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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 ontogenic shift described for warmer waters.

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 in 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

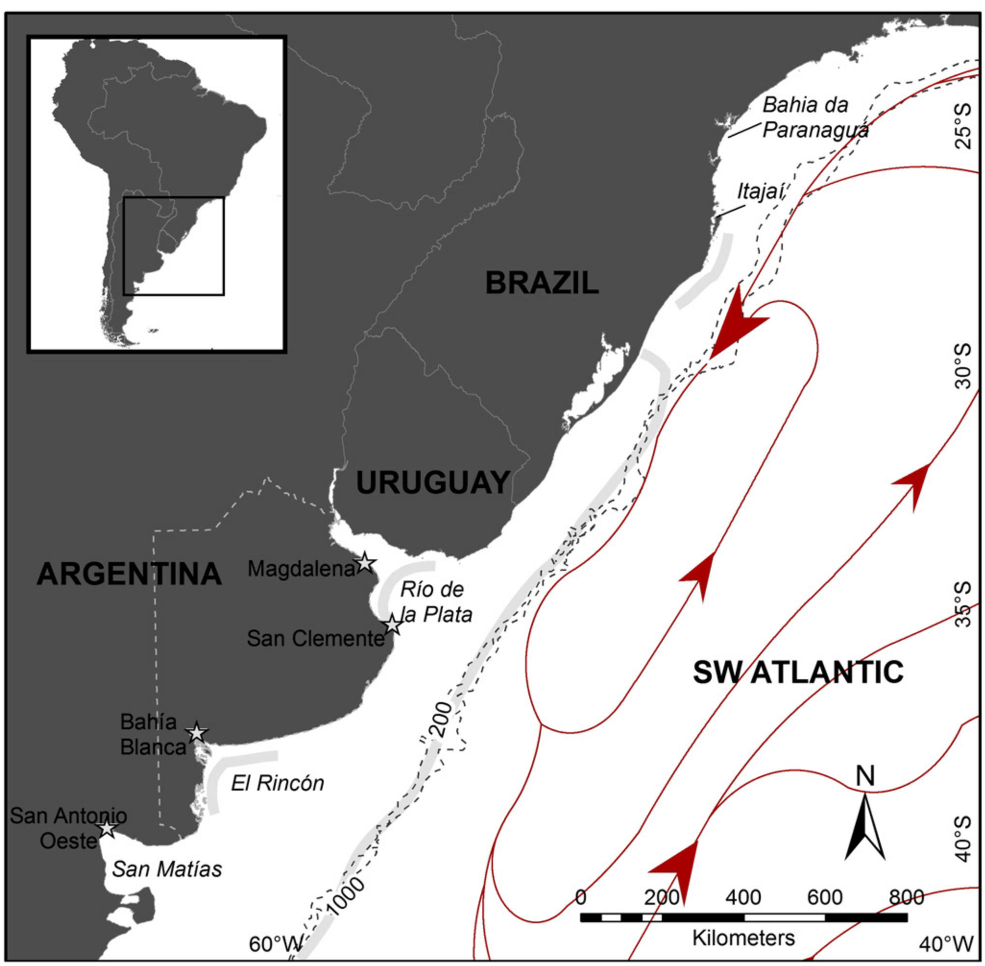

Fig. 1. Study area of juvenile green turtles in the SW Atlantic. Stars indicate localities on the Argentine coast where the turtles were captured. Black dashed lines show positions of 200 and 1000 m isobaths. Gray dashed lines show limits of the Buenos Aires province. Gray full lines show frontal areas.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