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Mixed-stock analysis reveals the migrations of juvenile hawksbill turtles (*Eretmochelys imbricata*) in the Caribbean Sea

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Abstract

Hawksbill turtles (*Eretmochelys imbricata*) migrate between nesting beaches and feeding habitats that are often associated with tropical reefs, but it is uncertain which nesting colonies supply which feeding habitats. To address this gap in hawksbill biology, we compile previously published and new mitochondrial DNA (mtDNA) haplotype data for 10 nesting colonies ($N = 347$) in the western Atlantic and compare these profiles to four feeding populations and four previously published feeding samples ($N = 626$). Nesting colonies differ significantly in mtDNA haplotype frequencies ($\Phi_{ST} = 0.588$, $P < 0.001$), corroborating earlier conclusions of nesting site fidelity and setting the stage for mixed-stock analysis. Feeding aggregations show lower but significant structure ($\Phi_{ST} = 0.089$, $P < 0.001$), indicating that foraging populations are not homogenous across the Caribbean Sea. Bayesian mixed-stock estimates of the origins of juveniles in foraging areas show a highly significant, but shallow, correlation with nesting population size ($r = 0.378$, $P = 0.004$), supporting the premise that larger rookeries contribute more juveniles to feeding areas. A significant correlation between the estimated contribution and geographical distance from nesting areas ($r = –0.394$, $P = 0.003$) demonstrates the influence of proximity on recruitment to feeding areas. The influence of oceanic currents is illustrated by pelagic stage juveniles stranded in Texas, which are assigned primarily (93%) to the upstream rookery in Yucatan. One juvenile had a haplotype previously identified only in the eastern Atlantic, invoking rare *trans*-oceanic migrations. The mixed-stock analysis demonstrates that harvests in feeding habitats will impact nesting colonies throughout the region, with the greatest detriment to nearby nesting populations.

Keywords: conservation genetics, control region, homing, international trade, mitochondrial DNA, sea turtles

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Introduction

Hawksbill turtles, *Eretmochelys imbricata*, inhabit tropical reefs and sponge habitats worldwide (Márquez 1990). This species shares key life history traits with other sea turtles, including adult migration between feeding and breeding habitats, but it is unique in foraging on sponges (Meylan 1988). Hawksbills are endangered in every ocean basin (Meylan & Donnelly 1999) due to widespread exploitation for 'tortoiseshell' scutes, which are used in a variety of artisan products (Parsons 1972). Corresponding conservation efforts are hindered by gaps in the life history of this migratory and cryptic marine reptile. In particular, the member-nations of the Convention on International Trade in Endangered Species (CITES) have debated whether to

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allow commerce in hawksbill shell, but it is uncertain how a harvest in one location will affect the natural resources (particularly the nesting populations) in surrounding states. An effective conservation strategy depends on understanding key aspects of hawksbill biology, including the degree of isolation among nesting colonies, migratory pathways of juveniles and adults and the source (nesting colony) for foraging populations.

The geographical scale of conservation efforts is determined by the extent of connectivity among nesting populations and feeding habitats. Like other marine turtles, hawksbill turtles can migrate long distances at each life-history stage. Tag returns indicate nesting-site fidelity by females (Miller *et al*. 1998; Meylan 1999a; Bellini *et al*. 2000), and natal homing has been confirmed by mitochondrial DNA (mtDNA) surveys of nesting colonies in the western Atlantic (Bass *et al*. 1996; Díaz-Fernández *et al*. 1999) and western Pacific (Broderick & Moritz 1996). These conclusions are based on a subset of regional nesting populations, so an overview of population structure in the greater Caribbean region (and Pacific) has yet to emerge.

Migratory patterns and the origins of juvenile foraging populations are nearly unknown, because of the difficulties in tracking individuals over a maturation period that may exceed 20 years (Boulon 1994). Juveniles congregate in shallow-water feeding areas after an open ocean interval suspected to span several years (Carr *et al*. 1966). The composition of these feeding areas may be influenced by the size of regional nesting populations, the distance from nesting areas and prevailing oceanic currents. Newly emerged hatchlings have a swimming frenzy to transport them to offshore habitats, and their migratory pathways are likely influenced by the energetic currents of the Caribbean, which reach 5 km per hour in some places.

In the absence of direct observations of migratory pathways, molecular genetic markers have proven useful for resolving migration patterns in sea turtles (Bowen & Karl 1996). Genetic isolation among nesting colonies, and corresponding mtDNA haplotype frequency differences, provide an opportunity to identify the origins of migratory juveniles and adults. This mixed-stock methodology was originally developed to identify the river source of salmon that mingle in coastal habitats of the northeastern Pacific (Grant *et al*. 1980). Early mixed-stock analysis employed a conditional maximum-likelihood approach to estimate the relative contributions of source populations to harvest areas (Pella & Milner 1987). This method has been used to identify the origins of hawksbill turtles on feeding grounds in the Indo-Pacific (Broderick *et al*. 1994) and several Caribbean locations (Bowen *et al*. 1996; Díaz-Fernández *et al*. 1999; Troëng *et al*. 2005).

Previous mixed-stock studies have postulated that two factors influence the recruitment of sea turtles to feeding habitats: size of source (nesting) populations and proximity between nesting and feeding areas (Bass 1996; Norrgard & Graves 1996; Lahanas *et al*. 1998; Rankin-Baransky *et al*. 2001; Engstrom *et al*. 2002; Witzell *et al*. 2002; Luke *et al*. 2004). Large nesting colonies are expected to contribute more to feeding areas than smaller colonies, and closer nesting colonies are expected to contribute more than distant ones. The first factor is intuitive and not controversial; the second factor (distance) is not as obvious because juvenile turtles have an oceanic interlude that may deposit them on feeding habitats far from their region of origin. However, Bowen *et al*. (2004) demonstrate that juvenile loggerhead turtles (*Caretta caretta*) return from oceanic habitat to coastal feeding areas near their rookery of origin, and hawksbill turtles may have a similar behaviour. A third factor, oceanic currents, could not be assessed with the previous studies of individual foraging habitats. Here, we compile a comprehensive data set of previously published and new mtDNA control region sequences from 10 potential source populations distributed across the western Atlantic ($n = 347$). We use haplotype data for juvenile hawksbills ($n = 626$) from four northern Caribbean Sea feeding areas (Bowen *et al*. 1996; Bass 1999; Díaz-Fernández *et al*. 1999) and contribute new samples from four additional feeding habitats in the US Virgin Islands (USVI), Dominican Republic, western Gulf of Mexico, and Bahamas (Fig. 1), to provide a basin-wide appraisal of juvenile migration, the composition of feeding habitats, and the factors that may influence the composition of foraging populations.

Materials and Methods

Blood from the cervical sinus for most collections (1992–1999), following the protocol of Owens & Ruiz (1980), was placed in lysis buffer (100 mM Tris-HCl, 100 mM EDTA, 10 mM NaCl, 1% SDS; pH 8.0) and stored at room temperature. Some nesting-area samples included moribund hatchlings, collected within 2 weeks (approximate renesting interval) to prevent the resampling of the same matriline. Samples of skin or muscle were taken from live animals with a 6 or 10 mm biopsy tool (1998) and stored in salt-saturated buffer (20% DMSO and 250 mM EDTA saturated with NaCl; pH 7.0) (Amos & Hoelzel 1991; Proebstel *et al*. 1992).

The present data set includes nesting-site haplotype frequencies from Bass *et al*. (1996), Díaz-Fernández *et al*. (1999) and Troëng *et al*. (2005), but with additional specimens from Barbados ($n = 9$, 1998), Arembepe, Brazil ($n = 4$, 1997), Buck Island, USVI ($n = 19$, 1995 –1998), Tortuguero, Costa Rica ($n = 15$, 1998 –1999) and Los Roques, Venezuela ($n = 7$, 1996) (Table 1).

Juveniles were collected in feeding areas near Mona Island, Puerto Rico ($n = 41$, Bowen *et al*. 1996; $n = 97$, Díaz-Fernández *et al*. 1999), at Yucatan, Mexico ($n = 21$) and at three locations around Cuba ($n = 210$, Díaz-Fernández *et al*. 1999). Additional specimens reported here for the first time

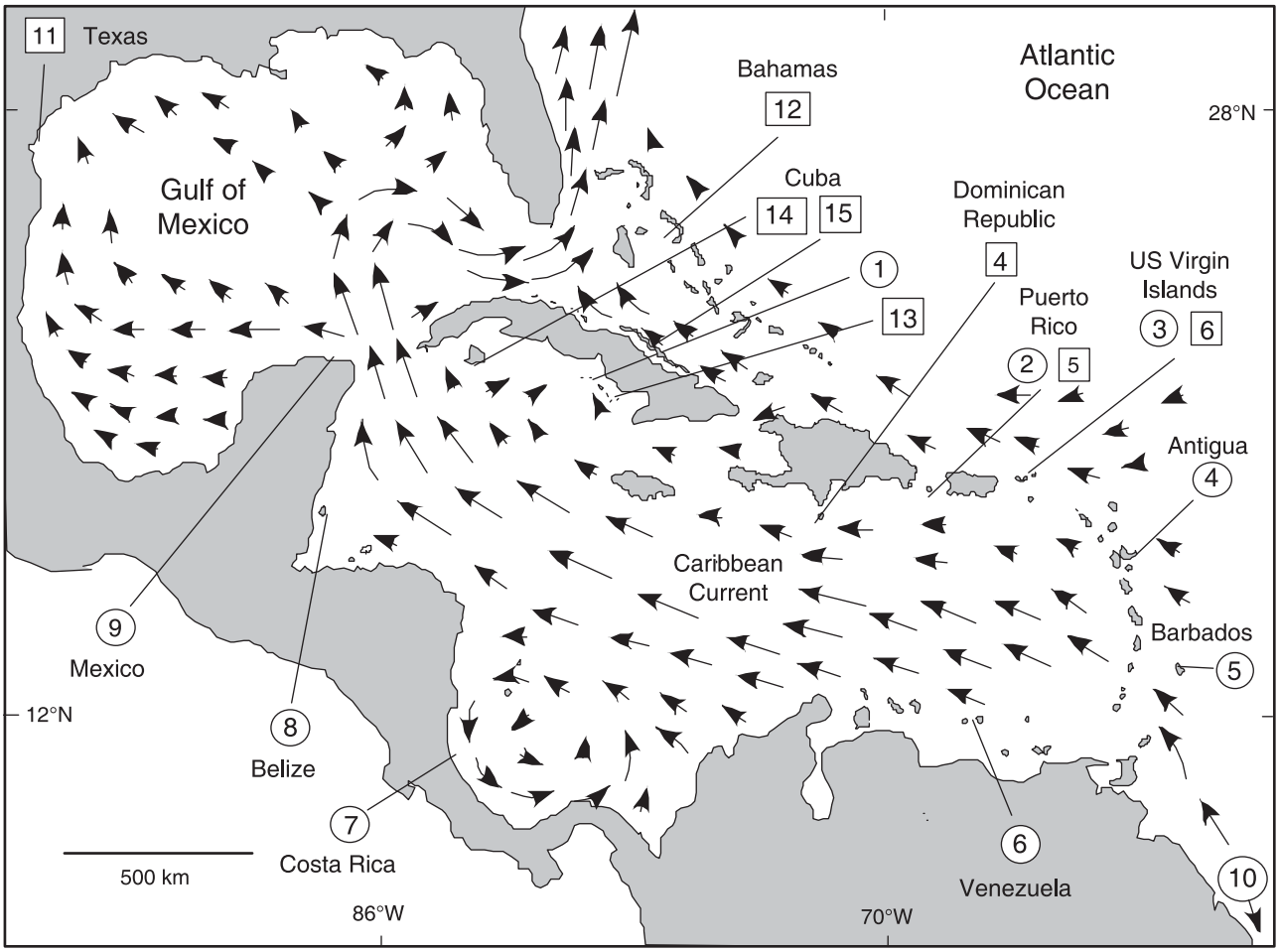

Fig. 1 Locations of samples from nesting (numbers in circles) and feeding areas (numbers in squares) and surface currents in the Caribbean Sea and Gulf of Mexico.

were collected near the Bahamas (n = 78, 1993–1997), Buck Island, US Virgin Islands (n = 69, 1995–1998), Dominican Republic (n = 90, 1996–1997) and Texas, USA (n = 42, 1996–1999). Previous studies used a 384-bp fragment of the control region, so we limited our analysis to this segment to maintain compatibility.

Total DNA was isolated from skin and blood samples with a standard phenol-chloroform protocol (Hillis *et al*. 1996). The mtDNA control region fragment was amplified with polymerase chain reaction (PCR) using primers TCR-5 (5′-TTGTACATCTACTTATTTACCAC-3′) and TCR-6 (5′-GTAAGTAAAACTACCGTATGCCAGGTTA-3′) (Norman *et al*. 1994) or TCR-5 and HDCM2 (5′-GCAAGTAAAACTACCGTATGCCAGGTTA-3′) (Allard *et al*. 1994). PCR cycling parameters followed one cycle of 94 °C (1 min), 25 cycles of (94 °C, 45 s +55 °C, 30 s +72 °C, 45 s) and one cycle of 72 °C for 3 min. Standard precautions included negative controls (template-free reactions) to test for contamination and to assure the fidelity of the PCR amplifications (Innis *et al*. 1990).

PCR amplicons were sequenced with an automated DNA sequencer (Applied Biosystems model 373A) at the DNA Sequencing Core, University of Florida. Sequences were aligned visually and matched with previously described haplotypes (Bass *et al*. 1996; Díaz-Fernández *et al*. 1999) with SEQUENCHER 3.0 (Gene Codes). New haplotypes were sequenced in both directions to assure accuracy. Haplotype designations follow Bass *et al*. (1996), Bowen *et al*. (1996) and Díaz-Fernández *et al*. (1999). Specimens from Brazil, identified as hawksbill–loggerhead (*Caretta caretta*) hybrids, were excluded from the analyses. No hybrids were detected in feeding populations or breeding populations outside Brazil.

Díaz-Fernández *et al*. (1999) used a larger control region DNA fragment in their analyses of Cuban, Mexican and Puerto Rican turtles that split the widely distributed haplotype F into three haplotypes and haplotype Q into two haplotypes. In the present study, these haplotypes were binned into haplotypes F or Q, because it was infeasible to re-sequence previously collected specimens. The effect

Table 1 Locations of samples, sample sizes (*N*), frequencies of mitochondrial DNA control region haplotypes in samples of hawksbill sea turtles from western Atlantic nesting and feeding areas, haplotype and nucleotide diversity and sources of haplotype frequency data. Haplotypes A through EATL correspond, respectively, to GenBank Accession nos U22368, DQ479326–DQ479329, U37804, DQ479330–DQ479336, U37805–U37807, DQ479350–DQ479352, DQ479341, DQ479339, DQ479340, DQ479342, DQ479345–DQ479349, DQ479343, DQ479344

Location (abbreviation)	*N*	Haplotype																															N_f§	*h* (SD)	θ_π (SD)	Source¶
		A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	BI1	α	β	γ	Cu3	Cu4	Cum	DR1	DR2	Mx1a	EATL				
Nesting areas																																					
1. Doce Leguas, Cuba (Cu)	70	62	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	1	1	0	0	0	0	0	566	0.213 (0.064)	0.0038 (0.0026)	A
2. Mona Island, Puerto Rico (PR)	35	1	0	0	0	0	13	0	0	0	2	1	2	2	12	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	179	0.751 (0.050)	0.0064 (0.0039)	A,B
3. Buck Island, US Virgin Islands (USVI)	51	5	1	0	0	0	43	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	80	0.255 (0.077)	0.0047 (0.0031)	B,C
4. Jumby Bay, Antigua (An)	15	9	4	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	133	0.590 (0.106)	0.0088 (0.0054)	B
5. Barbados (Ba)	24	20	0	0	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	50	0.301 (0.112)	0.0015 (0.0014)	B,C
6. Los Roques, Venezuela (Ve)	7	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0.0	0.0	C
7. Tortuguero, Costa Rica (CR)	57	0	0	0	0	0	33	6	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	10	0	0	4	0	0	0	0	0	0	8	0.641 (0.061)	0.0098 (0.0055)	C,D
8. Gale's Point, Belize (Be)	14	0	0	0	0	0	11	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	40	0.396 (0.159)	0.0064 (0.0041)	B
9. Yucatan, Mexico (Me)	69	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	64	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1459	0.139 (0.056)	0.0011 (0.0011)	A,B
10. Arembepe, Brazil (Br)	5 (18*)	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	2	1	1	0	0	0	0	0	0	0	0	0	0	0		0.0	0.0	B,C
Overall	347†																																		0.768 (0.015)	0.0102 (0.0056)	
Feeding areas‡																																					
11. Texas	42	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	38	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0		0.180 (0.077)	0.0005 (0.0007)	C
12. Bahamas	78	28	1	0	0	0	20	0	0	0	0	0	0	0	2	0	1	21	0	0	0	0	0	1	0	0	3	0	0	1	0	0	0		0.740 (0.024)	0.0093 (0.0053)	C
13. Cuba A	43	28	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	2	0	1	2	0	0	1	0	0	0		0.559 (0.083)	0.0081 (0.0048)	A
14. Cuba B	111	46	0	0	0	0	34	0	0	0	0	0	1	0	10	0	0	11	0	0	0	0	0	1	0	5	2	0	0	1	0	0	0		0.720 (0.027)	0.0103 (0.0057)	A
15. Cuba D	56	18	1	0	0	0	13	1	0	0	0	0	2	0	3	0	0	8	0	0	0	0	0	2	0	5	2	0	1	0	0	0	0		0.821 (0.031)	0.0105 (0.0059)	A
16. Dominican Republic	90	42	0	0	0	0	30	2	0	0	1	0	1	0	0	0	0	6	0	0	0	0	0	6	0	0	0	0	0	1	1	0	0		0.669 (0.034)	0.0102 (0.0057)	C
17. Puerto Rico pooled	138	38	2	0	0	0	62	0	0	0	0	0	3	0	8	0	0	18	0	0	0	0	0	5	1	1	0	0	0	0	0	0	0		0.705 (0.027)	0.0092 (0.0052)	
Puerto Rico 1993	41	7	1	0	0	0	18	0	0	0	0	0	1	0	3	0	0	7	0	0	0	0	0	2	1	1	0	0	0	0	0	0	0				E
Puerto Rico 1999	97	31	1	0	0	0	44	0	0	0	0	0	2	0	5	0	0	11	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0				A
18. Buck Island, USVI	68	28	2	0	0	0	17	0	0	0	0	0	0	0	6	0	0	9	0	0	0	0	0	3	0	1	0	0	1	0	1	0	1		0.750 (0.036)	0.0108 (0.0060)	C
Overall	626																																		0.749 (0.010)	0.0095 (0.0053)	

*Including hybrids with loggerhead turtle haplotypes R, S, T, U.

†Excluding hybrid haplotypes in the sample from Brazil.

‡Cuban haplotypes a, b, d, f, h, l, m, n, p, q, zz, and PAC were not included for Cuba or Puerto Rico. Only haplotypes known from nesting locations or observed at more than one feeding area are shown.

§Female census size, estimated from Meylan (1999b) and Garduño-Andrade (1999).

¶Sources of haplotype frequencies: A, Díaz-Fernández *et al*. (1999); B, Bass (1999); C, this study; D, Troëng *et al*. (2005); E, Bowen *et al*. (1996).

of binning the three new 'F' haplotypes was minimal, because two of them appeared only in the foraging aggregations at low frequencies, and in any case could not be used for mixed-stock analysis because they weren't detected in source populations. The two new Q haplotypes were found only in the nesting sample from Yucatan, Mexico. An additional haplotype, PR1 (Díaz-Fernández *et al*. 1999), was identified in nesting samples from Mona Island, Puerto Rico.

Haplotype diversities among nesting locations were estimated with equation 8.4 of Nei (1987), as implemented in ARLEQUIN 3.0 (Excoffier *et al*. 2005). Nucleotide diversities, which estimate the mutation parameter $2N\mu$, were calculated as θ_δ (Tajima 1983) in ARLEQUIN. AMOVA (ARLEQUIN) was used to partition the total haplotype variability among nesting colonies and among feeding aggregations. Sequence divergence between haplotypes was estimated under the Kimura 2-parameter model, following a gamma distribution with shape parameter $\alpha = 0.50$.

We used mixed-stock simulations in SPAM 3.7 (ADGF 1999; Debevec *et al*. 2000) to assess whether haplotype frequency differences among nesting areas (the baseline) were great enough to estimate the origins of feeding-area juveniles. Eight nesting-area samples (minus Venezuela and Brazil, see below) showed sufficient separation to proceed with a mixed-stock analysis. SPAM implements a conditional maximum-likelihood (ML) approach to estimate population origins in areas of mixing. Starting estimates included equal contributions from source populations (Chapman 1996). However, as ML estimates of mixed-stock proportions tend to underestimate small contributions to a mixed-stock (Chapman 1996), we also used a Bayesian algorithm with a Markov chain Monte Carlo (MCMC) estimation procedure (BAYES; Pella & Masuda 2001). MCMC runs of 50 000 in length were used for each potentially contributing nesting site with prior expectations of 0.93 for a particular nesting site and 0.01 for the seven other nesting sites. The shrink factor of Gelman & Rubin (1992) was used to assess convergence of the MCMC estimates to a desired posterior probability. Mixed stock composition was estimated from the mean of chains after 25 000 burn-in steps.

The effect of nesting-site abundance on feeding area composition was examined by regressing arcsine-transformed proportions from contributing populations on the log of population size (NTSYS 2.1; Exeter Software). Female abundances at rookeries in the Caribbean were collated from Garduño-Andrade (1999) and Meylan (1999b). Nesting-site abundance for each site was estimated by assuming an average of three nests per female. The effect of distance from nesting site on feeding area composition was examined by regressing arcsine-transformed proportions on various modifications of water distances between nesting and feeding areas. Two correlations were estimated: (i) an overall correlation between all nesting sites and feeding areas, and (ii) correlations between an individual feeding area and all nesting sites. For these correlations, distances were estimated from a chart in three ways: (i) unmodified water distances (km) represented the shortest swimming distance between potentially contributing nesting populations and juvenile feeding areas; (ii) 'Cuban' water distances through the Yucatan Channel and around the northern shores of Cuba representing the most likely migration path, given the strong currents through the Yucatan Channel; and (iii) 'current' distances modified by the directions and strengths of currents in the Caribbean and Gulf of Mexico. In the latter transformation, water distances were decreased by 10% if contributing populations were up-current of the juvenile feeding ground, increased by 10% if they were down-current and increased an additional 10% if the distance cut across strong currents. In addition, log transformations of unmodified distances were used in one correlation to resolve the contributions of nearby nesting sites to juvenile feeding areas. Finally, a stepwise regression was made between contributions to a feeding area and both the log-nesting population size and the distance from a nesting area.

Results

In the combined rookery data set ($n = 349$), 41 polymorphic sites define 27 haplotypes, including six transversions (Tv) and 36 transitions (Ti) (Table 1). Both a Ti and a Tv occur at site 309, and two Tv mutations are documented at site 148 (haplotype BI1: A-T; haplotype EATL1: A-C). A deletion is detected in haplotype D at position 59, and a 10-bp insertion begins at position 354 in MX1A; both indels are treated as single substitutions. Most of the observed haplotypes are separated by one or a few mutations (with two exceptions, see below), and relationships among haplotypes are described in Bass *et al*. (1996) and Díaz-Fernández *et al*. (1999). Kimura's 2-parameter sequence divergences between haplotypes are $d = 0.002–0.047$, with one exception.

The distribution of haplotype B, which was confined to the Antiguan nesting population in previous samples, now includes one nest specimen from Buck Island, USVI. This is the only case in which a previously endemic haplotype appeared in another population. A new haplotype, BI1, appears in one female from USVI and is notably divergent from other haplotypes in the Caribbean ($d = 0.028–0.047$). Another divergent haplotype, EATL1, is observed in the USVI feeding area ($d = 0.060–0.079$). This haplotype was previously detected in a sample of four turtles from a market in Sao Tome (eastern equatorial Atlantic) and is more similar to Indo-Pacific haplotypes than to Caribbean haplotypes (D. Broderick, personal communication). Haplotype α, which previously appeared in only foraging juveniles, is observed in nesting turtles at Costa Rica (Bowen *et al*. 1996; Díaz-Fernández *et al*. 1999; Troëng *et al*. 2005).

mtDNA diversities within and among nesting sites

Haplotype diversities among nesting colonies range from $h = 0.139$ to 0.751, with an overall estimate of $h = 0.768 \pm 0.015$ (Table 1). Nucleotide diversities within nesting populations range between $\theta_\pi = 0.0011$ and 0.0098, with an overall estimate of $\theta_\pi = 0.0102 \pm 0.0056$.

An AMOVA indicates that divergences among nesting sites are significantly greater than zero ($\Phi_{ST} = 0.588$; $P < 0.0001$). Nesting populations are further partitioned between the western and eastern Caribbean, which are separated by the high-energy Caribbean Current. In this comparison, the samples from Me, Be and CR differ significantly from samples from Cu, PR, USVI, An, Ba and Ve ($\Phi_{CT} = 0.559$, $P < 0.0001$; abbreviations in Table 1). In this latter model, haplotype frequencies among populations within each area also differ significantly from one another ($\Phi_{ST} = 0.607$, $P < 0.0001$).

mtDNA haplotype diversities within and among foraging areas

Not all nesting population haplotypes are detected in feeding areas (C, D, E, H, I, K, M, O, BI1, Cu4). Conversely, not all haplotypes in feeding samples are observed in nest samples (β, Cum, DR1, DR2, EATL). When present, these haplotypes occurred at low frequencies, and their absence did not detract from the accuracy of the mixed stock analysis. Haplotype diversities in feeding area samples ranged from $h = 0.180$ to 0.821, and nucleotide diversities ranged from $\theta_\delta = 0.0005$ to 0.0108. Much less divergence is apparent among feeding area samples than among nesting areas ($\Phi_{ST} = 0.089$, $P < 0.0001$).

Mixed-stock analysis

The mixed-stock simulations indicated that individuals from eight Caribbean nesting-area samples (Cu, PR, USVI, An, Ba, CR, Be, Me; see Table 1 for abbreviations) could be correctly re-assigned with at least 90% accuracy. Simulations consistently failed to correctly assign individuals from nesting areas in Ve and Br. The sample from Venezuela consisted of seven individuals with haplotype A, a haplotype occurring in most Caribbean nesting-site samples. The sample from Brazil included haplotypes R, S, T, U, which indicate loggerhead-hawksbill hybrids (Bass *et al*. 1996; Lara-Ruiz *et al*. 2006). Individuals with these four haplotypes were removed from the mixed-stock analyses, leaving only five individuals with haplotype A. Both Ve and Br were removed as potential source populations, because of these small sample sizes.

ML and Bayesian estimates of the nesting colony origins of juveniles in feeding areas are provided in Table 2. Shrink factors for Bayesian mixed-stock estimates were 1.02 or

Table 2 Percentage contributions of source populations to juvenile hawksbill sea turtles on Caribbean feeding grounds

	Feeding ground																											
	Texas			Bahamas			Cuba A			Cuba B			Cuba D			Dominican Republic			Puerto Rico			US Virgin Islands		
Source population	ML*	SD	Bayes	ML	SD	Bayes	ML	SD	Bayes	ML	SD	Bayes	ML	SD	Bayes	ML	SD	Bayes	ML	SD	Bayes	ML	SD	Bayes	ML	SD	Bayes
1. Cuba	0.00	0.00	0.30	36.90	6.24	36.11	72.51	6.98	72.14	45.81	5.39	45.31	43.18	7.15	43.44	44.71	5.61	32.07	23.45	4.59	20.28	36.98	7.51	32.23	13.26			
2. PR	0.00	0.00	0.72	3.96	2.99	4.09	0.01	0.00	0.60	15.69	4.76	18.98	10.74	5.99	12.16	1.82	1.99	1.82	11.06	3.77	12.42	14.66	5.71	18.06	8.49			
3. USVI	6.64	3.94	2.42	25.39	6.44	23.55	9.08	6.59	8.07	25.18	6.41	20.59	9.49	7.87	10.45	4.31	6.58	19.99	8.32	8.28	10.42	39.54	6.65	41.78	10.19	15.31	8.10	10.46	10.54
4. Antigua	0.00	0.00	0.32	1.19	3.38	1.63	0.00	0.00	1.03	0.15	3.60	0.96	2.13	2.72	3.44	2.83	4.00	0.01	0.00	0.74	3.32	1.03	3.10	1.77	3.84	7.18	5.54	10.86	12.59
5. Barbados	0.00	0.00	0.30	0.00	0.00	1.53	4.25	0.04	0.02	0.00	0.00	0.77	2.17	0.00	0.00	0.88	2.32	0.14	0.02	15.59	21.27	0.00	0.00	1.70	4.34	0.05	0.01	3.75	8.79
6. CR	0.05	0.01	1.19	2.91	3.04	1.98	3.37	11.69	7.87	11.25	7.76	2.39	2.48	1.61	2.80	19.19	9.75	19.74	8.94	24.45	7.59	31.78	10.79	11.17	4.65	8.05	6.87	10.19	5.85	8.84	8.13
7. Belize	0.60	0.09	2.00	3.31	0.00	2.17	5.41	0.00	0.00	2.17	4.53	0.00	0.00	1.87	4.88	0.00	0.00	2.02	4.49	0.00	0.00	3.34	7.21	0.00	0.00	0.87	3.48	0.00	0.00	2.37	5.72
8. Mexico	92.71	3.97	92.75	4.59	28.37	5.08	28.95	5.25	6.83	3.88	6.79	4.23	9.88	2.83	9.89	3.01	14.52	4.67	14.61	4.86	6.66	2.63	6.39	3.03	13.04	2.87	13.13	3.06	12.69	4.10	13.44	4.46
Unknown†	0.00			1.28			2.33			0.90			1.79			2.22						0.72			2.94					

*Maximum-likelihood (ML) estimates and standard deviations (SD) were calculated with SPAM (Debevec *et al*. 2000), and Bayesian estimates (Bayes) and standard deviations (SD) were calculated with BAYES (Pella & Masuda 2001).
†Orphaned haplotypes were included in the ML analysis, but are automatically removed from the Bayesian analysis by the program.

Table 3 Correlation between maximum-likelihood and Bayesian estimates of population admixture on feeding grounds

Feeding Location	*r*	df1	df2	*P*
1. Texas	0.998	1	6	0.000001
2. Bahamas	0.997	1	6	0.000001
3. Cuba A	0.997	1	6	0.000001
4. Cuba B	0.990	1	6	0.000001
5. Cuba D	0.992	1	6	0.000001
6. Dominican Republic	0.820	1	6	0.012200
7. Puerto Rico pooled	0.988	1	6	0.000001
8. Buck Island, USVI	0.964	1	6	0.000012
Overall	0.896	1	62	0.000001

R^2 is the regression coefficient, d.f. are degrees of freedom and *P* is the probability of R^2.

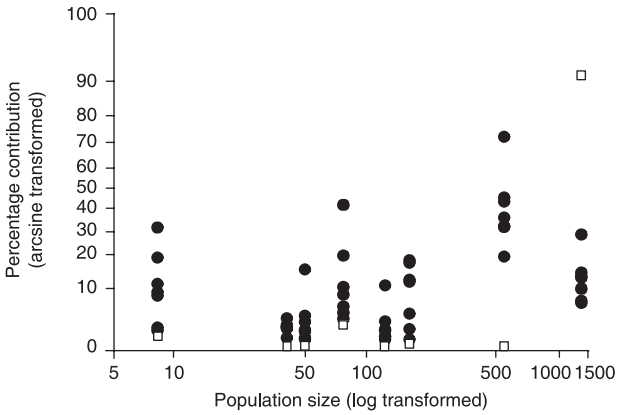

Fig. 2 Association between percentage contribution from a nesting site (arcsine transformation) and the size of the contributing population. Rookery sizes are from Table 1 and references therein. Contributions to the sample of juvenile beach strandings in Texas are indicated by squares.

less, indicating convergence among MCMC estimates. These two sets of estimates are highly correlated overall ($r = 0.896$, $P < 0.000001$; Table 3) and were generally correlated for individual samples with $r > 0.96$, except for DR ($r = 0.82$). In the latter sample, ML and Bayesian estimates of contributing populations differed for Cu, USVI, Ba, CR, often by several percentage points. Although the following analyses were computed for both ML and Bayesian estimates (Table 2), only the results for the Bayesian estimates are analysed further, as this approach may estimate extreme contributions more accurately (Pella & Masuda 2001), especially small contributions to feeding areas that are relevant to both behaviour and conservation.

The mixed stock analyses demonstrate that foraging habitats are occupied by turtles from multiple locations, with one notable exception. The sample of juvenile (stranded) turtles from Padre Island, Texas ($n = 42$) had an estimated contribution of 93% from the upstream rookery at Yucatan, Mexico. Point estimates of 1.2–2.4% came from Belize, CR and USVI, and estimates < 1% came from the remaining nesting areas. However, standard errors of these small contributions include zero.

As expected, the size of source-nesting populations demonstrably influences the composition of feeding areas, with larger populations contributing more juveniles. Annual nesting effort varies tremendously between rookeries, ranging from an estimated eight females at CR to 1459 females at Me. Corresponding correlation analyses include overall comparisons of nesting and feeding populations, and correlations for individual feeding populations. Estimated percentage contributions (arcsine transformed) from nesting sites were regressed on the log of nesting site population size, yielding a highly significant correlation ($r = 0.378$, $P = 0.004$, Fig. 2). To avoid an intractable analysis, this and subsequent correlations do not account for the standard errors around point estimates. Correlations for individual feeding-area samples were significant only for the Bahamas ($r = 0.807$, $P = 0.016$). The lack of significant correlations for individual samples may be due to small samples sizes or to confounding influences of currents and distance between source and feeding populations.

A regression analysis was used to test the effect of distance between nesting and foraging populations (Table 4). Direct water distances produced a highly significant negative correlation with percentage contribution ($r = -0.347$, $P = 0.009$). Direct water routes between nesting and feeding areas were also modified to account for possible effects of shoreline topography and current. One modification took into consideration current direction between nesting and feeding areas. This modification also yielded a highly significant correlation, but did not improve the correlation over direct water distance ($r = -0.294$, $P = 0.028$). A log transformation of distance, which places more importance on contributions from nearby populations, also yielded a significant correlation, but again did not improve the fit over unmodified water distances ($r = -0.289$, $P = 0.031$). Lastly, some direct distance routes involving western Caribbean populations traverse the fast-moving Caribbean Current. These migration pathways, which were routed through the Yucatan Channel and around the northern shores of Cuba, marginally improved the correlation between distance and percentage contribution ($r = -0.394$, $P = 0.003$, Fig. 3).

The strength of the correlation between distance and contribution varied considerably among feeding-area samples. With the adjustment for migration around Cuba, only the feeding areas at Ba and CuA showed a significant negative correlation between percentage contribution and distance from contributing nesting population (Table 4). The correlation for CuB was also large and nearly significant.

Table 4 Correlation between contribution to feeding area and geographical distance from contributing nesting population

Feeding area	*r*	df1	df2	*P*
1. Texas	–0.568	1	6	0.141
2. Bahamas	–0.523	1	6	0.183
	(–0.796	1	6	0.018)*
3. Cuba A	–0.796	1	6	0.018
	(–0.803	1	6	0.016)*
4. Cuba B	–0.438	1	6	0.278
	(–0.673	1	6	0.067)*
5. Cuba D	–0.438	1	6	0.441
6. Dominican Republic	–0.138	1	6	0.746
7. Puerto Rico pooled	–0.345	1	6	0.403
8. Buck Island, USVI	–0.118	1	6	0.784
Pooled				
Cuba*	–0.428	1	62	0.0004
Excluding Texas	–0.347	1	54	0.009
Unmodified†	–0.401	1	62	0.001
Excluding Texas	–0.294	1	54	0.028
Currents‡	–0.373	1	62	0.002
Excluding Texas	–0.394	1	54	0.003
LogDist§	–0.305	1	62	0.014
Excluding Texas	–0.289	1	54	0.031

*Distances between western Caribbean nesting sites and eastern Caribbean include a pathway through the Yucatan Channel, then around the northern shore of Cuba to account for the strong currents in these areas.
†Water distance between nesting and feeding areas.
‡Distances modified by up- and down-current positions of nesting and feeding areas.
§Log (10) transformation of water distance.

A stepwise regression of the percentage contribution at a feeding area on both the log-nesting population size and distance from nesting area yielded a highly significant correlation ($r = 0.484$, $P = 0.0009$).

Finally, most feeding habitat samples were benthic stage (older) juveniles, but the Texas strandings had a size range of 5.2–36.8 cm carapace length straight (mean 16.3 cm), indicating the oceanic juvenile phase. To determine whether this could influence conclusions about rookery size and distance from the feeding population, we reran correlation tests without the Texas strandings (Table 4). Dropping the Texas cohort reduced the correlation between distance and rookery contribution ($r = 0.428$ vs. r = 0.347 in one example), but corresponding *P* values remained highly significant ($P = 0.0004$ vs. $P = 0.009$).

Discussion

In the present study, the available mtDNA data for Caribbean and West Atlantic hawksbills (Bass *et al*. 1996; Bowen *et al*. 1996; Díaz-Fernández *et al*. 1999; Troëng *et al*. 2005) is augmented with four new feeding-area samples.

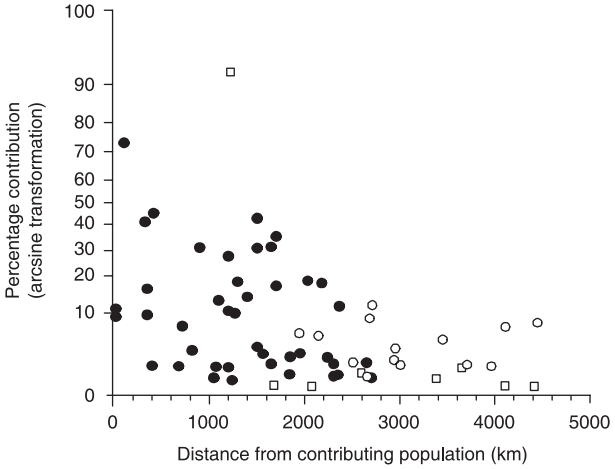

Fig. 3 Association between percentage contribution from a nesting site (arcsine transformation) and water distance from the nesting site to the feeding ground. Open circles represent dispersal pathways to the north of Cuba. Squares represent contributions to the sample of juvenile beach strandings in Texas.

The analysis of feeding-area composition, in addition to the analysis of population structure among nesting populations, permits a deeper understanding of the migratory behaviour of juvenile hawksbill turtles. Prior to dissecting these results, we address three caveats:

1 The estimated contributions to feeding areas illustrate general trends in hawksbill behaviour, but they should not be regarded as precise values for at least four reasons. First, estimates have large standard errors (Table 2), due primarily to the sharing of haplotypes among nesting colonies. Second, nesting effort has not been exhaustively sampled. The major nesting aggregates are included herein, but there is a substantial nesting effort by solitary females that is impossible to measure or adequately sample. Third, sample sizes are moderate and limit the extent of our inferences. In this highly endangered species, some rookeries have been reduced to a few dozen nesting females, and both nesting and feeding samples represent considerable effort. Fourth, most locations are represented by one-time sampling, and the extent of annual and decadal variability is largely unknown. Notably, nest samples collected at Puerto Rico in 1992 (Bass *et al*. 1996) and 1994 (Díaz-Fernández *et al*. 1999) are significantly different ($\chi^2 = 14.89$, $P = 0.009$). This difference may be due, in part, to the propensity of hawksbill females to nest at intervals averaging 2 to 3 years (Garduño-Andrade 1999; Richardson *et al*. 1999). No other significant differences were detected in resampled nesting populations, but the statistical power to detect such differences could be compromised by small sample sizes.

2 Feeding-area samples include a wide range of size classes, and it is possible that our samples include multiple life stages. Size class information indicates that the eight feeding samples are composed of juveniles, but individuals were not internally sexed and it is possible that a few adults are included. Further, the sample from Texas is composed primarily of smaller oceanic-phase juveniles (mean 16.3 cm carapace length straight). Unfortunately, our sample sizes for this endangered reptile are not large enough to support an analysis by size class or gender.

3 Human perturbations and conservation efforts may induce life-history changes that alter our results (Mrosovsky 1983; Mortimer 1988). Hawksbills have been reduced by two orders of magnitude in the Caribbean basin (Meylan & Donnelly 1999), their coral habitat has been reduced by perhaps 90%, and it is impossible to predict how these recent changes have altered migratory patterns. Head-started individuals, held in captivity for several months or years to enhance survival, may become residents near the point of release or may exhibit atypical migratory behaviour (Bowen *et al*. 1994).

Nesting populations

The results of our analyses of nesting hawksbill females corroborate the conclusions of earlier studies. Estimates of haplotype diversity do not differ significantly from those reported in Bass *et al*. (1996), although the overall haplotype diversity was slightly lower ($h = 0.768$ in this study and $h = 0.849$ in Bass *et al*. 1996), and nucleotide diversity was elevated ($\theta_\pi = 0.0102$ compared to $\theta_\pi = 0.0038$ in Bass *et al*. 1996) due to the divergent haplotypes BI1 and EATL1. Although criticisms have been raised about the sample sizes from nesting locations (Mrosovsky 1997), we note that haplotype diversity dropped with the larger sample size, suggesting that most of the mtDNA diversity in Caribbean hawksbill turtles has been identified. The results also confirm previous hypotheses (Bass *et al*. 1996; Díaz-Fernández *et al*. 1999) that individual nesting colonies are genetically distinct, indicating that natal- and spawning-site fidelity are predominant features of hawksbill female behaviour.

Effects of nesting-colony size on feeding-area composition

Estimated origins of juvenile hawksbills in feeding areas (Table 2) set the stage for assessing life-history features that are pertinent to conservation. First, what effect does nesting population size have on the recruitment of juveniles to feeding populations? A significant correlation between nesting population size and contribution to feeding areas supports the expectation that large populations contribute more juveniles ($r = 0.378$, $P = 0.004$). However, the scatter plot of population size and percentage contribution reveals two components of this correlation (Fig. 2). The increasing contributions from progressively larger populations drive the positive correlation, and this is consistent with the hypothesis that nesting population size sets the upper limit for contributions to feeding areas.

However, most of the (individual) estimated contributions are not correlated with nesting population size, and additional environmental and biological factors may be relevant. These include climate and oceanographic conditions, variable survivorship among populations and regional patterns of migratory behaviour. Major ocean-climate cycles take place on decadal timescales that are similar to maturation periods of hawksbills, and these cycles may alter recruitment to feeding areas. Most of these factors are beyond the scope of our study, but we can evaluate two prominent factors: geographical distance and the oceanic currents that sweep through the Caribbean.

Juvenile migratory behaviour

Our comparison of mixed-stock composition and distance from nesting colony yields a highly significant negative correlation ($r = -0.394$, $P = 0.003$). On the scale of the Caribbean Sea, contributions to feeding areas are strongly influenced by distance from the contributing colony. In most feeding areas, including Texas, Bahamas, Cuba A, Cuba B, Cuba D, Dominican Republic and Puerto Rico, the largest estimated contributions of juveniles are from nearby nesting colonies. However, a correlation between distance and contribution was negative and significant for individual feeding areas only in the Bahamas, Cuba A and (marginally) Cuba B. While the influence of nearby nesting areas on feeding area composition is robust, contributions from more distant colonies are more variable (Table 2).

Little is known about the migrations of post-hatchlings, but these may include a few years in the oceanic pelagic zone (Carr 1987; Musick & Limpus 1997), followed by recruitment to reef habitats at about 20–25 cm carapace length (Boulon 1994). Under these conditions, the presence of larger juveniles in feeding areas near their region of origin would mandate some degree of homing behaviour. After the pelagic stage, juveniles may move preferentially towards feeding habitats in the region of their natal beach. A similar phenomenon has been documented in loggerhead turtles, where small juveniles occupy pelagic habitats for about a decade (Bjorndal *et al*. 2000; Bolten 2003), after which large juveniles feed preferentially near their natal site (Laurent *et al*. 1998; Bowen *et al*. 2004, 2005). The Earth's magnetic field apparently guides this homing behaviour (Lohmann *et al*. 1999).

This preference for feeding 'closer to home' is not absolute, as indicated by connectivity between feeding and nesting habitats across the Caribbean basin (Table 2). Furthermore, we detected a haplotype in the USVI foraging

habitat (EATL) that is only known from a market sample obtained in Sao Tome in the eastern Atlantic, invoking the likelihood of occasional transoceanic migrations. This conclusion is supported by one tag recapture; a hawksbill turtle tagged in Brazilian waters and recovered in Gabon, Africa (Bellini *et al*. 2000).

Currents of the Caribbean Sea and Gulf of Mexico undoubtedly influence migration and hence regional patterns of feeding-area composition. This is most apparent in the sample of 42 oceanic-phase juveniles stranded in Texas. The mixed-stock analysis indicates a 93% contribution from the Yucatan nesting colony, which is directly upstream from the stranding site (Table 2). This pattern is fundamentally different from the more diverse contributions to the other seven (benthic) feeding populations. It seems likely that the water movements of the Caribbean Current (Fig. 1) combined with the semi- enclosed nature of the Gulf of Mexico, entrain juvenile turtles to a greater degree than the more open waters of the Caribbean Sea.

Implications for conservation

The hawksbill turtle is an ancient species, originating in the Miocene or earlier, and it has stirred the waters of the Caribbean Sea for millions of years. Conservation concerns for this species are immense because populations are severely reduced in every ocean basin. Nesting beaches in the Caribbean that historically hosted hundreds or thousands of turtles now have a few dozen nesting females. Corresponding breeding populations may be two orders of magnitude below pre-exploitation levels (Meylan & Donnelly 1999; Bjorndal & Jackson 2003), and over 80% of post-oceanic feeding habitat (Caribbean reefs) is severely damaged (Jackson 1997; Gardner *et al*. 2003). Despite severe decline and habitat loss, Caribbean hawksbills have retained high levels of mtDNA haplotype diversity, probably including most of the pre-exploitation variation. This is an expected outcome when the population depletion spans a few recent generations (Roman & Palumbi 2002). Population recovery at this stage would retain much of the corresponding mtDNA diversity. However, the prospects for recovery are not encouraging.

Harvests continue at local scales across the tropics, and international trade is a sleeping giant that may awaken at the next CITES meeting. In this realm, it is valuable to know how foraging populations are linked to nesting populations across the territorial waters of sovereign nations. Harvest in the Caribbean foraging areas will deplete nesting populations across multiple jurisdictions, and will also reduce the role of this unique spongivore on regional coral reefs. Clearly the appropriate scale for hawksbill conservation includes the greater Caribbean basin. Therefore, hawksbill conservation embodies a conflict between national and international interests, an area anticipated by the 1995 UN Straddling Stocks Agreement (Berkes 2005). Like many marine conservation issues, international cooperation is the last and best hope.

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