shrimp net	24 Apr 2008	10/14	297	989	5623	RDP ^a
C	47.8	13.5	Bahía Blanca	Shrimp net	17 Dec 2008	12/12	137	730	1530	URU ^b
D	46.0	8.5	Magdalena	Gillnet	8 Feb 2009	12/12	160	386	1769	SB
E	38.1	7.6	Bahía Blanca	Gillnet	17 Feb 2009	12/12	69	272	554	BA ^b
F	44.0	10.5	Bahía Blanca	Gillnet	10 Mar 2009	12/12	290	1461	5981	SB
G	48.0	12.5	San Clemente	Gillnet	5 Jan 2010	24/0	208	1354	4378	SB
H	39.5	6.8	San Antonio Oeste	Tidal pool	6 Mar 2010	12/12	358	2835	6734	RDP ^a
I	38.0	7.0	Bahía Blanca	Gillnet	15 Dec 2010	24/0	144	1614	2338	SB

^a Round-trip migration.

^b Transmissions stopped prematurely.

>30 m according to Boraso and Zaixso (2008), Boschi (1988), Mianzan et al. (2001) and Parodi (2004).

We also included information on isotherm distribution for February, May, August and November of 2009, meant to be representative of the seasonal variation in sea-surface temperature in the region for the studied period. Information came from the satellite MODIS/Aqua, with 9 km resolution, obtained through the online PO.DAAC Ocean ESIP Tool (POET) at the Physical Oceanography Distributed Active Archive Center (PO.DAAC), NASA Jet Propulsion Laboratory, Pasadena, CA.

3. Results

3.1. Turtles

Eight turtles were recovered from nets in artisanal fisheries at Magdalena, San Clemente and Bahía Blanca ports. One animal was found in a tidal pool in San Antonio Oeste (Fig. 1). They ranged in size from 38.0 to 48.0 cm CCL (mean \pm SD = 42.3 \pm 4.2 cm), and weighted from 7 to 13.5 kg (mean \pm SD = 9.2 \pm 2.5 kg) (Table 1).

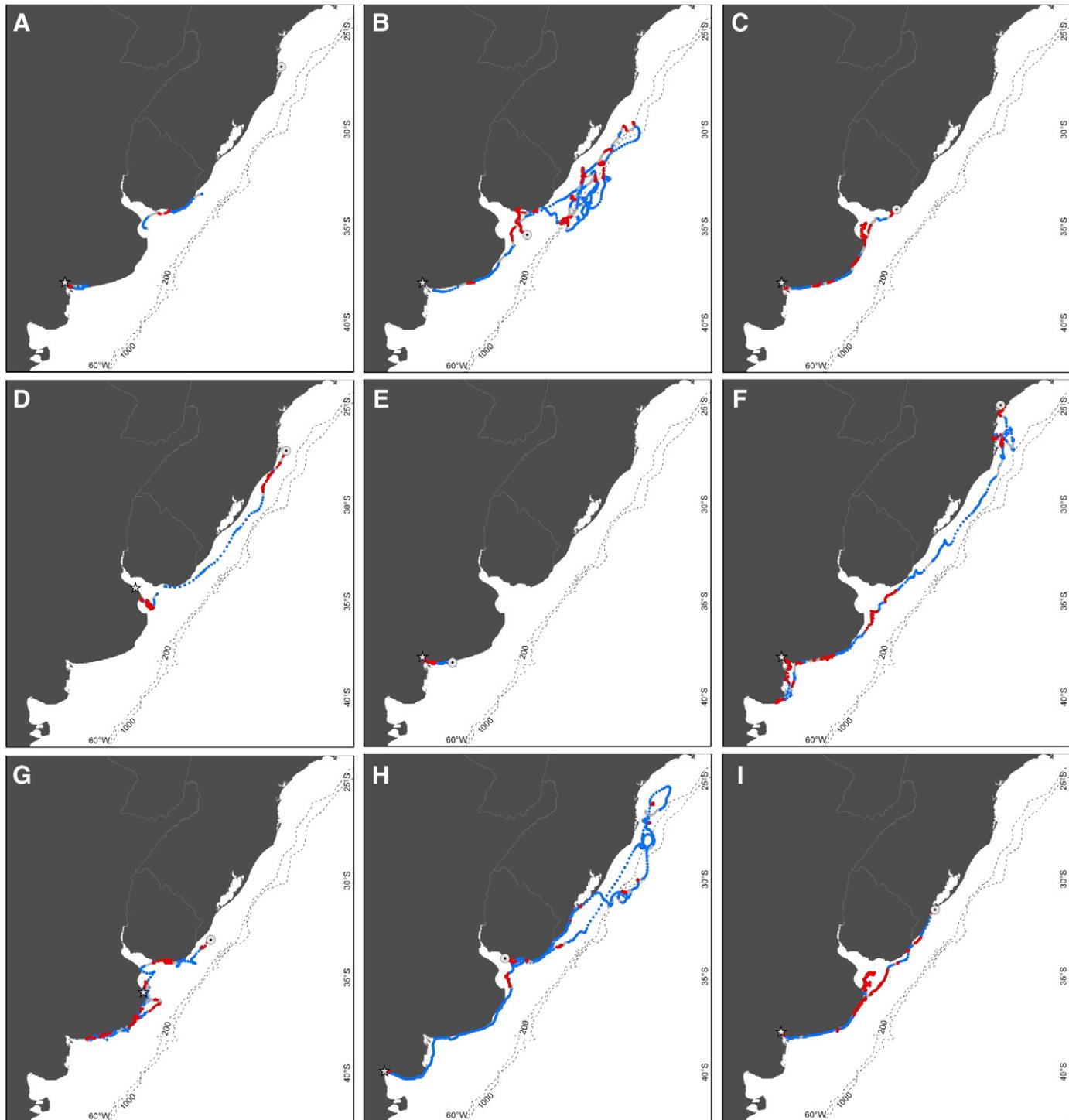


Fig. 2. Individual tracks of 9 juvenile green turtles (A–I) in the SW Atlantic. Stars indicate localities on the Argentine coast where the turtles were captured and circles indicate where transmission stopped. Red and blue dots indicate foraging and transiting positions, respectively. Gray dots show locations where behavior is uncertain.

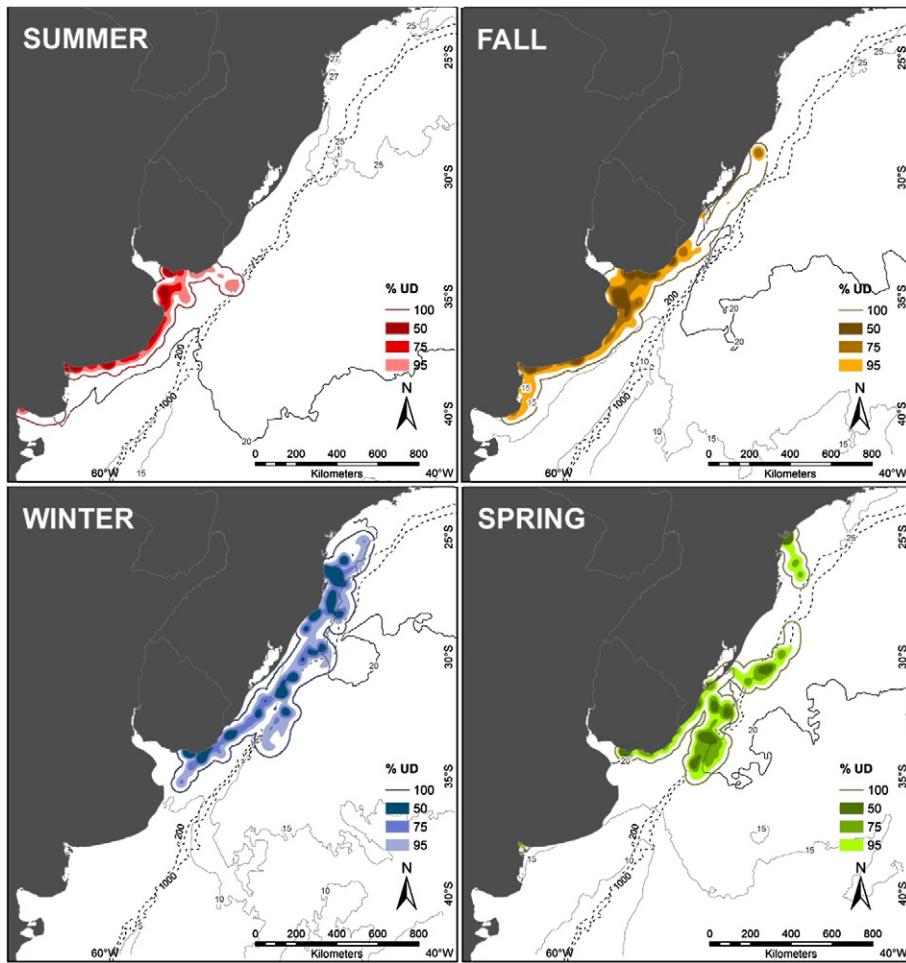


Fig. 3. Seasonal habitat use of juvenile green turtles in the SW Atlantic. The 100% and 50% UD represent the overall distribution range of the turtle and the core activity areas, respectively. Gray full lines represent monthly isotherm for February, May, August and November of 2009. The 20 °C isotherm is highlighted.

3.2. Satellite tracks

All turtles transmitted positions for a total of 9764 locations recorded during 1878 days of transmission. On average, tags transmitted 208 days and the range of days at large was 69 to 358. Mean travel speed for tracked turtles ranged from 0.5 to 1.24 km h⁻¹ (SD range = 0.61–1.46). The net distance traveled by the turtles ranged from 554 to 6734 km (mean \pm SD = 3381 \pm 2306 km) (Table 1). Seven out of the 9 tagged individuals reached southern Brazil, whereas the other two stopped transmitting prematurely along the Uruguayan and Argentine coasts (turtles C and E; Fig. 2). Turtle A sent its last transmission from coastal waters near Itají port (26°54' S, 48°40'W), although the relatively sporadic locations obtained during that period (every 2 to 5 days) did not allow the SSM to generate a complete track (Fig. 2).

3.3. Seasonal distribution

During summer and fall, tracked juveniles were located in the coastal waters off Argentina and Uruguay. They then migrated to southern Brazil to winter in warmer waters (Fig. 3). Migration started during the fall, as evidenced by an increase in mean movement rate and the northern position of the 20 °C isotherm (Figs. 3 and 4). In spring, most turtles remained in waters off Brazil and Río de la Plata (Fig. 3).

Green turtles occupied waters within a wide range of depths that encompassed neritic (depth < 200 m) as well as oceanic waters

(depth > 200 m, Fig. 3). During summer and fall they used almost exclusively shallow waters off the coast of Argentina and Uruguay, in contrast to winter and spring when they occupied shelf waters of Uruguay and Brazil, and even oceanic waters (summer/fall: median = 9.0 m, range = 0–256.0 m; winter/spring: median = 69.0 m, range = 0–2867.0; $F = 1390.5$, $p = 0$). Overall, green turtles expended ca. 38% of their time foraging in the Río de la Plata, El Rincón and deep water

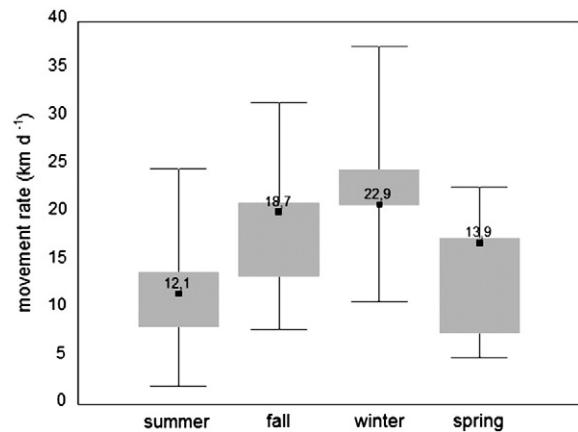


Fig. 4. Movement rate (km d⁻¹) of juvenile green turtles in the SW Atlantic. Black point indicates the median, rectangle indicates quartiles of 25 and 75% and whiskers indicates maximum and minimum values.

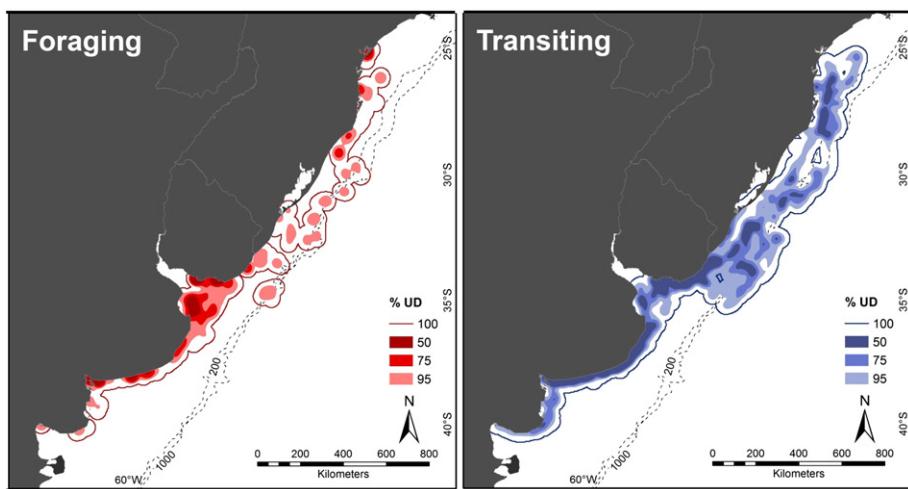


Fig. 5. Foraging areas and migratory routes of juvenile green turtles in the SW Atlantic, represented by the utilization distribution (UD) contours. The 100% and 50% UD represent the overall distribution range and the core activity areas, respectively.

areas. Distance to shore also varied between seasons, although it was not correlated with bathymetry. Turtles were closer to shore during summer and fall (summer/fall: median = 9.8 km, range = 0–181.9 km; winter/spring: median = 91.4 km, range = 0–295.1 km; $F = 202.3$, $p = 0$).

3.4. Migratory routes and foraging areas

During summer and fall, foraging occurred in nearshore waters. El Rincón, the Buenos Aires coast and Río de la Plata encompassed a highly used area of 11,282 km². During winter and spring, most foraging occurred in coastal waters of Uruguay and Brazil and in offshore waters, within an area of more than 5000 km² (Fig. 5, Table 2).

Some animals exhibited fidelity to nearshore waters off Argentina and Uruguay, suggesting that these habitats can be visited repeatedly by turtles. Turtles B and H performed a round-trip migration, using offshore waters to return to different parts of the Río de la Plata estuary (Fig. 2). In contrast, turtle F remained in Bahía da Paranaguá, Brazil (25°29'S, 48°33'W), after leaving Argentine waters.

4. Discussion

This work tracked green turtles in temperate waters and longer than previous studies on the species (Brill et al., 1995; Hart and Fujisaki, 2010; Makowski et al., 2006; McClellan and Read, 2009;

Seminoff et al., 2002). This extended tracking time and the novel analytical tool that combines SSM and KDE provide sound evidence that immature turtles can forage in habitats like the Río de la Plata and deep water areas void of submerged macrophytes (Boraso and Zaixso, 2008; Boschi, 1988; Mianzan et al., 2001; Parodi, 2004). As a consequence, they cannot be strictly herbivores in the temperate SW Atlantic. The behavior adapts to local conditions, which ultimately implies that the previously described ontogenetic shift would not be as abrupt and irreversible as proposed for the Greater Caribbean and eastern Australia. This is also the first study that documents the use of overwintering offshore areas by neritic immature green turtles.

Tag performance was good in general and only one tag transmitted for short time (see turtle E, Table 1). Among the reasons why tags usually stop transmitting are exhaustion of batteries, tag failure, antenna breakage, animal mortality and premature detachment, which in some cases can be identified on the basis of tag's diagnostic data (Hays et al., 2007). In our case, the shortest transmission time of tag on this turtle could be due to antenna breakage or premature detachment, although distinction between them is impossible. On the other hand, several tags stopped transmitting while turtles were occupying areas where bycatch is known to occur, such as turtles B, C, H and I (Fig. 2). Predation, which is relatively high at this immature stage (Crouse et al., 1987), could also be a reason.

Tracking data suggest that neritic juveniles spend ca. 5 months per year foraging in the Río de la Plata and El Rincón areas, where the community of species is characterized by large biomass of gelatinous macrozooplankton, especially *Lichnorhiza lucerna*, *Chrysaora lactea*, *Mnemiopsis mccradyi* and *Liriope tetraphylla* (Álvarez Colombo et al., 2003; Mianzan and Guerrero, 2000; Mianzan et al., 2001). Coherent with expectations, gelatinous remains were found in the stomach contents of green turtles from Río de la Plata (VGC, unpublished data). This result is similar to the described diet of the species off the Peruvian coast, where they prey on jellyfish (Quiñones et al., 2010). Outside the mentioned areas, but relatively close to them, the diet changes to herbivory. Off the coast of Uruguay, turtles feed on various macroalgae species (*Ulva lactuca*, *Chondracanthus teedii* and *Polysiphonia* sp.) and in Bahía da Paranaguá (Brazil) they graze on the seagrass *Halodule wrightii* (Guebert-Bartholo et al., 2011; López-Mendilaharsu et al., 2006). Juveniles may then be omnivorous in neritic environments of the SW Atlantic, feeding on macroalgae, seagrass and macrozooplankton, according to availability.

In addition to feeding in areas void of macrophytes such as the Río de la Plata and El Rincón, foraging was also estimated to occur in deep water areas where most seagrass or macroalgae do not grow. In fact,

Table 2

Foraging areas and migration routes of juvenile green turtles in the temperate SW Atlantic. Areas, in (km²) are for the 50 and 100% utilization distribution contours.

Foraging areas	Area
100%	254,741
50%	
Argentina coast	1182
El Rincón	1947
Río de la Plata	4987
Uruguay coast	3088
Bahía da Paranaguá	1176
<i>Migratory routes</i>	
100%	408,004
50%	
Argentina coast	21,448
Uruguay coast	19,144
Brazil continental shelf	18,497

two of our tracked animals spend the winter months in the offshore waters (depth > 200 m) of Uruguay and Brazil. Although exceptions can exist – some macroalgae species grow at more than 100 m according to Littler et al. (1985, 1986) – benthic feeding for shallow-divers such as small green turtles is unlikely in these waters (Brill et al., 1995; Hazel et al., 2009). Offshore areas were also described as feasible foraging environments for adult green turtles off the coast of Japan (Hatase et al., 2006).

The foraging areas described here are considerably larger than other studies of juvenile green turtles using comparable methods and sample sizes. We found that 50% contour areas are 10 to 100 times larger compared to those described in other studies (Table 2, see Hart and Fujisaki, 2010 for a review). Large foraging areas were also recorded for adult loggerheads from the NW Atlantic and the Mediterranean (Cardona et al., 2005; Hawkes et al., 2011; Revelles et al., 2007; Schofield et al., 2010). In these regions, a relaxed ontogenetic shift and therefore an adaptable behavior were proposed (Casale et al., 2008; Laurent et al., 1998; McClellan and Read, 2007; Witzell, 2002). Loggerheads might exhibit an “opportunistic amphihabitat stage”, in which they can exploit resources in the area they frequent: pelagic in oceanic habitats and both benthic and pelagic in neritic habitats. The decision of remaining in a habitat would depend therefore on the successful or unsuccessful experience of the turtle, on the basis of environmental parameters that are still poorly understood (Casale et al., 2008).

After foraging in temperate waters off Argentina, green turtles started migrating north possibly triggered by a decrease in sea-surface temperature (Fig. 3). Winter dormancy is known to occur in sea turtles, as evidenced by prolonged dive durations (Hochscheid et al., 2005). Our tags did not measure dives so we were not able to analyze green turtle behavior in relation to dormancy. However, the increased movement rate recorded during the fall and winter and the location of turtles in relation to the 20 °C isotherm suggest that, at least for the turtles studied, there is no evidence of such behavior. Cold-stunned turtles, probably those who had fallen behind, are usually recorded at the coastal waters of Argentina (VGC, unpublished data).

The foraging areas and migratory routes used by turtles in this study seem to be associated with major currents and frontal systems in the region. Animals migrating north would use shelf waters at variable distances from the coast to reach warmer areas. On their way back, they likely travel along offshore waters possibly using the southward flow of the warm Brazil Current (Fig. 1). Foraging areas intensively used may coincide with El Rincón, Río de la Plata, the Argentine shelf-break and the Cabo Santa Marta Grande fronts identified by Mianzan and Guerrero (2000) and Acha et al. (2004). Environmental conditions and resource availability need to be explored in the temperate SW Atlantic.

Why do green turtles in the SW Atlantic not fit the abrupt and irreversible ontogenetic shift reported for the Greater Caribbean and Australia? Juveniles venture to temperate waters that are too cold for them to overwinter. These waters offer, however, abundant resources that are predictable and concentrated. Juveniles benefit while the ocean conditions are feasible, but then they are forced to migrate, thus the large size of the areas used. The benefit of adapting the diet to these shifting environmental conditions should outweigh with the costs of migration and this is perhaps possible if the rate of acquisition of nutrients in temperate systems is larger than expected for habitats that facilitate an herbivorous diet. It is expected that shifting the behavior to local conditions would be selectively beneficial compared to a fixed pattern for the diet, unless the animals in the extreme of the distribution range of the species are forced to adopt behaviors that depart from the most convenient, being then exposed to higher mortality. The trade-off between venturing to temporary suitable waters and gaining access to abundant resources needs further research.

Describing variability in the life history of green turtles has implications for conservation. In addition to threats faced on land and in coastal waters (National Research Council, 1990; Seminoff, 2004), juveniles traveling in pelagic waters face the threat of being caught in pelagic longline fisheries. In fact, bycatch of juvenile green turtles have already been reported in the longline fleets operating in the temperate waters of the SW Atlantic (Sales et al., 2008). In the temperate SW Atlantic, turtles are part of the bycatch of artisanal and commercial fisheries (Gallo et al., 2006; González Carman et al., 2011; Sales et al., 2008); therefore the conservation of this population requires efforts in coastal and open waters.

The occurrence of green turtles in Argentine waters during summer and fall suggests that management for conservation should target these seasons and the fisheries which occur during these months. As the same individuals move across jurisdictions, management should also be coordinated with Uruguay and Brazil, as turtles live in their waters during the rest of the year. Argentina is a Party to the Inter-American Convention for the Protection and Conservation of Sea Turtles and the Convention on Migratory Species that provide the legal frame and dialog channel to work towards the conservation of the species in the SW Atlantic. Our results contribute to better management through the identification of areas intensively used by the species where conservation measures should be focused.

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