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Green Turtle (*Chelonia mydas*) Foraging and Nesting Aggregations in the Caribbean and Atlantic: Impact of Currents and Behavior on Dispersal

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Abstract

Although significant amounts of research have been dedicated to increasing the knowledge of the life history of green turtles (*Chelonia mydas*), large gaps exist in our understanding of juvenile migratory behavior. These gaps can be filled by genetic studies of foraging ground aggregations. Using mitochondrial DNA markers and Bayesian analyses, samples ($n = 106$) from a foraging aggregation in North Carolina indicated that animals from the east coast of the United States (54%) and Mexico (27%) dominate the composition with the remainder coming from other Caribbean and Atlantic nesting aggregations. These findings prompted a reanalysis of 4 regional foraging aggregations using Bayesian mixed stock analysis, analysis of molecular variance, and diversity measures. Significant regional population structure between northern and southern foraging aggregations in the Caribbean was detected ($\phi_{ST} = 0.27$, $P = 0.000$) in addition to significant nesting aggregation structure ($\phi_{ST} = 0.87$, $P = 0.000$). Haplotype diversity levels were highest at foraging aggregations located within the confluence of major current systems. These findings indicate that both currents and behavior have strong influences on the composition of foraging aggregations. In addition, our results provide evidence of juvenile homing to regional foraging grounds and highlight the difficulties of separating historical and current effects on recruitment patterns at foraging locations.

A globally distributed inhabitant of sea grass beds and coral reefs (Musick and Limpus 1997), the IUCN (International Union for the Conservation of Nature and Natural Resources)-listed endangered green turtle, *Chelonia mydas*, has been held in veneration by many cultures and served as an important food source (Parsons 1962). Recorded usage of this turtle as a food source in the Caribbean dates to the early 17th century when mariners utilized turtles for fresh meat on long voyages (Parsons 1962). The only member of Cheloniidae to forage on sea grasses, these turtles play an important ecological role as their grazing of the sea grass stimulates new growth while their feces replenish nutrients to this ecosystem (Thayer and others 1982; Aragones and Marsh 2000).

Green turtles inhabit both pelagic and neritic environments and follow the general life-history cycle proposed by Carr and others (1978). They are well adapted to long-distance travel in the sea and potentially spend a good proportion of their first years in a pelagic (oceanic) existence. Information about these first years is minimal, hence the use of the term the "lost years" as the posthatchlings are somewhat lost to scientific investigation. Because the majority of their life span is spent in the sea, specifics regarding much of their life history (with the exception of those relating to nesting) have proved elusive. Satellite tagging technology has enabled researchers to document the pre- and postnesting movements of reproductively active females as well as shuttling migrations between adult green turtle nesting and foraging locations (Luschi and others 2003). Data on male movements are scarce, and the application of these techniques to acquire the necessary data to accurately characterize

the movements of neonates and juveniles can be logistically difficult and expensive.

Although not replacing tagging studies, genetic analysis coupled with mixed stock analysis (MSA) has allowed researchers to examine the relationships among marine turtle nesting and juvenile foraging locations (Broderick and others 1994; Bowen and others 1995; FitzSimmons and others 1997; Bolten and others 1998; Lahanas and others 1998; Laurent and others 1998; Bass and Witzell 2000; Engstrom and others 2002; Luke and others 2004). Initially, MSA utilized a maximum likelihood (ML) algorithm to determine the relative contributions of sources, or stocks, to a hypothesized "mixed" population (Pella and Milner 1987). More recently, Bayesian statistics have been successfully incorporated into MSA (Pella and Masuda 2001).

Lahanas and others (1998) were the first to present an MSA of a juvenile green turtle foraging aggregation. After determining the relative contributions of multiple Caribbean nesting locations to the foraging aggregation in the Bahamas, these authors tested the importance of 2 possible determinants of foraging ground composition—the relative size of the nesting populations and the distance between nesting and foraging locations. Their analysis indicated that the size of the nesting populations played a key role in determining the composition of the foraging aggregation with approximately 80% of the foraging individuals coming from the largest nesting population in the Caribbean at Tortugeuro, Costa Rica (Bjorndal and others 1999). Multiple authors have tested this hypothesis at other Caribbean foraging locations, and the conclusions have been varied; in some cases, distance from nesting to foraging location appears to drive the composition (Bass and Witzell 2000). However, in a study of foraging greens off the coast of Barbados, Luke and others (2004) concluded that distance and size were not the driving determinants but suggested that currents play a more significant role in shaping the composition of the foraging aggregation.

In this study, we compile and reanalyze previously published data on multiple foraging aggregations in the Western Atlantic and include a new assessment of the relative contributions of green turtle nesting populations to the composition of a juvenile foraging area located along the eastern seaboard of the United States. Our primary goal is to examine the relative roles of currents and behavior on foraging ground recruitment on a regional as opposed to local scale and to postulate hypotheses for patterns in the genetic composition of these regional foraging grounds using both MSA and population genetic analyses. A second goal is to use the new foraging ground data to supplement long-term monitoring within the Core and Pamlico–Albemarle Sounds of North Carolina, United States. Designated by the National Marine Fisheries Service as a sea turtle index of abundance study area, this estuarine complex is an important foraging location for green, loggerhead (*Caretta caretta*), and Kemp's ridley (*Lepidochelys kempii*) turtles (Epperly and others 1995). This study area serves as a long-term monitoring site to track the status of populations, obtain data to support stock assessment and trend analyses, and provide life-history information (Epperly and Braun 1998).

Materials and Methods

A total of 106 blood samples were collected from juvenile green turtles incidentally captured in pound nets set in the study area (Core Sound, eastern Pamlico, and Albemarle Sounds, North Carolina) during September–December from 1995 to 1997. The mean straight carapace length of animals sampled was 32.8 ± 6.8 cm with a range of 24.8–74.4 cm. Approximately 1 ml of blood was placed in 9 ml of lysis buffer (100 mM Tris–HCl, 100 mM ethylenediaminetetraacetic acid, 10 mM NaCl, 0.5% sodium dodecyl sulfate; pH 8.0) and stored at room temperature. Whole DNA isolations from blood samples were conducted with the phenol/chloroform method described by Hillis and others (1996).

A 510-bp fragment located in the control region of the mitochondrial DNA genome was amplified using the primers LTCM1 and HDCM1 of Allard and others (1994) and standard reaction conditions. Cycle sequencing was conducted with an ABI Prism kit and fluorescently labeled dideoxynucleotides at the University of Florida DNA Sequencing Core. The labeled extension products were analyzed with an automated DNA sequencer (Applied Biosystems model 373A). Sequences were edited and aligned using the program SEQUENCHER (v. 3.0), which uses an exhaustive search-and-compare alignment algorithm. Visual inspection and removal of unnecessary gaps prevented misalignments. Polymorphic sites were identified and verified when unique or questionable by sequencing the fragment in the opposite direction. On confirmation of the sequences, they were compared with known green turtle haplotypes ($n = 194$ individuals surveyed by Encalada and others 1996 and Lahanas and others 1998; see also http://accstr.ufl.edu/cmmtdna.html). New haplotypes were deposited in GenBank.

Estimates of haplotype (h) and nucleotide (π) diversities were generated using ARLEQUIN (version 2.001; Schneider and others 2001). To determine how the molecular variation was partitioned within the Atlantic Ocean, an analysis of molecular variance (AMOVA) was performed using ARLEQUIN. For these analyses, the distances were computed using the Tamura–Nei model of nucleotide substitution as implemented in ARLEQUIN with 10 000 permutations to assess the significance of the associated P value. Additionally, exact tests of population differentiation based on haplotype frequencies were conducted using ARLEQUIN. For the exact tests of differentiation, default parameters (10 000 steps in the Markov chain and 1000 dememorization steps) were used.

The nesting, or source, populations used in this study correspond to those characterized in Encalada and others (1996) and Lahanas and others (1998). The green turtle rookeries originally surveyed are located at Ascension Island (United Kingdom), Atol das Rocas (Brazil), Aves Island (Venezuela), east coast of Florida (United States), Lara Bay (Cyprus), Matapica (Surinam), Pailoa (Guinea Bissau), X'cacel and Isla Cozumel (Mexico), and Tortuguero (Costa Rica) (Figure 1). The haplotype composition of these locations is shown in Table 1.

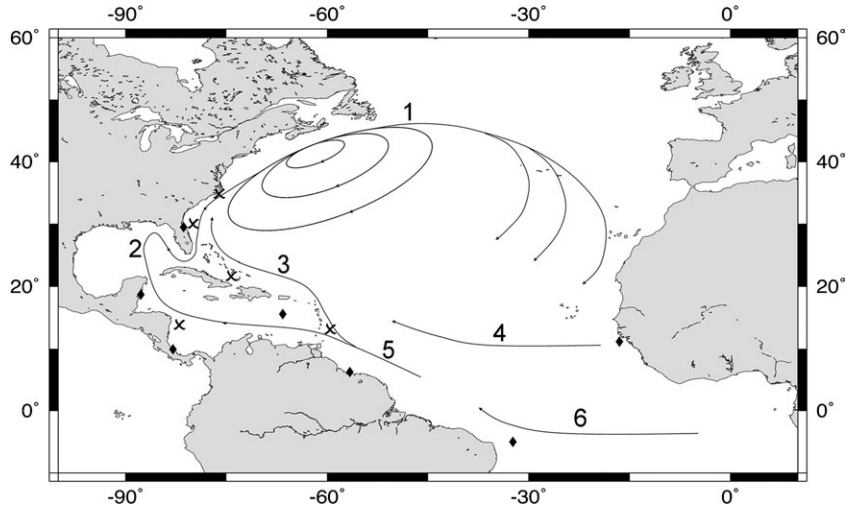

Figure 1. Map of Caribbean and Western Atlantic showing generalized current patterns and locations of nesting populations (♦) and foraging aggregations (×) sampled. 1 = Gulf Stream, 2 = Yucatán Loop, 3 = Antilles, 4 = North Equatorial, 5 = Guiana, 6 = South Equatorial.

Two approaches for estimating the relative contributions of the nesting (source) populations to the foraging aggregation were utilized: ML (SPAM, v. 3.5; Alaska Department of Fish and Game 2001) and Bayesian (BAYES; Pella and Masuda 2001). We used these different approaches because previous experience with ML and Bayesian approaches has yielded different results for loggerhead turtles (Bass and others 2004). These approaches are different in that the ML approach attempts to find a solution given the hypothesis that maximizes the likelihood of observing the data, whereas the Bayesian approach attempts to find a solution that has the greatest likelihood given the observed data. In addition, the Bayesian approach allows the incorporation of prior knowledge about the populations under study, such as population size. We utilized 2 different sets of priors to determine the relative contributions of Atlantic nesting populations to the

Table 1. Green turtle haplotype designations and frequencies of nesting populations and the North Carolina foraging aggregation. Nesting population sizes (minimum to maximum) as reported by Encalada and others (1996) and Lahanas and others (1998) and average population sizes used in the Bayesian analysis

Haplotype	United States	Mexico	Costa Rica	Aves/Surinam	Brazil	Ascension/Guinea Bissau	Cyprus	North Carolina foraging
CM-A1	11	7						34
CM-A2	1							2
CM-A3	12	5	40	3				43
CM-A4			1					
CM-A5		1		40				5
CM-A6				1				
CM-A7				1				
CM-A8					8	35		7
CM-A9					5	1		
CM-A10						3		
CM-A11					1			
CM-A12					2			
CM-A13							9	
CM-A14							1	
CM-A15		1						1
CM-A16		1						2
CM-A17		2						
CM-A18		3						3
N	24	20	41	45	16	39	10	97
Nesting population size	424	100–400	5000–23 000	300–500/2000	50–100	1600–3000/400	100	
Size used in prior	424	250	14 000	2400	75	2700	100	

North Carolina foraging aggregation to see if priors based on population size yielded significantly different results. In one analysis, Bayesian Model 1 (BM1), the baseline priors were determined by the pseudo-Bayes method and the haplotype composition of the stocks (Pella and Masuda 2001). Bayesian Model 2 (BM2) utilized priors based on the relative size of the individual nesting populations as a percentage of the total size of the Atlantic and Mediterranean nesting locations. Although Bass and Witzell (2000) previously concluded that rookery size was not significantly correlated with the estimates of relative contribution to the east-central Florida foraging area, we have used population size as a prior in the Bayesian analysis because this approach has proved useful in MSA of other marine turtles in this same study area (Bass and others 2004). For this analysis, we used population size estimates originally reported in Encalada and others (1996) and Lahanas and others (1998). In cases where a maximum and minimum nesting population estimate was given, an average of the maximum and minimum nesting population size was used to estimate the percentage of the total nesting effort in the Atlantic. Convergence of Markov chain Monte Carlo (MCMC) sampling with BAYES was assessed using the Gelman–Rubin shrink factor (Gelman and Rubin 1992). This shrink factor provides an indication of convergence by comparing the variation within a single chain to total variation among all chains. Values of the shrink factor greater than 1.2 indicate lack of convergence. All analyses of Bayesian and ML approaches to the estimate of the composition of the NC foraging location are presented to illustrate the general agreement among ML and Bayesian methods for the green turtle data set, which differs from the analyses of other species (see Bass and others 2004).

Data from foraging aggregations in the Miskito Cays, Nicaragua (Bass and others 1998), Great Inagua, Bahamas (Lahanas and others 1998), and east-central Florida (Bass and Witzell 2000) are included for comparative purposes and to search for trends in regional foraging locations. We reanalyzed the data sets from the east-central Florida, Bahamas, and Nicaragua foraging aggregations using the Bayesian algorithm and priors based on population size. In these analyses, United States and Mexico were treated as separate populations due to the large number of endemics in the Mexico nesting population. We did not treat Ascension Island and Guinea Bissau as separate populations as did the study on the Barbados foraging aggregation using Bayesian methods (Luke and others 2004). Reanalysis using Bayesian methods allows us to compare previous ML estimates with the Bayesian estimates, in addition to comparing all foraging aggregation estimates with each other.

Results

Ninety-seven of the 106 total sequences matched haplotypes observed at previously surveyed nesting locations (Table 1). The majority of animals were classified as haplotypes CM-A1 ($n = 34$) and CM-A3 ($n = 43$). Seven individuals were characterized as CM-A8, 5 as CM-A5, 3 as CM-A18, 2 each as CM-A2 and CM-A16, and 1 as CM-A15. The remaining 9 individuals had haplotypes not observed at previously surveyed nesting locations. The haplotypes of 3 animals matched CM-A28 (AF366257), which differs from CM-A1 by 2 nt. Two matched haplotype CM-A22 (AF366251), which differs from CM-A1 by 4 nt. Both CM-A22 and CM-A28 were identified previously in a Florida foraging population; however, the nesting origin is unknown. The remaining 4 animals represent newly identified haplotypes, CM-A26 (AF366255) and CM-A27 (AF366256), and both differ from CM-A1 by 1 nt. In general, the number of mutations that define all *C. mydas* haplotypes ranges from 1 to 10, including a 10-nt indel (Encalada and others 1996). Neither the newly identified haplotypes nor the haplotypes unassigned a rookery of origin were included in the MSA.

Haplotype (*h*) and nucleotide (π) diversity estimates for the North Carolina foraging aggregation are 0.7294 ± 0.0301 and 0.0053 ± 0.0031, respectively. The molecular diversity estimates for all other populations (both nesting and foraging) are listed in Table 2. The haplotype frequencies of the North Carolina foraging aggregation were significantly different ($P < 0.05$) from all nesting/source populations except the United States and Mexico. All other foraging aggregations were significantly different ($P \leq 0.05$) from all nesting populations except the east-central Florida foraging aggregation, which was not significantly different from the United States. The haplotype frequencies based on exact tests of differentiation of all foraging aggregations were significantly different ($P < 0.05$) from each other, except Nicaragua and the Bahamas ($P = 0.38$) (Table 3).

AMOVA in this and previously surveyed foraging aggregations and nesting populations yielded a significant $\phi_{ST} = 0.53$ ($P = 0.000$), indicating a greater degree of variation among populations than within. Including only the nesting populations or foraging aggregations generated values of $\phi_{ST} = 0.87$ ($P = 0.000$) and $\phi_{ST} = 0.15$ ($P = 0.000$), respectively. Because one of the foraging aggregations represents adult animals, only the juvenile foraging aggregations were examined, $\phi_{ST} = 0.15$ ($P = 0.000$), resulting in no change in the estimate of population subdivision. Pairwise comparisons of foraging aggregations indicated significant ϕ_{ST} values for all comparisons except Nicaragua versus the Bahamas and east-central Florida (Table 3). This finding differs from the exact test of differentiation based on the haplotype frequencies reported above, which indicated that Nicaragua was significantly different from east-central Florida. A final set of hierarchical groupings was conducted using AMOVA with northern versus southern groupings for foraging aggregations. The hierarchical grouping of northern foraging aggregations in North Carolina, east-central Florida, and Bahamas versus a southern foraging aggregation in Barbados yielded a greater degree of population subdivision with $\phi_{ST} = 0.27$ ($P < 0.005$).

Mixed Stock Analysis

The ML analysis indicated that 5 of the 7 potential stocks contributed to the North Carolina foraging aggregation

Table 2. Haplotype (*h*) and nucleotide (π) diversity estimates plus SDs for all nesting/source populations and foraging aggregations. Estimates were generated using ARLEQUIN (version 2.001)

	Haplotype (*h*) diversity	Nucleotide (π) diversity
Nesting/source populations		
United States	0.5616 ± 0.0468	0.0013 ± 0.0011
Mexico	0.8158 ± 0.0575	0.0051 ± 0.0032
Costa Rica	0.0488 ± 0.0459	0.0001 ± 0.0002
Aves/Surinam	0.2091 ± 0.0789	0.0035 ± 0.0023
Brazil	0.6765 ± 0.0753	0.0017 ± 0.0014
Ascension/Guinea Bissau	0.1930 ± 0.0812	0.0004 ± 0.0006
Cyprus	0.2000 ± 0.1541	0.0004 ± 0.0006
Foraging ground aggregations		
North Carolina, United States	0.7294 ± 0.0301	0.0053 ± 0.0031
Nicaragua	0.1831 ± 0.0621	0.0053 ± 0.0032
Barbados	0.7734 ± 0.0276	0.0102 ± 0.0056
Bahamas	0.3703 ± 0.0650	0.0064 ± 0.0037
East-central Florida, United States	0.4855 ± 0.0668	0.0031 ± 0.0021

(Table 4): United States (63%), Mexico (18%), Costa Rica (7%), Aves/Surinam (4%), and Ascension/Guinea Bissau (7%). The estimates of deviation and confidence intervals (CIs) were large.

When no priors were set in BM1, only the United States and Mexico were indicated as contributors to the foraging aggregation in North Carolina (Table 4). The Gelman–Rubin shrink factors were 1.00 for all estimates. When population size estimates were used to set the priors in BM2, 4 stocks were allocated a significant contribution to the North Carolina foraging aggregation: United States (mean = 0.5401, 97.5% CI = 0.1275–0.8156) Mexico (mean = 0.2672, 97.5% CI = 0.0699–0.6063), Costa Rica (mean = 0.1239, 97.5% CI = 0.0017–0.3372) and Ascension/Guinea Bissau (mean = 0.0465, 97.5% CI = 0.0000–0.1195) (Table 4). Gelman–Rubin shrink factors were all less than 1.20 indicating convergence in the MCMC chains. We consider the results of BM1 to be a conservative estimate of the number of contributors to the North Carolina foraging aggregation and believe that the estimates from BM2 are more biologically realistic. Qualitatively, the presence of CM-A6 and CM-A8, found only in Aves/Surinam and Brazil or Ascension/Guinea Bissau, respectively, suggests the presence of animals from nesting locales other than the United States and Mexico.

Reanalysis of the other foraging aggregations, excluding Barbados, yielded some differences in the ML point estimates generated previously (Table 5). For example, the Bayesian analysis attributed less of a contribution from the Mexican and Costa Rican nesting populations to the east-central Florida foraging aggregation, allocating more to the United States. In this case, the rare Mexico haplotype, CM-A18, found in the east-central Florida foraging aggregation (Bass and Witzell 2000) led the ML analysis to allocate a higher contribution to Mexico while the Bayesian analysis placed less importance on this rare haplotype. The effect of a rare haplotype, in this case in the Bahamas foraging aggregation, decreased the contribution for the United States and resulted in a point estimate much less than one for Mexico (not shown). Generally, the Bayesian methods did not improve the estimates of contribution to these foraging aggregations.

Discussion

Understanding the genetic composition of foraging aggregations allows researchers to track the status of populations, obtain data to support stock assessment and trend analyses, and provide life-history information (Epperly and Braun 1998). Individuals from the rookery in the United States (54%) dominate the foraging aggregation in North Carolina with significant contributions from the Mexican (27%) and Costa Rican (12%) nesting populations. The remaining proportion (7%) was allocated to nesting populations in the southern Atlantic. Point estimates from both the ML and Bayesian analyses had large CIs; therefore, these point estimates should be used as general indicators of source contributions as should all estimates shown in Table 5. The relatively high number of previously unidentified haplotypes, 4 haplotypes and 9 individuals, support either the presence of unsampled nesting locations contributing to the pool of mixed early juveniles or the occurrence of these haplotypes at low frequency in previously sampled nesting locations. Further research to identify the origin of these unidentified haplotypes and therefore determine the relative contribution of these unsampled nesting populations to North Carolina and other foraging aggregations is necessary for a more complete assessment of foraging aggregations in the Atlantic.

As noted previously, reanalysis of these data sets using Bayesian methods did not significantly improve estimates

Table 3. Results of pairwise comparisons of foraging aggregations based on both ϕ_{ST} as derived from Tamura–Nei distances and exact tests of differentiation as derived from observed haplotype frequencies. The *P* values for ϕ_{ST} are shown above the diagonal and for exact tests of differentiation are below the diagonal. Values not significant at 0.05 are indicated by an asterisk

	Nicaragua	North Carolina	Barbados	Bahamas	East-central Florida
Nicaragua	—	0.00098	0.00000	0.15820*	0.12598*
North Carolina	0.00000	—	0.00000	0.00586	0.03125
Barbados	0.00000	0.00000	—	0.00000	0.00000
Bahamas	0.33655*	0.00000	0.00000	—	0.01855
East-central Florida	0.00000	0.02970	0.00000	0.00095	—

Table 4. ML and Bayesian point estimates, SD, and CIs (95% and 97.5%, respectively) of contribution by nesting aggregations to the North Carolina foraging aggregation

Nesting aggregation	Mean	SD	CIs
ML			
United States	0.6308	0.1188	0.398–0.864
Mexico	0.1800	0.0707	0.041–0.318
Costa Rica	0.0717	0.0916	0.000–0.251
Aves/Surinam	0.0453	0.0246	0.000–0.094
Brazil	—	—	—
Ascension/Guinea Bissau	0.0723	0.0263	0.021–0.124
Cyprus	—	—	—
BM1			
United States	0.3984	0.3656	0.0000–0.8937
Mexico	0.6016	0.3656	0.1063–1.0000
Costa Rica	—	—	—
Aves/Surinam	—	—	—
Brazil	—	—	—
Ascension/Guinea Bissau	—	—	—
Cyprus	—	—	—
BM2			
United States	0.5401	0.1775	0.1275–0.8156
Mexico	0.2672	0.1429	0.0699–0.6063
Costa Rica	0.1239	0.0946	0.0017–0.3372
Aves/Surinam	0.0221	0.0274	0.0000–0.0938
Brazil	0.0001	0.0018	0.0000–0.0003
Ascension/Guinea Bissau	0.0465	0.0364	0.0000–0.1195
Cyprus	—	—	—

of contribution in the sense of lowering the standard deviations (SDs) and shrinking the CIs. Unlike other data sets that benefit from an informed Bayesian analysis, for example, loggerheads (Bass and others 2004; Bowen and others 2004), the green turtle data set does not seem to fit this category. On the contrary, contributions from the United States and Mexico to the Bahamas and east-central Florida foraging aggregations were affected such that no contributions from either source population were indicated. Although it has been suggested that informed priors in Bayesian analyses may alleviate some of the issues associated with rare haplotypes (Pella and Masuda 2001), we find them problematic (but see Bolker and others 2003).

Of the 5 foraging aggregations previously surveyed using MSA, Barbados and North Carolina aggregations exhibit a larger number of source populations (see Table 5) coupled with high haplotype diversity (Table 2). The Bahamian aggregation is composed primarily of turtles from Costa Rica and Aves/Surinam, both of which exhibit low haplotype diversity (Table 2). There are indications of other contributors such as Ascension Island/Guinea Bissau and the United States, but these appear to be minimal. Although turtles from the 4 juvenile green turtle foraging aggregations are similar in size (Table 5), the differences among their respective haplotype composition indicate a nonrandom distribution of animals among these foraging locations (Table 3).

The Nicaraguan sample is the only survey of an adult group, apparently composed primarily of turtles from the nesting beach in adjacent Costa Rica. If adult foraging grounds are adjacent to natal beaches, then it is not surprising that the diversity is lowest at this foraging ground as the adjacent nesting beach at Costa Rica also exhibits low haplotype diversity. A caveat is that only 60 animals were surveyed in the foraging ground study, and an increase in sample size may detect contributions from other nesting populations in the Caribbean. Nicaragua and the Bahamas are surprisingly similar in terms of contributors and proportions of contribution (Table 5). Neither are they highly variable in terms of haplotype diversity (Table 2) nor are they significantly different from each other in terms of the observed haplotype frequencies ($P = 0.38$). Pairwise comparisons of ϕ_{ST} indicated that the foraging aggregations at east-central Florida and the Bahamas were not significantly different from the Nicaragua aggregation, although, east-central Florida and the Bahamas were significantly different from each other ($P = 0.02$). This finding is surprising as the east-central Florida aggregation

Table 5. Summary of the estimated percent contributions (± SD) and size classes (straight carapace length) of 1 adult (Nicaragua) and 4 juvenile green turtle foraging aggregations located in the Caribbean and western Atlantic. The ML estimates were summarized from the following sources: Nicaragua (Bass and others 1998), Bahamas (Lahanas and others 1998), and East-Central Florida (Bass and Witzell 2000). The Bayesian contribution estimates for Nicaragua, Bahamas, and East-central Florida are from analyses using a prior based on population estimates and separating the United States and Mexico source populations. Only the Barbados Bayesian estimates are secondary data (Luke and others 2004). Bayesian estimates with SDs larger than the point estimate are italicized

	Foraging aggregation							
	Nicaragua		Bahamas		East-central Florida		North Carolina	Barbados
Nesting aggregation	ML	Bayesian	ML	Bayesian	ML	Bayesian	Bayesian	Bayesian
United States			0.05 (0.03)	*0.02 (0.03)*	0.37 (0.12)	0.48 (0.17)	0.54 (0.18)	0.18 (0.16)
Mexico					0.09 (0.06)	*0.04 (0.07)*	0.26 (0.14)	0.10 (0.10)
Costa Rica	0.91 (0.04)	0.89 (0.05)	0.80 (0.05)	0.83 (0.06)	0.49 (0.12)	0.44 (0.15)	0.12 (0.09)	0.19 (0.12)
Aves/Surinam	0.09 (0.04)	0.10 (0.05)	0.14 (0.04)	0.14 (0.04)	0.05 (0.03)	0.03 (0.03)	*0.02 (0.03)*	0.23 (0.06)
Brazil								*0.01 (0.02)*
Ascension Island			0.01 (0.01)	0.01 (0.01)			0.05 (0.04)	0.24 (0.08)
Guinea Bissau								*0.03 (0.05)*
Cyprus								
Size class (cm)	88.3–105.7		31–67		25–70		24–74	31–70

contains a high contribution from the adjacent US nesting aggregation (Table 5), whereas Nicaraguan turtles are nesting at the adjacent and largest green turtle rookery in the Caribbean—Tortuguero, Costa Rica (Bass and others 1998). Based on the natal homing behavior of adult green turtles and the similarity in genetic composition of their respective populations, it is likely that the majority of juveniles sampled from the Bahamas will join the adults foraging in Nicaragua once they are reproductively active. Tag returns of green turtles marked in the Bahamas provide support for the movement to Nicaragua (Bjorndal and others 2003), but whether this is concurrent with the shift to reproductive activity is not known. Further investigations of the Nicaraguan foraging aggregation and other adult foraging aggregations would augment our understanding of migration and life-cycle characteristics of green turtles.

Several studies have investigated the relationships between population size and distance and the proportional contributions to the foraging population. In the Bahamas, the estimated contribution of rookeries to a juvenile foraging ground was significantly correlated with population size, prompting Lahanas and others (1998) to suggest a life-cycle model of mixing of early juveniles in pelagic habitats and random settling into the benthic environment as a consequence of ocean currents. If hatchlings are uniformly mixed in the pelagic habitat and randomly settle into the benthic environment, then the composition of regional benthic foraging aggregations would be similar and controlled primarily by the size of the nesting (source) populations. However, our examination of green turtle foraging grounds on a regional scale indicates that the haplotype composition of juvenile foraging aggregations are significantly different from each other in terms of haplotype composition and, therefore, are not the product of random recruitment. If mixing within the pelagic habitat were disrupted by some factorss during recruitment to the benthic environment, then one would expect to see a nonrandom distribution of haplotypes among foraging locations.

One factor that could create a nonrandom distribution is continuous movement between foraging locations. We do not believe that individuals are moving between foraging locations in significant numbers unless they are shifting in response to the onset of reproductive activity. Juvenile residency (defined as an animal recaptured in the same area among years) on foraging grounds was documented in Florida with green turtles (Mendonça and Ehrhart 1982). Other factors that may create a nonrandom distribution of haplotypes among foraging aggregations include movements due to seasonal temperature changes in temperate areas, temporal variation in nesting population activity, continuous foraging aggregation recruitment due to the long maturation periods of marine turtles, currents, and behavior. We know of only one published attempt to assess temporal variation in foraging ground composition (Bass and others 2004) and no attempts to address the other factors. Hence, we will concentrate on currents and behavior as the leading hypothesis. We acknowledge that the relative influence of these 2 factors is hard to distinguish.

Multiple authors have suggested the importance of currents in marine turtle life cycles (Hughes 1974; Carr and Meylan 1980; Witham 1980). Witham (1980) proposed a model whereby early juveniles from Florida move into the Gulf Stream, are transported into the North Atlantic gyre, and are returned to the Caribbean and Florida by the North Equatorial Current (Figure 1). Based on the presence of numerous smaller gyres off the Gulf Stream, we suggest that on attaining an appropriate size/age, turtles will actively move out of the constraints of the Gulf Stream current and associated gyres and recruit to adjacent foraging locations. Smaller gyres may shunt early or late juveniles off the main Gulf Stream current and into the western Sargasso Sea, precluding a trans-Atlantic crossing and positioning the animals closer to foraging locations along the east coast of the United States and areas in the northern Caribbean. The entrapment in the Sargasso Sea could potentially explain the large number of Mexican turtles in North Carolina waters relative to other Caribbean foraging locations surveyed. Likewise, the strong influence of the Gulf Stream and North Equatorial Current may explain the presence of United States, Mexican, and Costa Rican turtles in Barbados (Luke and others 2004).

The high diversity of the foraging aggregations in Barbados, North Carolina, and to a lesser degree in east-central Florida may be a result of their positions relative to major and minor current systems. Barbados is positioned at the confluence of several major currents: the North and South Equatorial and Guiana Currents (Figure 1). The Florida Current, Gulf Stream, Antilles Current, and minor gyres located off the Gulf Stream influence both east-central Florida and North Carolina. It would seem that the Bahamas would exhibit a higher level of diversity, but the position of Great Inagua in the lower region of the chain of islands may result in fewer animals from the east coast of Florida and Mexico accessing this region. Modeling of currents in the Caribbean indicates a much more complex system, and the movement and dissipation of westward-moving eddies can greatly affect local (island level) currents (Murphy and others 1999). Seasonal and temporal variations of currents in the Caribbean may change the composition of foraging aggregations by affecting the distribution of animals at critical stages during their early life history. This phenomenon coupled with changes in population size of nesting aggregations and hatchling production could result in fluctuations in composition over time (Bass and others 2004). Long-term data on the composition of foraging aggregations would allow researchers to better understand the complex interactions of currents and population size on foraging ground recruitment.

Homing to a foraging area located in the proximity of a natal beach may also be affecting the architecture of the juvenile foraging aggregations. Encalada and others (1996) observed a phylogeographic division among nesting populations that reflected a western Caribbean and Mediterranean group and an eastern Caribbean, South Atlantic, and West African group. From a UPGMA (Unweighted Pair Group Method for Arithmetic Mean) haplotype tree, estimates of haplotype frequency shifts, and migration estimates, the authors hypothesized this division to be a result of multiple

dispersal events associated with glacial and climatic changes. Using AMOVA, we also find significant genetic partitioning among the nesting locations, indicating strong structure within the Caribbean and Atlantic. In fact, the estimates of genetic structure reported here for nesting and foraging aggregations are higher than those observed for loggerhead nesting and foraging aggregations ($\phi_{ST} = 0.42$ and 0.01, respectively; Bowen and others 2005). The MSA supports a regional grouping within the Caribbean as evidenced by the domination of northern foraging locations by animals from the northern nesting populations (United States, Mexico, and Costa Rica). When comparing juvenile foraging aggregations ($\phi_{ST} = 0.27$; $P < 0.005$), we find support for this phylogeographic split. The southern foraging ground aggregation in Barbados is dominated by the nesting populations located in the southern Caribbean or middle and eastern Atlantic (Aves Island, Surinam, Ascension Island, and Guinea Bissau). These findings indicate the prominent role that currents and initially passive migration of early juveniles play in the placement of green turtles within the large expanses of the Caribbean and western Atlantic. We predict that the composition of other green turtle foraging ground aggregations in the southern Caribbean will also be dominated by the southern nesting populations included here, reflecting the role of currents in shaping the composition of foraging aggregations. However, the influence of behavior cannot be discounted. Whereas loggerhead turtles (*C. caretta*) exhibit a tendency for juveniles to recruit to foraging locations adjacent to their natal beaches (Bowen and others 2004), green turtles may be doing the same but on a larger scale. The segregation of the juvenile foraging aggregations into a pattern that mirrors that of the phylogeography of the nesting populations supports this idea of juvenile natal homing. In conclusion, we suggest that the deposition of juvenile turtles into neritic foraging habitats is the result of an interaction between both contemporary currents and past colonization events that shaped the distribution of the nesting beaches and loosely the location of foraging aggregations.

The distribution of green turtles throughout the Caribbean and Atlantic highlights the lack of national boundaries in marine environments. Human-defined boundaries and border patrols do not regulate the passage of animals through the ocean basins. Our recognition of this fact and the importance of managing migratory marine populations within an internationally cooperative framework are absolutely necessary to assure the survival and success of marine turtle populations. Genetic studies of foraging ground aggregations highlight the mixing of marine turtle populations and provide frameworks for accessing life-history information necessary for successful management (Bowen and others 2005).

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