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GLOBAL PHYLOGEOGRAPHY OF THE LOGGERHEAD TURTLE (*CARETTA CARETTA*) AS INDICATED BY MITOCHONDRIAL DNA HAPLOTYPES

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Abstract.—Restriction-site analyses of mitochondrial DNA (mtDNA) from the loggerhead sea turtle (*Caretta caretta*) reveal substantial phylogeographic structure among major nesting populations in the Atlantic, Indian, and Pacific oceans and the Mediterranean sea. Based on 176 samples from eight nesting populations, most breeding colonies were distinguished from other assayed nesting locations by diagnostic and often fixed restriction-site differences, indicating a strong propensity for natal homing by nesting females. Phylogenetic analyses revealed two distinctive matrilineages in the loggerhead turtle that differ by a mean estimated sequence divergence $p = 0.009$, a value similar in magnitude to the deepest intraspecific mtDNA node ($p = 0.007$) reported in a global survey of the green sea turtle *Chelonia mydas*. In contrast to the green turtle, where a fundamental phylogenetic split distinguished turtles in the Atlantic Ocean and the Mediterranean Sea from those in the Indian and Pacific oceans, genotypes representing the two primary loggerhead mtDNA lineages were observed in both Atlantic–Mediterranean and Indian–Pacific samples. We attribute this aspect of phylogeographic structure in *Caretta caretta* to recent interoceanic gene flow, probably mediated by the ability of this temperate-adapted species to utilize habitats around southern Africa. These results demonstrate how differences in the ecology and geographic ranges of marine turtle species can influence their comparative global population structures.

Key words.—Biogeography, *Caretta caretta*, conservation genetics, marine turtles, mitochondrial DNA, phylogeography.

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Marine turtles of the family Cheloniidae encompass an ecological diversity that contrasts with their apparent morphological conservatism. In terms of feeding ecology, the spongivorous hawksbill (*Eretmochelys imbricata*) consumes sessile poriferids that are toxic to most vertebrates (Meylan 1988), the herbivorous green turtle (*Chelonia mydas*) grazes on sea grass and algal pastures (Bjorndal 1985), and the carnivorous loggerhead (*Caretta caretta*) feeds on crustaceans and mollusks (Mortimer 1982). With respect to reproductive ecology, green turtles and hawksbill turtles nest primarily in the tropics, whereas loggerhead turtles nest almost exclusively in warm temperate regions (Pritchard and Trebbau 1984).

To what extent might these and related ecological factors influence the phylogeography of

marine turtle species? In the green turtle (*Chelonia mydas*), continental barriers have been of overriding importance in partitioning phylogenetic lineages (Bowen et al. 1992). Since green turtles are primarily tropical in distribution, the southern extensions of Africa and South America represent prominent barriers to contemporary dispersal. By comparison, the loggerhead has a more temperate distribution, including an Indian Ocean rookery (Natal, South Africa) within 1000 km of the South Atlantic Ocean (Hughes 1974a,b). Given this temperate habitat, southern Africa may have been less formidable as a barrier to interoceanic gene flow in *Caretta caretta* than in the more tropical marine turtle species, a hypothesis that can be tested with molecular genetic data.

Adult loggerheads undertake reproductive migrations that range from tens to thousands of kilometers (Meylan et al. 1983; Hughes 1989; Limpus et al. 1992). Females typically nest on continental coastlines adjacent to warm temperate currents, and tag-recapture studies indicate that nearly all females return to the same nesting beach in successive nesting seasons (Dodd 1988). Major reproductive assemblages are known from the Mediterranean sea as well as the Atlantic, Indian, and western Pacific oceans, but nesting is rare or absent in the central and eastern Pacific (Ross 1982; Frazier 1985). Deraniyagala (1945) described putative subspecies based on subtle morphological differences between Atlantic (*Caretta caretta caretta*) and Indian-Pacific forms (*C. c. gigas*), but recent reviews have questioned these assignments (Pritchard and Trebbau 1984; Dodd 1988). Estimates of age at maturity range from 22–26 yr in the western Atlantic (Klinger and Musick 1995) to 30+ yr in eastern Australia (Limpus 1985).

In recent reports, analyses of maternally transmitted mitochondrial DNA (mtDNA) have proven useful for resolving questions about nesting behavior and population demography in marine turtles. Mitochondrial DNA data can yield information about gene flow over both contemporary and evolutionary timescales, thereby permitting appraisal of present-day philopatry to natal site (Meylan et al. 1990; Allard et al. 1994), historical patterns of global colonization (Bowen et al. 1991, 1992), and deeper evolutionary history (Bowen et al. 1993a). In a survey of regional population structure, the distribution of loggerhead mtDNA lineages among four locations in the southeastern United States revealed two genetic population units, corresponding to nesting beaches in (1) eastern and western Florida and (2) Georgia and South Carolina (Bowen et al. 1993b). These data are consistent with natal homing on a regional scale. Here we assess mtDNA haplotype relationships among nesting colonies on a global scale to resolve recent evolutionary history and patterns of historical dispersal for this temperate marine reptile.

MATERIALS AND METHODS

Between 1987 and 1992, 176 *Caretta caretta* nests were sampled from eight nesting aggregates, including rookeries in Greece, Brazil, South Africa, Oman, Japan, Australia, and two populations in the southeastern United States (table 1; fig. 1). These locations represent most of the ma-

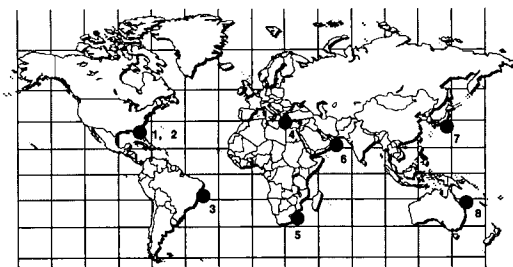


FIG. 1. Collection locales for *Caretta caretta*. The numbers refer to locations in table 1.

ajor nesting concentrations for *Caretta caretta* (Pritchard and Trebbau 1984; Dodd 1988). The nations represented in this survey constitute a subset of target locations for which permit agencies were accessible and receptive to biological research.

Each sample consisted of two eggs from a nest (to offset potential mortality during transportation—loggerhead eggs are highly sensitive to motion during the first few weeks of development [Limpus et al. 1979]), or a single hatchling. Eggs were removed from the nest during laying, transported to the laboratory, and incubated for 4 to 6 wk before processing. Hatchlings were euthanized and processed in the laboratory. Because both full- and half-siblings are expected to be identical with respect to mtDNA genotype, field collections were designed to ensure that no more than one nest per female was sampled.

Closed-circular mtDNA was isolated from whole embryos (eggs) or soft tissues (hatchlings) by CsCl-ethidium bromide density-gradient centrifugation (Lansman et al. 1981). Aliquots of purified mtDNA were digested with the 17 informative restriction enzymes (including four-, five-, and six-base recognition sequences) listed in table 2. In addition, representative samples were digested with *Bam*HI, *Cla*I, *Eco*RI, *Kpn*I, *Nsi*I, *Sac*I, *Sal*I, and *Sma*I, but these enzymes proved to be uninformative, producing either zero or one cut in preliminary tests. Digestion fragments were end-labeled with 35 S nucleotides and separated on 1.0%–1.7% agarose gels. Restriction fragments were visualized by autoradiography and assigned molecular weights through comparison to a 1-kb ladder.

Restriction-fragment profiles were compiled into composite letter codes that represented the observed mtDNA haplotypes. Estimates of nucleotide sequence divergence (p values) were calculated by the “site” approach (Nei and Li 1979).

TABLE 1. Sample locations, rookery sizes, and population information for *Caretta caretta*.

Rookery location	Sample size	Rookery size (females/yr)	Comments
Atlantic Ocean			
1. East and west Florida	29	10,000–25,000	Feeding grounds include the east coast of the U.S., the Bahamas, Gulf of Mexico, and Caribbean Sea
2. Georgia and South Carolina	63	1000–3000	Feeding grounds along east coast of U.S.
3. Bahia, Brazil	11	≈400	
Mediterranean			
4. Kiparissia Bay, Peloponnesus, Greece	21	≈300	Feeding grounds include Italy, Malta, and Tunisia
Indian Ocean			
5. Tongaland, Natal, South Africa	15	300–600	Feeding grounds include Tanzania, Madagascar, Kenya, South Africa, and Mozambique
6. Masirah Island, Oman	8	30,000	Largest rookery in the world; feeding grounds extend to the Horn of Africa, Red Sea, and Gulf of Arabia
Pacific Ocean			
7. Senrigahama Beach, Minabe, Wakayama Prefecture, Japan	15	100–300	Feeding grounds include the eastern China Sea
8. Mon Repos, Queensland, Australia	14	300–600	Feeding grounds include New South Wales, Solomon Islands, Indonesia, Papua New Guinea, and New Caledonia

References: 1, Meylan et al. 1983; Murphy and Hopkins 1984; Conley and Hoffman 1987; Ehrhart and Raymond 1987; 2, Richardson 1982; Murphy and Hopkins-Murphy 1989; 3, M. Marcovaldi pers. comm. 1993; 4, Margaritoulis 1988a,b; 5, Hughes 1974a,b, 1989, unpubl. data; 6, Ross and Barwani 1982; 7, Iwamoto et al. 1985; K. Goto pers. comm. 1993; 8, Limpus 1985; Limpus et al. 1992.

Haplotype diversities were estimated with methods described by Nei and Tajima (1981) and nucleotide diversities with methods described by Nei (1987). Relationships among mtDNA genotypes were assessed by UPGMA clustering (Sneath and Sokal 1973) using a program in the PHYLIP computer software package (version 3.4; Felsenstein 1989) and by an exhaustive search of branching networks using parsimony criteria in PAUP (version 3.1.1; Swofford and Olsen 1990; Swofford 1993). The bootstrapping option in PAUP (with 200 replicates) was used to assess statistical support for nodes in the parsimony network (Felsenstein 1985).

Nesting populations were tested in pairwise comparisons for significant differences in haplotype frequency using the *G* test with Yates' correction (Sokal and Rohlf 1981). Estimates of maternal gene flow among nesting populations (*Nm* values) were obtained using the cladistic approach (Slatkin and Maddison 1989). In cases where no haplotypes were shared between locations, an upper bound on the estimate of *Nm* was calculated with the approach described by

Slatkin (1989). An estimate of average migration rate among assayed nesting colonies was calculated with the private-allele method (Slatkin 1985), using the equation in Slatkin and Barton (1989).

RESULTS

Variation in mtDNA genome size was indicated by concordant differences in the relative mobility of mtDNA fragments across several restriction endonuclease profiles. For example, *SpeI* digests revealed length heterogeneity in an mtDNA fragment of approximately 3.0 kilobases (kb), with different individuals exhibiting homologous fragments ranging from 2.8 to 3.2 kb (fig. 2). Length variants were localized to a single region of the molecule, probably the control region (Bermingham et al. 1986). Because the inheritance of these size variants is uncertain, we excluded size variants from phylogenetic analyses. All subsequent discussion will concern restriction-site variation only.

Based on a mean of 82 restriction sites scored per individual, eight different mtDNA haplo-

TABLE 2. Description and distribution of mtDNA genotypes observed in *Caretta caretta*. Italicized letters refer to mtDNA restriction-fragment profiles produced by (from left to right): *Ava*II, *Bcl*I, *Bgl*I, *Bgl*II, *Bst*EII, *Bst*NI, *Dra*II, *Eco*RV, *Hind*II, *Hind*III, *Msp*I, *Nde*I, *Pvu*II, *Spe*I, *Sst*II, *Stu*I, and *Xba*I. For each enzyme, adjacent letters in the alphabet indicate that fragment profiles differed by a single restriction site gain or loss; nonadjacent letters differed by at least two sites.

Compos- ite code	mtDNA genotype	Rookery location	No. of nests
A	<i>DCCCCCCCCACCCCCBC</i>	Georgia-South Carolina, USA	2
B	<i>DCCCCCCCCBCCCCBC</i>	Georgia-South Carolina, USA	60
		Florida, USA	9
C	<i>DCCCCBCCCBCCCCBC</i>	Bahia, Brazil	11
		Florida, USA	1
D	<i>ACCCDCCCBBCCCCC</i>	Florida, USA	19
		Zakynthos, Greece	21
		Natal, South Africa	15
E	<i>ACCCDCBCBBCCCCC</i>	Georgia-South Carolina, USA	1
F	<i>DCCCCBCCCBCCCCBC</i>	Masirah Island, Oman	8
G	<i>BCCBCDCCCCBCCCCC</i>	Queensland, Australia	14
H	<i>BCCBCDCCCBCCCCC</i>	Wakayama, Japan	15

types were detected among assayed nesting populations (table 2). Digestion profiles are available from B.W.B. Overall haplotypic diversity among surveyed loggerheads was 0.732, slightly lower than the value of 0.874 reported for a comparable global mtDNA survey of green turtles (Bowen et al. 1992). Nucleotide diversity among surveyed specimens was 0.002, essentially identical to the value reported for green turtles. These estimates of mtDNA variation are near the low end of the spectrum of values reported for conspecific comparisons in vertebrates (Avice et al. 1987, 1989). Low levels of genetic variability also have been reported in a protein-electrophoretic survey of loggerhead turtles (Gyuris and Limpus 1988).

All differences among mtDNA restriction profiles could be interpreted as specific site gains or losses. The most prominent topological feature of the mtDNA phylogeny is a relatively deep bifurcation defining two distinct evolutionary lineages (haplotypes A, B, C, and F vs. D, E, G, and H) separated by a mean level of sequence divergence $p = 0.009$ (fig. 3). This divergence is similar in magnitude to the deepest fork observed within an mtDNA phylogeny of the green turtle ($p = 0.007$; Bowen et al. 1992). Representatives of the two primary loggerhead lineages were observed in both the Atlantic and Indian oceans.

On the basis of several restriction-site studies of mtDNA, a molecular clock for marine turtles has been tentatively calibrated at 0.2%–0.4% per my (Avice et al. 1992), a pace that is severalfold slower than conventional estimates for other vertebrate groups (Brown et al. 1979). From these

suspected evolutionary rates for marine turtle mtDNA, the deepest bifurcation in the loggerhead mtDNA phylogeny would be roughly 2–4 my old.

Within the Indian Ocean, samples from South Africa and Oman were fixed for separate haplotypes (D and F in table 2) that belong to the two distinct mtDNA lineages described in figure 3. In the Pacific, collections from northeastern Australia and Japan were fixed for alternate haplotypes (G and H in table 2) that differ by a single restriction-site change. In the Atlantic–Mediterranean, our sample from Greece was fixed for a mtDNA haplotype (D) that also was observed at 66% frequency in Florida samples (but notably

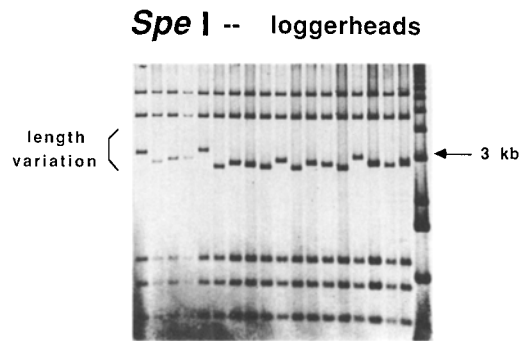


FIG. 2. *Spe*I digests of mtDNA from 18 loggerhead turtles collected in Georgia. Note the fragment at approximately 3.0 kb which varies in size among individuals. The specimen in the second lane from the right appears to be heteroplasmic for two mtDNAs differing by about 50 bp. The right lane is a molecular weight standard (1-kb ladder).

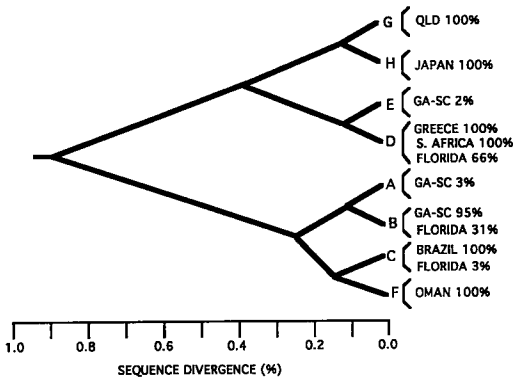


FIG. 3. UPGMA phenogram summarizing the relationships among the eight observed haplotypes described in table 2. The same branching order is observed in a parsimony analysis with minor rearrangements of genotypes A, B, C, and F. The distinction between the lineage containing genotypes A, B, C, and F versus the lineage containing genotypes D, E, G, and H is supported at a bootstrapping level of 100% in a parsimony analysis of restriction-site presence/absence data using an exhaustive search in the computer program PAUP. By the same criteria, the grouping of genotypes G and H is supported at 86%, and the grouping of genotypes D and E is supported at 60%, and no branching order for A, B, C, and F was supported above 50%. The geographic location(s) where each genotype was observed and the frequency of each genotype within these locations are indicated to the right. Abbreviations: GA-SC, Georgia and South Carolina; QLD, Queensland, Australia.

absent from the adjacent nesting population in Georgia and South Carolina) and at 100% frequency in the sample from South Africa. Thus, this haplotype was shared among nesting populations in three different ocean basins. Finally, samples from Brazil were fixed for a haplotype (C) that also was found at low frequency (3%) in Florida.

Notwithstanding these latter instances of haplotype sharing, the surveyed nesting populations were distinguished by significant differences in haplotype frequency in 27 of 28 pairwise comparisons (table 3). Pairwise estimates of inter-rookery gene flow (Nm values; table 3) are low. Based on the frequency of endemic or private haplotypes (i.e., those confined to a single population; Slatkin 1985), average gene flow between assayed nesting populations is $Nm \approx 0.1$. This value is qualitatively similar to migration estimates from green turtles: $Nm \approx 0.3$ for the Atlantic-Mediterranean and $Nm \approx 0.2$ for the Indian-Pacific (Bowen et al. 1992).

In general, Nm values greater than 1 to 4 in-

dicating that gene flow is sufficient to prevent fixation of alternate mtDNA genotypes in assayed populations, whereas lower values indicate that gene flow is insufficient to prevent divergence of isolated gene pools by genetic drift (Birky et al. 1983; Slatkin 1987; but see Allendorf 1983). However, Nm values based on mtDNA data must be interpreted with caution, because of a potentially high variance in migration estimates derived from single haploid genealogies, and possible violations of the equilibrium assumptions that support these estimates (see Slatkin and Barton 1989). For these reasons, Nm values presented here should be viewed as general indicators of the magnitude of genetic exchange over recent evolutionary timescales.

DISCUSSION

Population-Genetic Structure

If female loggerheads return to natal sites for nesting, then rookeries should tend to show pronounced differences with respect to female-transmitted genetic markers such as mtDNA (irrespective of the magnitude of male-mediated nuclear gene flow, possibly via interrookery matings; see Karl et al. 1992). Alternatively, in the absence of natal homing, rookeries would be subject to the homogenizing influence of female-mediated gene flow, and accordingly should exhibit little geographic partitioning of mtDNA haplotypes. In the Indian-Pacific basin, samples from all four surveyed rookeries exhibited fixed mtDNA haplotype differences from one another. These results are entirely consistent with a strong behavioral disposition for natal homing by female loggerhead turtles, at least on a regional scale, and extend the genetic evidence for natal homing presented previously for loggerheads in the Atlantic and Mediterranean basins (Bowen et al. 1993b).

Natal homing in loggerhead turtles cannot be absolute, because new nesting beaches must be colonized at some reasonable frequency by turtles hatched elsewhere (Carr et al. 1978). Over evolutionary timescales the availability and locations of appropriate nesting habitat no doubt change in response to alterations in climate, sea level, and geography. This may be reflected in the intraoceanic mtDNA phylogenies: genetic differentiation between nesting colonies within each ocean basin is generally shallow, a finding that indicates recent connections among colonies in a historical, phylogenetic sense. We suspect that

changes in climate and coastal geography drive an ongoing process of rookery extinctions and colonizations. This process, perhaps coupled with rare lapses in strict female natal homing, has a homogenizing effect whereby the accumulation of greater mutational separation among nesting populations is prevented. Overall, the mtDNA data suggest that loggerhead turtle rookeries within an ocean basin tend to be strongly isolated from one another over ecological timescales, but tightly connected over evolutionary time frames.

Marine Turtle Phylogeography

The absence of a clear matrilineal separation between oceanic basins in the temperate loggerhead turtle contrasts with phylogeographic patterns recently reported for two tropical marine-turtle assemblages. In the green turtle complex (*Chelonia mydas* and the nominal *C. agassizi*), a phylogeny for mtDNA haplotypes is characterized by a fundamental bifurcation that distinguishes all Atlantic-Mediterranean from all Indian-Pacific samples (Bowen et al. 1992). In the ridley complex (*Lepidochelys kempfi* and *L. olivacea*), morphological and genetic evidence indicate that an ancestral population may have been split by the Isthmus of Panama into Atlantic (proto-*L. kempfi*) and Pacific (proto-*L. olivacea*) forms about 3 to 4 mya (Pritchard 1969; Hendrickson 1980; Bowen et al. 1991). *Lepidochelys olivacea* may have subsequently colonized the Atlantic Ocean via southern Africa during recent evolutionary history (Pritchard 1969), a scenario supported by morphological data (Pritchard and Trebbau 1984), distributional data (Hughes 1972), and mtDNA analyses (Bowen et al. 1991, 1993a).

Representatives of the two primary mtDNA lineages in *Caretta caretta* were observed in both the Atlantic-Mediterranean and Indian-Pacific basins. We conclude that the temperate distribution of loggerhead turtles may have facilitated at least two effective transfers of matriline between the Atlantic and Indian oceans by gene flow around southern Africa. Based on the mtDNA haplotype distributions and phylogeny, we advance the following tentative scenario as one example of how such colonization events might have proceeded during the recent evolutionary history of *C. caretta*.

During cooler periods of the Pleistocene, loggerhead populations probably were isolated by geography and climate into Atlantic and Indian-

TABLE 3. Above diagonal: estimates of gene flow (*Nm*) between loggerhead turtle rookeries based on the cladistic approach (Slatkin 1989). The 95% confidence intervals are in parentheses. Below diagonal: *G* tests of independence for haplotype frequencies among rookeries. Abbreviation: GA-SC, Georgia-South Carolina.

Locale	1.	2.	3.	4.	5.	6.	7.	8.
1. Florida, USA	—	0.3 (0-0.8)	0.4 (0-1.2)	0.3 (0-0.9)	0.4 (0-1.2)	0.0 (0-0.4)	0.0 (0-0.3)	0.0 (0-0.3)
2. GA-SC, USA	<i>G</i> = 44.2 <i>P</i> < 0.001	—	0.0 (0-0.3)	0.0 (0-0.3)	0.0 (0-0.3)	0.0 (0-0.4)	0.0 (0-0.3)	0.0 (0-0.3)
3. Brazil	<i>G</i> = 33.0 <i>P</i> < 0.001	<i>G</i> = 52.3 <i>P</i> < 0.001	—	0.0 (0-0.3)	0.0 (0-0.3)	0.0 (0-0.4)	0.0 (0-0.4)	0.0 (0-0.4)
4. Greece	<i>G</i> = 8.6 <i>P</i> < 0.005	<i>G</i> = 83.9 <i>P</i> < 0.001	<i>G</i> = 32.4 <i>P</i> < 0.001	—	high	0.0 (0-0.3)	0.0 (0-0.3)	0.0 (0-0.3)
5. South Africa	<i>G</i> = 6.1 <i>P</i> < 0.02	<i>G</i> = 66.2 <i>P</i> < 0.001	<i>G</i> = 27.0 <i>P</i> < 0.001	<i>G</i> = 0 NS	—	0.0 (0-0.4)	0.0 (0-0.3)	0.0 (0-0.3)
6. Oman	<i>G</i> = 29.8 <i>P</i> < 0.001	<i>G</i> = 40.4 <i>P</i> < 0.001	<i>G</i> = 18.1 <i>P</i> < 0.001	<i>G</i> = 25.7 <i>P</i> < 0.001	<i>G</i> = 21.6 <i>P</i> < 0.001	—	0.0 (0-0.4)	0.0 (0-0.4)
7. Japan	<i>G</i> = 47.0 <i>P</i> < 0.001	<i>G</i> = 66.2 <i>P</i> < 0.001	<i>G</i> = 27.0 <i>P</i> < 0.001	<i>G</i> = 39.8 <i>P</i> < 0.001	<i>G</i> = 32.8 <i>P</i> < 0.001	<i>G</i> = 21.6 <i>P</i> < 0.001	—	0.0 (0-0.3)
8. Australia	<i>G</i> = 44.9 <i>P</i> < 0.001	<i>G</i> = 62.9 <i>P</i> < 0.001	<i>G</i> = 25.9 <i>P</i> < 0.001	<i>G</i> = 38.1 <i>P</i> < 0.001	<i>G</i> = 31.5 <i>P</i> < 0.001	<i>G</i> = 20.8 <i>P</i> < 0.001	<i>G</i> = 31.5 <i>P</i> < 0.001	—

Pacific basins. One mtDNA lineage (represented in our survey by haplotypes A, B, C, and F) may have evolved in the Atlantic, and another mtDNA lineage (represented by D, E, G, and H) may have evolved in the Indian-Pacific. Subsequently, warmer temperatures associated with interglacial periods allowed an expansion of loggerhead habitat to higher latitudes, opening a temperate corridor around southern Africa. During such periods, an Atlantic lineage (precursor to F) may have invaded the Indian Ocean, and an Indian-Pacific lineage (precursor to D and E) may have invaded the Atlantic. These particular lineages are indicated because (1) the A, B, C, F lineage is widely distributed in the Atlantic but represented by only one observed haplotype (F) in the Indian-Pacific, and (2) the D, E, G, H lineage is widespread in the Indian-Pacific but represented by only one common haplotype (D) and one rare haplotype (E) in Atlantic-Mediterranean samples. The low diversity of these lineages in the putative "invaded" ocean basin indicates that these transplantations occurred relatively recently, perhaps during the last 20,000 yr.

An alternative possibility, that both major mtDNA lineages have been retained in both ocean basins for several million years, cannot be excluded. If true, however, recent interoceanic exchange of mtDNA haplotypes is still implicated to account for the similarity of haplotypes in separate oceans. Under any of these or related scenarios, the coastline around southern Africa has provided (and may continue to offer) a stepping-stone for transplantation of loggerhead mtDNA genotypes between the Indian-Pacific and Atlantic-Mediterranean basins. Indeed, a recent investigation of hatchling movement from the Tongaland (South Africa) rookery has demonstrated "leakage" of neonates from this Indian Ocean rookery into the South Atlantic (G. R. Hughes unpubl. data). Perhaps these hatchlings, carried into the Atlantic through a narrow corridor of warm temperate water, are a source of Atlantic colonizers. This would explain the presence of haplotype D (observed at 100% frequency in Tongaland samples) in two surveyed Atlantic-Mediterranean nesting populations.

The presence of the two primary mtDNA lineages in both the Atlantic-Mediterranean and Indian-Pacific basins (fig. 3) is consistent with recent taxonomic reappraisals that have rejected subspecific designations for Atlantic and Indian-Pacific *Caretta caretta* (Hughes 1974a; Pritchard and Trebbau 1984; Dodd 1988).

Conservation Concerns

Although we have analyzed only a small fraction of the genetic architecture of loggerhead turtle populations (the matrilineal component), these results have special implications for the conservation biology of this species. First, the haplotypes defined in this report may aid in reconstructing the migratory routes and feeding ground demographics of *C. caretta*. In particular, four major nesting aggregates in the Indian and Pacific oceans (in South Africa, Oman, eastern Australia, and Japan) are characterized by fixed genetic differences in our assays. The mtDNA sequences therefore provide natural markers to detect the contributions of these populations to habitats outside the nesting area. In cases where feeding-ground populations are harvested or otherwise impacted by human activities, the conservation value of this data is readily apparent.

Secondly, the mtDNA data indicate a strong propensity for natal homing by females, such that each regional nesting population comprises an independent demographic unit. Although new nesting beaches must be occasionally colonized over evolutionary timescales, both tagging studies and mtDNA data (table 3) indicate that the frequency of such events over ecological timescales is low. Thus, a rookery extirpated by human encroachment or natural phenomena is not likely to be reestablished over a time frame relevant to human interests. This conclusion holds regardless of the level of interrookery exchange of nuclear genes that might be mediated by males. Accordingly, the protection of nesting habitats should remain a high conservation priority.

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