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Genetic composition of a green turtle (*Chelonia mydas*) feeding ground population: evidence for multiple origins

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Abstract Migratory marine turtles are extremely difficult to track between their feeding and nesting areas, and the link between juvenile and adult habitats is generally unknown. To assess the composition of a feeding ground (FG) population of juvenile green turtles (*Chelonia mydas* Linnaeus), mitochondrial DNA control region sequences were examined in 80 post-pelagic individuals (straight carapace length = 31 to 67 cm) sampled in September 1992 from Great Inagua, Bahamas, and compared to those of 194 individuals from nine Atlantic and Mediterranean nesting colonies. Evidence from genetic markers, haplotype frequencies, and maximum likelihood (ML) analyses are concordant in indicating that multiple colonies contribute to the Bahamian FG population. ML analyses suggested that most Bahamian FG juveniles originated in the western (79.5%) and eastern (12.9%) Caribbean regions, and these proportions are roughly comparable to the size of candidate rookeries. These data support a life-cycle model in which individuals become pooled in post-hatchling (pelagic) and juvenile (benthic) habitats as a consequence of ocean currents and movement among FGs. A substantial harvest of immature turtles on their feeding pastures will influence the reproductive success of contributing nesting populations over a wide geographic scale.

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Introduction

One of the perplexing problems encountered in the study of migratory marine animals is understanding juvenile movements. Often these life stages are difficult to follow due to the small sizes, long-distance movement patterns, and/or obscure habitat requirements of juveniles. This is particularly true with respect to marine organisms whose young may disperse across great expanses of open ocean. Recently, however, genetic tags have been useful in elucidating aspects of juvenile and adult life history in migratory marine organisms including salmon, whales and sea turtles (Utter and Ryman 1993; Baker et al. 1994; Norman et al. 1994). The applications of genetic markers in sea turtles have been particularly fruitful (Broderick et al. 1994; Norman et al. 1994; Bowen 1995; Bowen et al. 1995, 1996; Bass et al. 1996; Bolten et al. 1998). These long-lived marine reptiles have remarkably complex life histories that include aggregated nesting, pronounced developmental shifts in habitat and diet, and extended oceanic migrations. Such traits make the use of genetic tags valuable for long-term population and ecological studies of marine turtles.

The green turtle (*Chelonia mydas*) has emerged as a model organism for such long-term research. Population studies of maternally inherited mitochondrial DNA (mtDNA) have allowed the development of genetic "tags" for green turtles and have yielded valuable data on their molecular evolution, population structure, reproductive behavior, conservation, and migratory ecology (Bowen et al. 1992; Allard et al. 1994; Lahanas et al. 1994; Encalada et al. 1996). Female green turtles migrate thousands of kilometers between reproductive areas and feeding grounds (FGs), and long-term tag and recapture studies have indicated strong fidelity to these areas (Carr et al. 1978; Limpus et al. 1992). Despite our understanding of female reproductive migration cycles, the movements of green turtle hatchlings from the time they enter the surf to when they reappear at "dinner-plate size" on the benthic FGs – the "lost year" stage – remain

a mystery (Bolten and Balazs 1995; see also Bowen et al. 1995 and Bolten et al. 1998).

Sequences from the mtDNA control region were used to determine the genetic composition of a sample of immature green turtles obtained from a FG population at Great Inagua, Bahamas. Using genetic markers from an earlier study of nine nesting populations from the Greater Atlantic and Mediterranean (Allard et al. 1994; Lahanas et al. 1994; Encalada et al. 1996), we assessed nesting colony contributions to this FG population. We then used these genetic tags to resolve migratory patterns of early life-history stages in the green turtle. Understanding the origins of FG populations is essential for the development of long-range conservation strategies for this endangered species.

Materials and methods

Whole genomic DNA was isolated from blood samples drawn from 80 immature green turtles (*Chelonia mydas* Linnaeus) with straight carapace lengths from 31 to 67 cm, captured in September 1992 at Great Inagua, Bahamas. Standard DNA isolation procedures were used (Sambrook et al. 1989). The mtDNA control region (5′ end) was subjected to previously described cycle sequencing and alignment protocols (Allard et al. 1994; Lahanas et al. 1994). Tissue types and sources, DNA extraction procedures, purification methods and sequencing protocols for nine nesting population samples were reported previously (Bowen et al. 1992; Allard et al. 1994; Lahanas et al. 1994; Encalada et al. 1996). A total of 480 nucleotides of the control region, corresponding to sites 85 to 564 of Allard et al. (1994), were examined for each of the 80 FG individuals and then compared to corresponding sequences of 194 females from nine nesting colonies (Table 1; Fig. 1). The resulting 21 polymorphic sites resolved 21 haplotypes among the 274 individuals assayed. Of the 194 nesting females sequenced, 146 had been previously analyzed (Encalada et al. 1996), and 48 (26 collected from Tortuguero, Costa Rica, from July to September 1996, and 22 collected from Aves Island, Venezuela, from July to September 1994) were assayed for the current study using the automated sequencing protocols described by Encalada et al. (1996). The new sequences reported in this paper have been deposited in the GenBank database (Accession Nos. Z69886–Z69888).

Haplotype frequency differences between the FG and nesting populations were statistically compared with the Chi-squared test using the computer program CHIRXC (Zaykin and Pudovkin 1993). Probabilities for these tests were estimated using Monte Carlo randomization (Zaykin and Pudovkin 1993). The resulting probabilities were then corrected for multiple tests using the sequential Bonferroni method (Rice 1989).

Contributions to the Bahamian green turtle FG aggregate by sampled nesting populations were estimated using unconditional maximum likelihood (ML) (Pella and Milner 1987) calculated with the computer programs UCON (M. Masuda, NMFS Auke Bay Laboratory; Masuda et al. 1991) and SHADRACQ (Xu et al. 1994). ML employs an iterative algorithm to identify the most likely contributions of source populations to a mixed stock based on haplotype frequencies in both the source (nesting colonies) and mixed stock (FG) populations. While both UCON and SHAD-

Table 1 *Chelonia mydas*. Frequency distribution of Atlantic green turtle nesting colony and Bahamian feeding ground mtDNA haplotypes (Nesting colony location abbreviations are: *FL* Hutchinson Island, Florida, USA; *MEXI* Yucatán, Mexico; *CR* Tortuguero, Costa Rica; *AVES* Aves Island, Venezuela; *SURI* Matapica, Surinam; *BRAZ* Atol das Rocas, Brazil; *ASCE* Ascension Island, UK; *AFRI* Pailoa, Guinea Bissau; *CYPR* Lara Bay, Cyprus; *letters below* nesting locality abbreviations correspond to nesting colony sites in Tables 3 and 4, and Fig. 1). Expected numbers are adjusted for nesting colony population size. See Table 4 for population sizes and "Discussion" for further explanation of these expected counts

Haplotype	Nesting colony location									Feeding grounds	Expected numbers of FG haplotypes
	[a]FL A	[b]MEXI B	[a]CR C	[c]AVES D	[c]SURI E	[b]BRAZ F	[b]ASCE G	[b]AFRI H	[b]CYPR I		
I	11	7								2	1.2
II	1										
III	12	5	40	3						62	54.1
IV			1								
V		1		27	13					10	7.1
VI					1						
VII					1						
VIII						8	16	19		1	9.0
IX						5	1				
X							3				
XI						1					
XII						2					
XIII									8		
XIV									1		
XV		1									
XVI		1									
XVII		2									
XVIII		3									
XIX										1	
XX										1	8.6
XXI										3	("Other")
(*n*)	(24)	(20)	(41)	(30)	(15)	(16)	(20)	(19)	(9)	(80)	

[a] Data from Allard et al. (1994) and present study
[b] Data from Encalada et al. (1996)
[c] Data from Lahanas et al. (1994) and present study

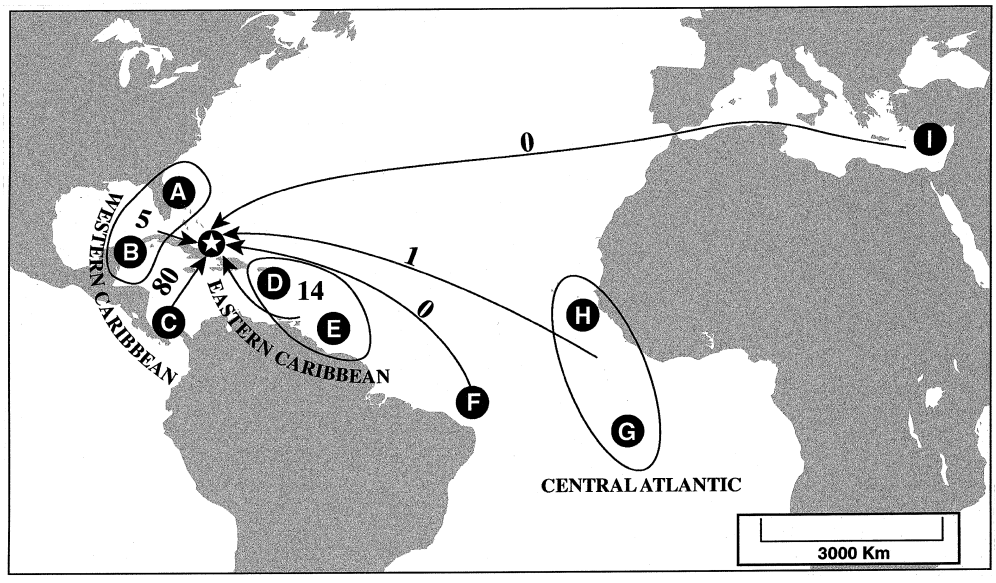

Fig. 1 *Chelonia mydas*. Origins of the Great Inagua, Bahamas FG population (*Letters A–I* correspond to nesting sites listed in Tables 1, 3 and 4; *star* identifies the Great Inagua, Bahamas FG). The contribution made to the FG population by each colony or encircled region is based on unconditional maximum likelihood estimates calculated by UCON (Table 3) and presented as percentages

RACQ are ML algorithms, they differ in the calculation of the maximum of the likelihood function. Therefore, comparing results from the two programs provides a more robust analysis. Standard deviation estimates based on the infinitesimal jackknife procedure were derived from the UCON analysis (SHADRACQ does not calculate standard deviations). Nesting colonies that showed no significant differences in haplotype frequencies were pooled into regional population units for this analysis. Because all mixed stock haplotypes must match source population haplotypes (Masuda et al. 1991), the three new FG haplotypes, XIX, XX, and XXI (five individuals) were excluded from the analysis. Thus, a FG sample size of 75 was used in the ML analysis and to convert ML proportions into estimated contributions.

To assess possible life-history correlates, source population size and distance were examined as a function of the estimated contribution to the FG determined from the ML analysis. Colonies were pooled into the same regional populations described in the ML analysis, and their expected contributions to a FG sample of 75 were calculated. The relative importance of distance and population size to colony contribution to the FG was determined using multiple regression analysis. A Student's *t*-test was used to determine statistical differences among estimates derived from ML and regression analyses. Chi-squared tests were used in all other cases.

Previous χ^2 tests using the sequential Bonferroni method performed on nesting populations (Encalada et al. 1996) indicated that no significant differences in haplotype frequency occurred between the Florida and Mexico (Yucatán Peninsula) populations, between Aves Island and Surinam populations, or between Ascension Island and Guinea Bissau populations. Subsequent χ^2 tests performed on the new samples from Aves Island also revealed no significant difference between this population and the Surinam nesting colony. These regional source populations were pooled for all regional-based analyses.

Results

Among the 80 FG samples, 14 polymorphic sites defined seven haplotypes. Four haplotypes corresponded to sequences identified in nesting populations (Table 1) and three were new (Table 2). The four haplotypes (I, III, V, and VIII), which matched rookery samples, accounted for 94% of the FG samples.

Due to the marked regional genetic structure among Atlantic green turtle populations (Bowen et al. 1992; Allard et al. 1994; Lahanas et al. 1994; Encalada et al. 1996) (Table 1), the FG haplotypes were readily assigned to either western Caribbean (Florida; Mexico; Costa Rica), eastern Caribbean (Aves Island, Venezuela; Surinam) or central Atlantic (Brazil; Ascension Island, U.K.; Guinea Bissau) geographic regions. The majority of individuals from the Great Inagua sample (77.5%) matched haplotype III, which is characteristic of western Caribbean nesting colonies (three haplotype III individuals occurred in the Aves Island population; Lahanas et al. 1994; present study), whereas 12.5% of the FG individuals matched haplotype V, which is observed in high frequencies only in rookery samples from the eastern Caribbean (although one haplotype V individual was found in the sample from the Yucatán Peninsula, Mexico). Two individuals had haplotype I which is

Table 2 *Chelonia mydas*. Sequence polymorphisms of three new mtDNA control region haplotypes recovered from the Great Inagua, Bahamas FG. Base positions correspond to alignment with the common haplotype III ($=A^{TAC}$; see appendix in Allard et al. 1994). Sequence polymorphisms for all other haplotypes are provided in Encalada et al. (1996)

Haplotype	Base position											
	204	220	242	244	321	343	355	438	481	502	504	558
XIX	G	C	C	A	T	C	T	G	T	A	G	A
XX	A	G	G	G	C	C	G	A	C	G	A	G
XXI	A	G	G	A	C	C	G	A	T	G	A	G
III	G	G	G	A	T	C	T	G	T	A	G	A

Table 3 *Chelonia mydas*. Expected composition of the Bahamian FG population estimated by unconditional maximum likelihood using the programs SHADRACQ and UCON. SHADRACQ expected contribution estimates sum to 0.99 due to rounding error. Standard deviations (*in parentheses*) were determined from the UCON analysis by the infinitesimal jackknife procedure

Location code	Population(s)	Expected contribution from SHADRACQ	Expected contribution (SD) from UCON
A/B	Florida/Mexico	0.05	0.05 (0.03)
C	Costa Rica	0.79	0.80 (0.05)
D/E	Aves Island/Surinam	0.14	0.14 (0.04)
F	Brazil	0.00	0.00 (0.00)
G/H	Ascension/Africa	0.01	0.01 (0.01)
I	Cyprus	0.00	0.00 (0.00)

observed only in Florida and Mexico. Finally, one individual had haplotype VIII, which is observed only in rookery samples from the central Atlantic (Fig. 1).

A comparison of the three new haplotypes to those previously known revealed that one (haplotype XIX) was most similar to the predominant Florida/Mexico haplotype I (differing by two transversions and one transition), whereas the two other new haplotypes (XX and XXI; Table 2) were most similar to haplotype V from Aves Island and Surinam, from which they differed by only one transition each (cf. Encalada et al. 1996). Finally, none of the FG haplotypes matched those from the Mediterranean nesting colony at Cyprus.

A comparison of haplotype frequencies revealed significant χ^2 differences between the FG and each of the nesting colonies ($\alpha = 0.05$).

Results of the two ML analyses (UCON and SHADRACQ) show high concordance and indicate contributions from all of the potential source populations except two of the most distant ones, at locations in Brazil and Cyprus (Table 3). Significant contributions were detected from the Aves/Surinam population ($t = 3.37$, $P < 0.05$) and the Costa Rican population ($t = 15.49$, $P < 0.001$). Smaller estimated contributions from Florida/Mexico and Ascension/Africa were not significantly greater than zero based on a Student's *t*-test, but these contributions of approximately 5 and 1%, respectively, are anchored by the presence of endemic Florida/Mexico and Ascension/Africa haplotypes in the feeding ground sample (Table 1). For this reason, we retain these small contributions in subsequent interpretation and discussion.

Discussion

Genetic composition

Evidence from genetic markers, haplotype frequencies, and ML analyses consistently indicate that the Bahamian FG contains cohorts from at least two geographically distinct source populations. Costa Rica overwhelmingly makes the largest contribution; the Aves/Surinam contribution is smaller, but significantly greater than zero. The presence of "endemic" haplotypes from Florida/Mexico and Ascension/Africa at low frequency indicates that these populations probably contribute as well.

What demographic or behavioral elements could account for this pattern? Two fundamental factors which may influence the composition of feeding aggregates are: (a) distance from the source colonies and (b) size of these nesting populations. If young turtles recruit preferentially to FGs near their natal nesting colonies, then this behavior should be reflected in extensive sharing of mtDNA haplotypes between proximal feeding and nesting areas. If turtles recruit from a general pool drawn from the entire region, then FG samples should approximate a random sample of haplotypes from candidate nesting colonies.

To ascertain which of the two factors played the larger role in determining contribution to the FG, multiple regression was performed incorporating distance and population size as independent variables. Regional assignments were maintained as before, and their means for population size and distance were used in the regression analysis. The results indicated a very strong correlation between the independent variables and ML estimates ($r = 0.98$), and that population size contributed significantly ($t = 6.77$, $P = 0.02$), whereas distance did not ($t = -0.26$, $P = 0.82$).

To determine the importance of population size alone, the relative expected contributions of each nesting colony to the pool of haplotypes in the FG sample were calculated as a function of colony size and genetic composition (Table 1). The Brazil and Cyprus samples were not considered in this analysis, because of their estimated contributions of 0.00 according to the ML comparisons (Table 3). Haplotypes represented in neither FG nor nesting colony samples were placed in the category "other". The predicted contributions of the other nesting colonies were then compared to the observed haplotype frequencies in the FG sample. Significant differences between the observed and expected frequencies for the FG sample were revealed by this test ($\chi^2 = 11.10$, $P = 0.025$). The greatest contribution to the χ^2 value (64%) came from the difference between the observed and expected counts for the Ascension/Africa regional population. The χ^2 test was rerun, but this time with the regional population samples from Ascension Island and Africa included in the "other" category. Under these conditions, the population-size model functioned as an excellent predictor of contribution to the FG ($\chi^2 = 1.10$, $P > 0.05$). The same conclusion was reached when the χ^2 test was performed for the expected contributions of regional colonies according to relative population sizes versus their ML estimates ($\chi^2 = 9.97$, $P < 0.05$ with Ascension/Africa included in the analysis; $\chi^2 = 1.91$, $P > 0.05$ with these two deleted from the analysis; Table 4).

These results prompt two conclusions. First, source population size appears to be the primary factor determining the contribution of nesting colonies to the Ba-

Table 4 *Chelonia mydas*. Comparison of expected nesting colony representation in a FG sample of 75[a] from Great Inagua, Bahamas. Expected values were derived from a reproductive population size model and unconditional maximum likelihood using UCON

Nesting colony location	Annual female reproductive population size[b]	Km to Bahamian feeding ground[c]	Expected no. as a function of population size	Expected no.; combined colonies into regional populations[d]	Expected no. based on ML; combined colonies
(A) Hutchinson Isl., Fla., USA	424	1 060	1.59	2.71	3.41
(B) Yucatán, Mexico	300	1 500	1.12		
(C) Tortuguero, Costa Rica	14 000	1 620	52.31	52.31	59.95
(D) Aves Isl., Venezuela	400	1 800	1.49	8.96	10.64
(E) Matapica, Surinam	2 000	3 340	7.47		
(F) Atol das Rocas, Brazil	150	4 450	0.56	0.56	0.00
(G) Ascension Isl., UK	2 300	6 500	8.59	10.08	1.00
(H) Guinea Bissau	400	5 600	1.49		
(I) Lara Bay, Cyprus	100	10 500	0.38	0.38	0.00
Totals	20 074		75	75	75

[a] Five FG individuals representing three new haplotypes were not included in the analyses

[b] Represents estimates of average annual effective population size derived from data obtained from Conley and Hoffman (1987) and A. Meylan (personal communication) (A); Zurita et al. (1993) (B); Bowen et al. (1992) (C–I)

[c] Represents aquatic straight-line distance between nesting colony and the Great Inagua, Bahamas FG

[d] Nesting colony samples that showed no significant ($P > 0.05$) haplotype frequency differences were combined into regional populations as indicated

hamian FG, for colonies relatively close (<3500 km) to the FG. If size is important, as the regression analysis suggests, then it seems likely that Costa Rica was the origin of most assayed individuals. Costa Rica has an average annual reproductive population that is one order of magnitude larger than Aves/Surinam and two orders of magnitude larger than either Florida or Mexico (Table 4). This conclusion is consistent with the null hypothesis advanced by Chapman (1996). Chapman (1996) suggested that mixed stock analyses are hampered by a lack of a null hypothesis and concluded that a reasonable null hypothesis would be that all nesting populations contribute to mixed stocks in proportion to their relative abundance. Additional FG studies will be necessary to determine if this is a universal feature of green turtle population biology.

Second, geographic distance between a nesting colony and the FG becomes important only when distances exceed a threshold. The low (or zero) estimated contributions from source populations in the mid-Atlantic, Brazil, Africa and the Mediterranean could be explained by geographical separations on the order of 4500 to 10 000 km from the Bahamian FG and/or by those rookeries feeding into different current systems that do not overlap with those from which the Bahamian FG population is derived.

An important caveat to these estimates is that the ML model assumes that all potential source populations have been sampled and that all rookery haplotypes are known. Because this assumption is unlikely to be met for any migratory marine species with widely scattered breeding areas, some caution is indicated in transferring the results of the model to the interpretation of natural history patterns. The nine surveyed nesting populations represent the vast majority of nesting effort in the Atlantic and Mediterranean basins. However, of the 80 juvenile green turtles that we sampled, five (6%) had haplotypes that were not detected in Atlantic green turtle nesting populations and therefore could not be included in the maximum likelihood analyses. These three new haplotypes were all observed at low frequency (Table 2): two haplotypes were represented by only a single individual and one haplotype was observed in three turtles. These rare haplotypes may have been missed in the genetic survey of nesting populations, or they may occur in small nesting populations that have not yet been sampled. In the Atlantic, small numbers of green turtles nest in areas – such as the Bahamas and Cuba – that have not been sampled because of logistic or political restrictions. Samples from these remaining nesting populations would be informative and may provide some of the missing rare haplotypes. However, because of the small size of these unsampled populations, results of such work would be unlikely to alter our conclusion that the Bahamian FG population is a mixed stock with rookery contributions roughly proportional to the sizes of the West Atlantic rookeries. The four haplotypes (I, III, V, and VIII) that are shared between nesting and FG populations account for 86% of samples collected (Table 1).

Green turtle life cycle

The stochastic distribution of haplotypes in the Bahamian FG green turtle population may be explained in terms of early life history. The influence of ocean currents on the dispersal and distribution of hatchling sea turtles has been widely acknowledged (Hughes 1974; Balazs 1976). Rather than simply transporting hatch-

lings directly to a given downstream FG, however, ocean currents (at least in some regions) may instead mix cohorts from different source populations, and thereby combine haplotypes that are highly structured among regional nesting colonies.

Carr and coworkers (Carr 1980) presented a model of ontogenetic changes in the green turtle life cycle in which hatchlings enter a pelagic "lost year" habitat, and subsequently transfer through a series of "developmental" benthic habitats. After emerging from the nest, hatchlings enter prevailing currents of the Greater Atlantic system and begin a planktonic, pelagic existence (Wyneken and Salmon 1992). Time spent in this period was originally believed to be relatively brief. When the slow growth rate of green turtles was understood (Bjorndal and Bolten 1988), it was realized that several years, perhaps up to ten, were spent in the pelagic stage. Individuals spending several years in these waters might make several rotations through various current systems of the Greater Atlantic before shifting to a benthic feeding habitat. Thus, hatchlings that begin life in close proximity may eventually be separated by thousands of kilometers during the planktonic, pelagic stage by microgeographic differences in ocean currents and marine hydrology (Ingrahm 1979). Over extended periods, these dynamics would tend to mix hatchlings (and therefore, randomize haplotypes) from different nesting colonies in the Caribbean and northern tropical Atlantic region. The data presented here are consistent with expectations of the Carr recruitment hypothesis and bolster our understanding of some of the more elusive aspects of the green turtle's life cycle.

We suggest that this mixing is one key to understanding the distribution of haplotypes observed in the Great Inagua juvenile feeding aggregate. Recapture data indicate that immature turtles >20 cm carapace length move between benthic FGs separated by open ocean. Immature green turtles tagged in the shallow waters of the Bahamian FG have been recaptured hundreds or thousands of kilometers away at deeper water feeding areas such as the Miskito Bank, Nicaragua, and off the coast of Colombia (KAB and ABB unpublished data). Movement among FGs by immature individuals undoubtedly contributes to the further mixing of haplotypes on feeding pastures. To distinguish between the effects of pelagic and post-pelagic mixing on the development of mixed stocks on benthic FG, the haplotype frequencies of turtles newly recruited from pelagic habitats would have to be compared with those of older turtles.

A comparison to hawksbill turtles

Although green turtles and hawksbill turtles (*Eretmochelys imbricata*) differ in aspects of nesting biology and migratory behavior (Meylan 1982; Parmenter 1983; Bjorndal et al. 1985), they show similar patterns of contributions to FG assemblages. Bowen et al. (1996) found significant haplotype frequency differences between a nesting population on Mona Island, Puerto Rico, and a nearby (Mona Island) feeding population. As with green turtles, this finding suggested that the FG population did not come directly from the nearby nesting populations, but from other areas of the Caribbean. An analysis of ML indicated that the hawksbill FG population at Mona Island received significant contributions from at least four Caribbean rookeries greater than 100 km from the FG, but a Brazilian breeding population 7000 km from the Mona Island FG made no detectable contribution.

A qualitative difference between Atlantic hawksbill and green turtles is the relative contributions made by nesting populations to their respective FG assemblages. In hawksbills, these contributions were relatively uniform among the six colonies assayed, whereas approximately 80% of the green turtle Bahamian FG population was derived from a single nesting site in Costa Rica. Differences in relative sizes of nesting colonies between these two species may account for differences in their FG contributions. Hawksbill turtles nest widely throughout the Caribbean in relatively small rookeries (Bowen et al. 1996), and have been shown to move between adjacent nesting beaches in the Seychelles (Diamond 1976) and eastern Australia (Limpus et al. 1983). In contrast, the majority of green turtle nesting in the Atlantic occurs at a single colony at Tortuguero, Costa Rica. These differences have led to modes of FG contribution in both hawksbill and green turtles that are consistent with the hypothesis that breeding population size, and not proximity to the FG, is the primary determinant of FG contribution.

Green turtle conservation

The geographically widespread origins of the Great Inagua feeding population have important conservation implications. The results presented here indicate that minimally two and probably several Atlantic nesting colonies are represented in this developmental habitat. Therefore, any source of mortality on FGs, such as those at Great Inagua, Bahamas, is likely to impact nesting populations throughout the Caribbean and wider Atlantic region. The degree of impact will vary inversely with the size of the nesting population. Likewise, overharvesting of eggs or females on nesting beaches is likely to diminish distant feeding populations. These data reinforce the view that management of green turtles must be conducted on a regional scale. A dilemma, therefore, surrounds the stewardship of these natural resources, as management on a strictly national level is clearly inadequate. The 1982 U.N. Convention on the Law of the Sea stipulates that biological resources captured on the high seas are the domain of the nations hosting these animals in coastal developmental habitat (Van Dyke 1993). The 1983 U.N. Convention on the Conservation of Migratory Species (the Bonn Convention) prohibits taking endangered species during feeding

or reproductive migrations, even if such migrations place the animal within the territorial boundaries of sovereign nations (Hykle 1992). If these principles are applied to green turtles, nesting and FG populations constitute a shared resource for which no single nation may claim exclusive jurisdiction. Regional cooperation and international agreements will be required to manage these complex migratory populations effectively.

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