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Sea turtle population structure and connections between oceanic and neritic foraging areas in the Atlantic revealed through trace elements

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ABSTRACT: Assessing population structure and connectivity of species that have cryptic life stages, such as sea turtles, is a challenge in conservation biology. The early oceanic stage of sea turtles, also known as the 'lost years', is poorly known. Green turtle *Chelonia mydas* hatchlings emerge from their nests, enter the sea, and inhabit oceanic (open ocean) habitats where they are rarely seen until they recruit to coastal (neritic) foraging grounds several years later. Therefore, the location of and population structure in oceanic foraging grounds, as well as the connections between oceanic and neritic foraging grounds, are difficult to determine. Given that long-term tracking devices are not available for sea turtle hatchlings, the use of other markers, such as trace elements and stable isotopes, is necessary to study the oceanic stages of sea turtles. We analyzed the elemental composition and ratios of stable isotopes of carbon and nitrogen of scute tissue that was deposited when turtles were in the oceanic habitat to characterize 6 oceanic foraging areas used by green turtles in the Atlantic Ocean. We determined that there is significant structuring among oceanic green turtle aggregations and multiple links between oceanic and neritic foraging areas. We discuss the conservation implications of structured oceanic aggregations with multiple links, as well as the use of trace elements (particularly titanium, chromium, zirconium and barium) in the characterization of oceanic regions.

KEY WORDS: Green turtle · Oceanic stages · Trace elements · Open ocean · Population connectivity

INTRODUCTION

Determining population structure and movements of individuals among subpopulations that are geographically separated and constitute a metapopulation is one of the major goals of conservation biology, as it allows us to determine the resilience of populations to either stochastic or anthropogenic disturbances (Cowen et al. 2007, Fogarty & Botsford 2007). However, assessing population structure and connections is a challenge when dealing with organisms that have cryptic life stages that occur in unknown or inaccessible locations, such as sea turtles.

Sea turtles are highly migratory organisms that move between foraging areas and nesting areas (Musick & Limpus 1997). For most species of sea turtles, hatchlings emerge from their nests, enter the sea, and inhabit oceanic (open ocean) habitats until they recruit to coastal (neritic) foraging grounds several years later. The location of oceanic developmental areas of young turtles other than loggerheads *Caretta caretta* (Carr 1986, Bolten 2003a,b) remains a

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mystery — commonly known as the 'lost years' (Carr 1986). We have learned much about the connections between neritic foraging grounds (after 'lost years' turtles have recruited to neritic areas; Bass & Witzell 2000, Hart & Fujisaki 2010) and nesting beaches used by adult sea turtles (Lahanas et al. 1998, Luke et al. 2004). However, until we locate the oceanic foraging areas of these young sea turtles and understand how they connect to other developmental areas, we cannot identify potential threats or protect the turtles.

Despite advances in the development of tracking devices for a vast array of marine organisms, including juvenile and adult sea turtles (Luschi et al. 1998, Mansfield et al. 2009, Godley et al. 2010), tracking devices for sea turtle hatchlings are still limited to very short spatio-temporal scales (Thums et al. 2013). Therefore, other types of markers, such as trace elements and stable isotopes, are needed to evaluate population structure and connections within metapopulations of sea turtles during their early oceanic stage, or 'lost years'.

Trace metals and stable isotopes occur naturally in the environment (Kabata-Pendias & Mukherjee 2007, Hobson 2008). Ratios of carbon and nitrogen isotopes have shown a clear geographic variation among coastal areas of the northwest Atlantic and these signatures are reflected in the tissue of organisms foraging in these areas (Pajuelo et al. 2012). The abundance of trace elements varies geographically depending on factors such as temperature, depth, distance from the coast and other oceanographic features (Boyle et al. 1982, Brown et al. 1994, Newman et al. 2000, Grousset & Biscaye, 2005). Because of their differential geographic distribution, trace elements have also been used to identify locations of various marine organisms (Kunito et al. 2002, Born et al. 2003, Thorrold et al. 2007, Carson et al. 2008, Doubleday et al. 2008).

Organisms obtain trace elements and stable isotopes from their environment, thus acquiring the elemental signature of the place in which they feed and grow, which makes it possible to identify changes of habitat when the appropriate tissue is analyzed (Ramos et al. 2009). Inert tissues with continuous growth such as stylets, otoliths, baleen, feathers and hair are ideal for determining changes of habitat because their elemental composition is mainly determined either by the chemistry of the water (e.g. stylets and otoliths; Elsdon & Gillanders 2004, Walther & Thorrold 2006) or by their diet (e.g. baleen, feathers, hair; Gray 2002, Gray et al. 2008). Once they are deposited, inert tissues do not change, thus preserving a history of the places where the organism has been (Elsdon & Gillanders 2005). Evaluating these environmental changes in sequential subsections of such tissues has allowed the study of population structure and connectivity of different marine organisms with cryptic life stages (Born et al. 2003, Thorrold et al. 2007, Doubleday et al. 2008).

The scute of sea turtles is an inert keratinized tissue that covers the bony plates of the carapace. Scute grows by deposition of new keratinized skin directly under the old tissue (Alibardi 2005). As a result, the oldest tissue is found on the dorsal surface of the scute, whereas the youngest tissue is found on its ventral surface. Although the oldest tissue is sloughed, previous studies on oceanic juvenile green turtles have found a retention time between 0.8 and 2 yr (Vander Zanden et al. 2013). By analyzing the elemental composition of the scute tissue that was deposited when the turtle was in the oceanic habitat, we could determine where the turtle was during its 'lost years' if the geographic distributions of trace elements were known.

The extent of connections among subpopulations can be determined by the patterns of migratory pathways among developmental areas. In general, populations with more connections among subpopulations have greater genetic variation and usually have greater resilience to disturbances because many geographically distributed subpopulations can replace losses in one area. When connections are fewer, populations usually have lower genetic variation and their resilience to strong disturbances is lower (Gaines et al. 2007).

In our study, we used trace elements and stable isotopes to determine (1) whether oceanic aggregations of green turtles *Chelonia mydas* in the Atlantic are structured among different regions, (2) the connections between oceanic and neritic foraging grounds, and (3) whether green turtles and loggerheads *Caretta caretta* use the same areas during their oceanic stage.

We used a conceptual model (Fig. 1) to address the first 2 objectives. The conceptual model illustrates the 3 hypothetical scenarios of connections that can result from the analysis of trace elements and stable isotopes in the oceanic scute tissue of green turtles on neritic foraging grounds. The first scenario (Fig. 1A) has a single oceanic foraging ground contributing to multiple neritic foraging grounds. Turtles in these neritic foraging grounds would have the same oceanic signatures and therefore no variability either between or within neritic foraging grounds. The next 2 scenarios (Fig. 1B,C) have multiple oceanic foraging grounds (spatial structure) contributing to several

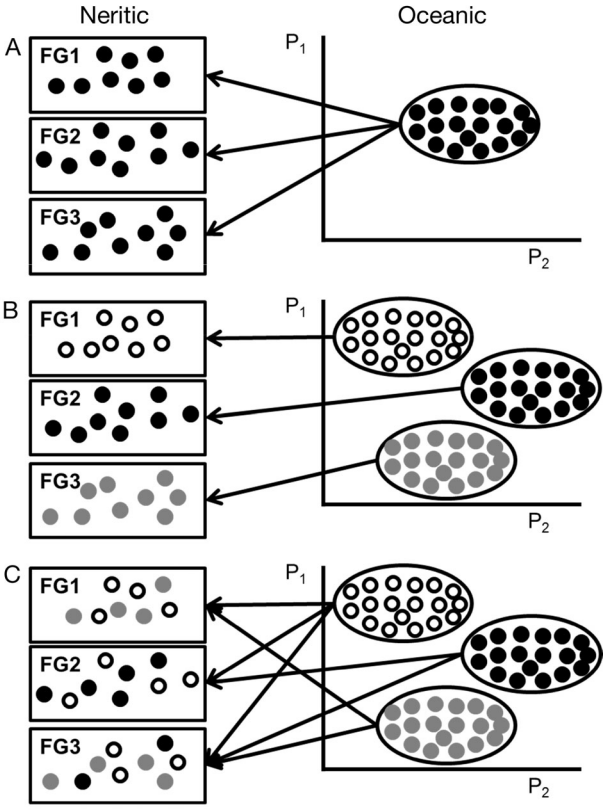

Fig. 1. Conceptual model of possible scenarios resulting from the analysis of trace elements in the oceanic scute tissue of green turtles from 3 different neritic foraging grounds (FG). P_1 and P_2 on the *y*- and *x*-axes represent different combinations of trace elements and their concentrations. Ovals represent oceanic foraging grounds. (A) Single oceanic foraging ground contributes to different neritic foraging areas. (B) Multiple oceanic foraging grounds, each contributes to one neritic foraging ground. (C) Multiple oceanic foraging grounds contribute to multiple neritic foraging grounds

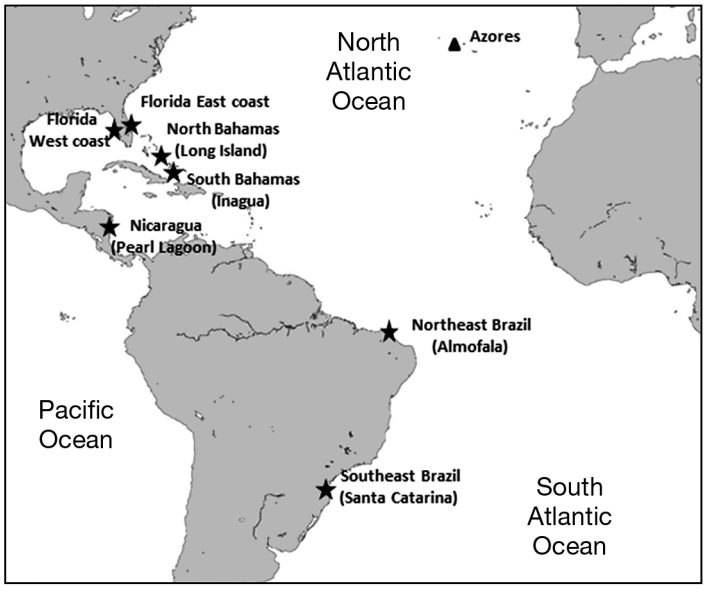

Fig. 2. *Chelonia mydas* and *Caretta caretta*. Sample collection sites. Neritic foraging grounds of green turtles are denoted by stars. The triangle represents the only oceanic foraging ground where loggerheads were sampled. Map created with www.seaturtle.org/maptool

neritic foraging grounds, but with differences in the number of connections. In the second scenario (Fig. 1B), each oceanic foraging ground contributes to only one neritic foraging area. In this case, oceanic signatures would vary among neritic foraging grounds but not within them. In the third scenario (Fig. 1C), each oceanic foraging ground contributes to several neritic foraging areas, that is, there are multiple connections between oceanic and neritic foraging grounds. In this scenario, oceanic signatures would vary within the coastal foraging grounds and, perhaps, among them.

MATERIAL AND METHODS

Sample collection

Scute samples were collected from 174 green turtles smaller than 55 cm straight carapace length (SCL; range 24.7 to 54.6 cm) at 7 coastal foraging grounds at different latitudes in the Atlantic Ocean: east (n = 32) and west (n = 25) coast of Florida, north (Long Island; n = 16) and south (Inagua; n = 26) Bahamas, Nicaragua (n = 27), and north (Almofala; n = 26) and south (Santa Catarina; n = 22) Brazil (Fig. 2). The work of Reich et al. (2007) demonstrated that oceanic-stage green and loggerhead turtles can occupy similar habitats and forage in the same trophic levels. Furthermore, the scute tissue formation process is the same in both species with small differences in the number of epidermal layers (Solomon et al. 1986). Therefore, the incorporation of trace elements into the scute tissue of both species should be similar. Given that small green turtles occasionally strand in the Azores, scute samples were collected from 11 juvenile loggerhead turtles smaller than 30 cm SCL (range 8.3 to 23.3 cm) stranded dead in the Azores to determine the trace element signature of scute in the region and to assess the extent to which green turtles use these oceanic waters as well. Using sterile 6 mm biopsy punches, 2 adjacent scute samples were collected from the central region of the second right lateral scute. Samples were air dried and stored until their preparation in the lab.

Stable isotope analysis

We used stable isotopes of carbon and nitrogen to identify the scute tissue that was deposited while the turtles were in oceanic habitats (Reich et al. 2007). One of the 2 scute samples from each individual was lipid-extracted with petroleum ether using an accelerated solvent extractor and then sub-sampled in 50 µm layers using a carbide end mill. Each layer was analyzed for carbon and nitrogen isotopic composition to determine how many layers had an oceanic signature. Analyses were conducted at the Department of Geological Sciences Light Stable Isotope Lab at the University of Florida using an ECS 4010 elemental analyzer (Costech) interfaced via a ConFlo III to a DeltaPlus XL isotope ratio mass spectrometer (ThermoFisher Scientific). Stable isotope abundances (ratio of heavy to light isotopes) were expressed in delta notation (δX in Eq. (1), where X is either C or N), defined as parts per thousand (‰) relative to the standard:

$$\delta X = (R_{sample}/R_{standard} - 1) \times 1000 \quad (1)$$

where R_{sample} and $R_{standard}$ are the ratios of heavy to light isotopes ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) in the sample and international standard, respectively. The standards used were Vienna Pee Dee Belemnite for ^{13}C and atmospheric N_2 for ^{15}N. L-glutamic acid (reference material USGS40) was used to normalize all results. The standard deviation of the reference material was 0.09‰ for $\delta^{13}C$ values (n = 136) and 0.10‰ for $\delta^{15}N$ values (n = 146). Repeated measures of loggerhead scute used as a laboratory reference material was used to examine consistency in a homogeneous sample of similar isotopic composition. Standard deviation of the loggerhead scute was 0.08‰ for $\delta^{13}C$ values and 0.13‰ for $\delta^{15}N$ values (n = 59).

The isotope values used to distinguish between scute deposited in oceanic and neritic habitats were <–14‰ for $\delta^{13}C$ values and >5‰ for $\delta^{15}N$ values for oceanic tissues (Reich et al. 2007). We used the results of the stable isotope analyses as a reference to select the oceanic layers in the second scute sample. Only samples with at least 2 consecutive layers with similar stable isotope values representing the oceanic habitat were considered for the analysis of trace elements, except for the samples from Brazil. In Brazilian turtles, there was no significant difference between neritic and oceanic stable isotope values in the scute layers, but all turtles were smaller than 55 cm SCL (range 25.0 to 54.6 cm). For these turtles, we used the 2 oldest 50 µm layers of each sample.

Trace element analysis

The second scute sample from each turtle was ultra-cleaned in 4× distilled water for 5 min using a sonicator to eliminate possible contamination of trace elements from the environment. These samples were also sub-sampled in 50 µm layers using a carbide end mill. Based on the stable isotope analysis of carbon and nitrogen, the consecutive oceanic layers of each sample were combined and analyzed as a single sample. Each sample was weighed in acid-cleaned Teflon vials and digested in a 2:1 concentrated nitric acid (HNO_3): 30% hydrogen peroxide (H_2O_2) solution for 24 h on a hot plate at 100°C to digest all organic material. After this time, sample vials were opened and contents were dried on the hot plate. After evaporation, 4 ml of 5% HNO_3 spiked with 8 parts per billion (ppb) rhenium (Re) and rhodium (Rh) was added to the residue, and closed vials were left on the hot plate at 100°C overnight to ensure complete dissolution. A small amount of the sample was removed and diluted again with 0.8 N HNO_3, spiked with 8 ppb Rh and Re to make the final dilution around 2000. The final dilution for trace element analyses was determined by mass for each sample. The trace element analyses were conducted on an Element2 HR-ICP-MS (Thermo-Finnigan) in medium resolution using Rh and Re as internal standards at the Department of Geological Sciences, University of Florida. Samples from different sites, e.g. Florida, Nicaragua, Brazil, were loaded in sequence (all samples from one location followed by the samples of another location) and run the same day. Results were quantified by external calibration using a combination of gravimetrically prepared ICP-MS standards obtained from QCD Analysts. Concentration of trace elements is reported in parts per million (ppm). The detection limits were 0.0003 ppm for magnesium, aluminum, vanadium, manganese, iron and zinc; and 0.00003 ppm for titanium, chromium, cobalt, nickel, copper, rubidium, strontium, yttrium, zirconium, cadmium, cesium, barium, thallium, lead, thorium and uranium.

Statistical analysis

We used a correlation matrix to eliminate trace elements that were highly correlated and provided repetitive information to ensure numerical stability of cluster analysis. To determine the number of oceanic foraging grounds from which the sampled turtles were derived, we conducted model-based cluster

analyses using the package MCLUST in R (Fraley & Raftery 2006). A model-based cluster method uses a mixture of normal distributions to explain the dispersion of the trace elements in the samples and evaluates different combinations of normal distributions based on possible orientation, volume and shape of the covariances among variables in the input (i.e. using the mean and the variance of each element) to determine the optimal number of clusters and the number of variables that best separate such clusters using a Bayesian information criterion (BIC; Fraley & Raftery 1998). BIC is a model selection statistic that scores how well the mixture of normal distributions explains the between and within variation among clusters. BIC also penalizes for the number of trace elements input in the model, allowing us to compare fairly among models with different combinations of trace elements. All trace elements were standardized according to their mean and variance to build comparable models. We first found the BIC score for the model that included all 20 standardized trace elements, and the carbon and nitrogen isotope values (full model). Then we programmed the cluster analysis to choose every subset of covariates from 1 to 19 (a total of $2^{20} - 1$ combinations) and calculated their BIC scores. Overall, the best BIC score represents the model that best separates groups and simultaneously has the most informative elements. Because of the large number of models to test, we used the high-performance computing cluster at the University of Florida. We conducted these steps twice: the first time to obtain the best models for green turtles only, and the second time to see whether the number of clusters, the assignment of individuals and the uncertainty of classification to each cluster changed when loggerhead turtles from the Azores were included.

An analysis of multiple variances was performed with the resulting clusters of the best model (highest BIC score) to determine whether the clusters were significantly different. We considered each cluster as one oceanic foraging ground. Based on the assignment of each individual to each cluster by the model-based cluster analysis, we determined the contribution of these oceanic areas (clusters) to the different coastal areas by calculating the proportion of individuals sampled at the different coastal foraging grounds assigned to each oceanic cluster. We used a chi-square contingency table test to determine whether the contributions of the oceanic clusters were equal in all neritic foraging grounds.

RESULTS

Of the 174 scute samples collected, only 128 had 2 or more consecutive layers with similar stable isotope values representing the oceanic habitat. The number of samples by coastal foraging ground was: east coast of Florida, n = 24; west coast of Florida, n = 15; north Bahamas, n = 14; south Bahamas, n = 15; Nicaragua, n = 17; north Brazil, n = 26; south Brazil, n = 17. The mean and range of the stable isotope values of the oceanic layers are shown in Table 1.

A total of 22 trace elements were measured in the scute of green and loggerhead turtles (Table 2). The concentrations of 6 of the 22 elements were significantly different between the 2 species (multivariate analysis of variance (MANOVA) $F_{1,137} = 7.35$, $p < 0.0001$). From the correlation matrix of the concentrations of all elements, we reduced the number of trace elements to 18 (Table 2) to avoid redundancy of data.

The model-based cluster analysis performed with only the green turtles indicated that the best model had 3 trace elements (titanium, chromium, zirconium) forming 5 distinct groups (Table 3) or oceanic areas used by green turtles in the Atlantic. The level of uncertainty in the classification was low, with 93% of the turtles having uncertainty levels equal to or below 0.2. The second best model for green turtles was one with 4 trace elements, the same 3 of the best model and barium (Table 3). However, the number of clusters in the second best model was 7. The uncertainty of classification of the second best model was higher than the best model, with 88% of the turtles with uncertainty levels below 0.2.

When loggerhead turtles from the Azores were included in the analysis, the resulting best model had

Table 1. *Chelonia mydas*. Mean values and range of stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) in the oceanic layers of scute of green turtles sampled at 7 coastal foraging grounds in the Atlantic

	$\delta^{13}C$ (‰)		$\delta^{15}N$ (‰)	
	Mean	Range	Mean	Range
West Florida	−17.37	−19.01 to −12.73	8.03	4.84 to 12.42
East Florida	−17.54	−19.38 to −12.52	7.28	2.93 to 11.40
North Bahamas	−19.69	−29.71 to −14.77	6.81	5.04 to 8.56
South Bahamas	−17.62	−18.63 to −16.50	6.77	3.53 to 8.32
Nicaragua	−16.78	−18.50 to −14.85	6.35	4.91 to 7.93
North Brazil	−18.80	−23.96 to −16.57	8.48	5.95 to 13.45
South Brazil	−17.48	−19.80 to −14.84	8.10	5.67 to 11.82

Table 2. *Chelonia mydas* and *Caretta caretta*. Trace elements detected in the scute of green turtles (n = 128) and loggerhead turtles (n = 11) in the Atlantic. Elements in bold were excluded from other analyses as they had a high correlation with other elements. Concentrations are given as mean (ppm) ± SD. *Elements that were significantly different between species based on a multiple ANOVA

Trace element	Green turtles	Loggerhead turtles
Mg*	301 ± 201	481 ± 207
Al*	77.6 ± 127.0	173 ± 163
Ti	19.6 ± 97.4	3.1 ± 3.5
V*	0.71 ± 0.74	2.4 ± 1.7
Cr	1.2 ± 4.1	0.62 ± 0.55
Mn	3.0 ± 6.3	3.6 ± 2.4
Fe	51.0 ± 71.4	81 ± 131
Co	0.13 ± 0.17	0.19 ± 0.15
Ni	1.8 ± 4.9	1.4 ± 1.5
Cu	2.1 ± 3.4	3.6 ± 3.4
Zn*	145.0 ± 91.4	277 ± 88
Rb*	0.4 ± 0.4	1.1 ± 1.0
Sr	9.1 ± 10.9	14.6 ± 16.3
Y	0.06 ± 0.13	0.06 ± 0.05
Zr	0.74 ± 2.60	0.80 ± 0.87
Cd*	0.16 ± 0.39	0.72 ± 0.71
Cs	0.03 ± 0.06	0.04 ± 0.01
Ba	1.1 ± 3.2	1.3 ± 1.5
Tl	0.02 ± 0.02	0.02 ± 0.02
Pb	0.49 ± 0.89	0.60 ± 0.38
Th	0.02 ± 0.04	0.02 ± 0.01
U	0.03 ± 0.05	0.04 ± 0.03

a higher BIC score than the best model for only green turtles (Table 3). This model classified the turtles in 6 different groups instead of 5 (Fig. 3). The same elements of the best model for green turtles — titanium, chromium and zirconium — were present in this new model as well as barium. The new cluster (Cluster 4; Table 4) included most of the Azores turtles (8 out of 11 turtles) and the concentrations of barium, zirconium and titanium were significantly different from the other clusters (Fig. 4). The uncertainty level of this model was also low, with 93.5% of the turtles having uncertainty levels below 0.2, which supports the suggested number of clusters. Bi-dimensional scatterplots with the 95% credible intervals for each of the clusters suggested by the model-based cluster analysis are shown in Figs. S1 to S4 in the Supplement at www.int-res.com/articles/suppl/m490p233_supp.pdf.

From these analyses, we concluded that the green turtle populations we sampled in the Atlantic use 6 distinct oceanic foraging areas. The analysis of multiple variance showed that the 6 clusters (Fig. 3) were significantly different (MANOVA $F_{5,133} = 5.5592$, $p < 0.001$), which supports the results of the model-based cluster analysis. In general, the mean concentrations of titanium, chromium, zirconium and barium varied among the clusters, but not all elements were significantly different among all clusters (Fig. 4).

To determine the contribution of oceanic areas to neritic foraging grounds of green turtles and establish the connections between these developmental habitats, we calculated the proportion of individuals sampled at the different coastal foraging grounds that were assigned to each oceanic cluster (Table 4). The results showed that oceanic areas contribute in different proportions to the different neritic foraging grounds ($\chi^2 = 273.6041$, df = 30, $p < 0.0001$; Fig. 5), with oceanic areas contributing to all or only some of the coastal foraging grounds. This indicates that there are multiple connections between oceanic and neritic foraging grounds.

DISCUSSION

The oceanic stage of green turtles has been a mystery for decades. The location of oceanic foraging areas, how the oceanic developmental aggregations are structured and how these areas connect to other developmental sites (coastal foraging grounds) are critical questions. We have demonstrated that there is structure in the oceanic-stage aggregations — there is not just one oceanic foraging (panmictic) area — and each oceanic foraging aggregation is connected to several neritic areas. Our data support the third hypothesis of connections between geographically discrete oceanic aggregations and several neritic foraging grounds of green turtles in the Atlantic (Fig. 1C). The mixture of different oceanic signatures in each of the coastal foraging areas indicates that the contribution of these oceanic areas to neritic foraging grounds is not in the same proportion. This could be due to a number of factors that control recruitment from oceanic to neritic foraging areas, such as distances between areas, ocean currents or the influence of water temperatures on movements, as turtles prefer to be in warmer waters (Musick & Limpus 1997, Proietti et al. 2012).

Identifying locations of oceanic foraging grounds with trace elements

Owing to their differential geographic distribution, trace elements have been used to identify locations of various marine organisms, such as the minke whale *Balaenoptera acutorostrata*, the rock fish *Sebastes*

Table 3. *Chelonia mydas* and *Caretta caretta*. Bayesian information criterion (BIC) scores of the best models obtained in the cluster analysis of the elemental composition of green turtles and all turtles combined (loggerhead turtles included). Best fit model for green turtles only and best fit model for all turtles are indicated in **bold**

Models (number of elements)		BIC score	Best parameters (elements)	Number of clusters
2	Green only	784.3667	Ti, Zr	3
	All turtles	823.808	Ti, Zr	4
3	**Green only**	**909.0112**	**Ti, Cr, Zr**	**5**
	All turtles	929.4573	Ti, Cr, Zr	6
4	Green only	904.7073	Ti, Cr, Zr, Ba	7
	All turtles	**940.7244**	**Ti, Cr, Zr, Ba**	**6**
5	Green only	842.4538	Ti, Cr, Zr, Ba, Cd	6
	All turtles	838.93	Ti, Cr, Zr, Ba, Cd	6
6	Green only	749.1124	Ti, Cr, Zr, Ba, Cd, Y	5
	All turtles	752.8325	Ti, Cr, Zr, Ba, Cd, Y	7
7	Green only	579.8948	Ti, Cr, Zr, Ba, Cd, Y, Mn	8
	All turtles	602.8961	Ti, Cr, Zr, Ba, Cd, Y, Mn	8
8	Green only	485.5459	Ti, Cr, Zr, Ba, Cd, Y, Mn, Al	8
	All turtles	305.6228	Ti, Cr, Zr, Ba, Cd, Mn, Sr, Tl,	8
9	Green only	287.4794	Ti, Cr, Zr, Ba, Cd, Y, Mn, V, Cu	9
	All turtles	149.3097	Ti, Cr, Zr, Ba, Cd, Y, Mn, Cu, Co,	9
10	Green only	4.7913	Ti, Cr, Zr, Ba, Cd, Y, Mn, V, Cu, Pb	9
	All turtles	−118.2502	Ti, Cr, Zr, Ba, Cd, Y, Mn, Al, Pb, Fe	7
11	Green only	−220.18	Ti, Cr, Zr, Ba, Cd, Y, Mn, V, Cu, Pb, Rb	8
	All turtles	−353.7967	Ti, Cr, Zr, Ba, Cd, Y, Mn, Al, Pb, Fe, Cu	8
12	Green only	−460.2792	Ti, Cr, Zr, Ba, Cd, Y, Mn, V, Cu, Pb, Fe, Sr	7
	All turtles	−766.4207	Ti, Cr, Zr, Ba, Cd, Y, Mn, Al, Pb, Fe, Cu, Co	8
13	Green only	−676.2756	Ti, Cr, Zr, Ba, Cd, Y, Mn, Al, V, Cu, Pb, Fe, Sr	6
	All turtles	−1039.511	Ti, Cr, Zr, Ba, Cd, Y, Mn, Al, Pb, Fe, Cu, Co, V	9
14	Green only	−1019.778	Ti, Cr, Zr, Ba, Cd, Y, Mn, Al, V, Cu, Co, Pb, Fe, Sr	7
	All turtles	−1438.854	Ti, Cr, Zr, Ba, Cd, Y, Mn, Al, Pb, Fe, Co, V, Zn, Sr	8
15	Green only	−1392.378	Ti, Cr, Zr, Ba, Cd, Y, Mn, Al, V, Cu, Co, Pb, Fe, Sr, $\delta^{13}C$	9
	All turtles	−1858.35	Ti, Cr, Zr, Ba, Cd, Y, Mn, Al, Pb, Fe, Co, V, Zn, Cu, $\delta^{15}N$	9
16	Green only	−1814.114	Ti, Cr, Zr, Ba, Cd, Y, Mn, V, Cu, Pb, Fe, $\delta^{13}C$, Al, Co, Zn, Sr	9
	All turtles	−2217.74	Ti, Cr, Zr, Ba, Cd, Y, Mn, V, Cu, Pb, Fe, $\delta^{13}C$, Al, Co, Rb, Mg	8
17	Green only	−2256.322	Ti, Cr, Zr, Ba, Cd, Y, Mn, V, Cu, Pb, Fe, Rb, $\delta^{15}N$, Al, Co, Zn, Mg	9
	All turtles	−2533.98	Ti, Cr, Zr, Ba, Cd, Y, Mn, V, Cu, Pb, Fe, $\delta^{13}C$, Al, Co, Rb, Mg, Sr	7
18	Green only	−2530.164	Ti, Cr, Zr, Ba, Cd, Y, Mn, V, Cu, Pb, Fe, Rb, $\delta^{15}N$, Al, Co, Zn, $\delta^{13}C$, Sr	9
	All turtles	−3146.613	Ti, Cr, Zr, Ba, Cd, Y, Mn, Cu, Pb, Fe, Rb, $\delta^{15}N$, Al, Co, Zn, $\delta^{13}C$, Mg, Sr	8
19	Green only	−3045.404	Ti, Cr, Zr, Ba, Cd, Y, Mn, V, Cu, Pb, Fe, Rb, $\delta^{15}N$, Al, Co, Zn, $\delta^{13}C$, Sr, Tl	9
	All turtles	−3633.253	Ti, Cr, Zr, Ba, Cd, Y, Mn, V, Cu, Pb, Fe, $\delta^{15}N$, Al, Co, Zn, $\delta^{13}C$, Mg, Sr, Tl	9
20	Green only	−3729.398	Ti, Cr, Zr, Ba, Cd, Y, Mn, V, Cu, Pb, Fe, Rb, $\delta^{15}N$, Al, Co, Zn, $\delta^{13}C$, Sr, Tl, Mg	4
	All turtles	−4196.825	Ti, Cr, Zr, Ba, Cd, Y, Mn, V, Cu, Pb, Fe, Rb, $\delta^{15}N$, Al, Co, Zn, $\delta^{13}C$, Sr, Tl, Mg	5

atrovirens, the yellow damselfish *Pomacentrus amboinensis*, the porcelain crab *Petrolisthes cinctipes* and the octopus *Octopus maorum* (Kunito et al. 2002, Born et al. 2003, Thorrold et al. 2007, Carson et al. 2008, Doubleday et al. 2008). Trace elements were effective in differentiating among oceanic areas for these species because environmental availability has a great effect on the concentration of these elements. Once trace elements are incorporated into inert tissues, they do not change (Doubleday et al. 2008). Thus, the trace element concentrations in the scute tissue of oceanic-stage green turtles can reflect the chemical differences in the oceanic areas they use. For these reasons, we are confident that the 6 clusters identified by the model analysis represent geographically distinct oceanic foraging areas.

Trace elements enter the ocean in different ways. These processes can be natural, such as aerosol particles from dust, volcanic eruptions and riverine inputs, or anthropogenic, i.e. from combustion emissions (Hoffmann et al. 2012). Because of the nature of these sources, their input varies greatly over time and space depending on climate and other conditions (Jickells et al. 2005). The distribution of trace elements in the open ocean are not sufficiently known to allow detailed mapping of oceanic turtle distributions. How-

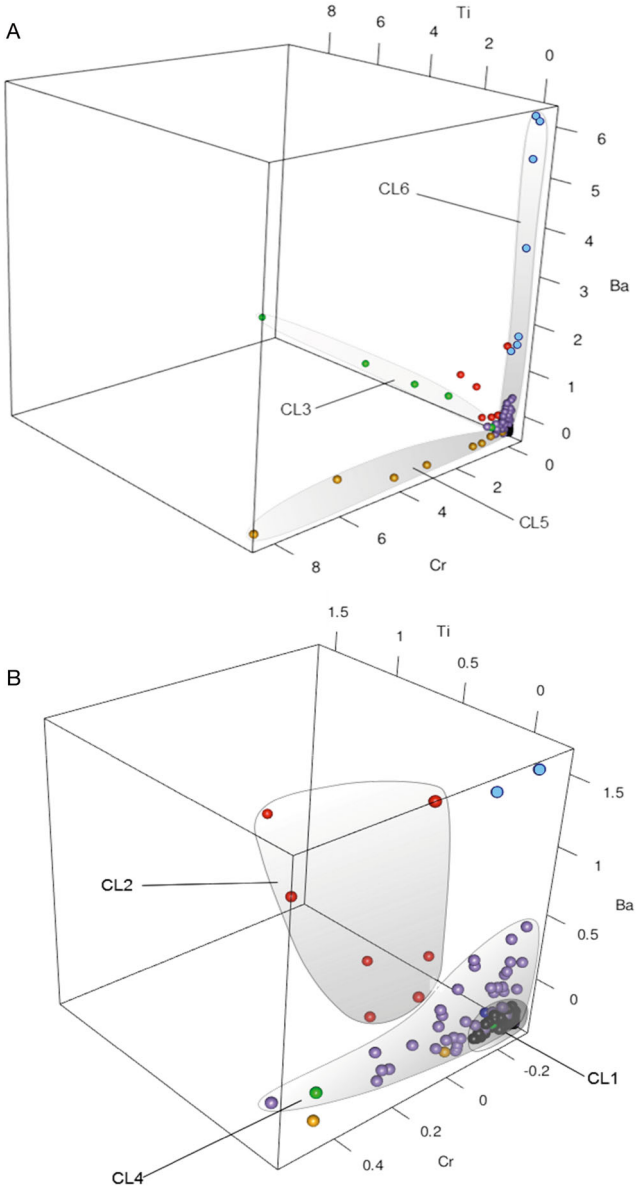

Fig. 3. (A) The 6 clusters (CL) identified by the model-based cluster analysis in multi-dimensional space using 3 of the 4 most informative elements (barium, chromium and titanium). Note that Clusters 3, 5 and 6 have high variance and the 3 clusters with low variance cannot be distinguished. (B) Close up of the lower right corner of panel A to show the separation of Clusters 1, 2 and 4, which had the lowest variance. Note the change in the scale. Cluster 1 is black, 2 is red, 3 is green, 4 is purple, 5 is yellow and 6 is blue

Table 4. *Chelonia mydas* and *Caretta caretta*. Number of turtles captured in each coastal foraging area and classified in each of the 6 groups determined by the model-based cluster analysis. Turtles from the Azores are loggerheads, the rest are green turtles. CL= cluster

Coastal foraging ground	Number of turtles	CL1	CL2	CL3	CL4	CL5	CL6
West Florida	15	7	1	3	3	1	0
East Florida	24	8	4	2	9	0	1
North Bahamas	14	10	0	0	2	2	0
South Bahamas	15	11	1	0	1	0	2
Nicaragua	17	5	1	2	6	3	0
North Brazil	26	15	0	0	9	1	1
South Brazil	17	10	0	0	3	1	3
Azores	11	1	0	1	8	0	1
Total	139	67	7	8	41	8	8

ever, some hypotheses about the possible locations of the 6 oceanic foraging grounds identified by the cluster analysis can be made with caution. We present a map (Fig. 6) showing very tentative locations of the 6 oceanic clusters as an example of what could be determined if distributions of trace elements were better known in the Atlantic and samples from more green turtle coastal foraging grounds were available.

We base the provisional map (Fig. 6) on the following. Titanium, chromium, zirconium and barium were the most important elements in the formation of clusters (Table 3). The input of these elements into the Atlantic comes from different terrigenous sources. Although all 4 elements are terrigenous, it is believed that zirconium and chromium are controlled mainly by riverine sources, while titanium comes from dust deposition (Dupré et al. 1996, Dammshäuser et al. 2011). Furthermore, about half of the chromium in the environment at present is contributed by anthropogenic activities (Rauch & Pacyna 2009). These 4 elements show very low concentrations in seawater with low ppb ranges for barium and parts per trillion ranges for titanium, chromium and zirconium (Faure 1998). The residence times are short for titanium and zirconium (160 yr) and longer for chromium (1600 yr) and barium (5000 yr; Faure 1998). As typical for trace elements in seawater, they are considered non-conservative elements — that is, their concentrations are higher close to their source and lower in oceanic environments, where their concentrations remain relatively constant in the water column (Connelly et al. 2006, Dammshäuser et al. 2011).

The high concentration of titanium in Clusters 2 and 3 could be due to the influence of Saharan dust as this is the major source of this element in the North Atlantic. Saharan dust is transported by winds through the

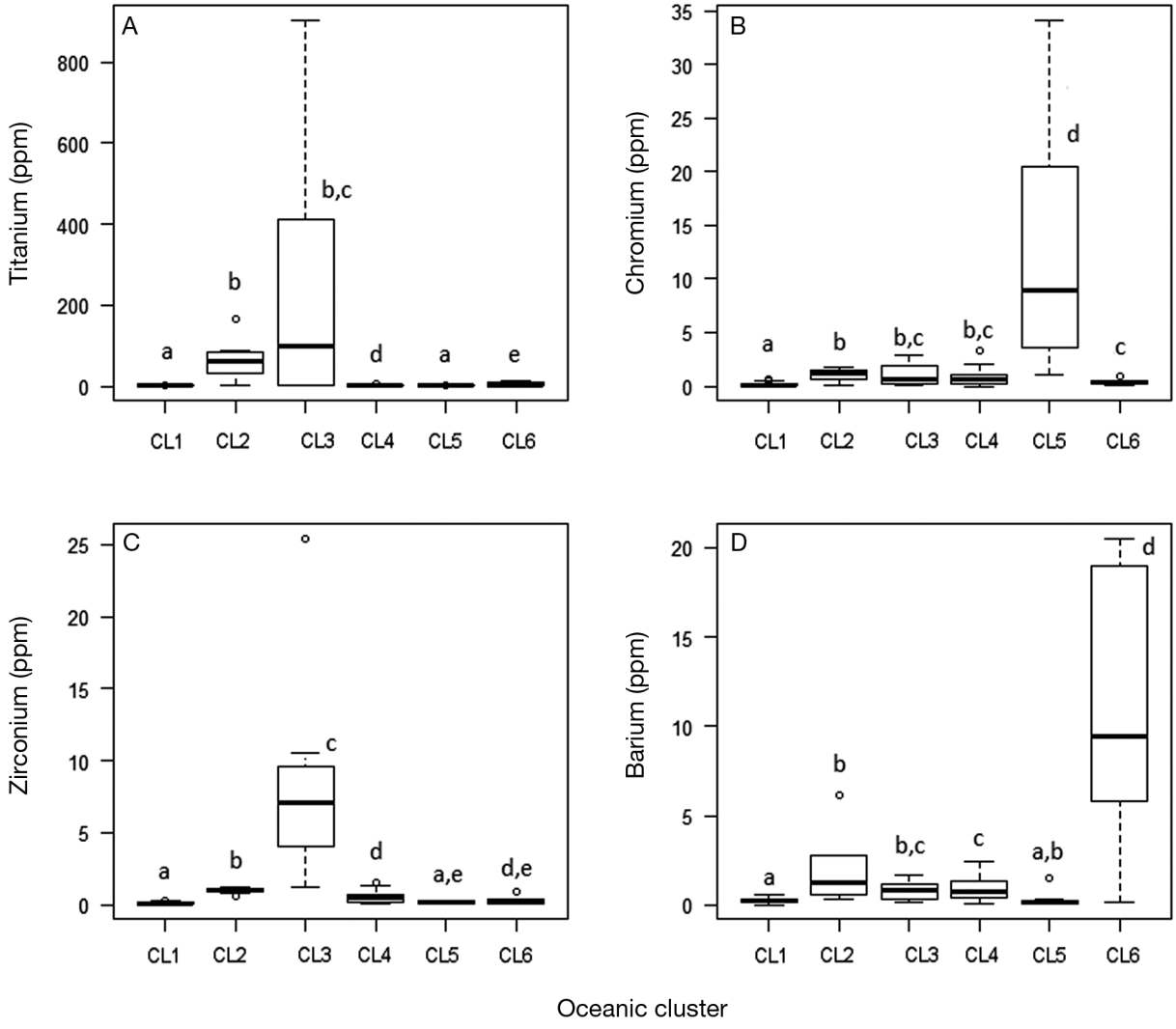

Fig. 4. *Chelonia mydas* and *Caretta caretta*. Box and whisker plots of concentrations of (A) titanium, (B) chromium, (C) zirconium and (D) barium in the scute of green and loggerhead turtles grouped by cluster (CL). Boxes represent the distribution of data (lower and upper quartiles) around the median (bold line). Open circles denote outliers. Statistically different groups identified by a multiple ANOVA are denoted by lower case letters

Atlantic into the Caribbean, and to the southern and eastern coasts of the US (Prospero 2007). High concentrations of titanium exist in the tropical and subtropical North Atlantic (Duce et al. 1991, Jickells et al. 2005), and there is also a decrease in titanium concentration from east to west (Duce et al. 1991), which might explain why clusters 1 (farther to the west) and 4 (farther to the north) had lower titanium concentrations. However, the zirconium concentration in Cluster 3 is higher than that in cluster 2, suggesting that Cluster 3 might also be influenced by riverine inputs (Fig. 5). Cluster 5 also seems to be influenced by a riverine source with a high concentration of chromium compared with the other clusters (Figs. 3 & 4). The 3 major riverine sources in the Atlantic are the Amazon on the Brazilian coast, the Mississippi River in the Gulf of Mexico, and the Congo River on the west coast of Africa. Chromium is transported in suspended sediments to the ocean. According to the average concentration of chromium in suspended sediments and the sediment flux of world rivers, the Mississippi River has the highest concentration of chromium, followed by the Congo River and then by the Amazon (Syvitski et al. 2005, Viers et al. 2009). Therefore, we can speculate that the waters near the Mississippi River can potentially have higher chromium content compared with the Amazon and Congo rivers (Fig. 6).

The concentration of barium in oceanic waters has been found to be inversely correlated with depth and

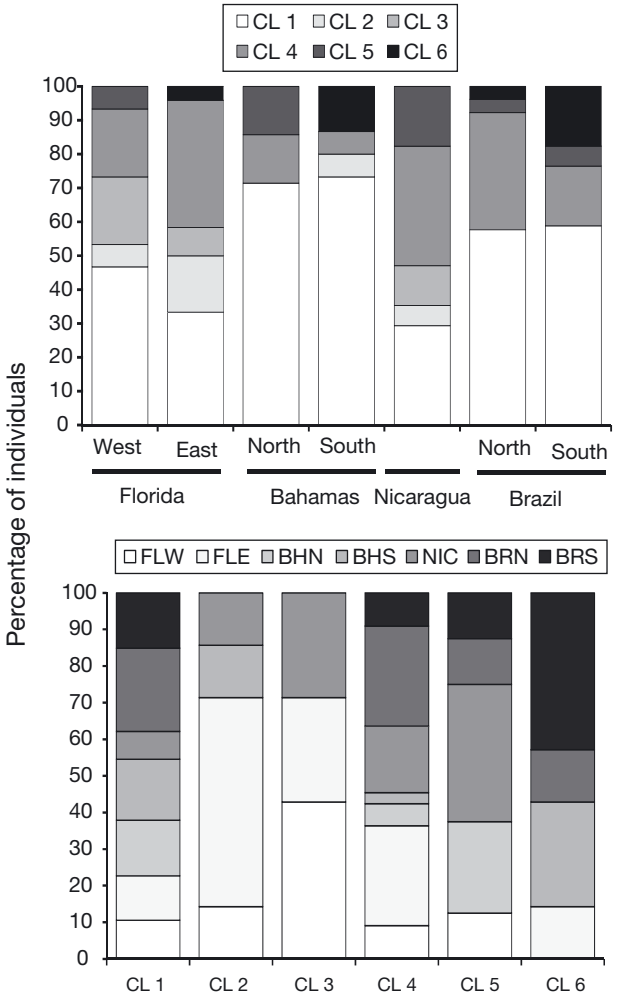

Fig. 5. *Chelonia mydas* and *Caretta caretta*. (A) Contributions of 6 oceanic clusters (CL) to 7 neritic foraging grounds of green turtles studied in the Atlantic. (B) Percentage of each neritic foraging ground derived from each cluster not including loggerheads from the Azores. FLE = east Florida, FLW = west Florida, BHS = south Bahamas, BHN = north Bahamas, NIC = Nicaragua, BRN = north Brazil, BRS = south Brazil

temperature (Lea et al. 1989, Zumholz et al. 2007). Barium concentrations are usually low in warm surface waters and high in cold subsurface waters (Dehairs et al. 1991). In areas of upwelling, however, barium concentrations can be high as a result of cold, nutrient-rich waters moving to the surface (Lea et al. 1989). The high concentration of barium in Cluster 6 suggests that it might be an oceanic area influenced by the high productivity of upwelling areas. Such areas in the Atlantic occur along the coasts of Africa (Kostianoy & Zatsepin, 1996, Rubio et al. 2009) and Brazil (Campagna et al. 2006) (Fig. 6).

Clusters 1 and 4 have the largest numbers of turtles (n = 67 and n = 41, respectively; Table 4). The concentrations of titanium, chromium, zirconium and barium were significantly higher in Cluster 4 (Figs. 3 & 4) and most of the Azores loggerheads (8 out of 11) were in this cluster. Although young green turtles are rare in the Azores, given the slightly higher concentration of the elements and the location of the Azores, we suggest that Cluster 4 could represent an oceanic area in the eastern Atlantic as this area also receives Saharan dust input (Fig. 6). On the other hand, Cluster 1 could be an area in the tropical western Atlantic (Fig. 6); the concentration of barium is very low, which is expected in the nutrient-poor oceanic waters of the tropics (Dehairs et al. 1991). The low concentration of chromium, zirconium and titanium could be due to the loss of influence of riverine inputs. Also, Cluster 1 had one turtle from the Azores, but given the small size of the turtle (16.3 cm SCL), it is possible that the scute layers still had the chemical signature from the Florida coast and had not acquired the signature from the Azores.

Although different oceanic regions can be characterized based on the concentration of trace elements, there are constraints that need to be considered. Trace element concentrations are not constant; they can change spatially and temporally due to climate conditions (Jickells et al. 2005, Hoffmann et al. 2012) and anthropogenic activities. We have been able to predict what elements and what concentrations can be found in certain areas based on input sources (e.g. Saharan dust plume, river effluents, known volcanic areas), but these are also variable in space and time. This means that the chemical signatures of the 6 oceanic areas reported in our study could change in the future. Long-term measures of trace elements in the open ocean, such as the international GEOTRACERS program, might help detect these signature changes and also determine the variability of trace elements in the ocean.

In other marine studies, stable isotope ratios of carbon and nitrogen have provided information on foraging habitat use of migratory species (Hatase et al. 2002, Pajuelo et al. 2012). However, stable isotopes did not contribute significantly in distinguishing among oceanic clusters in our study. Perhaps $\delta^{13}C$ and $\delta^{15}N$ values in oceanic green turtles are not informative because the habitat has similar values over a broad geographic range at lower latitudes (similar $\delta^{13}C$ values) (Graham et al. 2010) and oceanic green turtles feed at the same trophic level (similar $\delta^{15}N$ values). Furthermore, trace elements can reflect the chemistry of the habitat of green tur-

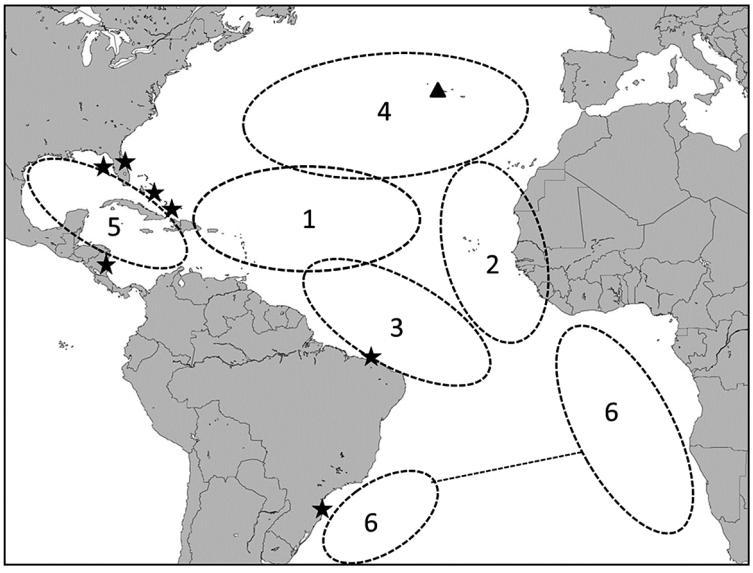

Fig. 6. *Chelonia mydas* and *Caretta caretta*. Speculative locations of the 6 clusters based on trace element analysis. Stars represent the 7 neritic foraging grounds and the triangle is the oceanic foraging ground of loggerheads indicated in Fig. 2

tles more accurately than stable isotope values of carbon and nitrogen, because even though animals feed on the same trophic level and occupy the same type of habitat (oceanic), the chemistry of the environment in different regions of the Atlantic is different and that will be reflected in trace element concentrations in the scute.

Conservation implications of population structure

The structure in oceanic aggregations and the connections between oceanic and neritic developmental areas of green turtles can have conservation implications because of the effects on the resilience of populations. Aggregations with many connections (Fig. 1C) between oceanic and neritic developmental areas, which was the case in our study, benefit the green turtle population because it creates a higher level of resilience (Gaines et al. 2007). In the event of a disturbance (whether natural or anthropogenic) in any oceanic area, the effect on the neritic foraging grounds will be minimized by the contributions from the other oceanic areas. Local extinctions on neritic foraging grounds would be rarer than in the populations with fewer connections. Conservation efforts can be directed to those oceanic areas that contribute the most to neritic foraging grounds. However, it is necessary to establish how much variation there is in the contribution of oceanic foraging grounds, and what is causing such variation.

Populations with limited connections tend to have lower resilience (Gaines et al. 2007). In the first hypothetical case where there is only one oceanic foraging ground (a panmictic aggregation), the risk of local extinction on neritic foraging grounds as a result of threats on the oceanic foraging ground is relatively high as all neritic areas rely on this single oceanic area. In the second scenario of spatially structured aggregations with limited connections, local extinctions would be more common as the disturbance of a given oceanic area would have catastrophic results in the corresponding neritic area. Conservation efforts in these 2 scenarios need to be different. In the case of a panmictic oceanic foraging ground (Fig. 1A), the implementation of protection plans in parts of the oceanic area could help recover all neritic foraging grounds. However, in spatially structured aggregations with limited connections (Fig. 1B), conservation efforts should focus on all oceanic foraging grounds as they all contribute to the genetic variability of the population.

The variation in the number of juveniles recruiting annually to neritic foraging grounds can also be affected by the connections between oceanic and neritic areas, especially when they are spatially structured. Hatchling production varies greatly from year to year at nesting beaches (Bjorndal & Bolten 2008), and assuming each rookery connects to 1 or 2 oceanic foraging grounds, the number of hatchlings that reach these oceanic areas will also vary greatly in response to hatchling production. In structured aggregations with few connections (Fig. 1B), a much larger variation in the abundance of juveniles in neritic foraging grounds could occur from year to year because only 1 oceanic area is contributing to 1 neritic foraging ground. However, in structured populations with many connections (Fig. 1C), the abundance of juveniles in neritic foraging grounds would be less variable because there are many oceanic foraging grounds contributing to the neritic area. In the case of a panmictic oceanic foraging area (Fig. 1A), the variation in the number of juveniles recruiting to neritic foraging areas should also be small as the oceanic area is receiving hatchlings from all of the rookeries.

CONCLUSIONS

Trace elements are a useful tool to assess population structure and connections between developmental areas of marine species with cryptic life stages. We were able to characterize the trace element signature of 6 oceanic foraging grounds used by green turtles and determine how these areas contribute in different proportions to neritic foraging grounds. The elemental signatures of some of the green turtles were similar to those obtained from loggerheads in the Azores. This suggests that these species may use some of the same areas during their oceanic stage. However, more samples from the Azores are necessary to determine if these species do share the same oceanic areas or if they use different areas with similar chemical signatures. The terrigenous elements titanium, chromium, zirconium and barium were the most informative trace elements for differentiating among oceanic areas and indicate where these foraging areas could be. However, the exact location of these oceanic areas is still unknown. Further studies should focus on creating maps of trace element abundances in oceanic areas. The use of other biological markers might help assign oceanic foraging areas to a specific region of the ocean; we are currently evaluating lead stable isotopes. Furthermore, the number of oceanic clusters in this study is based on the sampling of only 7 neritic foraging grounds in the western Atlantic. More neritic areas, especially in the eastern Atlantic, should be included for a better understanding of the spatial distribution of oceanic foraging grounds and their connections with neritic areas. The addition of more samples of young turtles from different coastal foraging areas, particularly in the eastern Atlantic, could reveal a more distinct geographic pattern in the distribution of oceanic foraging grounds.

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