RESEARCH ARTICLE

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Origins of green turtle (*Chelonia mydas*) feeding aggregations around Barbados, West Indies

Abstract Although green turtles (*Chelonia mydas* Linnaeus) do not nest in Barbados, the easternmost island in the Caribbean archipelago, juveniles are regularly seen foraging in nearshore waters. To examine the stock composition of this foraging population, mitochondrial (mt) DNA control region sequences were analysed from 60 juvenile (31–70 cm curved carapace length) green turtles and compared with data published for key nesting populations in the Atlantic, as well as other feeding grounds (FGs) in the Caribbean. Eight distinct haplotypes were recognised among the 60 individual green turtles sampled around Barbados. Three of the haplotypes found have only previously been reported from western Caribbean nesting beaches, and two only from South Atlantic beaches. The nesting beach origin of one of the Barbados FG haplotypes is as yet unidentified. Stock mixture analysis based on Bayesian methods showed that the Barbados FG population is a genetically mixed stock consisting of approximately equal contributions from nesting beaches in Ascension Island (25.0%), Aves Island/Surinam (23.0%), Costa Rica (19.0%), and Florida (18.5%), with a lesser but significant contribution from Mexico (10.3%). Linear regression analysis indicated no significant effects of rookery population size or distance of the rookery from the FG on estimated contributions from the source rookeries to the Barbados FG. Our data suggest that the similar-sized green turtles sampled on the Barbados FG are a mixed stock of more diverse origins than any previously sampled feeding aggregations in the Caribbean region. The relatively large contribution from the Ascension Island rookery to the Barbados FG indicates that hatchlings from distant rookeries outside the Caribbean basin enter the North Atlantic gyre and become a significant part of the pool from which eastern Caribbean foraging populations are derived. These data support a life cycle model that incorporates a tendency of immatures to migrate from their initial foraging grounds at settlement towards suitable foraging grounds closer to their natal rookeries as they mature.

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Introduction

Studies of maternally inherited mitochondrial DNA (mtDNA) in endangered (cf. IUCN: the World Conservation Union) green turtles (*Chelonia mydas*) have been useful in understanding the population structure and reproductive behaviour of these highly migratory marine animals (Bowen et al. 1992; Allard et al. 1994; Lahanas et al. 1994; Norman et al. 1994; Encalada et al. 1996). MtDNA analyses of adult females nesting at nine rookeries around the Atlantic and Mediterranean (Florida, Costa Rica, Aves Island, Surinam, Mexico, Brazil, Ascension, Guinea Bissau, and Cyprus) have indicated that there are significant genetic differences between populations (Lahanas et al. 1994; Encalada et al. 1996), providing support for natal homing in this species (Allard et al. 1994) and demonstrating the existence of distinguishable stocks for management purposes (Bowen and Karl 1997).

The movements of immature green turtles from the time that they leave the beach as hatchlings, through their developmental years as juveniles in various marine habitats, have been more difficult to elucidate. However, the presence of fixed or nearly fixed differences between specific nesting populations has now been sufficiently well characterised in the Atlantic region (Lahanas et al. 1994; Encalada et al. 1996) such that mtDNA alleles can be used as genetic markers to determine the natal origins of juvenile turtles sampled in their developmental

habitats or along migratory pathways (Bass et al. 1998; Lahanas et al. 1998; Bass and Witzell 2000).

All feeding ground (FG) studies to date indicate stocks of mixed origins, differing significantly from location to location. Lahanas et al. (1998) showed that juvenile green turtles sampled on their FG in Great Inagua, Bahamas originated from multiple nesting colonies, but that over three-quarters (79.5%) originated from nesting beaches in Costa Rica, 5% from Florida and Mexico, 12.9% from beaches in the eastern Caribbean at Aves Island and Surinam, and 1% from central and east Atlantic locations of Ascension Island/Guinea Bissau. Bass et al. (1998), in their study of adult green turtles from an important FG off the northeast coast of Nicaragua, found only two different haplotypes in the population sampled and concluded that 90% of the animals originated from the nearby Tortuguero rookery in Costa Rica and 10% from the Aves Island/Surinam nesting beaches. Bass and Witzell (2000) found significant differences between the juveniles sampled on the east central Florida FG of their study (53% Costa Rica, 42% Florida/Mexico, and 4% Aves Island/Surinam) and the juveniles sampled from the Bahamas (Lahanas et al. 1998), despite the two locations being only a few hundred kilometres apart. Although there were differences between the east central Florida juvenile FG and the adult FG sampled in Nicaragua, the juvenile Bahamian population did not differ from the Nicaraguan sample (Bass et al. 1998).

Lahanas et al. (1998) hypothesised that individuals emerging from different nesting beaches become pooled in pelagic and benthic habitats as a result of ocean currents and the movement of animals between feeding grounds, and that FG composition is largely determined by population size of rookeries (at least those within 3,500 km). Bass and Witzell (2000) suggested that proximity of the nesting location to a FG may be more important than the size of the nesting population and hypothesised that as juveniles mature, they may move towards feeding grounds near their natal beaches from where they will ultimately make their reproductive migrations.

Barbados is the most easterly island in the Caribbean archipelago, positioned where the north equatorial current of the Atlantic gyre and the south-westerly Guiana/south equatorial current first enter the Caribbean. It is closer to the Aves Island/Surinam and Ascension Island rookeries than any previously studied FG population in the Atlantic. Green turtles have never been known to nest in Barbados, and adults are rarely seen foraging around the island. However, juvenile green turtles ranging between 31 and 70 cm curved carapace length (CCL) are found coincident with seagrass and algal habitats. The objectives of this study were (1) to compare the mtDNA haplotypes of the foraging green turtles around Barbados with haplotypes that have been identified from the Atlantic and Mediterranean nesting beaches, to ascertain natal origins of the Barbados foragers, (2) to compare the composition of haplotypes on the Barbados FG with that of foraging populations sampled elsewhere in the Caribbean, and (3) to comment on the relative importance of rookery proximity, rookery population size, and oceanographic current patterns as predictors of FG composition.

Materials and methods

MtDNA d-loop sequence analysis was carried out on tissue samples collected from 60 juvenile green turtles ranging in CCL from 31 to 70 cm, which were obtained at sites off the western, south-western, and eastern coasts of Barbados between March 1999 and September 2000. The samples were preserved using a 20% dimethyl sulphoxide (DMSO) solution saturated with sodium chloride (Dutton 1996). DNA was isolated from 44 samples using standard phenol/chloroform extraction techniques (Sambrook et al. 1989) whilst the remaining 16 were extracted using the Fast Prep DNA isolation kit (Bio101). Amplification of mtDNA was performed by PCR using the primers HDCM2 and LTCM2, designed to target 488 bp at the 5′ end of the control region of the mitochondrial genome (Lahanas et al. 1994). Template DNAs were amplified in 50 μl PCR reactions on a Perkin Elmer 480 thermocycler using the following profile: initial denaturation at 94°C for 2 min, followed by 36 cycles of (1) DNA denaturing at 94°C for 50 s, (2) primer annealing at 52°C for 2 min, and (3) primer extension at 72°C for 1 min 30 s, concluding with a final primer extension for 5 min at 72°C. The sizes of the amplified products were determined using electrophoresis in a 2% agarose gel stained with ethidium bromide. PCR products were then purified using the Qiaquick PCR purification kit (Qiagen 1995) and stored at 4°C. Direct cycle sequencing reactions of the light strand were performed on 2 μl of purified PCR product combined with 2 μl of ABI Prism dRhodamine terminator cycle sequencing kit, 3 μl of primer LTCM2. and 5 μl purified water. The labelled extension products were then purified via ethanol precipitation and analysed with an Applied Biosystems model 377 automated DNA sequencer. The sequences were analysed for uncalled and miscalled bases using either Gene Codes Sequencher 3.1.1 or ABI SeqED v. 1.0.2.

Statistical analysis comparing haplotype frequencies found within the Barbados foraging population with previously reported haplotype frequencies for nine nesting colonies as described in Lahanas et al. (1998) was conducted using the chi-square test. The sequential Bonferroni method was used to correct the probabilities obtained by the chi-square test for multiple tests (Rice 1989).

The biases inherent in the standard maximum likelihood (ML) techniques typically used to estimate rookery contributions to foraging grounds have long been recognized (Chapman 1996; Pella and Masuda 2001), although they have continued to be applied for lack of alternatives. The Bayesian method, using Markov chain Monte Carlo (MCMC) estimation, offers an approach that allows for rare haplotypes that are actually present in a particular rookery but not detected in a small sample and has the potential to correct for problems of bias better than the standard ML methods (Pella and Masuda 2001). Although the MCMC method gives more accurate confidence limits than ML with bootstrapping, which tends to underestimate small contributions, there is little qualitative difference between point estimates of sea turtle stock contributions using MCMC and ML methods (Bolker et al. 2003). We therefore used the new Bayesian methods as implemented in the program BAYES (Pella and Masuda 2001). Estimates of contributions by different nesting populations to the Barbados FG were based on Bayesian analysis using MCMC estimation from 6,320 resamplings of four stock mixtures composed of green turtles from eight major nesting stocks. The baseline rookery data are the same as those used in previous mixed-stock-analysis FG studies. Previous chi-square tests comparing haplotype frequencies of Aves Island and Surinam have shown no significant differences (Encalada et al. 1996; Lahanas et al. 1998) and are lumped as a single rookery in the

Bayesian analysis used in the present article. FG frequency comparisons between Barbados and the Bahamas, east central Florida, and Nicaragua were conducted using similar chi-square techniques. To test whether rookery size and/or distance from Barbados correlated with contributions to the FG, a regression analysis was conducted with size of rookery (both minimum and maximum estimates of rookery size) and distance of the rookery from the FG as independent variables and the MCMC estimates of contributions to the FG (arcsine transformed) as the dependent variable. Great circle distances between the source rookeries and Barbados were calculated using exact longitude and latitude coordinates. Minimum and maximum rookery population size estimates were obtained from Bass and Witzell (2000).

Results

Eight distinct haplotypes were recognised among the 60 individual green turtles sampled around Barbados. Three of the haplotypes found (I, III, and XVII) have only previously been reported from western Caribbean nesting beaches, and two (IX and X) only from South Atlantic beaches (Table 1). Haplotypes V and VIII have been reported from more widely separated nesting beaches, that is, Mexico, Aves Island, and Surinam for haplotype V, and Brazil, Ascension Island, and Guinea Bissau for haplotype VIII. The nesting beach origin of haplotype XXII is as yet unidentified, but haplotype XXII represents only 1.7% ($n = 1$) of the FG samples from Barbados. Haplotypes found in Cyprus were not observed in this study.

Haplotype frequencies indicate that the green turtle foraging population around Barbados is a genetically mixed stock consisting of individuals originating from nesting beaches of the western and eastern Caribbean (Florida, Mexico, Costa Rica, Aves Island, Surinam), the South Atlantic (Ascension Island and possibly Brazil), and possibly the east Atlantic (Guinea Bissau; Table 1). Of the 60 individuals sampled, 35% ($n = 21$) exhibited haplotype III, 23.3% ($n = 14$) exhibited haplotype VIII, and 21.7% ($n = 13$) exhibited haplotype V. Amongst the remaining 12 individuals, five additional haplotypes were found [haplotypes I ($n = 7$), X ($n = 2$), and IX, XVII, and XXII (each with $n = 1$; see Table 1]. There was no difference in the mean CCL of turtles identified as haplotypes I and III from predominantly western Caribbean rookeries (50.6 cm), those identified as haplotype V from eastern Caribbean rookeries (47.6 cm), and those identified as VIII, IX, and X predominantly from central Atlantic rookeries (48.6 cm; $F = 0.42$, $P > 0.05$).

A comparison of haplotype frequencies revealed significant differences between the Barbados FG population and each of the nesting colonies ($\alpha = 0.05$). The difference in haplotype frequencies between samples from the Barbados and Bahamas FG ($\chi^2 = 32.3$, $df = 3$), Barbados and the east central Florida FG ($\chi^2 = 29.1$, $df = 3$, and Barbados and the Nicaraguan FG ($\chi^2 = 38.1$, $df = 3$) were all highly significant ($P < 0.001$ in each case). For each FG comparison, the chi square was calculated conservatively using the four most common haplotypes

to minimise the possibility of type I errors caused by small cell sizes (Clewer and Scarisbrick 2001).

Results of the Bayesian analysis indicate that the Barbados FG aggregation is likely composed of contributions from all of the potential source populations surveyed to date, except Cyprus (Table 2). We estimated approximately equal contributions from nesting beaches in Ascension Island (25%, including a haplotype X that is endemic to Ascension) and Aves Island/Surinam (23%), with lesser but significant contributions from Costa Rica (19.1%), Florida (18.5%), and Mexico (10.3%), and minor contributions of approx 3.1% from Guinea Bissau and 1.1% from Brazil (see Fig. 1).

To investigate hypotheses concerning factors that might affect contributions to the Barbados FG, only those populations that were estimated to contribute to the FG are considered (Table 2). Estimated results of contributions from the various rookeries were first compared with expected values based on equal contributions from each of the seven potential source stocks. The hypothesis predicting that all rookeries have an equal probability of contributing individuals to the FG was rejected ($\chi^2 = 26.8$, $df = 6$, $P < 0.001$). Linear regression analysis indicated no significant effects of either minimum rookery population size and distance of the rookery from the FG ($F = 0.89$, $P > 0.05$) or maximum population size and distance of the rookery from the FG ($F = 0.38$, $P > 0.05$) on estimated contributions from the source rookeries to the Barbados FG.

Discussion

Immature green turtles are thought to spend up to 10 years in the pelagic stage making several rotations through the various current systems of the Atlantic before shifting to a benthic feeding habitat at about 25–40 cm straight carapace length (SCL; Bjorndal and Bolten 1988; Lahanas et al. 1998). Previous FG studies of juveniles of a similar size range to the present study (i.e. 25–70 cm SCL) have revealed that the populations are composed of different mixed stocks (Lahanas et al.1998; Bass and Witzell 2000). In their FG study, Lahanas et al. (1998) found that the juvenile green turtles (31–67 cm SCL) around the Bahamas were composed primarily of individuals originating from the western Caribbean Costa Rican rookery (80%), and to a lesser extent, the eastern Caribbean Aves Island/Surinam rookeries (13%). Bass and Witzell (2000) sampled a similar size class (25–70 cm SCL) a few hundred kilometres away off east central Florida but found almost equivalent contributions from Costa Rica (53%) and Florida/Mexico (42%), and markedly less from Aves Island/Surinam (4%). Our data suggest that the similar-sized green turtles sampled on the Barbados FG (31–70 cm CCL) are a mixed stock of more diverse origins than any previously sampled feeding aggregations in the Caribbean region. The Barbados FG turtles derived in approximately equal measure from Ascension

Table 1 Green turtle haplotype composition for the Barbados feeding ground (FG) population compared with rookery data from Allard et al. (1994), Lahanas et al. (1994, 1998), and Encalada et al. (1996), and FG data from Bahamas (Lahanas et al. 1998), east central Florida (Lahanas et al. 1998), and Nicaragua (Bass et al. 1998). *Asterisk* denotes haplotype not identified at any rookery sampled to date. Haplotype XXII most closely resembles that of XVII

Haplotype	Nesting colony location									Bahamas FG	East central Florida FG	Nicaragua FG	Barbados FG
	Florida	Mexico	Costa Rica	Aves	Surinam	Brazil	Ascension Island	Guinea Bissau	Cyprus				
I	11	7								2	12	54	7
II	1										1		
III	12	5	40							62	43		21
IV			1										
V		1		27	13					10	3	6	13
VI					1								
VII					1								
VIII				3				19		1			14
IX						8	16						1
X						5	1						2
XI							3						
XII						1							
XIII						2							
XIV									8				
XV									1				
XVI		1											
XVII		1											
XVIII		2									2		1
XIX		3								1			
XX										1			
XXI										3			
XXII*											1		1

Table 2 Estimates of contributions by different nesting populations to the Barbados foraging ground population, based on Markov chain Monte Carlo (MCMC) estimations from 6,320 resamplings of four stock mixtures composed of green turtles from eight major nesting stocks in the Atlantic and Mediterranean. If a foraging population haplotype had not been previously identified at a nesting location (i.e., XXII), the sample was excluded from the analysis, resulting in $n = 59$ used in the analysis. Median and 95% confidence limits (2.5% and 97.5% quantiles) are shown

Nesting stock	Mean	SD	Median	Lower quantile	Upper quantile
Florida	0.1848	0.1556	0.1624	0.0000	0.5046
Mexico	0.1031	0.1031	0.0726	0.0000	0.3651
Costa Rica	0.1906	0.1211	0.2007	0.0000	0.4150
Surinam/Aves Island	0.2300	0.0634	0.2280	0.1137	0.2280
Brazil	0.0110	0.0240	0.0006	0.0000	0.0813
Ascension Island	0.2497	0.0835	0.2528	0.0670	0.4112
Guinea Bissau	0.0307	0.0560	0.0027	0.0027	0.1986
Cyprus	0.0000	0.0000	0.0000	0.0000	0.0000

Island, Aves Island/Surinam, Costa Rica, and Florida, indicating important contributions from the central Atlantic, eastern Caribbean, and western Caribbean source regions, respectively (Lahanas et al. 1998), with a markedly lower contribution from the Gulf of Mexico nesting stock.

One should be cautious when interpreting the results of green turtle FG mixed-stock analysis, since not all rookeries have been adequately sampled around the Atlantic. Our finding of one turtle with a haplotype on the Barbados FG that has not been identified on a nesting beach illustrates this. Use of larger sample sizes than those published to date may result in detection of additional rare haplotypes at nesting beaches. It is possible that the haplotypes that so far appear to be endemic to Ascension Island may be detected by future studies in some of the green turtle rookeries in

West Africa or elsewhere. It is also possible that the contributions of Brazil or Guinea Bissau to the Barbados FG mix may be underestimated in our analysis, if indeed larger sample sizes reveal the presence of the rare haplotypes IX and X in either population. Whether or not this proves true, our notable finding, that we detected a relatively large contribution from a source population outside the Caribbean basin, would remain the same.

Factors found to influence the contribution of various rookeries to FGs vary. Lahanas et al. (1998) concluded that the size of nesting colonies was an important factor in influencing FG composition, at least for those nesting colonies within 3,500 km of the FG. The Tortuguero green turtle rookery in Costa Rica is at least an order of magnitude larger than any other known rookery that can potentially contribute to Caribbean FGs. It has been suggested that the relative abundance of Costa Rican haplotypes in the gene pool compared to those from other nesting beaches is a primary reason why all Caribbean FGs might be expected to have significant contributions from this rookery (see Lahanas et al. 1998). However, Bass and Witzell (2000), working on a FG a few hundred kilometres away from that of Lahanas et al. (1998), found that the distance between rookery locations and the FG may be more important than the size of the source rookeries. The results of the present study found no significant influence of either size or distance of the source rookery from the FG on the estimated contributions of different rookeries to the Barbados FG.

The three largest Atlantic rookeries identified to date are Costa Rica, Aves Island/Surinam, and Ascension Island. Between them, they are estimated by Bayesian analysis to contribute more than 65% to the Barbados FG. However, instead of a significantly larger contribution coming from the largest rookery, Costa Rica, contributions from the three rookeries are almost equal (Ascension Island 25%, Aves Island/Surinam 23%,

Fig. 1 Map of the Atlantic region showing green turtle (*Chelonia mydas*) rookeries (excluding Cyprus) relative to Barbados' foraging population. Mean percentage contributions by the different nesting populations, as estimated by Markov chain Monte Carlo estimation, are indicated. Note: the pathways shown are not indicative of migratory corridors
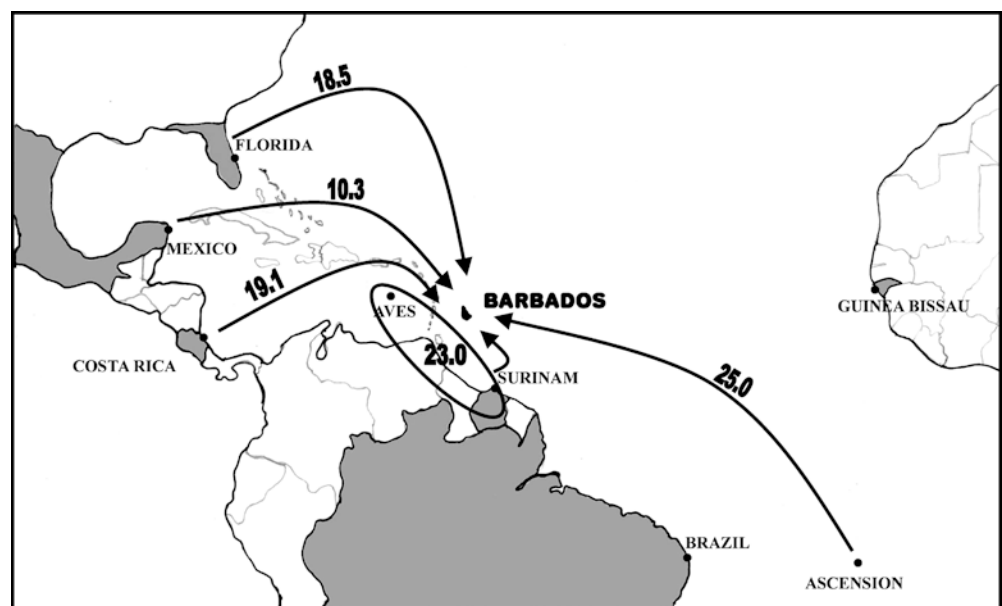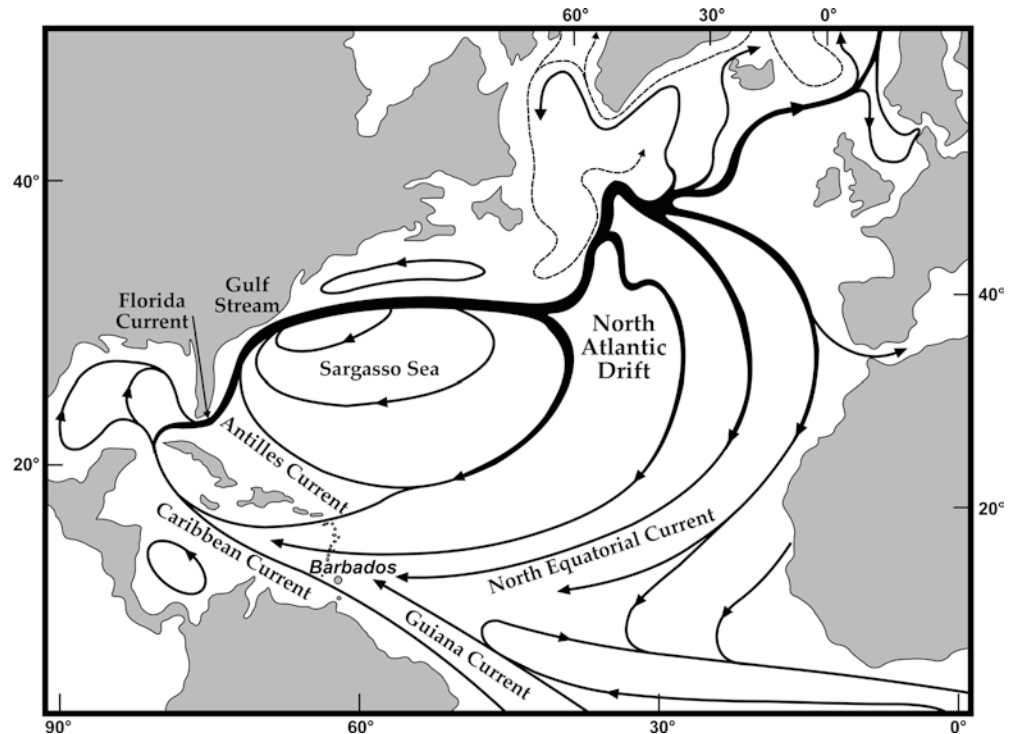
Fig. 2 The major Atlantic currents affecting the Caribbean region

Costa Rica 19%). Furthermore, a similar contribution (18.5%) is estimated from the much smaller Florida rookery.

The large contributions from Aves Island/Surinam and Ascension Island to the Barbados FG could be explained by a tendency for turtles to move to FGs closer to their natal beaches as they mature (Bass and Witzell 2000). However, the absence of any size classes larger than about 70 cm CCL around Barbados, the significant contribution from the relatively small Florida rookery, and the lack of any significant difference in size of turtles originating from western Caribbean, eastern Caribbean, and central Atlantic rookeries, tend to suggest that this is not the major explanation for stock composition around Barbados.

One plausible explanation for the finding of large contributions from Ascension, Aves/Surinam, and Florida is the location of Barbados at the point where the north equatorial and south equatorial currents coalesce (Fig. 2). The pool of haplotypes from which post-pelagic green turtles that settle around Barbados is composed may consist of relatively large numbers of individuals from those rookeries that feed directly into these major Atlantic current systems, for example, Florida, Aves Island/Surinam, and Ascension Island, rather than from rookeries where young turtles have a greater chance of being caught up in smaller gyres within the western Caribbean and Gulf of Mexico, for example, the Costa Rica and Mexico rookeries (see Fig. 2). If substantial numbers of green turtles originating from rookeries in Costa Rica and Mexico are trapped in the recirculation gyre of the Sargasso Sea rather than entering the north equatorial current system, this is likely to increase their contribution to FGs in shallow areas of the continental shelf and around islands in the western Caribbean.

Finally, the lack of any significant contribution from Ascension Island to Caribbean FGs other than Barbados is interesting and suggests that these animals may not typically migrate much further northwards if they make landfall in the south eastern Caribbean. Instead, these animals may migrate southwards towards suitable FGs that are closer to their natal rookery. Consistent with this, the only tag return record of a green turtle tagged in Barbados is that from a 66.5 cm CCL juvenile that was subsequently caught 300 km to the south of Barbados off the coast of Trinidad.

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