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Genetic Diversity and Origin of Leatherback Turtles (*Dermochelys coriacea*) from the Brazilian Coast

Sarah M. Vargas, Flávia C. F. Araújo, Danielle S. Monteiro, Sérgio C. Estima, Antônio P. Almeida, Luciano S. Soares, and Fabrício R. Santos

From the Laboratório de Biodiversidade e Evolução Molecular, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, Caixa Postal 486, Belo Horizonte, MG, 31270-901, Brazil (Vargas, Araújo, and Santos); the Núcleo de Educação e Monitoramento Ambiental, NEMA, Rua Maria Araújo, 450, Rio Grande, RS, 96207-480, Brazil (Monteiro and Estima); the Projeto Tamar-ICMBio, Reserva Biológica de Comboios s/n, Regência, Caixa Postal 105, Linhares, ES, 29900-970, Brazil (Almeida); and the Fundação Pró-Tamar, Caixa Postal 2219, Salvador, BA, 41950-970, Brazil (Soares).

Address correspondence to F. R. Santos at the address above, or e-mail: fsantos@icb.ufmg.br.

The leatherback sea turtle (*Dermochelys coriacea*) population that nests in Brazil is restricted to a few individuals, but high densities of pelagic individuals are observed along the southern and southeastern Brazilian coast. We investigated the diversity of the mitochondrial DNA (mtDNA) control region in order to understand the relationship between nesting and pelagic leatherbacks from Brazil and elsewhere. High-quality 711-bp sequences were generated, analyzed, and compared with published data from worldwide populations. We detected the presence of shared haplotypes between nesting and pelagic aggregates from Brazil, as well as haplotypes shared with other nesting areas from the Atlantic and Pacific. Furthermore, the use of longer control region sequences allowed the subdivision of the common Atlantic haplotype A into 3 different haplotypes (A1, A3, and A4), thus improving the resolution of mtDNA-based leatherback phylogeography. The use of longer sequences partially supported a closer association between nesting and pelagic individuals from Brazil and pointed to a complex origin for the pelagic individuals in the Brazilian coast.

The leatherback turtle (*Dermochelys coriacea*) is a pelagic marine species with a worldwide tropical and subtropical distribution. It is highly adapted for life in the open seas, feeding on jellyfish, salps, and other gelatinous organisms distributed in the water column (Marquez 1990). Major leatherback nesting sites in the Atlantic Ocean include populations in the French Guiana and Suriname in South America, Trinidad in the southern Caribbean, and Gabon and Congo in Africa (Spotila et al. 1996; Rivalan et al. 2006).

The population of leatherbacks nesting in Brazil is restricted to a few individuals, located on the northern coast of the State of Espírito Santo, eastern Brazil, around lat 19°S (Thomé et al. 2007). Although small, the leatherback population shows an increasing trend in the annual number of nests: 92 nests were recorded in the 2003/2004 nesting season in Espírito Santo (Thomé et al. 2007) as compared with 6 in 1993/1994. Furthermore, rare nesting leatherbacks have been observed in other places in Brazil (Barata and Fabiano 2002) and leatherbacks are often seen along the Brazilian coast, with a higher concentration of individuals along the southern and southeastern coast (Barata et al. 2004).

Dermochelys coriacea is classified as "Critically Endangered" by the World Conservation Union. Population declines have been observed around the world, mainly in the Pacific and Indian Oceans, since the early 1980s (Chan and Liew 1996; Spotila et al. 1996, 2000). Major threats include incidental catches by industrial fisheries (also called "bycatch," Lewison et al. 2004) and destruction of coastal nesting habitats (Pritchard 1996).

The leatherback turtles can travel very large distances (Pritchard 1976), reaching cold waters where no other marine reptile occurs (Goff and Lien 1988). Current available information from tag returns and stranding records in the western Atlantic suggests that adults engage in routine migrations between boreal, temperate, and tropical waters, presumably to optimize both foraging and nesting opportunities (Pritchard 1976).

Sea turtles have been subjected to intensive studies with molecular markers for over a decade (Avise and Bowen 1994). Genetic diversity data in sea turtles have already allowed the identification of complex phylogeographic patterns (Bowen et al. 2005; Lara-Ruiz et al. 2006) and the demonstration of a phylopatric behavior and natal homing for females (Fitzsimmons et al. 1997; Bowen et al. 2004),

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but few studies have been performed on leatherbacks (Dutton et al. 1999; Crim et al. 2002).

The genetic identification of the origin of bycatch or nesting sea turtles is currently performed with mitochondrial DNA (mtDNA) sequence analyses in a global scale. The published mtDNA sequences of leatherback turtles are restricted to very few populations. In this work, we aimed to describe the Brazilian nesting and pelagic *D. coriacea* populations and to compare the data obtained with previous reports. Our analyses allowed us to establish the relationship between nesting leatherbacks from Brazil and elsewhere, as well as to ascertain the origin of the pelagic aggregate individuals. Furthermore, the use of longer mtDNA control region sequences proved to be a valuable tool in obtaining more consistent genealogical relationships of mtDNA haplotypes and individuals of *D. coriacea* populations.

Materials and Methods

Samples were collected from nesting and pelagic leatherbacks in Brazil (Figure 1). Females ($n = 11$) were sampled from a nesting area in the Espírito Santo State, and the pelagic aggregate includes individuals incidentally caught by fisheries in Brazilian waters ($n = 6$) or stranded on beaches during a massive event in the Rio Grande do Sul State ($n = 46$) in December 2005. Fresh skin biopsies were taken from the anterior flipper of females during oviposition or from individuals incidentally caught in fisheries' nets. Biopsies from skin and other tissues were also collected from dead individuals found on beaches. All samples were stored in ethanol 70% at room temperature, and total DNA was extracted as previously published (Lara-Ruiz et al. 2006). The mtDNA control region was entirely amplified using the specific primers LCM 15382, H950 (Abreu-Gobrois FA, personal communication), and HDCM1 (5′ actaccgtatgccaggtta 3′) (Allard et al. 1994). Polymerase chain reaction (PCR) mixes of 12.5 μl included 2 μl of genomic DNA (~40 ng), 1 U of *Taq* polymerase (Phoneutria, Belo Horizonte, Brazil), 200 μM of deoxynucleoside triphosphates, 1× Tris–KCl buffer with 1.5 mM $MgCl_2$ (Phoneutria), and 0.5 μM of each primer. The amplification program consisted of 5 min at 94 °C, followed by 35 cycles of 30 s at 94 °C, 30 s at 51 °C, 1 min at 72 °C, and a final extension step of 9 min at 72 °C. PCR products were further processed and sequenced as previously described (Lara-Ruiz et al. 2006).

Some procedures were adopted in order to generate high-quality sequences, namely: 1) sequences longer than 1000 bp were amplified, 2) at least 2 different PCR products were obtained for the sequencing reactions for each individual, 3) chromatograms were carefully checked for ambiguities, 4) high-quality consensus sequences were generated with forward and reverse sequences from at least 2 independent PCR products, and 5) consensus sequences produced for each individual in the present study were aligned and compared among them and with other sequences of *D. coriacea* obtained from the GenBank.

Consensus sequences (GenBank accession numbers: EF513272–EF513278) were obtained after careful analyses with the softwares Phred v. 0.20425 (Ewing et al. 1998), Phrap v. 0.990319 (http://www.phrap.org), and Consed 14.0 (Gordon et al. 1998). Sequence alignments were performed with Clustal X implemented in MEGA 3.1 (Kumar et al. 2004), with manual edition when necessary. Sequence divergence among different haplotypes was estimated through the software MEGA 3.1 using Kimura 2-parameter (K2p) distance model. MEGA 3.1 was also used to construct trees by neighbor joining (NJ) based on the K2p model and maximum parsimony (MP), both with branch topology tested by 10 000 bootstrap replicates. We also used the median joining (MJ) network analysis (Bandelt et al. 1999) to depict the relationships among Brazilian *D. coriacea* haplotypes (711 and 496 bp) as implemented in the Network 4 software (http://www.fluxus-engineering.com). Population pairwise Fst's and ϕst's, analyses of molecular variance (AMOVAs) among nesting populations, exact tests of population differentiation and Tajima's *D* and Fu's *Fs* neutrality tests were calculated with Arlequin version 3.1 (Excoffier et al. 2005).

The origin of pelagic leatherbacks in the Brazilian coast was investigated by comparisons with different nesting populations found in the Atlantic and Pacific regions. We performed a mixed stock analysis (MSA) to estimate the relative contributions of different nesting colonies to the pelagic aggregate. We used the Bayesian algorithm with a Markov Chain Monte Carlo (MCMC) estimation procedure implemented in BAYES (Pella and Masuda 2001), which has higher statistical power and is more accurate than traditional maximum likelihood estimates (Antonovich and Templin 2003). For comparison purposes, we also computed admixture coefficients from molecular data as implemented in Admix 2.0 (Bertorelle and Excoffier 1998; Dupanloup and Bertorelle 2001). Only short haplotypes (496 bp) could be used in these analyses. We used 2 baseline stocks (Atlantic and Indo-Pacific populations) to run 2 MCMC chains of size 200 000, 1 chain per baseline stock with a starting point of 0.90 for the first and 0.1 for the second one. Convergence of MCMC estimates to a desired posterior probability was assessed using the Gelman–Rubin shrink factor (Gelman and Rubin 1992), increasing the MCMC size until all values obtained were less than 1.2. The Brazilian pelagic aggregate composition was estimated from the mean of 2 chains after 100 000 burn-in steps.

Results and Discussion

High-quality 711-bp long sequences were generated and analyzed in 2 ways: using the complete sequence or only 496 bp to compare with available data from the literature. When 496-bp sequences were analyzed, 5 distinct haplotypes (Dc_A, A2, C, D, and I) were defined by 5 polymorphic sites. When using 711-bp sequences, 7 haplotypes (Dc_A1, A2, A3, A4, C, D, and I) were defined by 9 polymorphic sites (Table 1). Thus, the use of longer control region

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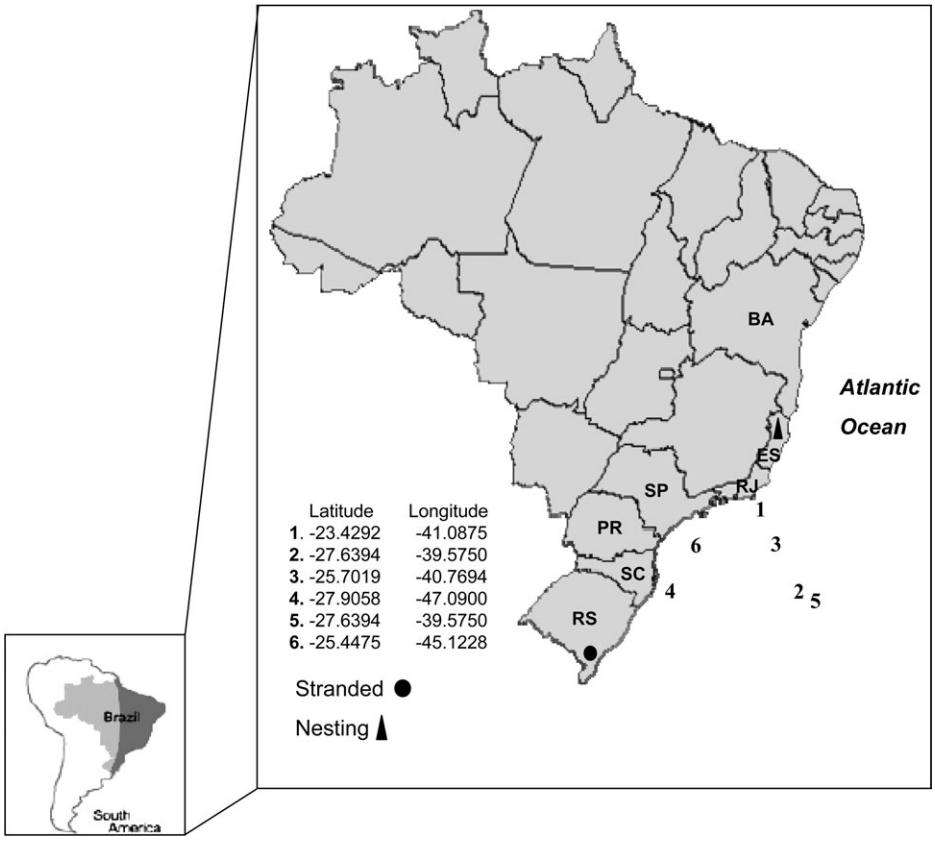

Figure 1. Approximate location of sampling sites along the Brazilian coast (RS—Rio Grande do Sul State, SC—Santa Catarina State, PR—Paraná State, SP—São Paulo State, RJ—Rio de Janeiro State, ES—Espírito Santo State, and BA—Bahia State) and geographic coordinates for 6 sampling sites of pelagic (stranded/incidentally caught) animals.

sequences clearly improved the resolution of mtDNA haplotypes.

The genetic diversity indexes for the nesting population ($n = 11$) were similar when using short or long sequences ($h = 0.182$ and $\pi = \pm 0.00147$) and only 2 haplotypes were present (Dc_A1 and Dc_C). For pelagic (stranded and incidentally caught) leatherbacks ($n = 52$), we observed 5 haplotypes, $h = 0.369$ and $\pi = 0.00138$ when using 496 bp, whereas 7 haplotypes, $h = 0.553$ and $\pi = 0.00166$ were found when using 711-bp sequences. Slightly, higher diversity values were observed in the pelagic aggregate because more haplotypes were discriminated with longer sequences.

The AMOVA indicated that *D. coriacea* populations are significantly structured ($P < 0.0001$) in 2 macrogeographic groupings, Atlantic and Indo-Pacific, with low differentiation among individual nesting populations within each group. The nesting populations from Brazil, Florida (USA), Costa Rica (Atlantic), Trinidad, Suriname/French Guyana, Saint Croix, and South Africa were grouped in an Atlantic nesting group and the populations from Malaysia, Solomon Islands, Mexico, and Costa Rica (Pacific) were grouped in an Indo-Pacific population (Table 2).

The global ϕst for all the nesting leatherback populations was 0.6351, with 52.8% of the variation occurring between the Atlantic and Indo-Pacific groups, 36.5% found within populations, and only 10.7% among populations within the Atlantic and Indo-Pacific groups. These results revealed that the Atlantic and Indo-Pacific leatherback populations are distinct and should be considered separate demographic units (Table 2).

Table 1. MtDNA control region polymorphisms and haplotype designations for *D. coriacea* assayed using 496 bp (Dc_A, A2, C, D and I) or 711 bp sequences (Dc_A1, A2, A3, A4, C, D and I). Polymorphisms from positions 150 to 308 are also included in the 496 bp haplotypes.

	Base position		
	496 bp haplotypes	12223 51250 05898 6667 2390 2203	711 bp haplotypes
Haplotypes	Dc_A	GAGGA AACT	Dc_A1
	Dc_A2	...A.	Dc_A2
	Dc_A	C	Dc_A3
	Dc_A	....T.	Dc_A4
	Dc_C	AGA.G .G..	Dc_C
	Dc_D	.GA.G .G..	Dc_D
	Dc_I	....G GG..	Dc_I

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Table 2. Absolute haplotype frequencies, haplotype (h) and nucleotide (π) diversities for *Dermochelys coriacea* populations using 496 bp: pelagic aggregate and nesting populations from Brazil, compared with data from other worldwide nesting populations (Dutton et al. 1999)

Location	Haplotypes												*n*	Haplotype diversity (h)	Nucleotide diversity (π)
	A	A2	B	C	D	E	F	G	H	I	K	L			
Brazil (pelagic aggregate)	**41**	**6**	**0**	**2**	**1**	**0**	**0**	**0**	**0**	**2**	**0**	**0**	**52**	**0.369**	**0.0014**
Atlantic nesting populations															
Brazil	10	0	0	1	0	0	0	0	0	0	0	0	11	0.182	0.0015
Florida	10	0	0	0	0	0	0	0	0	0	0	0	10	0	0
Costa Rica	26	0	0	2	0	0	0	0	0	0	0	0	28	0.138	0.0005
Trinidad	16	0	0	11	0	0	0	0	0	0	0	0	27	0.501	0.0019
Suriname/French Guyana	20	0	0	0	0	0	0	0	0	0	0	0	20	0	0
St Croix	12	0	8	2	0	0	0	0	0	0	0	0	22	0.589	0.0011
South Africa	8	0	0	0	0	0	0	0	0	0	0	0	8	0	0
Indo-Pacific nesting populations															
Malaysia	3	0	0	0	2	3	0	0	1	0	0	0	9	0.806	0.0019
Solomon Islands	1	0	0	0	0	0	0	0	2	5	0	0	8	0.607	0.0021
Mexico	0	0	0	0	8	0	0	2	6	0	1	1	18	0.712	0.0017
Costa Rica	0	0	0	0	14	0	1	3	4	0	2	1	25	0.663	0.0016
Overall (nesting)	**106**	**0**	**8**	**16**	**24**	**3**	**1**	**5**	**13**	**5**	**3**	**2**	**186**	**0.382**	**0.0011**

One individual of the Brazilian nesting population presented the Dc_C haplotype that was also found in other nesting populations in the Atlantic coast of Costa Rica, Trinidad, and Saint Croix (Atlantic Ocean). However, 10 individuals (89.9%) presented the Dc_A haplotype (711 bp Dc_A1), which has also been found in the previously cited regions and in 5 other areas of the Atlantic and Indo-Pacific: Suriname, Florida, South Africa, Malaysia, and Solomon Islands (Dutton et al. 1999). Despite the small sample size, this Brazilian nesting population could be significantly differentiated from all Indo-Pacific populations ($P < 0.01$), although not from other Atlantic populations.

In the pelagic aggregate ($n = 52$), 2 individuals (3.9%) had the Dc_I haplotype, previously found only in the Solomon Islands; one individual (1.9%) had the Dc_D haplotype, commonly found in the Pacific Coast of Costa Rica, and 6 individuals (11.5%) presented a new haplotype (Dc_A2). Furthermore, the pelagic population included haplotypes previously described in nesting populations of the Atlantic: 41 individuals (78.8%) with haplotype Dc_A (711 bp: Dc_A1: 65.4%, A3: 11.5%, A4: 1.9%), the most frequent in the Brazilian nesting population (89.9%, all 711 bp Dc_A1), and 2 individuals (3.9%) with the Dc_C haplotype found in the Brazilian nesting site (11.1%), but frequent in Trinidad (Dutton et al. 1999). Although we could speculate that the animals with the haplotype Dc_A from the Brazilian pelagic aggregate may have a Pacific origin, it is more parsimonious to assume that their origin is from the closest Brazilian (or another Atlantic) nesting population. This conclusion is also supported by the use of 711-bp haplotypes, according to which both Brazilian populations have the Dc_A1 haplotype as the most frequently found (Figure 2B). Unfortunately, further comparisons are hindered by the lack of studies describing long mtDNA sequences from other Pacific or Atlantic leatherbacks. Nevertheless, we observed a high diversity (7 haplotypes) in the pelagic aggregate, which was composed by 43 individuals with haplotypes Dc_A and C found mainly in the Atlantic, 3 animals with haplotypes Dc_D and I found in the Pacific, and 6 animals with the haplotype Dc_A2, not described for any known nesting site yet. These results indicate a complex origin for *D. coriacea* foraging in the coast of Brazil, which includes individuals from the Pacific.

The genealogical relationships among the 12 *D. coriacea* 496-bp haplotypes are shown in Figures 2A and 3. The MP (Figure 3) and NJ (not shown) trees indicated that the haplotype Dc_B is likely the basal *D. coriacea* haplotype. Dc_A (the most frequent haplotype observed in Brazil and other regions of the Atlantic Ocean), Dc_B, and Dc_A2 (the new haplotype only found in the stranded/incidentally caught Brazilian leatherback population) are sister lineages (Figure 3). A network with 7 haplotypes based on the 711-bp sequences is shown in Figure 2B. In this case, the nesting population is still represented by only 2 haplotypes, (Dc_A1 and Dc_C), but the Dc_A haplotype (496 bp) has been subdivided into Dc_A1, A3, and A4. The MJ network (Figure 2B) and the MP and NJ trees (data not shown) for these haplotypes indicated the existence of 2 clusters: one composed of Dc_A1, A2, A3, and A4 and the other joining Dc_C and D; with Dc_I appearing as a separate lineage. Although these phylogenetic analyses suggest a close relationship between Dc_C and Pacific (Eastern and Indo-Pacific) haplotypes, its occurrence among Brazilian pelagic leatherbacks is more parsimoniously explained by an Atlantic origin. Haplotype Dc_C also appears in the Brazilian nesting site (11.1%) and is one of the most frequent haplotypes found in the Trinidad nesting population (Dutton et al. 1999).

The future use of longer mtDNA sequences in other Pacific and Atlantic populations could help to better resolve

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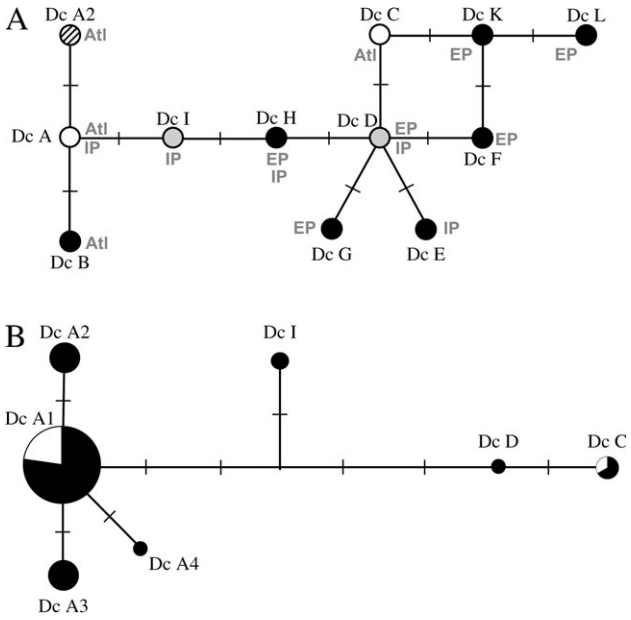

Figure 2. (**A**) MJ network describing the relationship among the 12 *Dermochelys coriacea* mtDNA haplotypes (496 bp). Haplotypes Dc_A to Dc_L found by Dutton et al. 1999. Haplotypes Dc_A, C, D, I, and A2 (new 496-bp haplotype) found in our work. Gray: Haplotypes found in pelagic population of Brazil. White: Haplotypes found in the nesting population and pelagic population of Brazil. Black: Haplotypes found in other populations by Dutton et al. 1999. Hatched: Haplotype found exclusively in the pelagic population of Brazil. Presence of haplotypes in the Atlantic (Atl), in the Indian and Pacific (IP) and Eastern Pacific (EP) oceanic regions are also indicated. (**B**) MJ network describing the relationships among 7 *D. coriacea* mtDNA 711-bp haplotypes (Dc_A1, A2, A3, A4, C, D, and I) found in nesting (white: $n = 11$) and pelagic populations (black: $n = 52$) along the Brazilian coast. Nucleotide substitutions are shown on the branches as small transverse bars.

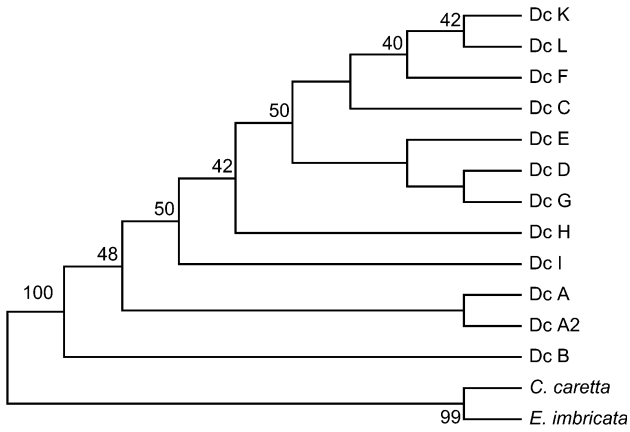

Figure 3. MP consensus tree produced from an alignment of control region sequences with 12 *Dermochelys coriacea* mtDNA haplotypes (496 bp) found in this study and elsewhere (Dutton et al. 1999). Bootstrap support values are shown on the branches. *Caretta caretta* and *Eretmochelys imbricata* sequences were used as outgroup. Identical tree topology was obtained using NJ (results not shown).

this phylogeny and to discriminate between haplotypes that have been found both in the Atlantic and in the Pacific, such as Dc_A.

The MSA performed in Bayes was run using an input file with haplotypes from the pelagic leatherbacks found in Brazil and from nesting populations found worldwide. Six pelagic individuals were excluded from the analysis because they represented the new orphaned haplotype (Dc_A2). The source populations were grouped as Atlantic or Indo-Pacific, as suggested by the AMOVA results. All chains consistently indicated a major contribution to the Brazilian pelagic aggregate from Atlantic nesting populations (mean 96.1%) and a lower contribution from the Indo-Pacific (mean 3.9%). These results are likely due to the presence of a haplotype in 2 Brazilian individuals that has only been previously found in the Solomon Island nesting population.

These results are in agreement with the biology of *D. coriacea*, known to be long distance disperser (James et al. 2005; Billes et al. 2006). The MSA performed with the Admix 2.0 software also produced similar results (data not shown). Thus, present comparisons using known haplotype distributions and MSA reveal a diverse origin for the Brazilian pelagic aggregate including individuals from Atlantic (mainly Brazil) and Pacific nesting sites. However, future stock analysis using longer mtDNA sequences from most Indo-Pacific and Atlantic nesting sites will likely provide much better clues for the origin of Brazilian pelagic leatherbacks. Indeed, leatherbacks flipper tagged in Gabon (western Africa) beaches were recently recovered in Brazil and Argentina (Billes et al. 2006), and our analysis of a single individual from Gabon revealed that it bears the Dc_A3 haplotype (Vargas S, Soares LS, Santos FR, unpublished data), frequently found in Brazilian pelagic leatherbacks (12%).

Conclusions

We described and compared the haplotypes of nesting and pelagic leatherbacks from Brazil with worldwide populations. This study provided relevant data to better understand the relationships among and within different rookeries as well as the migration pattern of leatherbacks found in Brazil and worldwide. Furthermore, we showed that the use of longer mtDNA sequences provide a more discriminating phylogeography, particularly useful in further ascertainment studies and MSA involving the critically endangered leatherbacks. These conclusions can be incorporated in future studies and conservation programs of this species aiming at avoiding regional and global extinction.

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Corresponding Editor: Hector Seuanez

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