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Phylogeography of the green turtle, *Chelonia mydas*, in the Southwest Indian Ocean

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Abstract

Patterns of mitochondrial DNA (mtDNA) variation were used to analyse the population genetic structure of southwestern Indian Ocean green turtle (*Chelonia mydas*) populations. Analysis of sequence variation over 396 bp of the mtDNA control region revealed seven haplotypes among 288 individuals from 10 nesting sites in the Southwest Indian Ocean. This is the first time that Atlantic Ocean haplotypes have been recorded among any Indo-Pacific nesting populations. Previous studies indicated that the Cape of Good Hope was a major biogeographical barrier between the Atlantic and Indian Oceans because evidence for gene flow in the last 1.5 million years has yet to emerge. This study, by sampling localities adjacent to this barrier, demonstrates that recent gene flow has occurred from the Atlantic Ocean into the Indian Ocean via the Cape of Good Hope. We also found compelling genetic evidence that green turtles nesting at the rookeries of the South Mozambique Channel (SMC) and those nesting in the North Mozambique Channel (NMC) belong to separate genetic stocks. Furthermore, the SMC could be subdivided in two different genetic stocks, one in Europa and the other one in Juan de Nova. We suggest that this particular genetic pattern along the Mozambique Channel is attributable to a recent colonization from the Atlantic Ocean and is maintained by oceanic conditions in the northern and southern Mozambique Channel that influence early stages in the green turtle life cycle.

Keywords: *Chelonia mydas*, control region, Indian Ocean, mitochondrial DNA, Mozambique Channel, phylogeography

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Introduction

The green turtle (*Chelonia mydas*) is a large, long-lived, herbivorous reptile that grazes on marine macrophytes in shallow tropical and subtropical waters around the world (Limpus *et al*. 1994; Limpus & Chaloupka 1997). Because green turtle hatchlings are rarely seen between the time they leave their natal beach and when they first appear in shallow water foraging habitats (Musick & Limpus 1997), Carr (1987) named this interval the 'lost year'. Available evidence now indicates that this lost year involves at least several years of drifting in oceanic gyre systems in a passive migration that may circumnavigate entire ocean basins (Bowen *et al*. 1995; Bolten *et al*. 1998; Lahanas *et al*. 1998). Green turtles grow slowly, often taking some 25–30 or more years to reach maturity (Limpus & Walter 1980). During this developmental period, they occupy a series of foraging habitats dispersed over an extensive area. Upon

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reaching adulthood, reproductive females typically make long distance migrations between feeding sites and their natal breeding beaches (Limpus *et al*. 1992). They show great fidelity to both nesting (Meylan 1982) and feeding grounds (Limpus *et al*. 1992), even though these may be separated by thousands of kilometres (Mortimer & Carr 1987). They typically lay multiple clutches within a season (Carr & Ogren 1960), with 1–9 or more years separating successive breeding seasons (Le Gall *et al*. 1985; Limpus *et al*. 1994, 2001; Miller 1997).

Attempts have been made to define green turtle population boundaries for this globally distributed endangered species in order to identify functional units of management. Although flipper tagging (Le Gall & Hugues 1987), satellite (Pelletier *et al*. 2003) and acoustic telemetry (Taquet *et al*. 2006) provide useful information about contemporary demography, site fidelity and migrations of individual animals, the data produced are strongly biased towards females and intensively surveyed locations, especially nesting beaches. In contrast, genetic studies tend to focus on the population rather than on the individual level that can offer unique perspectives on historical population dynamics. When complemented by tagging studies, genetic tools can elucidate the geographical boundaries of breeding populations and provide information about their migrations through feeding, breeding and developmental ranges (Bowen & Karl 1997).

Mitochondrial DNA (mtDNA) has proven particularly effective for detecting population structure in marine turtles (FitzSimmons *et al*. 1999), and several studies have successfully used mtDNA variants to resolve population boundaries among breeding sea turtles (Bowen *et al*. 1992, 1994, 1998; Broderick *et al*. 1994; Norman *et al*. 1994; Bass *et al*. 1996; Encalada *et al*. 1996; Dutton *et al*. 1999). In general, these studies have revealed a significant level of population subdivision on both regional and global scales and found that rookeries, often separated by hundreds of kilometres, may form genetically discrete populations or management units (Moritz 1994). The maternal inheritance of mtDNA also tends to accentuate genetic differences among populations compared to nuclear genes because it has a smaller effective population size. In many circumstances, female-inherited markers offer a distinct advantage because they provide perspectives on female reproductive behaviour that are paramount to species survival (FitzSimmons *et al*. 1999). Nevertheless, mtDNA does not capture the entire population genetic history of a particular species and inferences of population connectivity and isolation can be misleading especially if male–mediated gene flow is substantially different to that of females, as it was shown in some green turtle populations (Karl *et al*. 1992; FitzSimmons *et al*. 1997a, b, 1999; Roberts *et al*. 2004).

Among the significant green turtle rookeries that occur in the Southwest Indian Ocean, some have been well described. At the French Eparses Islands (Europa, Juan de Nova, Tromelin and Glorieuses), green turtle populations have been monitored since the 1980s (Le Gall *et al*. 1985; Le Gall & Hugues 1987; Le Gall 1988). The green turtles of the Seychelles archipelago are well known (Frazier 1984; Mortimer 1984; Mortimer *et al*. in press), especially those at Aldabra (Frazier 1971; Mortimer 1988). Other studies include those of green turtles at Mayotte (S. Ciccione, unpublished data), Comoros (Frazier 1984; S. Ciccione, unpublished data), Northeast of Madagascar (J. Bourjea, unpublished data), Kenya (Okemwa *et al*. 2004), and Tanzania (Muir 2005). These studies have shown that the patterns of movements and behaviour of green turtles in this region conform to those found elsewhere in the world, but a detailed appraisal of the entire region has yet to emerge. In fact, information on nesting turtles is either sparse or lacking in other adjacent countries, especially Mozambique, South of Madagascar and Somalia, where both nesting and foraging habitat as well as human exploitation of this species occur (Le Gall & Hugues 1987; Rakotonirina & Cooke 1994).

The Southwest Indian Ocean, especially the Mozambique Channel, is of particular biogeographical interest. Suitable green turtle feeding habitat, due to warm water flows, are found very close to the tip of South Africa while suitable habitat is absent from the west coast of South Africa due to upwelling and cold water flows. Previous protein and total mtDNA restriction fragment length polymorphism (RFLP) genetic studies inferred that cold waters of South Africa have been a major biogeographical barrier for green turtle dispersal (Bonhomme *et al*. 1987; Bowen *et al*. 1992). Bowen *et al*. (1992) found no evidence of gene flow occurring between Indian and Atlantic Oceans over the last 1.5 million years but they did not sample rookeries in the Mozambique Channel. If there is any contact between green turtles in the Indian and Atlantic Oceans, then the Mozambique Channel is the most likely place for this to occur.

The purpose of this study is to survey the patterns of mtDNA control region sequence variation of nesting green turtles at 10 different rookeries in the Southwest Indian Ocean, principally along the Mozambique Channel. The patterns of mtDNA variation will be used to: (i) define groups of rookeries that comprise discrete genetic populations; (ii) investigate the patterns of dispersal and subdivision of rookeries in this region; and (iii) determine if there is any evidence of contact between green turtles from Indian and Atlantic Oceans.

Materials and methods

Sampling

A total of 288 nesting females were sampled on different dates from 10 different nesting sites in the western Indian

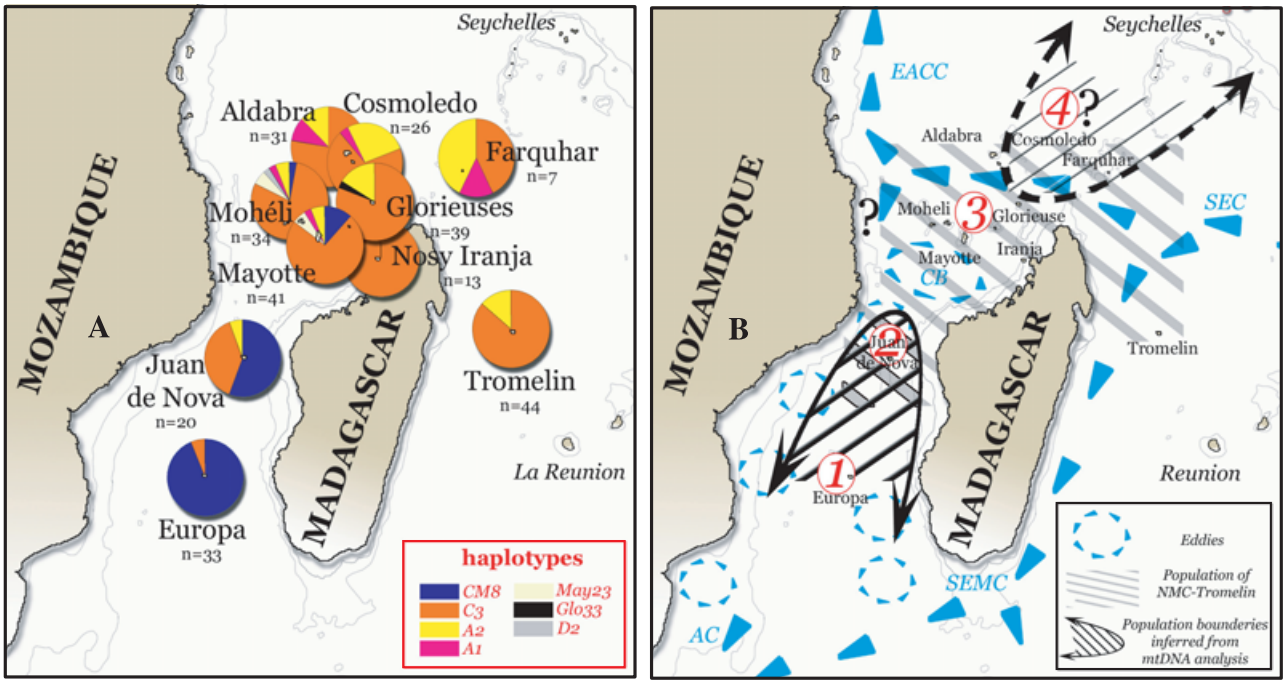

Fig. 1 (A) Geographical locations of the 10 green turtle nesting sites sampled in the Southwest Indian Ocean. The piechart shows the frequencies of the haplotypes per nesting site. (B) Main oceanic movements in the Southwest Indian Ocean and nesting green turtle population boundaries inferred from mtDNA data. The following abbreviations were used: SEC, South Equatorial Current; SEMC, Southeast Madagascar Current; EACC, East African Coastal Current; AC, Agulhas Current; CB, Comoro Basin. The numbers (1, 2, 3, and 4) in red show the different nesting green turtle genetic stocks proposed in this study.

Table 1 Mitochondrial DNA variants detected among green turtle populations nesting in 10 different sites in the Southwest Indian Ocean. Haplotype (*h*) and nucleotide diversity (π) for the 10 populations in the North Mozambique Channel (NMC) and South Mozambique Channel (SMC)

	Location	Date of sampling	CM8	C3	May23	D2	Glo33	A1	A2	Total	Haplotype diversity (*h*)	Nucleotide diversity (π)
SMC	Europa	1997/2003	31	2						33	0.1174	0.0076
	Juan de Nova	1999	11	8					1	20	0.5632	0.0360
	Total SMC		42	10					1	53	0.3425	0.0221
NMC	Nosy Iranja	2004		13						13	0	0
	Mayotte	2004	5	30	2			1	3	41	0.4524	0.0231
	Mohéli	2004	1	27	2	1		1	2	34	0.3708	0.0133
	Glorieuses	2004		31			1		7	39	0.3441	0.0168
	Cosmoledo	1996		24				3	4	31	0.3871	0.0210
	Aldabra	1996		18				1	7	26	0.4646	0.0249
	Farquhar	1996		3				1	3	7	0.7143	0.0342
	Total NMC		6	146	4	1	1	7	26	191	0.3964	0.01962
	Tromelin	1997		38					6	44	0.2410	0.0132
	Total		48	194	4	1	1	7	33	288	0.5063	0.0289

Ocean (Fig. 1A and Table 1), that geographically fall into three groups. Those from the South Mozambique Channel (called here SMC) include Europa and Juan de Nova (French Eparses islands); while those from the North Mozambique Channel (called here NMC) include the Mohéli (Comoros), Mayotte (French territory), Nosy Iranja (Madagascar), Glorieuses (French Eparses Island), and three sites in the Republic of Seychelles. The last group,

out of the Mozambique Channel, is composed only by Tromelin (French Eparses Island). In the French Eparses islands, Europa was sampled in 1997 ($n = 24$) and again in 2003 ($n = 9$), for a total of 33 samples; Tromelin ($n = 44$), Juan de Nova ($n = 20$) and Glorieuses ($n = 39$) were sampled, respectively, in 1997, 1999 and 2004. Mayotte ($n = 41$), Mohéli ($n = 34$), Nosy Iranja ($n = 13$) were sampled in 2004. In the Republic of Seychelles, Aldabra ($n = 31$), Cosmoledo ($n = 26$), and Farquhar ($n = 7$) were sampled in 1996.

Typically, the source of mtDNA for the majority of turtles was either skin or blood. Blood samples were taken from the cervical sinus (*after* Owens & Ruiz 1980) and stored in either lysis buffer or frozen in ACD-B (Becton Dickinson solution). Skin samples were taken from either the neck or flipper region and stored in 20% DMSO (Dimethyl Sulfoxide) saturated salt solution (Dutton 1996). All adult turtles encountered in this study were tagged. In some cases, however, mtDNA was obtained from tissues of dead embryos or hatchlings found in the bottom of hatched-out nests (Mortimer & Day 1999) with only one sample per clutch and per female to avoid resampling the same matriline.

Mitochondrial DNA control region extraction, amplification and sequencing

DNA was extracted from small amounts of blood (20 µL) or tissue (0.1 g) by overnight digestion at 56 °C in a 1x TE buffer, proteinase K (0.5 mg/mL) and SDS (0.01%) solution. Digested proteins and cellular material were salted out by centrifugation (17 000 *g* for 20 min at 4 °C) in the presence of Ammonium acetate. The DNA was subsequently pelleted by adding 1 volume of cold EtOH to the supernatant and further centrifugation (13 000 r.p.m. for 20 min at 4 °C). Residual salts were removed by rinsing the DNA pellet twice with 100% and 70% EtOH wash, respectively. The DNA was resuspended in 1x TE buffer. An alternative rapid protocol was also used and involves a proteinase K (0.2 mg/mL) digestion in 0.5 mL of 1x TE buffer and 5% Chelex (Biorad) solution for 4–12 h at 55–60 °C with frequent vortexing. The suspension was heated at 95 °C for 5 min and then centrifuged for 5 min at 13 000 r.p.m. The supernatant was collected and used as template for subsequent polymerase chain reaction (PCR) amplifications.

A portion (~396 bp) of the mtDNA control region was amplified by PCR using the TCR-5 (5′-TTGTACATTACTT-ATTTACCAC-3′) and TRC-6 (5′-GTACGTACAAGTAA-AATACCGTATGCC-3′) primers (Norman *et al*. 1994). Amplifications were performed in a total volume of 25 µL containing 5–50 ng of whole DNA, 10 mM of each dNTP, 10 µM of each primer, 0.5 U of high fidelity Advantage 2 polymerase mix (BD Biosciences) and the corresponding reaction buffer (1x). Cycling parameters were 93 °C for 1 min, followed by 35 cycles at 93 °C for 40 s, 55 °C for 50 s, and 72 °C for 40 s, and a final extension at 72 °C for 2 min (FitzSimmons *et al*. 1997a). Amplification was verified by electrophoresis of 4 µL of each reaction in a 1% agarose gel, together with a 100-bp DNA ladder (New England Biolabs).

Products were purified with the SEQueasy Kleen Kit (Biorad) and run through a 3730XL sequencing analyser (Applied Biosystems). The sequencing reactions (forward and reverse) were performed with dye terminators (BigDye 3.1, Applied Biosystems) on a Primus 96 thermocycler (MWG Biotech).

Data analysis

Sequence alignments were performed with the software CLUSTAL W (Thompson *et al*. 1994). Neighbour-joining analysis (Saitou & Nei 1987) was implemented with the NEIGHBOUR procedure of the program PHYLIP 3.5 (Felsenstein 1993). Bootstrap analysis was computed using of the SEQBOOT (500 replicates) and CONSENSE procedures from the PHYLIP package. The neighbour-joining tree was drawn with the software TREEVIEW 1.5 (Page 1996).

Differentiation between populations was assessed with Wright's fixation index F_{ST} (10 000 replicates; Wright 1951), estimated by θ (Weir & Cockerham 1984) with the GENETIX 4.02 software package (Belkhir *et al*. 2001). This software was also used to estimate the number of migrants per generation (Nm). AMOVA (analysis of molecular variance approach, Excoffier *et al*. 1992) was performed using ARLEQUIN version 2.0 (Markov chain length: 10 000; Schneider *et al*. 2000) to examine genetic structuring among rookeries and among different groups of regional rookeries.

Correlation between genetic (measured as $F_{ST}/(1 - F_{ST})$ following Rousset 1997) and geographical distance matrices was tested with a Mantel nonparametric permutation test (Mantel 1967) as implemented in GENETIX 4.02. The geographical distances between the different nesting sites corresponded to the shortest sea distance between rookeries.

Results

Mitochondrial DNA polymorphism

A total of 40 polymorphic sites were found (Table 2) corresponding to 39 substitutions, one insertion and one deletion. Seven mtDNA haplotypes were observed among the 288 green turtles sampled from 10 rookeries in the southwestern Indian Ocean (Table 1 and Fig. 1A). Six of the seven haplotypes described here have been found elsewhere: CM8 (GenBank Accession no. Z50130) occurs in South Atlantic and West African Rookeries (Encalada *et al*.

Table 2 Polymorphic sites corresponding to the seven green turtle haplotypes detected in the Southwest Indian Ocean from a 396-bp fragment of mtDNA control region sequence

Base positions	32	45	71	82	87	88	89	92	93	95	108	109	110	111	112	135	136	146	147	149
Haplotypes																				
Glo33	T	C	A	G	T	A	C	T	C	G	A	A	T	A	C	G	G	C	T	T
May23	T	C	A	A	T	A	C	T	T	G	A	A	G	A	C	G	G	C	T	T
D2	T	C	A	G	T	A	C	T	T	G	A	A	G	A	C	G	G	C	T	T
CM8	T	C	G	A	T	G	C	C	T	G	A	A	G	C	T	A	A	C	C	C
A2	C	C	A	A	C	G	T	T	T	A	G	G	A	A	C	G	A	C	C	C
A1	C	—	A	A	C	G	T	T	T	A	A	G	A	A	C	A	A	T	C	C
C3	T	C	A	G	T	A	C	T	T	G	A	A	G	A	C	G	G	C	T	T

Base positions	151	153	155	163	222	226	236	248	290	307	328	329	336	343	344	345	347	353	359	360
Haplotypes																				
Glo33	A	C	A	C	C	A	A	G	A	T	A	T	A	T	G	G	T	A	C	—
May23	A	C	A	C	C	A	A	G	A	T	A	T	A	T	G	G	T	A	C	—
D2	A	C	A	C	C	A	A	G	A	T	A	C	A	T	G	G	T	A	C	—
CM8	G	T	G	T	T	G	C	G	G	C	G	T	A	T	A	A	T	G	T	T
A2	A	T	G	T	T	A	A	A	A	T	A	T	G	C	A	A	T	A	C	—
A1	A	T	G	T	T	A	A	A	A	T	A	T	G	T	A	A	C	A	C	—
C3	A	C	A	C	C	A	A	G	A	T	A	T	A	T	G	G	T	A	C	—

1996) and is the first time this variant has been found in the Indian Ocean. Haplotypes C3, D2, A1 and A2 are known to occur in several other rookeries throughout the Indo-Pacific (Dethmers *et al*. submitted; GenBank Accession nos AY955204, AY955205, AY955215 and AY955219, respectively). May23 haplotype was found in the Comoros (Formia 2002) and registered in GenBank as Accession no.. AF529030. A new haplotype is described here for the first time: Glo33 (GenBank Accession no. DQ256086).

The observed seven haplotypes differed by between one and 25 substitutions, corresponding to 0.3–6.5% (mean = 4.2%) estimated sequence divergence. The neighbour-joining tree of the seven haplotypes (Fig. 2) identified three distinct clades of haplotypes: clade 1 (CM8 alone), clade 2 (including A1 and A2) and clade 3 (including C3 and the rare haplotypes May23, D2 and Glo33). The new haplotype Glo33 forms a clade with common C3 haplotype and differs by only two substitutions.

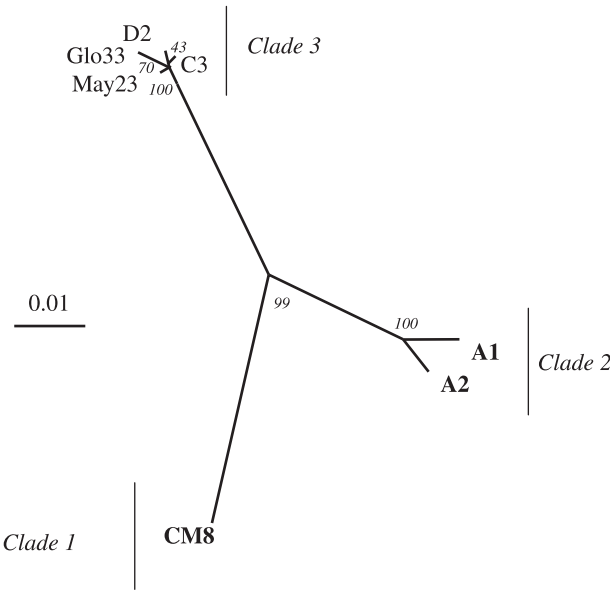

Fig. 2 Neighbour-joining tree based on the mtDNA control region sequences. Bootstrap values (500 replicates) are indicated on the branches. Three clades of haplotypes were identified, called, respectively, 1, 2 and 3. Haplotype Cm8 is nested in the Atlantic Ocean clade B of Encalada *et al*. (1996). Haplotypes A1 & A2 and haplotypes C3 & D2 are nested in the Indo-Pacific Ocean clades V and I, respectively, of Dethmers *et al*. (submitted).

Within-population diversity

Within-population diversity range from one haplotype at Nosy Iranja ($n = 13$) to six (haplotype diversity: $h = 0.3708$; Table 1) at Mohéli ($n = 34$; Table 1 and Fig. 1A). The northern (NMC-Tromelin) regional set of rookeries has higher levels of haplotypic heterogeneity (mean 3.3 haplotypes, $h = 0.3723$) compared to those from the south (SMC, mean 2.5 haplotypes, $h = 0.3425$). All seven haplotypes were found in the NMC rookeries, with C3 at high frequencies, A2 at intermediate frequencies and several rarer haplotypes (CM8, May23, D2, A1 and Glo33). In contrast for the SMC, only three haplotypes were found in Juan de Nova ($h = 0.5632$; CM8 at high frequency, C3 at intermediate frequency and a single occurrence of haplotype

Table 3 Genetic differentiation (F_{ST}) between the 10 locations sampled in the Southwest Indian Ocean (above diagonal) and estimation of the number of migrant per generation (*Nm*; below diagonal). The significance of permutation test (10 000 permutations) are shown for $P < 0.05$ (*) and $P < 0.001$ (**)

F_{ST} *Nm*	Europa	Juan de Nova	Nosy Iranja	Mayotte	Mohéli	Glorieuses	Cosmoledo	Aldabra	Farquhar	Tromelin
Europa		0.3030*	0.9113**	0.6465**	0.7343**	0.7497**	0.7125**	0.7388**	0.7368**	0.8031**
Juan de Nova	1.22		0.5831**	0.3151**	0.4160**	0.4502**	0.5280**	0.3757**	0.4189**	0.5280**
Nosy Iranja	0.03	0.19		0.0793	0.0406	0.0842	0.1742	0.078	0.5011*	0.0466
Mayotte	0.13	0.49	4.46		−0.0106	−0.017	0.0304	0.004	0.1473*	0.0326
Mohéli	0.09	0.32	14.97	∞		−0.0023	0.0374	−0.0111	0.2027*	0.0023
Glorieuses	0.08	0.27	5.07	14.97	∞		0.0035	−0.0112	0.1604	−0.0118
Cosmoledo	0.1	0.39	1.52	7.03	6.43	70.41		−0.0001	0.0124	0.0425
Aldabra	0.09	0.32	4.6	89.66	∞	∞	∞		0.1317	0.0014
Farquhar	0.09	0.54	0.34	1.39	0.98	1.09	19.98	1.65		0.2911*
Tromelin	0.06	0.2	10.17	7.12	106.43	∞	5.63	173.86	0.61	

A2; Table 1) and only two haplotypes were found in Europa ($h = 0.1174$; CM8 in high frequency and C3 in low frequency). Nucleotide diversities on the other hand were similar in both the NMC and Tromelin ($\pi = 0.0184$) and SMC ($\pi = 0.0221$) because most rookeries are comprised of a mixture of divergent haplotypes.

Differentiation among nesting sites population structure

Tests for population differentiation were estimated using Wright's fixation index (F_{ST}) based on haplotype frequency. Results are presented in Table 3. Comparisons between SMC rookeries (Europa and Juan de Nova) and all other rookeries were highly significant [$F_{ST} = (0.307–0.912)$; $P < 0.001$]. There is also a significant differentiation inside SMC between Europa and Juan de Nova populations ($F_{ST} = 0.303$; $P < 0.05$). Farquhar has a small sample size but it is also slightly but significantly differentiated from most other NMC rookeries [$F_{ST} = (0.147–0.501)$; $P < 0.05$] with the exception of Glorieuses, Cosmoledo and Aldabra [$F_{ST} = (0.160–0.012)$; $P = (0.066; 0.340)$]. But all comparisons among the NMC rookeries excluding Farquhar were not significant [$F_{ST} < 0.17 - P = (0.056; 0.610)$]. Comparisons between pooled NMC rookeries and Tromelin were also statistically insignificant [$F_{ST} < 0.0466 - P = (0.081; 0.558)$]. We therefore recognize two genetic stocks in SMC (Europa and Juan de Nova) and a single genetic stock in the NMC comprising Aldabra, Cosmoledo, Glorieuses, Nosy Iranja, Mohéli, Mayotte, Farquhar and Tromelin.

The screening of mtDNA variation shows a frequency shift of haplotypes from Europa to Tromelin Atolls. The CM8 haplotype is the most common in the SMC (Europa and Juan de Nova) whereas the C3 haplotype is most frequent in the NMC (Seychelles, Nosy Iranja, Mohéli, Mayotte and Glorieuses) and in Tromelin. The change in frequency of the CM8 haplotype from south to north Mozambique Channel is particularly informative. It is nearly fixed at Europa (94%), dominant at Juan de Nova (55%), present at Mayotte (12%), rare at Mohéli (3%) and is absent from the other NMC rookeries surveyed (Fig. 1A).

Estimates of gene flow (Table 3) show that there is little exchange between SMC and NMC rookeries ($Nm < 1$) compared to exchange among rookeries within each of these regions (typically $Nm > 1$). There was some evidence for restricted gene flow between Farquhar and some of the more distant rookeries within the NMC rookeries [$Nm = (0.34–1.65)$] compared to the closest rookery Cosmoledo ($Nm = 19.98$).

AMOVA was used to compare four hypotheses about hierarchical structuring among Southwest Indian Ocean rookeries (Table 4). The first model (GP1) had two groups, all the NMC rookeries and all the SMC rookeries. The second model (GP2) had three groups, Farquhar, the remainder of the NMC rookeries and SMC rookeries. The third model (GP3) had three groups, Europa, Juan de Nova and all the NMC rookeries. The fourth model (GP4) had four groups — Europa, Juan de Nova, Farquhar and the remainder of the NMC rookeries. According to among-group variance (F_{CT}) component test results, all four models were statistically significant but the GP3 model explained the highest among group variance (F_{CT}) and is consistent with our earlier identification of just three genetic stocks within this region.

We used a Mantel test to determine if the observed patterns of population genetic structure were consistent with a one-dimension isolation-by-distance model (Fig. 3) and found a significant correlation ($P < 0.001$, $R^2 = 0.3565$; slope = 0.002) between genetic and geographical pairwise distance measures. Concerned that the divergent SMC rookeries might be driving this pattern, we ran the same model without Europa and Juan de Nova and found no correlation between the genetic and geographical distance measures ($P = 0.147$; $R^2 = 0.018$; slope = 0.00004).

Table 4 Analysis of molecular variance (AMOVA) results for the Southwest Indian Ocean groups of green turtle nesting sites. AG is the among-groups component variance; AP/WG is the among-populations/within-group component of variance; WP is the within-population component of variance. The significance of permutation test (10 000 permutations) are shown for $P < 0.05$ (*), $P < 0.01$ (**) and $P < 0.001$ (***)

Name	Grouping scheme	Variance component	% of variance	*F* statistics
GP1		AG	55.84	$F_{CT} = 0.55835$*
Group 1	Europa — Juan de Nova	AP/WG	2.9	$F_{SC} = 0.06562$*
Group 2	Other islands	WP	41.27	$F_{ST} = 0.58733$***
GP2				
Group 1	Europa — Juan de Nova	AG	53.96	$F_{CT} = 0.53959$*
Group 2	Farquhar	AP/WG	2.43	$F_{SC} = 0.05272$*
Group 3	Other islands	WP	43.61	$F_{ST} = 0.56388$***
GP3				
Group 1	Europa	AG	57.18	$F_{CT} = 0.57178$*
Group 2	Juan de Nova	AP/WG	1.46	$F_{SC} = 0.03413$*
Group 3	Other islands	WP	41.36	$F_{ST} = 0.58640$***
GP4				
Group 1	Europa	AG	55.65	$F_{CT} = 0.55653$**
Group 2	Juan de Nova	AP/WG	0.76	$F_{SC} = 0.01720$
Group 3	Other islands	WP	43.58	$F_{ST} = 0.56416$***
Group 4	Farquhar			

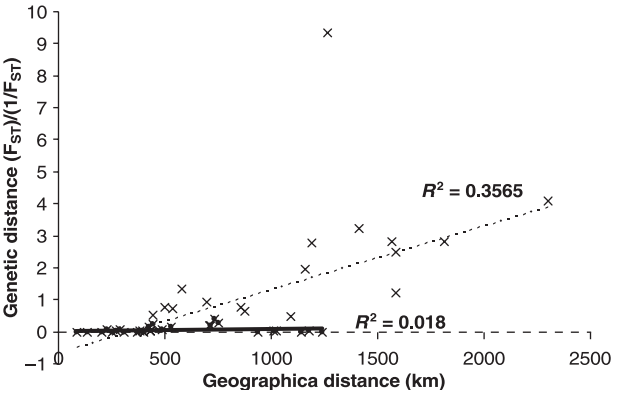

Fig. 3 Regression of genetic distances, $F_{ST}/(1\text{-}F_{ST})$, vs. geographical distances (km) in the 10 green turtle nesting sites sampled for mitochondrial DNA data. Regressions were performed with (×) and without (●) Europa and Juan de Nova.

Discussion

Evidence for gene flow around the Cape of Good Hope

Most of the haplotypes identified in this study conform to expectations and occur elsewhere in Indo-Pacific Oceans rookeries (Dethmers *et al*. submitted) or are novel and occur in low frequency. The remarkable discovery of an Atlantic Ocean haplotype (CM8 Encalada *et al*. 1996) represents the first time that any Atlantic Ocean haplotype has been recorded among any Indo-Pacific nesting populations. The observation of this Atlantic variant mixed with Indo-Pacific haplotypes in a same rookery (Table 1) reinforces the fact that Atlantic and Indo-Pacific lineages are not cryptic species. Until now, several green turtle genetic studies have shown that there is a fundamental phylogenetic split distinguishing all green turtles in Atlantic Ocean and the Mediterranean Sea from those in Indian and Pacific Oceans (Bonhomme *et al*. 1987; Avise *et al*. 1992; Bowen *et al*. 1992). Because of prevailing cold water conditions, the Cape of Good Hope has been commonly assumed to be an absolute barrier to the mixing of Atlantic and Indo-Pacific populations of green turtles but it has not been an impermeable barrier to all tropical species (Briggs 1974).

Had Bowen's *et al*. (1995) total mtDNA study surveyed populations from the Southwest Indian Ocean, they would have found the same remarkable pattern despite the present studies enhanced power using mtDNA sequence data. Using microsatellite data Roberts *et al*. (2004) demonstrated recent or ongoing male-mediated gene flow among populations within Indian and Atlantic Ocean Basins. Although their study did not include samples from the Southwest Indian Ocean it did provide compelling evidence that at least the occasional male was capable of rounding the Cape of Good Hope. Our study of Southwest Indian Ocean rookeries demonstrates for the first time a recent matrilineal link between Atlantic and Indian Ocean green turtle populations. The observation that an Atlantic mtDNA haplotype occurs in adjacent Indian Ocean waters and not vice versa is a significant observation, as it indicates that the direction of matrilineal gene flow is likely to be from the Atlantic to the Indian Ocean. Likewise, the observation that only a single Atlantic haplotype has been

observed and that it occurs in high frequency among SMC rookeries suggests that gene flow is not ongoing. If the Indian and Atlantic Oceans were connected by substantial amounts of contemporary gene flow then we would expect to detect additional Atlantic haplotypes in the SMC. If the colonization event was more ancient then we would expect to have detected novel variants of the CM8 haplotype with our intensive sampling of the SMC region.

A growing number of studies document an Indian and East Atlantic phylogeographical connection in different marine species, like bigeye tuna (Chow *et al*. 2000; Durand *et al*. 2005), hammerhead sharks (Duncan *et al*. 2006), trumpetfishes (Bowen *et al*. 2001) and the urchin diadema (Lessios *et al*. 2001). Almost all cases of marine dispersal in this region are from the Indian to the Atlantic Ocean, usually attributed to passive drift by larvae in the Agulhas Current. However, in a recent study on hammerhead shark (*Sphyrna lewini*), Duncan *et al*. (2006) showed a connection between these two oceans. The authors strongly support that the Indo-West Pacific hammerhead shark haplotypes most closely related to the Atlantic lineage are the product of a recent dispersal from the Atlantic into the Indo-Pacific, and that gene flow in this opposite direction is possible because this species is an active swimmer at every life stage (Duncan *et al*. 2006). Green turtles are also active swimmers at every life stage and may present the second example of active dispersal from the Atlantic into the Indian Ocean.

Regional differentiation

The analysis of the genetic variability of nesting turtles in the Southwest Indian Ocean shows a significant population differentiation between those in the SMC including Europa and Juan de Nova, and the remaining nesting sites that were sampled in the NMC including Mohéli, Mayotte, Glorieuses, Nosy Iranja, Seychelles and Tromelin (Fig. 1A, Table 3). For example, there is a high genetic differentiation (F_{ST} = 0.646, Table 3) between Europa and Mayotte although the two populations are less than 1200 km apart. Inside SMC, there is a significant population differentiation between Europa and Juan de Nova. Our data also show that Farquhar may be differentiated from both rookeries in the NMC (excluding Cosmoledo) and Tromelin (Table 3). This result must be taken with caution as the sample size of Farquhar is small (n = 7) due to the limited number of nesting females present at this remote island when the survey was conducted. However, more intensive sampling may not necessarily lead to the identification of further population genetic structuring here as the well sampled and more distant comparisons of Tromelin and pooled SMC rookeries were also insignificant.

It is rare to see such clear patterns of isolation by distance (IBD) in marine turtles even though it is expected in a species that has natal homing. Our results showed a pattern of IBD (Fig. 3) when run on the entire data set. However there was no relationship between genetic and geographical distance for comparisons among rookeries in the NMC and Tromelin. The decreasing frequency of the CM8 variant from SMC rookeries to NMC rookeries points to IBD operating within the Mozambique Channel but not among rookeries in the rest of the Southwest Indian Ocean. This pattern is consistent with a colonization process whereby rookeries closest to the Atlantic Ocean source populations (e.g. Europa) receive more immigrants than those more distant (e.g. Juan de Nova). In subsequent generations, migration and possible selection could act to further disperse the CM8 lineage throughout the Mozambique Channel beyond the initial founder populations.

Data from turtle tagging studies in the Mozambique Channel (Hughes 1982; Le Gall & Hugues 1987) are consistent with the general observation that most nesting turtles migrate less than 1000 km between breeding and foraging habitat; although distances greater than 2600 km have been recorded for sea turtles (Miller 1997). These observations indicate that the length of the Mozambique Channel is not a biological barrier during the migration of adult turtles. As highlighted by Pelletier *et al*. (2003), we suggest that the unique and unusual oceanography in the Mozambique Channel may contribute to the green turtle population structure observed in the Mozambique Channel, influencing particularly the early stages in the life cycle of green turtles.

Oceanography in the Mozambique Channel

At the seabird nesting islands in the Mozambique Channel, studies have shown that subspecies of *Phaethon lepturus* (Le Corre & Jouventin 1999), *Puffinus lherminieri* (Le Corre 2000b) and *Sula sula* (Le Corre (1999), nesting in Europa (South Mozambique Channel), have phenotypic patterns that differ from the equivalent species nesting in other islands of the Indian Ocean. Le Corre (1999); 2000a, b) suggested that few successful exchanges of individuals occur between the North and South Mozambique Channel and that Europa seabird populations are isolated from the other nesting colonies of the Indian Ocean. This biogeographical pattern may be linked to oceanic conditions in the Mozambique Channel particularly at the south end where there is a peculiar pattern of sea-surface temperatures (Le Corre 2000b).

Several authors have already emphasized the unusual oceanic conditions that occur in the southern Mozambique Channel, where there is an increase of sea-surface temperature (Piton *et al*. 1981), the occurrence of meanders (Lutjeharms *et al*. 1981; Donguy & Piton 1991), and a convergence zone between different currents (Piton & Magnier 1976; Piton & Laroche 1993). Recent studies in the Mozambique Channel showed that the average drift in the

southern part is a dynamic area swept by an intermittent train of large anticyclonic eddies (~200 km in diameter) leading to a southward transport along the African coast (Lutjeharms *et al*. 2000; De Ruijter *et al*. 2002; Schouten *et al*. 2003; Quartly & Srokosz 2004; Fig. 1B. These currents are likely to play a role in hatchling dispersal as they spend the first few years of their life in oceanic waters (Carr 1987). Hatchlings emerging from nests south of the Mozambique Channel should drift southward. On the western side of the Mozambique Channel, oceanic movement consists of strong anticlockwise eddies (De Ruijter *et al*. 2002), whereas on the eastern side the flow is weak and variable. In the northern part of the Mozambique Channel, the flow seems to be quite variable, but on average may consist of an anticlockwise gyre in the Comoro Basin (Lutjeharms 2005). The South Equatorial Current carries water westward in North of the Comoros, but part of this will go south into the Mozambique Channel, part northward as the East African Coastal Current (Fig. 1B; Schouten *et al*. 2003). As Girard *et al*. (in press) have showed that currents around Europa act as a constraint for adult green turtles, one theory would be that juveniles from the NMC do move part northward and part southward, but are mostly retained in this way in the intense western Mozambique Channel eddies. This would mean that they would only occasionally pass close to Juan de Nova and on the whole would not reach Europa Island. A test for this theory would come from the haplotypes found at the Mozambique and southwest Madagascar coasts: if these have Indo-Pacific genetic characteristics, the unusual characteristics at Europa Island would be a localized exception.

Those oceanic elements may contribute to the green turtle genetic structuring in the Mozambique Channel, slowing down the exchanges between these two opposite zones. Further studies are needed to fully elucidate the genetic structure of green turtles nesting along the Mozambique Channel and to distinguish the relative importance of ongoing oceanographic processes from historical patterns of colonization. An expanded study incorporating rookeries from the East African coast, and eastern and southwestern coasts of Madagascar will help us to better understand the mechanisms responsible for structuring among NMC-Tromelin and the SMC green turtle populations. Of particular interest would be the relationships between genetic characteristics of the nesting green turtles, oceanography and seasonality of nesting. For instance, do nesting green turtles in Mozambique coast, at the same latitude of Europa (22°21′S), have the same mtDNA genetic structure as those nesting at Europa?

Green turtle management units

Several rookeries of the Southwest Indian Ocean are important nesting sites for green turtles (Frazier 1984; Mortimer 1984, 1988; Le Gall 1988; Van Buskirk & Crowder 1994; Mortimer & Day 1999). Genetic analysis of sea turtle population structure can provide an essential management tool to identify genetically distinct management units (MUs) within a region (Dizon *et al*. 1992; Moritz 1994). Our genetic data suggest that rookeries of green turtles in Europa, Juan de Nova and the NMC-Tromelin belong to three separate genetic populations and should be considered as independent MUs. Our inability to differentiate Tromelin from other NMC rookeries most likely reflects the limitations of a single locus marker and a recent shared history rather than ongoing gene flow.

The genetic markers we have characterized for each MU are suitable for assessing stock composition in regional harvested and resident populations of green turtle. The assessment of multiple harvests and feeding assemblages throughout this region will help to define the geographical extent of migration and threatening processes that impact on green turtle populations. The delineation of management areas for each MU relies on a combination of tag returns, satellite tracking and genetic analysis of foraging and harvested populations all of which are currently being evaluated for this region.

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