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Individual specialization and behavioral plasticity in a long-lived marine predator

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ABSTRACT

Individual specialization in vertebrates is often related to morphological variability, but can also reflect a diversity of trajectories during the learning sensitive period in early life. In both cases the capacity of adults to adapt to new environments can be limited if further morphological or behavioral change is not possible. Adult loggerhead turtles *Caretta caretta* (Linnaeus, 1758) from Cape Verde (NW Africa) may forage in the open ocean or on the continental shelf. Oceanic foragers prevail in the population, but neritic foragers grow larger, have a higher reproductive output and produce best fitted offspring. Previous research suggests that the high prevalence of oceanic foragers is because the migratory routes followed by juvenile turtles during their early life results into a low probability of settlement on the African shelf. The stable isotope ratios of C and N in 60 μm carapace layers from 14 adult females have been analyzed to reconstruct retrospectively their individual habitat use patterns and test the hypothesis that adult loggerhead turtles remain faithful to their foraging grounds even if sub-optimal. Only two turtles exhibited clear oceanic—neritic shifts, approximately 22 and 15 years before sampling. The remaining turtles had foraged in neritic (3) or oceanic (9) habitat as long as recorded in the carapace scutes (approximately 8–37 years), despite the smaller body size and the lower reproductive output associated to oceanic foraging. These results suggest that habitat shifts during adulthood are unlikely in this species and support the hypothesis that only during the juvenile stage loggerhead turtles are flexible enough to adapt to contrasting environments.

1. Introduction

Individual specialization is widespread in vertebrates (Bolnick et al., 2003) and has major consequences for community structure and dynamics (Araujo et al., 2011). Morphological variability is often at the basis of individual specialization (e.g. Grant and Grant, 1996; Svanbäck and Eklöv, 2002), but this is not always true and other factors such intraspecific and interspecific competition, predation risk and ecological opportunity are often involved (Araujo et al., 2011; Svanbäck and Bolnick, 2007). Individual specialization is expected to be irreversible when based on morphological traits that cannot be modified at advanced life stages (Svanbäck and Bolnick, 2007), but could be reverted otherwise if individuals learn new foraging tactics (Mery and Burns, 2010).

Adult hard-shelled marine turtles exhibit high levels of individual specialization on habitat use (Cardona et al., 2014; Ceriani et al., 2012; Eder et al., 2012; Hatase et al., 2013; Pajuelo et al., 2012; Vander Zanden et al., 2010, 2013; Vander Zanden et al., 2016; Pajuelo et al., 2016) and very little temporal change (Vander Zanden et al., 2010, 2013; Vander Zanden et al., 2016; Pajuelo et al., 2016). However, the quality of foraging grounds used by female adult hard-shelled marine turtles is heterogeneous and the reproductive output of females and the quality of the offspring varies accordingly (Cardona et al., 2014; Eder et al., 2012; Hatase et al., 2013; Vander Zanden et al., 2014; Vieira et al., 2014; Zbinden et al., 2011). Given the capability of other chelonians for spatial learning (López et al., 2001), hard-shelled marine turtles settled in sub-optimal habitats as juvenile might be expected to shift to better habitats with age to improve their fitness and reproductive performance, as far as they improve their spatial knowledge (Eder et al., 2012). Previous research has reported several cases of long-term site fidelity in hard-shelled turtles but also a few cases of habitat shifts in adult females (Broderick et al., 2007; Hawkes et al., 2011; Vander Zanden et al., 2010, 2013) and males (Pajuelo et al., 2016). It has been speculated that adult hard-shelled marine turtles may shift habitat more likely where resource availability is lower (Pajuelo et al., 2016), but they are known to remain faithful to their foraging grounds

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even after major anthropogenic impacts (Vander Zanden et al., 2016).

Satellite tags are widely used to track marine turtles, but they last usually for less than a year (e.g. Broderick et al., 2007; Hawkes et al., 2011), which is a major shortcoming for the study of long term movements in a long-lived organism (Avens et al., 2015). The analysis of stable isotopes offers an alternative method to document ontogenetic habitat shifts, because carapace scutes are metabolically inert once formed and offer a record of the foraging habitats used by individual turtles during several years (Cardona et al., 2009; Cardona et al., 2010; Reich et al., 2007; Vander Zanden et al., 2010, 2013; Vander Zanden et al., 2016; Pajuelo et al., 2016).

The Cape Verde archipelago hosts an important, isolated and endangered population of the loggerhead *Caretta caretta* (Linnaeus, 1758) (Casale and Marco, 2015; Marco et al., 2012; Monzón-Argüello et al., 2010) where adult males and females primarily feed in oceanic habitats (Eder et al., 2012; Hawkes et al., 2006; Pikesley et al., 2015; Scales et al., 2015; Varo-Cruz et al., 2013). The proportions of oceanic and neritic females nesting in the archipelago match habitat availability and random settlement between the archipelago and mainland Africa at the end of the developmental migration may explain it (Eder et al., 2012). However, females using neritic habitats along the coast of north-western Africa grow larger, have a higher reproductive output and produce better quality offspring than oceanic females foraging in the upwelling area between the archipelago and mainland Africa (Eder et al., 2012; Vieira et al., 2014). Adult males foraging in neritic grounds are also larger than oceanic foragers (Varo-Cruz et al., 2013). Hence, a potential habitat shift might be expected as adult loggerhead turtles grow older and improve their spatial knowledge of the area and navigational skills (Eder et al., 2012). Here, the frequency of habitat shift in 14 adult female loggerhead turtles from Cape Verde has been assessed to test this hypothesis. Individual patterns of habitat use have been reconstructed retrospectively through the analysis of C and N stable isotope ratios in the layers of carapace scutes.

2. Material and methods

2.1. Sample collection

Five samples of the jellyfish *Pelagia noctiluca* (Forsskål 1775) were collected off Cape Verde in 2010 to characterize the stable isotope ratios of oceanic prey and five samples of the benthic octopus *Octopus vulgaris* Cuvier 1797 were collected off Mauritania to characterize the stable isotope ratios of benthic prey. Jellyfish and octopus samples were preserved at − 20 °C until analysis.

The third lateral carapace scute from 14 adult females found dead on nesting beaches in Boavista Island (Cape Verde) were collected during the 2008, 2009 and 2010 nesting seasons (Table 1). Females were selected from a larger sample to cover the whole range of nesting adults (Hawkes et al., 2006; Eder et al., 2012). Curved carapace length (CCL) was measured with a fiberglass tape measure (± 0.1 cm) and dry scutes were stored without preservatives in plastic bags at ambient temperature (15–25 °C) until analysis.

2.2. Stable isotope analysis

Whole jellyfish and pieces of octopus mantle were dried into a stove at 60 °C and powdered using mortar and pastel. Lipids were removed from 1 g of powdered sample by rinsing it several times with a 2:1 chloroform:methanol solution until the liquid was clear.

Once in the laboratory, scutes were slightly brushed and sub-sampled with a 6 mm biopsy punch at a site close to the posterior lower margin (Reich et al., 2007). The sub-samples were embedded in paraffin and micro-sampled with a FM AG microtome (model Rotary 3003) in successive layers (30 μm) to provide a chronological sequence. This layer thickness was selected for convenience, because thicker sections were harder to cut. Nevertheless, successive carapace sections were combined in pairs to obtain enough material for the stable isotope analysis, thus resulting into an effective layer thickness of 60 μm. Sections were kept into a stove at 60 °C overnight, rinsed daily with a 2:1 chloroform:methanol solution for five days and dried again for 24 h at 60 °C. A previous trial demonstrated that this procedure removed any paraffin trace and after rinsing with chloroform:methanol and drying, the $\delta^{13}C$ and $\delta^{15}N$ values of the sample did not differ from those of control samples in which paraffin was not used (Fig. 1).

On average, 0.3 mg of sample was used for stable isotope analysis of both prey and carapace samples. Samples were weighed in tin cups (3.3–5 mm) and combusted at 1000 °C in a continuous flow isotope ratio mass spectrometer (Flash 1112 IRMS Delta C Series EA, Thermo Finnigan, Bremen, Germany). Atropine was used as a standard system

Table 1
Descriptive characteristics of the 14 adult loggerhead turtles from Cape Verde (NW Africa).

Specimen	Year	CCL (cm)	Scute thickness (μm)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
CV50	2009	99.0	2220	− 16.2 ± 0.7	13.7 ± 0.3
CV1	2008	93.0	800	− 15.6 ± 0.1	12.7 ± 0.1
CV69	2010	93.0	2700	− 16.2 ± 0.7	12.1 ± 0.8
CV42	2009	92.0	1620	− 15.3 ± 0.5	12.5 ± 0.2
CV59	2010	89.5	3720	− 17.1 ± 0.4	11.1 ± 0.4
CV51	2009	89.0	1620	− 18.3 ± 2.0	8.7 ± 0.7
CV29	2009	87.5	1500	− 18.1 ± 0.6	9.4 ± 0.7
CV58	2010	87.0	1100	− 15.3 ± 0.3	12.4 ± 0.3
CV68	2010	86.0	1380	− 17.7 ± 0.4	10.0 ± 0.4
CV66	2010	85.5	1470	− 17.5 ± 0.5	10.2 ± 0.6
CV79	2010	78.5	1320	− 18.1 ± 0.3	9.3 ± 0.7
CV55	2010	74.0	1080	− 17.9 ± 0.4	10.1 ± 0.2
CV53	2010	76.0	1860	− 17.2 ± 0.5	9.3 ± 07
CV40	2009	75.0	2220	− 18.0 ± 0.3	9.7 ± 0.5

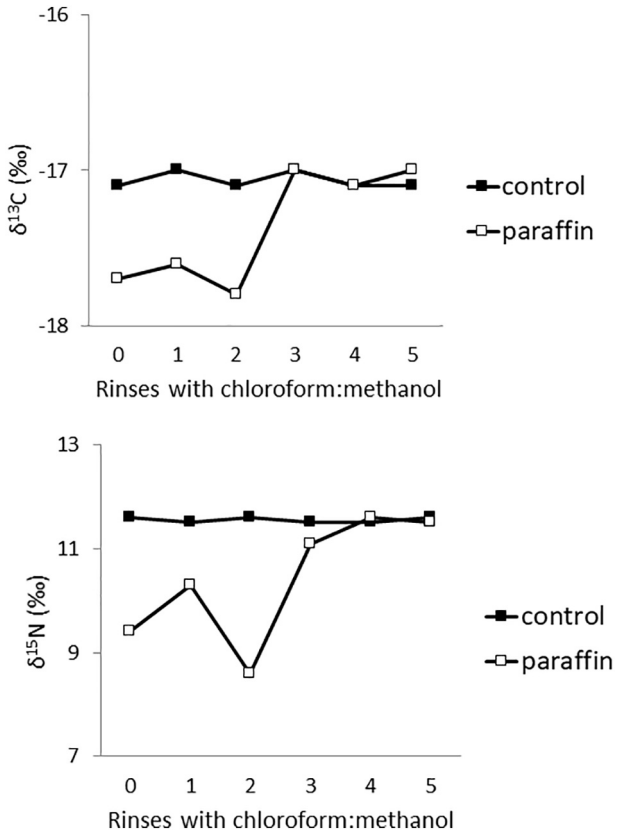

Fig. 1. Effect of rinses with a 2:1 chloroform:methanol solution to remove paraffin traces from carapace scute sections.