

# 14 *Population genetic structure and developmental migrations of sea turtles in the Chagos Archipelago and adjacent regions inferred from mtDNA sequence variation*

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Patterns of mitochondrial DNA variation were used to determine genetic relationships among hawksbill (*Eretmochelys imbricata*) and green turtle (*Chelonia mydas*) populations in the Chagos Archipelago (Central Indian Ocean) and those in three adjacent localities: the Republic of Seychelles, the Arabian Peninsula, and western Australia. Nesting hawksbills in Seychelles and Chagos are both characterized by high frequency mtDNA variants not recorded elsewhere in the world and differ from each other by significant haplotype frequency shifts. The few nesting green turtles sampled from Chagos had haplotypes shared with green turtle populations in both the eastern and western Indian Ocean but distinct from those in the Arabian Peninsula.

Populations of foraging juvenile hawksbill turtles from the Chagos and Seychelles could not be genetically differentiated from each other and their pooled mtDNA frequencies are not significantly different from either Seychelles or Chagos rookeries, but are more similar to Seychelles rookeries. Notably, none of the haplotypes observed in western Australian rookeries were detected in these foraging populations. These data indicate that Seychelles is a major source of juveniles in both Seychelles and Chagos foraging populations but the possibility of Arabian Peninsula or other unsampled stocks in the region also making significant contributions cannot be precluded. Additional samples from both hawksbill and green turtle rookeries in the Chagos are needed to elucidate these patterns.

## INTRODUCTION

The Chagos Archipelago, Central Indian Ocean (5°13'–17°27'S; 71°16'–72°30'E) hosts significant populations of nesting hawksbill (*Eretmochelys imbricata*) and green turtles (*Chelonia mydas*) (Mortimer & Day, Ch. 12, this volume). Both green and hawksbill turtles conform to generalised marine turtle life histories. Each nesting season, turtles migrate from resident foraging grounds, often long distances away, to breed at natal regions (Limpus *et al.*, 1992; Meylan, 1982). The average female lays several egg

clutches during a season, returning to nest at intervals of two, three or more years (Hirth, 1971; Witzell, 1983; Mortimer & Bresson, 1999). After incubation, hatchlings emerge *en masse* and disperse into pelagic habitat. This pelagic phase is thought to last for several years and to involve the circumnavigation of entire ocean basins (Carr, 1982, 1987; Bowen *et al.*, 1995; Lahanas *et al.*, 1998; Bolten *et al.*, 1998) such as the Indian Ocean.

After the pelagic phase, juvenile turtles take up residence in shallow water habitat which may be hundreds or thousands of kilometres from where they were born (Carr, *et al.*, 1978; Broderick *et al.*, 1994; Lahanas *et al.*, 1998). Turtles may shift habitats as they develop but tagging studies indicate they find a permanent residence upon maturity, from which adult turtles migrate back to their natal nesting beaches to breed. This life history, which encompasses a large geographic spread, can result in nesting populations comprising animals from multiple foraging populations (Carr *et al.*, 1978; Mortimer & Carr, 1987). Conversely, each foraging population can comprise turtles from several nesting populations (Carr, 1975; Broderick *et al.*, 1994; Lahanas *et al.*, 1998). Effective management of sea turtles is further complicated by extensive migrations which often cross international boundaries. The relationship between the migrations and genetic affinities of the sea turtles inhabiting Chagos and those elsewhere in the region are of particular interest given the isolation of Chagos in the Central Indian Ocean, approximately 3200 km south of the Arabian Peninsula, 2000 km east of the Granitic Seychelles, and 5100 km west of Australia. While the abundant coral reefs in Chagos provide ample foraging habitat for hawksbills, marine angiosperm pastures where green turtles typically forage are sparse (Mortimer & Day, Ch. 12, this volume).

This study uses mtDNA to elucidate the genetic relationship between the breeding and foraging populations of sea turtles in the Chagos Archipelago with those at key localities elsewhere in the region to: i, determine whether nesting sea turtle populations of Chagos have a stronger affinity to those of the western Indian Ocean, western Australia, or the Arabian Peninsula; ii, determine the stock composition of juvenile foraging populations; and iii, suggest possible mechanisms to explain patterns observed.

## MATERIAL AND METHODS

### *Sample Collection*

From nesting hawksbills, a total of 127 genetic samples were collected at the following sites: Chagos Archipelago (Diego Garcia, n=3; Peros Banhos atoll, n=5; and Salomon atoll, n=1), obtained for this study, and Seychelles (n=73), Saudi Arabia (n=14), and western Australia (n=31) representing samples collected for a global analysis (Broderick *et al. in prep.*). From foraging hawksbills, a total of 241 samples were collected at Chagos (Diego Garcia, n=40; Peros Banhos, n=4; Salomon atoll, n=5; and Chagos Bank, n=1) and Seychelles (n=191). Nesting green turtle samples collected at Chagos (Salomon atoll, n=1; Danger Island, n=1; and Nelson Island, n=1) were compared with five other key breeding localities in the Indian Ocean: Seychelles, Arabian Peninsula, Tromelin Island, Europa atoll, and western Australia (Broderick *et*

*al.*, unpublished data). From foraging green turtles, only a single sample was collected in the Chagos (Diego Garcia,  $n=1$ ). Typically the source of mtDNA for the majority of turtles was either skin (preserved in a 20% DMSO solution saturated with salt) or blood (stored whole in lysis buffer *after* Bowen *et al.*, 1996). In some cases however, mtDNA was obtained from tissues of dead embryos or hatchlings found in the bottom of hatched-out nests (Mortimer & Day, Ch. 12, this volume) with due care taken to sample only one clutch per female to avoid resampling the same matriline.

### *Molecular Methods*

Small amounts of tissue or blood (typically 0.1 g) were digested overnight in a 1xTE, Proteinase K (0.5mg/ml) and SDS (0.001%) solution. Digested proteins and cellular material were 'salted out' by centrifugation in the presence of 3.5M AmAc @ 4°C, the supernatant (containing DNA) was subsequently pelleted with the addition of cold EtOH and further centrifugation. Templates for polymerase chain reaction (PCR) procedures were obtained by resuspending the DNA pellet in a 1xTE and 5% chelex solution. A segment of the mtDNA control region was amplified using TCR5 and TCR6GC primers (modified after Norman *et al.* (1994) with the latter primer containing a 41bp GC clamp). Typically, 1–2 µl of template was used in 25 µl PCR reactions using standardized conditions (denaturing @ 94°C - 10s, annealing @ 54–56°C - 30s and extension @ 72°C - 40s for 32 cycles).

Individuals were either sequenced manually ( $P^{33}$  labeled cycle sequencing) or with an ABI 373A automated sequencing machine following standardized protocols; and some samples were sequenced using both methodologies to validate results. Sequences were aligned using Clustal IV (Higgins *et al.*, 1992) and estimates of nucleotide diversity and divergences were calculated using REAP (McElroy *et al.*, 1992). Several tests were used to examine genetic structure among populations: I, Chi-square tests with 10000 replicates (Roff & Bentzen, 1989); II, Exact Tests (Raymond & Rousset, 1995); and III, AMOVA (Excoffier *et al.*, 1992). The last two tests were conducted using the genetic software package Arlequin 1.1 (Schneider *et al.*, 1997).

To process the large number of samples, we developed (Norman *et al.*, 1994; Broderick, in prep.) a rapid yet sensitive screening protocol using denaturant gradient gel electrophoresis (DGGE) to detect DNA polymorphisms. This technique uses the melting behaviour of DNA fragments to detect genetic site substitutions. The standard application of this technique detects some, but not all, single base pair changes. The sensitivity of this technique was increased by using heteroduplex analysis which hybridises candidate DNA variants with known sequence variants in a process of heating and cooling. When hybrids are re-run on a DGGE gel, any differences in genetic composition between the control and candidate DNA will produce multiple fragments (heteroduplexes) of differing mobilities. An advantage of this method over PCR-RFLP analysis (but see Abreu-Grobois *et al.*, 1996) lies in its ability to detect, with greater sensitivity, new as well as known mtDNA variants. The screening strategy we employed was to: I, score samples relative to the mobility of known mtDNA control variants in a size marker; II, confirm their identity using heteroduplex analysis; and III, sequence representatives from each genotype/locality combination for final verification and to test sensitivity.

## RESULTS

*Nesting Turtles**Hawksbill Turtles*

Genetic assessment of 127 nesting hawksbill turtles across four Indian Ocean populations revealed ten mtDNA variants shown in Table 1. These mtDNA variants (A1, A6, A7, B3, B10 and E1-5) fall into three distinct clades each separated by an average of 3–4% sequence divergence (Broderick, *in prep.*; Broderick *et al.*, 1994). The E1-5 variants are unique to turtles nesting in the Seychelles and Chagos Islands not having been detected in other extensive Indo-Pacific (Broderick *et al.*, 1994; Broderick & Moritz, 1996) or Atlantic Ocean (Bass *et al.*, 1996; Bass, 1996) genetic surveys. The B3 variant is common in Seychelles and Peninsular Malaysia rookeries but is not found in any other surveyed populations. The A1 variant occurs at a low frequency in the Seychelles (n=2) and was not recorded in the limited Chagos sample, but is fixed in the adjacent Arabian Peninsular population. This variant has an impressively broad distribution occurring at several nesting populations from the eastern Pacific to the western Indian Ocean (Broderick *et al.*, 1994.). All of the mtDNA types found in the Indo-Pacific are distantly related (4–7% sequence divergence) to the mtDNA types found in the Atlantic Ocean (Broderick, *in prep.*).

Average nucleotide divergence among surveyed populations was 2.47% but ranged from 0.39% (Chagos - Seychelles) to 4.24% (Chagos - Australia). High nucleotide divergences (3.79%) were also found between Chagos and Arabian Peninsular populations. Several tests (Chi-squared, AMOVA and Exact tests) for population subdivision all confirmed ( $p < 0.001$ ) that hawksbill turtles nesting at the Seychelles and Chagos

TABLE 1 Distribution of mtDNA variants among (*top*) nesting and (*bottom*) juvenile foraging hawksbill turtles in the Indian Ocean.

LOCATION	A1	A6	A7	B3	B9	B10	E1	E2	E3	E4	E5	W	TOTAL
NESTING													
Chagos							7	1	1				9
Seychelles <sup>†</sup>	2			24			36	10			1		73
Arabian	14												14
W Australia		26	5										31
TOTAL	16	26	5	24			43	11	1		1		127
FORAGING													
Chagos	5			19		1	20	4		1			50
Seychelles <sup>‡</sup>	14			54	1	1	90	23	3	4		1	191
TOTAL	19			73	1	2	110	27	3	5		1	241

<sup>†</sup> Granitic Islands (n=32), Amirantes (n=23), Platte Island (n=13), Farquhar (n=1), Cosmoledo (n=2), Aldabra (n=2)

<sup>‡</sup> Aldabra (n=103), Amirantes (n=63), Providence (n=19), Platte Island (n=6)

Islands are readily distinguishable from all other rookeries sampled in the region. Tests for population subdivision between Seychelles and Chagos revealed that the difference between these two populations is slight. While the results were comparable among tests, those incorporating nucleotide divergences tended to describe more population subdivision than those using frequencies of mtDNA haplotypes alone and is reflected in their range of  $p$  values ( $0.026 < p < 0.058$  and  $0.062 < p < 0.066$ , respectively). The power of these tests however, is hampered by small sample size from Chagos rookeries ( $n=9$ ). In a simulated population that had alleles in the same frequency as Chagos but twice the number of samples, all tests for population subdivision between the Seychelles population became highly significant ( $p < 0.007$ ). Similarly, it is predicted that further sampling of Chagos rookeries will confirm their distinctiveness among nesting populations of hawksbill turtles in the region. Contingent upon further sampling of Chagos rookeries, we recognize that turtles nesting at Chagos belong to a unique stock, effectively isolated from those stocks in the adjacent Arabian Peninsular, Seychelles, and western Australian populations.

### *Green Turtles*

Too few samples were obtained from Chagos ( $n=3$ ) to draw strong conclusions about their genetic affinities among the five other Indian Ocean green turtle nesting populations considered in this study. Nevertheless, the Aa and C3 haplotypes found in one and two individuals respectively, are known to occur in several other rookeries throughout the Indo-Pacific (including Seychelles, Tromelin Atoll, and west Australia) but none of these haplotypes occur among Arabian Peninsular nesters.

### *Juvenile Foraging Hawksbill Turtles*

The majority of the 241 individuals screened in the Chagos and Seychelles juvenile foraging hawksbill populations contained mtDNA variants that are commonly found in adjacent nesting populations (Table 1(*bottom*)). Screening uncovered four mtDNA variants in nine foraging individuals (3.7%) that are not known to occur elsewhere. Chi-square randomisation tests failed to detect any genetic differences among surveyed foraging populations; even differences between pooled Chagos and Seychelles populations were insignificant. The frequencies of mtDNA variants found among combined hawksbill turtles foraging in the Western and Central Indian Ocean differ from all other stocks in the region ( $p < 0.001$ ) except for Chagos ( $p < 0.198 \pm 0.004$ ) and Seychelles ( $p < 0.369 \pm 0.005$ ). Again, these results are contingent on further sampling but it does appear that foraging populations of hawksbill turtles in this area share greater affinities with Seychelles nesters than with those animals nesting in Chagos. Indeed, preliminary maximum likelihood stock analysis (GIRLSYM; Masuda *et al.*, 1991) suggests that the contribution of individuals from Seychelles rookeries into these juvenile foraging populations may be as much as ninety percent. While this implies that offspring from Seychelles rookeries are the major source of recruitment into adjacent foraging populations throughout the surveyed area, it does not exclude the possibility of contributions from adjacent Arabian Peninsular, Chagos, or even other unsampled stocks.

## DISCUSSION

Additional samples from both hawksbills and green turtle rookeries in the Chagos are needed to define patterns of genetic structure in the region more adequately; the following results should therefore be regarded as preliminary. With this caveat, genetic comparisons suggest that: I, nesting hawksbill turtles in Chagos represent a distinct stock that is most similar to Seychelles turtles; II, resident foraging populations of juvenile hawksbill turtles at Chagos and Seychelles are indistinguishable; and III, resident foraging populations in this region appear to be recruited primarily from Seychelles stock. Our sampling of Chagos green turtles is too small to permit statistical analysis; however, they appear to be more closely related to eastern and western Indian Ocean populations than to Arabian Peninsular populations.

The relatively greater contribution of offspring from Seychelles to the foraging populations is consistent with the fact that Seychelles hosts the largest remaining hawksbill nesting population in the western Indian Ocean (Humphrey & Salm, 1996). An estimated 1000–2000 females nested annually in Seychelles in the early 1980s (Mortimer, 1984) and only 300–700 in Chagos in 1996 (Mortimer & Day, Ch. 12, this volume). Significant populations of hawksbills also nest on the Arabian Peninsula, some 600–800 annually in the Sultanate of Oman (Salm *et al.*, 1993; Baldwin & Al-Kiyumi, *in press*), 100 in Saudi Arabia (Ross & Barwani, 1982; Miller, 1989), and perhaps as many as 1000 in Iran (Ross & Barwani, 1982). Recruitment of offspring from Arabian populations some 3000 km to the north may explain the relatively high representation of the A1 haplotype in the Chagos and Seychelles foraging populations (Table 1). On the other hand, although significant numbers of hawksbills nest in western Australia (C. Limpus, *pers. comm.*), the A6 and A7 haplotypes that characterise those rookeries did not contribute at detectable levels to the juvenile foraging populations of either Chagos or Seychelles (Table 1). These findings suggest that in the Indian Ocean, juvenile hawksbills may disperse over distances greater than 2000–3000 km, but less than 5000 km. Bowen *et al.* (1996) documented recruitment to central Caribbean feeding grounds from hawksbill rookeries located hundreds of km away, but not from as far away as Brazil (7000 km). Ultimately, the potential for long range dispersal of juvenile turtles is probably not so limited by distance as by the relationship between ocean currents and the locations of suitable breeding and foraging habitats.

The distribution of mtDNA variants for nesting hawksbill turtles within the Indian Ocean is curious. Individuals from rookeries throughout the area are characterised by mtDNA variants that have both localised and widespread distributions. For example, the majority of hawksbills nesting in Chagos have mtDNA variants with localised distributions (Chagos and Seychelles), while hawksbills nesting in the Arabian Peninsula are fixed for the A1 variant, which commonly occurs in several other rookeries throughout the Indo-Pacific (Broderick & Moritz, 1996). Despite the presence of widespread mtDNA variants, we observed genetic structure among the key localities surveyed, indicative of low or negligible contemporary gene flow. The balance between natal philopatry and long distance dispersal are the key to understanding, and hence reconstructing, the phylogeographic histories of these animals.

The low genetic affinity between populations of hawksbill turtles in the Arabian Peninsula with those in the western and central Indian Ocean is consistent with the

patterns described for corals (Rosen, 1971). Cluster analysis using assemblages of coral species showed geographic groupings in the Arabian area, in the Red Sea, and in the southwest and central Indian Ocean areas, with the Arabian group being the most distinct (Sheppard, 1998). Sheppard (Ch. 5, this volume) also reported that the affinities of the Chagos coral fauna are mainly with the western, rather than the eastern, Indian Ocean, as is the case with hawksbills. Although the reef fishes of Chagos show affinities to communities of both the eastern and western Indian Ocean, like the corals, their greater affinity is with those of the Western Indian Ocean (Winterbottom & Anderson, 1997). Moreover, the high rate of endemism documented for reef fishes of the Arabian Peninsula (Randall & Hoover, 1995) suggests that the factors causing genetic isolation of corals and sea turtles in the region may also affect the fish.

The similarities between the biogeographic patterns of hawksbills and coral species might be explained, in part, by the dependence of hawksbills on coral reefs as primary foraging habitat. Adult hawksbills in the western Indian Ocean (Seychelles) may also engage in relatively limited post-nesting migrations, as evidenced by the lack of international tag returns (Mortimer & Bresson, unpublished data) and the relatively restricted movements observed in post-nesting female hawksbills tracked by satellite telemetry (Mortimer *et al.*, unpublished data). Juvenile hawksbills, on the other hand, may disperse more widely, first as hatchlings that are carried long distances on oceanic gyres, and later when they temporarily settle at remote developmental habitats. Juvenile turtles comprised the foraging animals sampled in the present study, and our data show that while populations throughout the central and western Indian Ocean are genetically indistinguishable from one another, they appear to be recruited primarily from Seychelles breeders. Data from other studies suggest that hatchling green, hawksbill, and loggerhead (*Caretta caretta*) turtles disperse widely within an ocean basin during their post-hatchling pelagic stage, but later settle on benthic foraging habitats located nearer their natal rookeries (Carr, 1986; Bass *et al.*, 1996; Bolten *et al.*, 1998; Laurent *et al.*, 1998).

Corals and fish are, to a large degree, passive dispersers, carried by ocean currents. Isolation has apparently driven the differentiation of faunal groupings, and patterns of ocean currents may enhance or reduce such isolation. Our study suggests that genetic architecture of sea turtle populations is influenced by similar factors that shape coral and fish biogeography. Nevertheless, the ability of sea turtles to migrate (and navigate) long distances, and their potential for long distance dispersal, is also likely to influence their population genetic structure and may account for some of the genetic anomalies that have been recorded.

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