

## Origin and genetic diversity of leatherbacks (*Dermochelys coriacea*) at Argentine foraging grounds



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### ABSTRACT

To conduct conservation of migratory species, such as marine turtles, is important to understand the population structure throughout the entire distribution of the species. We study the genetic composition of the leatherback turtles, *Dermochelys coriacea* foraging in waters off Argentina by analyzing 763 bp sequences of the mtDNA control region in order to determine the nesting origin of these animals. A total of 40 samples were collected from adult leatherbacks (mean 143.5; 180–123 cm curved carapace length) captured (10%) in fisheries or encountered as strandings (90%). Based on analysis of mtDNA sequences we detected 4 haplotypes, the most common ( $n = 26$ ) being DC1.1, and the other two rarer DC1.3 ( $n = 4$ ), DC13.1 ( $n = 2$ ), and DC1.4 ( $n = 1$ ). The genetic diversity was evaluated through the haplotype ( $0, 3712 \pm 0, 1000$ ) and nucleotide diversities ( $0, 000521 \pm 0, 000553$ ). Bayesian Mixed Stock Analysis (MSA) showed that the Buenos Aires foraging leatherbacks come primarily from the West African rookeries (Ghana and Gabon, mean estimate = 69% and 14% respectively). MSA results are consistent with those from mark–recapture studies, since four leatherbacks captured in Argentinean waters were adult females that were originally tagged on the nesting beaches in Gabon, West Africa. Our findings demonstrate the connection between nesting and foraging areas in the South Atlantic and illustrate the importance of the Malvinas ecoregion to the survival of migratory marine vertebrates, such as leatherbacks.

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### 1. Introduction

The Southwest Atlantic is an important breeding and feeding area for many groups of marine vertebrates, largely due to the favorable oceanographic characteristics generated by the convergence of the Malvinas and Brazil currents (Peterson and Stramma, 1990). It is among the most productive ecoregions in the world and is home to populations of over 600 vertebrate species, including seabirds, marine mammals and sea turtles (Miloslavich et al., 2011). Most of these species exhibit seasonal migrations such as humpback whales (*Megaptera novaeangliae*), Southern right whales (*Eubalaena australis*) and Manx shearwater (*Puffinus puffinus*). The feeding habitats of right whales occur in higher latitudes where cold, nutrient rich waters generate large amounts of plankton. Calving, nursing, and breeding habitats occur in lower latitudes where warm, shallow waters are favorable for reproduction (Acevedo and Martínez, 2013; Guilford et al., 2009; Rasmussen et al., 2007; Zerbinì et al., 2011). Sea turtles are an example of endangered and threatened species that have complex life cycles

spread across different habitats (Wallace et al., 2013). Nesting grounds are frequently separated by thousands of kilometers from neritic and oceanic feeding grounds (Bolten, 2003a, 2003b; Musick and Limpus, 1997). Understanding the connectivity among populations using these different habitats at different life stages is important for conservation, since threats to animals at distant foraging and developmental areas will impact specific breeding populations differently (Fossette et al., 2014; Wallace et al., 2011).

The leatherback turtle is widely distributed from 71° N to 44° S throughout all oceans of the world (Eckert et al., 2012; Marquez, 1990). Leatherbacks are on the IUCN threatened species list (Wallace et al., 2013) due to dramatic population declines, particularly in Pacific populations (Mast and Pritchard, 2006; Sarti et al., 1996; Spotila et al., 1996, 2000). Adults typically undertake periodic long distance migrations from temperate foraging grounds to tropical nesting beaches to breed (Bailey et al., 2012; Benson et al., 2011; Fossette et al., 2010a, 2010b; Hughes et al., 1998; James, 2000; James et al., 2006; López-Mendilaharsu et al., 2009).

Nesting areas for leatherback turtles are distributed from southeastern USA to northern Brazil in the western Atlantic and from Mauritania to Angola in the eastern Atlantic (Barata et al., 2004; Dutton et al., 1999, 2013; Eckert et al., 2012). The largest Atlantic nesting populations occur

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in French Guiana, Suriname and Gabon (Girondot et al., 2007; Pritchard and Trebbau, 1984; Witt et al., 2009). Recent studies with satellite telemetry and mark–recapture have provided information about habitat use and movements for this species (Fossette et al., 2014). Fossette et al. (2010a, 2010b) and Witt et al. (2011) showed that the adult female leatherbacks tagged at the nesting beaches in West Africa migrate to multiple foraging areas, including waters off the coast of South America. Results of mark–recapture studies at nesting beaches in Gabon have demonstrated that tagged individuals occur in Argentinean waters, which are the most important feeding grounds in Southwest Atlantic (Billes et al., 2006; Fossette et al., 2010a, 2014; López-Mendilaharsu et al., 2009). These studies are limited to adult females tagged on nesting beaches, and it is unclear where the males and juveniles foraging off Argentina are from. Leatherback turtles feed mainly on jellyfish in this region, primarily in the estuaries of the Rio de la Plata (RP) and El Rincón (ER) at Buenos Aires (BA) province from December to March (González-Carman et al., 2011) (Fig. 1). The seasonal and regional occurrence of this species in southernmost waters is strongly associated with high-density of gelatinous organisms (Fossette et al., 2010a; López-Mendilaharsu et al., 2009; Mianzan and Guerrero, 2000). Activities of economic importance such as maritime transport, domestic and industrial waste discharge, tourism, and fishing occur in Argentinean coastal waters, potentially affecting the survival of this species (Domingo et al., 2006; González-Carman et al., 2011; López-Mendilaharsu et al., 2009; Mianzán et al., 2001).

Over the last two decades, studies of intraspecific genetic variation using molecular markers have been useful in the analysis of the population structure and phylogeography of sea turtles (Avice, 2007; Bowen et al., 2004, 2005; Fitzsimmons et al., 1997; Lara-Ruiz et al., 2006; Lee,

2008). Mitochondrial DNA (mtDNA) in particular has been used to identify the origin and stock composition of foraging populations and infer migratory routes (Bass et al., 2006; Bolker et al., 2007; Bowen et al., 1994, 2007; Jensen et al., 2013; Luke et al., 2004; Naro-Maciel et al., 2007).

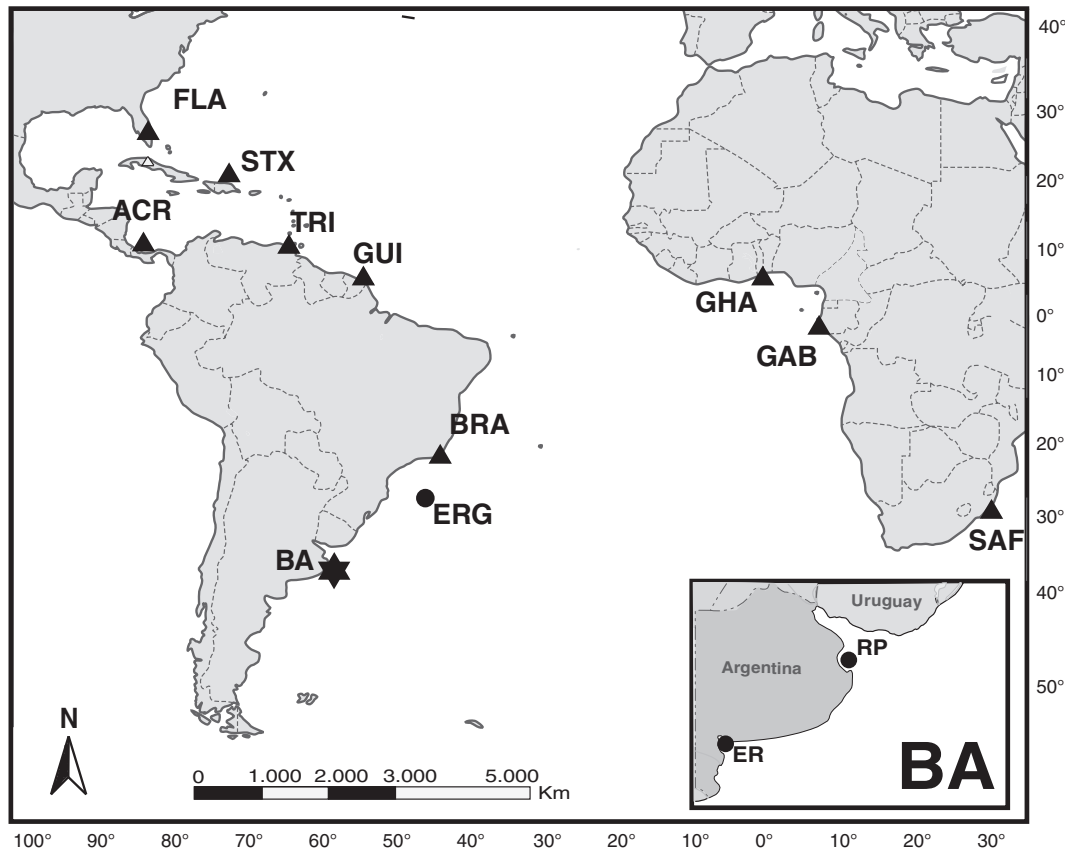
Previous studies using short mtDNA sequences (496 bp) have characterized nesting colonies from the Atlantic, Pacific and Indian Oceans and one feeding area in the Atlantic (Brazil) and demonstrated low variation (Dutton et al., 1999, 2007; Vargas et al., 2008). Recent studies using longer (763 bp) sequences have revealed additional variation in the mtDNA control region that has improved the ability to detect population structure in leatherback (Dutton et al., 2013).

In the present work we analyzed mtDNA sequences (long sequences, 763 bp) and morphometric data obtained from leatherback foraging aggregations in Argentine waters in order to improve our knowledge about the migratory patterns of this species. Our specific objectives were to i) determine the life history stage, ii) analyze the genetic diversity, and iii) to estimate the nesting stock composition of leatherback turtles in foraging areas of Argentina. Understanding which nesting colonies use these southernmost feeding areas will help determine which nesting populations are potentially impacted by threats, such as fishing and pollution, great distances away.

## 2. Materials and methods

### 2.1. Sample collection

A total of 40 leatherback turtles were sampled by Regional Program for Sea Turtle Research and Conservation of Argentina (PRICTMA)



**Fig. 1.** Map showing locations of the main nesting populations throughout the Atlantic (east and west) and the feeding grounds in our study in the western Atlantic. Rio de la Plata (RP) and El Rincón (ER) estuaries (see inset) are located in Buenos Aires (BA) province, Argentina (symbolized by stars). Nesting colonies, considered possible sources of turtle feeding at BA (indicated by triangles) are as follows: ERG (Elevação do Rio Grande), ES (Espírito Santo), TR (Trinidad), GUI (French Guiana and Suriname), FL (Florida in the United States), STX (St. Croix in the U.S. Virgin Islands), GHA (Ghana), GAB (Gabon) and SAF (South Africa) in South West Indian Ocean. Elevação do Rio Grande (ERG) feeding grounds are indicated by circles (Dutton et al., 2013; Vargas et al., 1999).

between 2004 and 2010 along the coasts of Buenos Aires province (Argentina) (33°01'S, 58°31'W to 39°26'S, 62°28'W) (Fig. 1). Samples came from turtles encountered as bycatch in trawl fisheries (10%), or as strandings (90%). The blood samples were collected in EDTA and stored at  $-15^{\circ}\text{C}$ . Muscle and skin samples were collected in alcohol 90% and stored at  $-4^{\circ}\text{C}$  (Dutton, 1996). Curved carapace length (CCL) was measured for all individuals as described by Bolten (1999), and used to infer the life stage according to Stewart et al. (2007). Where possible, sex was determined by external examination of the genitalia and examination of gonads from dead necropsied turtles.

## 2.2. Molecular techniques

Standard phenol/chloroform methods were used for DNA extractions as described by Sambrook et al. (1989). A 763 bp fragment of the mtDNA control and tRNA pro gene was sequenced using primers LCM 15382 and H950 (Abreu-Grobois et al., 2006).

Polymerase chain reaction (PCR) (1.5 mM  $\text{MgCl}_2$ ,  $1\times$  PCR buffer, 0.2 mM each dNTPS, 0.5  $\mu\text{M}$  each primer, 5 U Taq (Invitrogen Life Technologies), 1  $\mu\text{l}$  template DNA and  $\text{H}_2\text{O}$  to a total volume of 50  $\mu\text{l}$ ) was carried out under the following conditions: 5 min at  $94^{\circ}\text{C}$ , 35 cycles of 30 s at  $51^{\circ}\text{C}$ , 1 min at  $72^{\circ}\text{C}$  and followed by 9 min at  $72^{\circ}\text{C}$  (Vargas et al., 2008), using a MGW Biotech Primus PCR System. The samples were purified and sequenced by Macrogen Inc., Korea.

## 2.3. Data analysis

Sequences were edited and aligned using BioEdit v 7.0 (Hall, 1999) and Clustal programs (Higgins and Sharp, 1988) against a reference dataset from Dutton et al. (2013). Polymorphic sites were identified using GenAlex 6 (Peakall and Smouse, 2006). Haplotypes were classified according to those based on reported 763 bp sequences (Dutton et al., 2013).

The haplotype diversity ( $h$ ) and nucleotide diversity ( $\pi$ ) were estimated according to Nei (1987) using the Arlequin program v 3.11 (Excoffier et al., 2005).

The sequence data obtained in the present study were compared with those obtained for the feeding ground of Elevação do Rio Grande (ERG, Brazil), the only Atlantic leatherback feeding area characterized to date using 763 bp fragment of the mtDNA (Vargas et al., 2008). Genetic differentiation between feeding sites was studied through analysis of molecular variance (AMOVA) (Excoffier et al., 2005) based on  $F_{ST}$  (by means of haplotype frequencies) and  $\Phi_{ST}$  (by means of genetic

distances with Kimura algorithm) using the program Arlequin v 3.11 (Excoffier et al., 2005).

We performed MSA using the program BAYES (Pella and Masuda, 2001) to estimate the stock composition of leatherback turtles in Argentina using published mtDNA haplotype frequencies for the nine potential source rookeries in the Atlantic and Indian Oceans (Dutton et al., 2013; Vargas et al., 2008). These included French Guiana/Surinam (GUI), Trinidad (TRI), St. Croix (STX) in the U.S. Virgin Islands, Espiritu Santo (BRA) in Brazil, Florida (FLA) in the United States, Costa Rica (ACR), South Africa (SAF), Gabon (GAB) and Ghana (GHA) (Fig. 1). Because pairwise comparisons of genetic differentiation between GUI and TRI and between FLA and ACR nesting beaches did not exhibit significant haplotype heterogeneity (Dutton et al., 2013), they were combined for further analysis into SWC (South West Caribbean) and NWC (North West Caribbean) respectively. A total of 15,000 Markov Chain Monte Carlo (MCMC) steps were run for 7 chains. A burn-in of 10,000 runs was used to calculate the posterior distribution. We performed MSA using two different models. One model used equal prior probabilities (flat priors) for all parameters (source rookeries), and in the second model the potential contributions of different source rookeries were weighted relative to the size of the nesting population (population size priors, Bass et al., 2004). The latter model assumes that larger source populations contribute more individuals to the mixture than smaller ones, and it may be beneficial to incorporate priors when there are shared haplotypes among the source populations (Bolten, 1999). Although reliable abundance data is not available for all the South Atlantic leatherback nesting populations, sufficient knowledge exists on general relative population sizes. For instance, the Brazilian nesting population is very small, less than hundred nesting females, while Gabon is believed to be one of the largest in the world, with thousands of nesting females (Witt et al., 2009). We compiled nesting population data from published and unpublished sources for the purposes of choosing priors for our MSA (Table 1) and compared results of the analysis with and without priors. The Gelman and Rubin shrink factor diagnostic was computed to ensure that all chains had converged, as was indicated by a shrink factor of less than 1.2 for each chain (Pella and Masuda, 2001). Individuals with haplotypes that had not been previously observed in any of the potential source rookeries ('orphan' haplotypes) were removed from the analysis by the program as these are non-informative.

Relationships among western Atlantic feeding grounds and nesting beaches were also examined by multidimensional scaling (MDS) analysis based on  $\Phi_{ST}$  values. We used the nonparametric correlation test of

**Table 1**

Haplotype frequencies at leatherback rookeries and feeding grounds, based on mtDNA 763 bp sequences in there Atlantic and SW Indian Oceans. References and abbreviations correspond with Fig. 1.

Haplotype frequency	Nesting areas									Feeding areas	
	BRA	ACR	FLA	STX	TRI	GUI	GHA	GAB	SAF	ERG	BA
DC1.1	9	119	209	98	65	98	47	178	34	34	26
DC1.3							11	12		6	4
DC1.4							1		7	1	1
DC2.1				21							
DC3.1	14	10	10	4	11	20		5		2	
DC3.2		2			11	20					
DC4.1							1	2		1	
DC9.1										2	
DC13.1							1	35		6	2
DC17.1			3								
DC19.1		1									
N	23	132	222	123	87	138	61	232	41	52	33
( $h$ )	0.4980 (0.0530)	0.1830 (0.0440)	0.1120 (0.0280)	0.3380 (0.0470)	0.4150 (0.0580)	0.4570 (0.0440)	0.3790 (0.0068)	0.3870 (0.0370)	0.2980 (0.0780)	0.3690 (0.0809)	0.3712 (0.1000)
( $\pi$ )	0.0032 (0.0020)	0.0011 (0.0009)	0.0006 (0.0006)	0.0008 (0.0007)	0.0027 (0.0017)	0.0030 (0.0018)	0.0006 (0.0006)	0.0008 (0.0007)	0.0004 (0.0004)	0.0014 (0.0012)	0.0005 (0.0005)
Distance to BA (km)	2300	10,225	10,470	9550	8064	7050	7500	7750	7543	1680	
Nesting females	50	2500	750	250	5000	3000	100	6000	50		

$h$  = Haplotype diversity,  $\pi$  = nucleotide diversity,  $N$  = Sample size. Standard deviations are indicated in brackets.

Spearman STATISTICA program (STATISTICA Stat Soft Inc., 1996) to determine whether stock contributions are affected by the distance between each of the nesting and feeding areas. The geographic distances between nesting areas and Argentina were estimated with the Google Earth 5.0 considering continental contours (Table 1).

### 3. Results

#### 3.1. Morphometric data

The 40 leatherback turtles (13 females; 11 males and 16 undetermined by a high degree of decomposition) ranged from 180 to 123 cm CCL length with a mean of 143.5 cm ( $\pm 14.24$  standard deviation), and thus were all determined to be adults.

#### 3.2. Genetic diversity in foraging grounds

A 763 bp fragment of the mtDNA control region was successfully amplified from 33 out of 40 turtles sampled in Buenos Aires (BA) province. A total of four haplotypes were identified at the BA feeding grounds. The most frequent haplotype at the BA feeding grounds was

DC1.1 ( $n = 26$ ). This haplotype was also widely distributed in nesting colonies of the Atlantic and SW Indian Oceans (Table 1). The other haplotypes, detected in a low proportion, DC1.3 ( $n = 4$ ), DC13.1 ( $n = 2$ ) and DC1.4 ( $n = 1$ ) at the BA feeding grounds, were only identified in West Africa nesting areas.

Genetic diversity based on the 763 bp mtDNA sequence was also analyzed in Elevação do Rio Grande (ERG, Brazil), the only southwestern Atlantic feeding grounds characterized to date (Vargas et al., 2008). Seven haplotypes were identified in ERG and were submitted to GenBank under the name of Dc A1, Dc A2, Dc A3, Dc A4, Dc C, Dc D and Dc I (Accession numbers EF513272–EF513278). These haplotypes correspond to haplotypes DC1.1, DC13.1, DC1.3, DC1.4, DC3.1, DC4.1 and DC9.1 described by Dutton et al. (2013) for Atlantic nesting beaches (Table 1). For the ERG feeding ground the most common haplotype (DC1.1) was shared by 65.4% of the samples, with second common haplotypes (DC1.3 and DC13.1) shared by 11.5% (Vargas et al., 2008).

The haplotype diversity in BA ( $0.3712 \pm 0.1000$ ) was similar to that detected ERG whereas the nucleotide diversity estimated in BA feeding area ( $0.000521 \pm 0.000553$ ).

Analyses of molecular variance (AMOVA) based on haplotype frequencies and on genetic haplotype divergence did not reveal significant

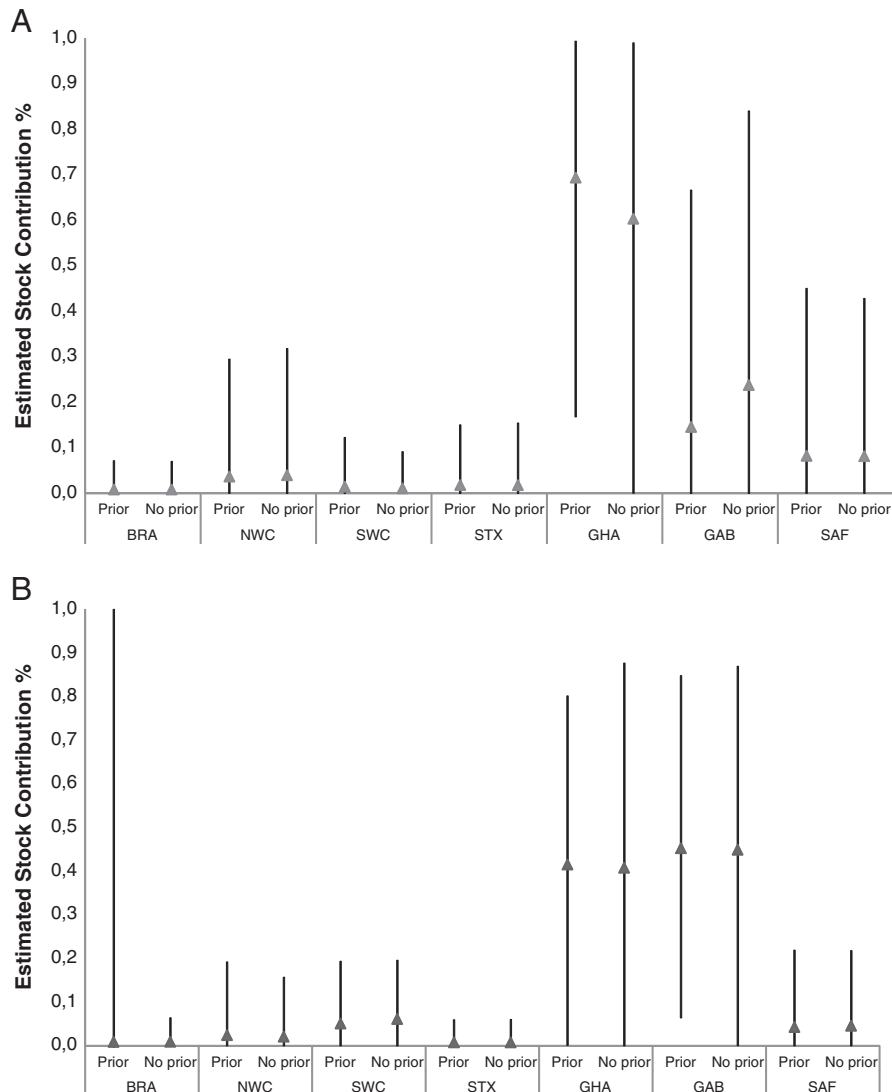


Fig. 2. Estimated mixed stock analysis (MSA) stock contributions from Atlantic leatherback rookeries at A) Argentine (BA) and B) Brazil combined (BA + ERG) foraging aggregations using weighted rookery size and flat priors. Confidence intervals (95%) are indicated. Abbreviations correspond with Fig. 1 and Table 1.

differences between the BA and the ERG feeding areas ( $F_{ST} = 0.00056$ ,  $P = 0.36$ ;  $\Phi_{ST} = 0.01$ ,  $P = 0.25$  respectively).

### 3.3. Mixed stock analysis

The MSA indicated that the Argentine leatherback foraging aggregation was primarily composed of animals of West African (WA) stock origin, with Ghana (estimated mean 69%) and Gabon (estimated mean 14%), together comprising 83% (Fig. 2). The confidence intervals around these estimates were large and overlapping (Fig. 2). Results were similar for MSA using flat and informed priors, although the point estimates were marginally higher for Ghana than Gabon with flat priors, the confidence intervals remained large (Fig. 2). Only minor potential contributions were estimated from nesting areas in the Caribbean and South Africa (Fig. 2). Since haplotype frequencies at BA and ERG foraging sites were not statistically different, we combined them and conducted another set of MSA. The MSA based on this larger combined foraging ground dataset still resulted in a combined mean estimate of approximately 84–86% for West Africa, but more evenly split between Gabon (~45%) and Ghana (~41%), although confidence intervals remained large (Table 1 and Fig. 2). No significant relationships were detected between MSA results and the geographic distance from nesting colonies ( $r = 0.34$ ;  $P = 0.45$ ).

Accordingly the MDS based on  $\Phi_{ST}$  values (stress value = 0.05) indicated that ERG and BA foragers grouped together along with Ghana and Gabon nesting beaches (Fig. 3). An interesting result is that the MSD ordination demonstrated low affinity of Brazil nesting beaches with respect to feeding grounds in the southwestern Atlantic.

## 4. Discussion

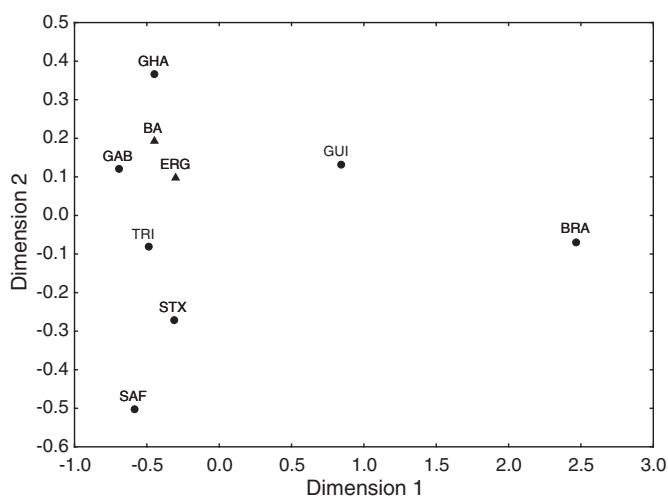
Our results represent the first MSA for leatherbacks with informative longer mtDNA sequences and taken together with the results of the MDS analysis indicate that the leatherback foraging grounds off Brazil and Argentina are linked to the breeding populations off West Africa. These results are consistent with those obtained from mark–recapture studies in Argentina and preliminary genetic findings from ERG feeding grounds (Billes et al., 2006; Dutton et al., 2013; Vargas et al., 2008).

Although the use of the longer mtDNA sequences in leatherbacks improves the ability to conduct meaningful MSA for Atlantic (Dutton et al., 2013), our results should be interpreted with caution. For instance, the large confidence intervals surrounding estimates for the Gabon and Ghana contribution are likely due to the shared common

haplotypes found at these regional rookeries, and may not accurately reflect fine scale differences (see Jensen et al., 2013). Relative population sizes are also important to consider. Although comprehensive population census data are not available, the Brazilian nesting population is generally thought to be orders of magnitude smaller than the large populations in West Africa (Witt et al., 2009), so the relatively minor presence of Brazilian leatherbacks detected in our study in Argentine foraging grounds likely reflects the relative population sizes of the source stocks. Threats to survival of the relatively fewer Brazilian turtles at the South American foraging areas (BA and ERG) would still have a large impact on the already depleted Brazilian nesting population. Incorporating relative population sizes into a weighted MSA did not substantially change the estimated relative contribution of Ghana versus Gabon rookeries, both analyses yielded mean estimates with large confidence intervals. The larger combined ERG and BA dataset resulted in a more even split of the West Africa contribution between Ghana and Gabon, suggesting that larger sample sizes of the mixed stock may change the outcomes of MSA, but the large confidence intervals caution over-interpretation of these fine-scale differences. There are also additional nesting sites along the West African coast that have not been characterized. The use of multiple nuclear markers allows more precise detection of weakly differentiated stocks (Dutton et al., 2013), and accurate stock assignment of individual animals, as demonstrated by Stewart and Dutton (2013) for leatherbacks encountered at foraging grounds in the North Atlantic and offers a feasible approach for further analysis in the future. Finally, more comprehensive studies that incorporate data from multiple foraging populations throughout the geographic range are needed to allow more sophisticated MSA using “many-to-many” approaches that avoid potential biases described by Bolker et al. (2007) in order to obtain more accurate point estimates of stock composition. Nevertheless, for the purposes of our present study, the predominant presence of leatherbacks from the West African rookeries at the South American feeding grounds can be conclusively established.

Recent studies using satellite tracking data have identified coastal marine habitat in our study area in Argentina, as well as Uruguay and Brazil as High Use Areas (HUAs) for leatherbacks whose presence is associated with the seasonal distribution and abundance of prey as well as the oceanographic conditions, linking both the BA and ERG feeding areas in the western South Atlantic (Fossette et al., 2010a, 2014; López-Mendilaharsu et al., 2009). This supports our findings of genetic homogeneity in terms of stock composition between the ERG and BA foraging aggregations of leatherbacks, and further suggests that animals move between these different sites along the temperate zones off the Atlantic coast of South America. Leatherback turtles feed on soft-bodied animals such as jellyfish and ctenophores (Den Hartog and Van Nierop, 1984; James and Herman, 2001). Cabreira et al. (2006) highlighted the role of the Rio de la Plata convergence front, in generating a large accumulation of organic matter and plankton off the coast near Buenos Aires and hence providing an important area for the development of gelatinous organisms such as *Lychnorhiza lucerna* and *Chrysaora lactea* (Scyphozoa), which are favored leatherback prey items (Estrades et al., 2007; López-Mendilaharsu et al., 2009).

Ocean currents are another important factor influencing migratory patterns of leatherback turtles in the South Atlantic that help explain the connectivity patterns indicated by our genetic results. Satellite tracking studies have shown that the movement of leatherback turtles from nesting areas of Africa to feeding and development grounds off America is associated with ocean currents (Almeida et al., 2011; Eckert, 2006; Eckert et al., 1986; Ferraroli et al., 2004; Fossette et al., 2010a, 2010b; Hays et al., 2004; Luschi et al., 2006; Sales et al., 2006; Witt et al., 2009, 2011). The distribution of this species is likewise influenced by trophic conditions as suggested by telemetry studies indicating that adult movements are associated with patterns of food abundance (Fossette et al., 2010a; Grant et al., 1996; López-Mendilaharsu et al., 2009; Witt et al., 2007).



**Fig. 3.** Results of multidimensional scaling (MDS) analysis showing relationships among the 2 feeding grounds (BA and ERG) and the 7 Atlantic nesting sites. The analysis, which integrates genetic and geographic proximity, was done with two dimensions. Abbreviations correspond with Fig. 1 and Table 1.

The results of the present study together with the findings of satellite tracking research and knowledge of gelatinous organism distribution could be incorporated into threat assessment models and provide the basis for national and regional conservation programs for this species that implement mitigation measures and temporal and spatial management of fishing practices in the region. The frequent reports of turtles incidentally captured in artisanal and industrial fisheries and mass-stranding events off the coast of Argentina, Uruguay and Brazil (Domingo et al., 2006; González-Carman et al., 2011; Laporta et al., 2006; Sales et al., 2008) indicate that this region is a foraging “hotspot” that overlaps with fishing (Fossette et al., 2014). In addition to fishing, the Argentine and Brazilian coastal waters are increasingly impacted by economic activities, such as maritime cargo transport, tourism, and the discharge of domestic and industrial waste that further threaten survival of this species (Fossette et al., 2014; López-Mendilaharsu et al., 2009). Our results help further define the boundaries of the Regional RMU proposed by Wallace et al. (2010), contributing to the critical data needs and show that threats on Argentine foraging grounds will impact the southwestern leatherback RMU. These findings further illustrate the importance of the Malvinas ecoregion to the survival of migratory marine vertebrates in the South Atlantic and highlight the need to coordinate international conservation efforts on an ocean-wide scale.

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