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DNA and dispersal models highlight constrained connectivity in a migratory marine megavertebrate

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Population structure and spatial distribution are fundamentally important fields within ecology, evolution, and conservation biology. To investigate pan-Atlantic connectivity of globally endangered green turtles *Chelonia mydas* from two National Parks in Florida, USA, we applied a multidisciplinary approach comparing genetic analysis and ocean circulation modeling. The Everglades (EP) is a juvenile feeding ground, whereas the Dry Tortugas (DT) is used for courtship, breeding, and feeding by adults and juveniles. We sequenced two mitochondrial segments from 138 turtles sampled there from 2006–2015, and simulated oceanic transport to estimate their origins. Genetic and ocean connectivity data revealed northwestern Atlantic rookeries as the major natal sources, while southern and eastern Atlantic contributions were negligible. However, specific rookery estimates differed between genetic and ocean transport models. The combined analyses suggest that post-hatchling drift via ocean currents poorly explains the distribution of neritic juveniles and adults, but juvenile natal homing and population history likely play important roles. DT and EP were genetically similar to feeding grounds along the southern US coast, but highly differentiated from most other Atlantic groups. Despite expanded mitogenomic analysis and correspondingly increased ability to detect genetic variation, no significant differentiation between DT and EP, or among years, sexes or stages was observed. This first genetic analysis of a North Atlantic green turtle courtship area provides rare data supporting local movements and male philopatry. The study highlights the applications of multidisciplinary approaches for ecological research and conservation.

Newly available and state-of-the-art bioinformatic tools are uncovering fundamental and previously obscured aspects of population structure, history, and spatial distribution. High-resolution ocean circulation models and advanced experiments have shed light on mysteries of marine animal movements, including geomagnetic orientation by salmon and sea turtles (Putman et al. 2012, 2014a, 2015), and larval retention in reef fishes despite the potential for extensive dispersal (Cowen et al. 2007, Staaterman and Paris 2014). The genomics field is booming as cutting-edge technology enables faster and expanded gene sequencing at lower cost. Deeper genomic coverage has improved phylogeographic resolution in many marine taxa including species with pan-global distributions, such as marine turtles (Shamblin et al. 2011, 2012a, b, 2015a, b, Roden et al. 2013, Ellegren 2014, Naro-Maciel et al. 2014a). The combination of these technologies shows considerable promise for better understanding cryptic life history stages such as the marine turtle 'lost years' (Putman and Naro-Maciel 2013).

After hatching from nests on beaches, neonate sea turtles head for the water and engage in a ~ 24–48 h swimming 'frenzy', then alternate between diurnal swimming and nocturnal drifting during the post-frenzy period and into their 'lost years' (Wyneken and Salmon 1992). The latter stage is thus named because little is known of the whereabouts and general biology of pelagic post-hatchlings (Carr 1967). The classic hypothesis is that small turtles drift with the currents for several years before recruiting to coastal feeding grounds, or FGs (Carr 1967). Recently, high resolution ocean circulation models have begun to simulate the movements of 'lost years' turtles under a range of behavioral scenarios, many of which question the preponderance of passive drift (Gaspar et al. 2012, Putman et al. 2012, 2014b, 2015, Putman and He 2013, Putman and Naro-Maciel 2013, Naro-Maciel et al. 2014b, Putman and Mansfield 2015). A case study from Palmyra Atoll (Central Pacific), for example, revealed pronounced differences between genetic and ocean connectivity estimates, suggesting that many pelagic turtles were retained in the Eastern Pacific (Naro-Maciel et al. 2014b). Further, the first study to deploy passive drifters alongside pelagic-stage turtles (14–29 cm straight carapace length [SCL]), showed tracks of individual turtles diverged substantially from what would be expected if movements were primarily the result of ocean circulation processes (Putman and Mansfield 2015).

In green turtles *Chelonia mydas* of the North Atlantic, the 'lost years' period is estimated to last 3–5 yr (Reich et al. 2007), after which turtles generally leave the open

ocean for neritic feeding grounds (IUCN 2015, Seminoff et al. 2015). Some FGs, such as the mangroves within the Everglades National Park (EP) World Heritage Site, Wetland of International Importance, and International Biosphere Reserve, are developmental areas composed solely of juveniles (Hart and Fujisaki 2010). Other FGs, such as the Dry Tortugas National Park (DT) include juveniles and adults foraging in seagrass pastures over a sandy bottom. Containing courting, nesting, and feeding grounds, DT not only represents a rare opportunity to study a courtship area (CA), it also may house an uncommonly non-migratory resident breeding population (Hart et al. 2013). The site further offers a rare opportunity to investigate philopatry in males, which is less understood than in females (that are more accessible when coming ashore to nest).

Nesting green turtles tend to return to their natal areas to reproduce, resulting in genetic differentiation among rookeries (Bowen and Karl 2007). Feeding grounds are considered 'mixed stocks' because they are usually drawn from multiple rookeries. Atlantic green turtle mixed stock analyses (MSAs) have shown that rookery population size, geographic distance from source populations, ocean currents, and juvenile natal homing (a behavior in which juveniles ultimately recruit to neritic waters in the vicinity of their natal site) likely influence FG population composition (Fig. 1 and references therein). However the small section of the mitochondrial genome sequenced in most studies (~ 481 bp) may be limited in terms of genomic representation and resolution; there are many shared sequences among sites (Supplementary material Appendix 1, Table A1) and MSA 95% probability intervals are generally broad. Such limitations can be mitigated through multidisciplinary approaches, including testing null hypotheses generated by ocean connectivity models with genetic data (Putman and Naro-Maciel 2013), and deeper genomic sequencing. Promising methods include sequencing the mitochondrial longer control region segment (CR, ~ 800 bp) and the short tandem repeat or STR (Abreu-Grobois et al. 2006, Shamblin et al. 2012b, 2015a, b, Tikochinski et al. 2012).

Globally endangered and highly migratory green turtles may be threatened by direct harvest, bycatch, climate change, habitat loss, pollution and other factors throughout their life cycles (Wallace et al. 2011, Seminoff et al. 2015). Understanding their distribution is therefore a research and conservation priority in sea turtle management (Hamann et al. 2010, Wallace et al. 2011, Seminoff et al. 2015). Previous work carried out in Florida points to its utility as an index site for assessing species status (Witherington et al. 2006, Seminoff et al. 2015). The *Sargassum* mats off of Atlantic Florida and in the Gulf of Mexico represent one

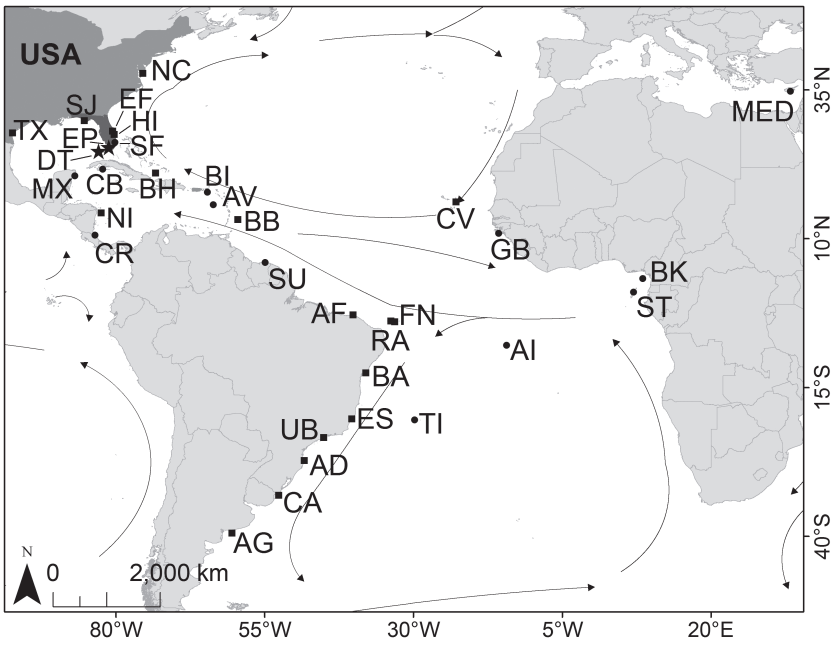

Figure 1. Map of the Dry Tortugas (DT) and Everglades National Park (EP) study sites (symbolized by stars) in the context of major oceanic circulation patterns (depicted as arrows), and other green turtle groups previously characterized genetically. References and abbreviations for other FGs (symbolized by squares) are as follows: Almofala (AF, Naro-Maciel et al. 2007); Argentina (AG, Prosdocimi et al. 2012); Arvoredo (AD, Proietti et al. 2012); Bahamas (BH, Lahanas et al. 1998, Bolker et al. 2007); Barbados (BB, Luke et al. 2004); Cape Verde (CV, Monzon-Arguello et al. 2010); Casino Beach (CA, Proietti et al. 2012); eastern central Florida (EF, Bagley 2003); Hutchinson Island, Florida (HI, Bass and Witzell 2000); Nicaragua (NI, Bass et al. 1998); North Carolina (NC, Bass et al. 2006); Rocas Atoll (RA, Bjorndal et al. 2006); St Joseph's Bay, Florida (SJ, Foley et al. 2007); Texas (TX, Anderson et al. 2013) and Ubatuba (UB, Naro-Maciel et al. 2007). Rookeries that were assessed (symbolized by circles) were: Hutchinson Island, Florida USA (FL); Quintana Roo, Mexico (MX); Aves Island, Venezuela (AV); Matapica, Surinam (SU, Encalada et al. 1996); east central and southern Florida (EF, SF, Shamblin et al. 2015); Lara Bay, Cyprus (CY, Encalada et al. 1996, Kaska 2000); Cuba (CB, Ruíz-Urquiola et al. 2010); Tortuguero, Costa Rica (CR, Encalada et al. 1996, Bjorndal et al. 2005); Ascension Island, UK (AI); Poilao, Guinea Bissau (GB, Encalada et al. 1996, Formia et al. 2006); Bioko Island, Equatorial Guinea (BK); Sao Tome (ST, Formia et al. 2006); Trindade Island, Brazil (TI, Bjorndal et al. 2006); and Rocas Atoll, Brazil (RA, Encalada et al. 1996, Bjorndal et al. 2006).

of the few studied 'lost years' pelagic habitats (Witherington et al. 2012). The first tracks of 'lost years' green turtles were obtained in the Gulf of Mexico (Putman and Mansfield 2015). Satellite tracking also revealed localized habitat use by older green turtles at DT and EP (Hart and Fujisaki 2010, Hart et al. 2013). Mark–recapture studies have uncovered Florida green turtle connectivity primarily within the Northwestern Atlantic and Caribbean (Meylan 1995, Bagley 2003, Witherington et al. 2006). Florida is thus part of the Atlantic Northwest Regional Management Unit (RMU), a complex of multiple rookeries jointly considered for conservation (Wallace et al. 2010). Despite the importance of these advances, tagging methods suffer from small sample size, tag loss, incomplete monitoring, and other issues, highlighting the need for complementary methods.

Here we researched the origins of green turtles foraging in DT and EP using multi-locus mitochondrial genetic data and a high-resolution ocean circulation model. Specifically, we aimed to investigate: 1) genetic composition at two mitochondrial loci; 2) structure within the study FGs, including among years, stages, and sexes; 3) links to other FGs; 4) natal sources; 5) ocean connectivity; and 6) applications for conservation and management.

Methods

Genetic analysis

Sampling and laboratory procedures

Following standard and previously used protocols (Naro-Maciel et al. 2007, 2012), blood or tissue samples were obtained from in-water green turtles captured at DT between May and September (and 4 samples collected in October 2011) from 2008–2014 (n = 116), and at EP between November and May from 2006–2015 (n = 22; Fig. 1). Blood samples were stored on cards and tissue samples were stored in ethanol. The SCL of sequenced turtles ranged from 22.7–112.7 cm (average = 54.8 cm) in the DT, and 23.8–67.5 cm (average = 37.5 cm) at EP. Each individual was examined, measured, sampled, PIT tagged for individual identification, and released.

Qiagen DNeasy Kits were used to extract DNA according to manufacturer's instructions (Qiagen). To increase mitogenomic coverage, the primers LCM15382 and H950 were employed to amplify a ~ 856 bp fragment of the mtDNA control region and two tRNAs (Abreu-Grobois et al. 2006). Primers CM-D-1 F and CM-D-5 R (Tikochinski et al. 2012) were used to amplify ~ 90 bp of a mitochondrial microsatellite repeat, while primer 16284seqF was used for forward sequencing (Shamblin unpubl.). Standard conditions and negative controls were employed and sequencing was done in both directions (Naro-Maciel et al. 2007, 2012). GENEIOUS ver. 6.1-8.0.5 (Biomatters) was used to align and edit sequences. Control region segments were named following standardized Archie Carr Center for Sea Turtle Research (ACCSTR) designations. Mitochondrial STRs were named by counting the number of AT repeats within each of four repetitive subsegments separated by conserved sequences (Tikochinski et al. 2012, Shamblin et al. 2015b).

Genetic diversity and differentiation

Differentiation among possible population subgroups (sites, years, stages, sexes) was assessed to determine if they should be pooled or considered separately. To test the null hypotheses of no genetic differentiation among sites, the control region sequences were necessarily truncated to ~ 481 bp for comparison to previous studies shown in Fig. 1. Analyses within and between the DT and EP study sites and other areas with available data were carried out using these truncated segments, in addition to the longer control region sequences (~ 856 bp), mitochondrial repeats, and concatenated control region + repeat. Samples were compared among years to evaluate the MSA assumption of temporal constancy. To test for differences among stages, turtles ≤ 67.5 SCL were considered juveniles (n = 96), and larger turtles whose gender was identified using morphological characteristics were considered adults (n = 42; two turtles measuring ~ 73 cm whose sex could not be determined, were alternately analyzed as juveniles or adults with similar results, and were ultimately considered juveniles). We note that laparoscopy was not carried out and visual gender assignments must be interpreted cautiously. To test the possibility of single origins for these FGs prior to MSA, the pairwise tests described above were used to compare them to rookeries shown in Fig. 1.

The number of haplotypes (a) as well as haplotype (h) and nucleotide (π) diversities using pairwise differences (Nei 1987) were calculated with ARLEQUIN ver. 3.11 (Excoffier and Lischer 2010). As is standard for sequence data such as ours, and considering available software, this program was used to implement pairwise and global exact tests of population differentiation (Raymond and Rousset 1995) in addition to pairwise tests and analysis of molecular variance (AMOVA) using F-statistics based on haplotype frequencies only (Shamblin et al. 2012b). As recommended, the few slightly negative F_{ST} values that resulted from greater genetic variation within than between populations, were interpreted as $F_{ST} = 0.000$. As described in the ARLEQUIN manual, for accuracy significance values were obtained from 10 000 permutations (of haplotypes between populations to compute sampling distributions of F_{ST} values under the null hypothesis, using the standard significance level of $p = 0.05$). All significant tests were corrected for multiple comparisons using the sequential Bonferroni procedure (Rice 1989).

Mixed stock analysis

Bayesian MSAs (Pella and Masuda 2001) were carried out to investigate DT and EP natal origins at individual rookeries and Regional Management Units (RMUs) using available genetic data (Supplementary material Appendix 1, Table A1, Fig. A1). Bayesian MSAs provide for assessment of stock mixtures, accounting for uncertainty in sampling from potential source populations contributing to the mixture, and allowing for the incorporation of prior information about the mixture composition. The MSAs were carried out on a pooled FG sample (DT + EP) using the individual rookeries as potential sources. MSAs for DT + EP were also run with individual rookeries grouped into RMUs (Regional Management Units) due to a lack of genetic differentiation among some individual rookeries. Due to spatial overlap, the RMUs are hereafter defined as the following clusters (Monzón-Argüello et al. 2010): 1) central western Atlantic

(AV and SU with BI added here; corresponds to Atlantic South Caribbean RMU); 2) MED (Mediterranean RMU); 3) northwestern Atlantic (FL, MX and CR, with CB added here; Atlantic Northwest RMU); and 4) southwestern and eastern Atlantic (RA, TI, AI, GB, BK and STP; corresponds to Atlantic East, South Central, and Southwest RMUs).

We compared two MSAs with different priors for the stock proportions: one with a 'neutral, low information prior' (Pella and Masuda 2001, p. 151) and one with an informative prior based on independent information on the stock proportions. The first prior (used in MSA_1) had parameters equal to 1/(number of rookeries or geographic regions), while the second prior (used in MSA_2) had parameters weighted to reflect estimated nester abundance at each possible source and then normalized. Both sets of parameters sum to 1 and are equivalent to adding a single individual to the mixture sample (Pella and Masuda 2001). The low information prior allows data patterns to override the prior (Pella and Masuda 2001). The informative prior allows independent, ecological data, such as source population size, to be incorporated as prior knowledge to improve the precision of stock composition estimates (Pella and Masuda 2001, Okuyama and Bolker 2005, Bolker et al. 2007). The parameters for MSA_2 were calculated by dividing the best estimates of each rookery's population size (Seminoff et al. 2015; Supplementary material Appendix 1, Table A1) by the total Atlantic rookery population size (Bass et al. 2004, Okuyama and Bolker 2005, Naro-Maciel et al. 2007).

Five haplotypes unique to the Florida FGs (CMA22, 26, 30, 47, 68; 7.25% of their green turtles) were excluded by the BAYES program since the sequences were not observed in any of the source rookeries and therefore BAYES had no information by which to assign those individuals. Sixteen MCMC chains, one per rookery, were run for 20 000 samples. Each chain had a dispersed starting composition: 95% contribution from one rookery and 5% equally divided among the remaining rookeries (Pella and Masuda 2001). The running of multiple chains from dispersed starting points is recommended to ensure convergence of the samples to the posterior distribution of unknowns (Gelman and Rubin 1992, Pella and Masuda 2001). Once convergence of the chains was confirmed, the first half of each chain was discarded as burn-in, while the remaining 10 000 samples were combined over chains and used as simulated draws from the posterior distribution of the unknown parameters.

Stock composition estimated from the particle tracking data, independent of the genetic data, was compared to MSA-estimated stock composition using Pearson linear correlation tests. We also examined if particle tracking estimates (described below) were included in the MSA 95% probability intervals, and conversely if the MSA estimates were included in the particle tracking 95% confidence intervals.

Particle tracking

Estimating ocean connectivity

Methods used to estimate oceanic connectivity between DT + EP and major green turtle rookeries followed 'backtracking' simulations previously described (Putman and Naro-Maciel 2013). A polygon encompassing DT and EP served as a release zone for numerical backtracking experiments (vertices at 24.786735°N, 83.883362°W; 24.392130°N, 82.823181°W; 26.155438°N, 80.735779°W; 26.155438°N, 81.493835°W). The movement of virtual particles was simulated using ICHTHYOP (v2) particle-tracking software (Lett et al. 2008) and the output of the Global Hybrid Coordinate Ocean Model (HYCOM; Chassignet et al. 2007). HYCOM is forced using wind stress, wind speed, heat flux, precipitation, and river discharge. HYCOM assimilates satellite altimetry data, sea surface temperature and in situ measurements from a global array of expendable bathythermographs, Argo floats, and moored buoys to produce hindcast model output. Thus, HYCOM accurately resolves mesoscale processes such as meandering currents, fronts, filaments and oceanic eddies (Chassignet et al. 2007). The HYCOM output used here was from the newly released Global Reanalysis (<http://hycom.org/dataserver/glb-reanalysis>), and output is a daily snapshot of current velocity at 00:00 h (GMT) at a spatial resolution of 0.08° (approx. 6–9 km grid spacing) – sufficiently high resolution to depict ocean circulation processes at scales important for depicting the movement of animals at the ocean surface (Putman and He 2013).

For the model years 2012, 2011, 2010, 2009, and 2008, 100 virtual particles were released at 5-d intervals (Putman and Naro-Maciel 2013) and tracked backwards through time for a total of 3 yr (Naro-Maciel et al. 2014a, b). Particles were advected using a Runge–Kutta fourth-order, time-stepping method whereby particle position was calculated each half an hour. Thus, ICHTHYOP determined where a total of 36 500 particles came from to reach their final location in the DT + EP FG. We recorded the percentage of particles entering major green turtle rookeries throughout the Atlantic (defined as 2.5° latitude × 2.5° longitude zones; Putman and Naro-Maciel 2013). To determine the likely contribution of each rookery to the FG, particle-tracking results were weighted by nester abundance (Seminoff et al. 2015). Additionally, we performed two modeling scenarios exploring the sensitivity of transport predictions to 'recruitment time'. In one scenario we calculated population contributions in which no time restrictions were placed on particles (as in previous studies). In the other, particles were only counted as arriving from a particular rookery after they had drifted for 1 yr. For comparison with genetic data we focused our attention on 16 sequenced rookeries (Supplementary material Appendix 1, Table A1). The average particle contributions for each rookery are reported as well as the minimum and maximum values predicted across the 5 yr modeled.

Results

Genetic analysis

Genetic diversity and differentiation

Most of the DT and EP control region sequences belonged to Lineage A (Cluster A, Encalada et al. 1996), with CMA-3 and CMA-1 (and their CM-A3.1 and CM-A 1.1 subhaplotypes) being the most common (Table 1, Supplementary material Appendix 1, Table A1). One previously undescribed

Table 1. Green sea turtle mtDNA control region haplotypes, subhaplotypes, and frequencies, at the study sites, with sample size (n).

Haplotype (481 bp)	Subhaplotype (856 bp)	Study sites	
		DT	EP
CM-A1	CM-A1.1	22	6
	CM-A1.2	7	
	CM-A1.3	1	
	CM-A1.4	1	
CM-A2	CM-A2.1	1	
CM-A3	CM-A3.1	52	10
	CM-A3.4	1	
CM-A5	CM-A5.1	7	1
CM-A16	CM-A16.1	5	
	CM-A16.2	1	
CM-A18	CM-A18.1	1	1
	CM-A18.2	1	
CM-A21	CM-A21.1	1	
CM-A22	CM-A22.1	2	
CM-A26	CM-A26.1	5	
CM-A27	CM-A27.1	4	2
CM-A28	CM-A28.1	1	
CM-A30	CM-A30.1	1	
CM-A47	CM-A47.1	1	
CM-A48	CM-A48.3		2
CM-A68	CM-A68.1	1	
Sample size (n)		116	22

haplotype was found at Dry Tortugas and assigned the standardized ACCSTR designation CM-A68 (GenBank Accession KT441099). The sequence differed by a single transition (C –> T at position 81) from CM-A16. Analysis of the longer segments (~ 856 bp) revealed 5 previously unpublished subhaplotypes (CMA-1.1, JF308465; CMA-1.2, JF308466; CMA-16.2, CMA-30.1, and CMA-68.1, KT441098-100; Table 1). The longer segment (LS) completely spanned and extended the shorter (SS) by 100 bp at the 5′ end, and ~ 276 bp at the 3′ end. There were several new STR haplotypes as well (GenBank KT441101-121). The distribution of control region segments among the study sites is shown in Table 1, and along with the STRs in Table 2. No significant differentiation was found among sexes, stages, or years sampled, at either study site or marker (Table 3).

Genetic diversity measures at DT and EP are slightly higher than average in comparison to other FGs (Table 4). Global tests revealed highly significant differentiation among Atlantic FGs grouped by geographic region (n = 20; SS: $F_{ST} = 0.351$; 64.94% of variation within and 31.57 among groups, p = 0.000, exact p = 0.000). Pairwise comparisons showed significant differentiation between DT + EP and FGs outside the USA's southeast coast ($F_{ST} > 0.022$, $p < 0.001$; exact p = 0.000). However there was no significant differentiation between DT and EP at any marker (SS: $F_{ST} = 0.000$, p = 0.822; exact p = 0.518; LS: $F_{ST} = 0.000$, p = 0.619; exact p = 0.519; STR: $F_{ST} = 0.000$, p = 0.901; exact p = 0.938; LS + STR: $F_{ST} = 0.003$, p = 0.298; exact p = 0.915), or between our study sites and other east coast US FGs after SB corrections.

The DT CA (in-water males and females) was not differentiated from DT nesters (Shamblin et al. 2015a, b; LS: $F_{ST} < 0.016$, p > 0.196, exact p > 0.118). Following SB corrections for F_{ST}, the DT juveniles were also undifferentiated from the nesters. DT nesters were not significantly differentiated, after SB corrections, from FGs from NC to FL and into the Caribbean. Males and females at the DT and Rocas Atoll (Naro-Maciel et al. 2012) CAs had similar levels of differentiation (SS males: $F_{ST} = 0.524$, p = 0.000; exact p = 0.000; females: $F_{ST} = 0.462$, p = 0.000; exact p = 0.000).

With respect to other rookeries, DT+EP was undifferentiated from Mexico ($F_{ST} = 0.027$, p = 0.088, exact p = 0.360), and possibly Cuba after SB corrections ($F_{ST} = 0.032$, p = 0.046, exact p = 0.007). All green turtle FGs including DT + EP are mixed stocks (Fig. 1 and references therein), and genetic similarity was attributed to recent

Table 2. Green sea turtle mtDNA microsatellite repeat (STR) and control region subhaplotypes, and frequencies, at the study sites, with sample size (n).

MtDNA CR (856 bp)	Study sites		
	STR	DT	EP
CMA1.1	6 8 4 4	5	
	7 7 4 4	17	6
CMA1.2	6 8 4 4	5	
	7 7 4 4	1	
	8 10 4 4	1	
CMA1.3	7 7 4 4	1	
CMA1.4	7 8 4 4	1	
CMA2.1	7 7 4 4	1	
CMA3.1	5 8 4 4	5	1
	5 9 4 4	3	1
	6 7 4 4	1	
	6 7 4 5	2	
	6 8 4 4	23	7
	6 9 4 4	1	
	7 7 4 4	6	
	7 7 4 5	3	
	7 8 4 4	5	1
	7 12 4 4	3	
CMA3.4	7 8 4 4	1	
CMA5.1	5 13 4 4	1	
	6 8 4 4	1	
	6 13 4 4	1	
	7 11 4 4	2	
	7 12 4 4	2	1
CMA16.1	5 7 6 4	2	
	5 8 6 4	2	
	5 10 6 4	1	
CMA16.2	5 8 6 4	1	
CMA18.1	7 7 4 4	1	1
CMA18.2	7 7 4 4	1	
CMA21.1	7 11 4 4	1	
CMA22.1	5 8 4 5	1	
	7 7 4 4	1	
CMA26.1	6 8 4 4	2	
	7 8 4 4	3	
CMA27.1	5 8 4 4		1
	5 9 4 4	1	
	5 9 8 4	3	1
CMA28.1	5 8 5 4	1	
CMA30.1	7 8 4 4	1	
CMA47.1	7 7 5 5	1	
CMA48.3	6 7 4 4		2
CMA68.1	5 6 6 4	1	
Sample size		116	22

Table 3. Genetic structure of the study sites. Sample size (n) is given with results of tests for different markers among years, sexes, and stages at DT and EP, when applicable. No significant differentiation was found among sexes, stages, or years sampled, at either study site or marker following sequential Bonferroni (SB) corrections, and post-SB non-significant comparisons are abbreviated "ns" and labeled with *. Samples with n = 1 were not tested.

	Genetic diversity				Genetic differentiation		
	P	A	h	π	Sexes	Stages	Years
DT n = 116							
Haplotypes	18	14	0.716	0.005	$n_{male} = 16$, $n_{female} = 26$; $F_{ST} = 0.002$, p = 0.360; exact p = 0.518	$n_{juvenile} = 74$, $n_{adult} = 42$; $F_{ST} = 0.009$, p = 0.173; exact p = 0.270	$n_{2008} = 23$, $n_{2009} = 21$, $n_{2010} = 11$, $n_{2011} = 28$, $n_{2012} = 7$, $n_{2013} = 13$, $n_{2014} = 13$; $F_{ST} < 0.135$, p > 0.054*; exact p > 0.072 *except 2009 vs 2011: $F_{ST} = 0.088$, p = 0.009; ns after SB
Subhaplotypes	28	20	0.756	0.003	$n_{male} = 16$, $n_{female} = 26$; $F_{ST} = 0.016$, p = 0.237; exact p = 0.241	$n_{juvenile} = 74$, $n_{adult} = 42$; $F_{ST} = 0.008$, p = 0.187; exact p = 0.350	$n_{2008} = 23$, $n_{2009} = 21$, $n_{2010} = 11$, $n_{2011} = 28$, $n_{2012} = 7$, $n_{2013} = 13$, $n_{2014} = 13$; $F_{ST} < 0.080$, p > 0.114*, exact p > 0.063 *except 2009 vs 2010: $F_{ST} = 0.071$, p = 0.040; 2009 vs 2011: $F_{ST} = 0.066$, p = 0.021; ns after SB
STRs	30	22	0.830	0.059	$n_{male} = 16$, $n_{female} = 26$; $F_{ST} = 0.062$, p = 0.051; exact p = 0.167	$n_{juvenile} = 74$, $n_{adult} = 42$; $F_{ST} = 0.011$, p = 0.129; exact p = 0.088	$n_{2008} = 23$, $n_{2009} = 21$, $n_{2010} = 11$, $n_{2011} = 28$, $n_{2012} = 7$, $n_{2013} = 13$, $n_{2014} = 13$; $F_{ST} < 0.071$, p > 0.145*, exact p > 0.080* *except 2008 vs 2009: $F_{ST} = 0.071$, p = 0.025, exact p = 0.041; 2009 vs 2011: $F_{ST} = 0.065$, p = 0.023; 2011 vs 2013: exact p = 0.029, ns after SB
STRs + Subhaplotypes	58	41	0.930	0.008	$n_{male} = 16$, $n_{female} = 26$; $F_{ST} = 0.000$, p = 0.553; exact p = 0.702	$n_{juvenile} = 74$, $n_{adult} = 42$; $F_{ST} = 0.007$, p = 0.129; exact p = 0.361	$n_{2008} = 23$, $n_{2009} = 21$, $n_{2010} = 11$, $n_{2011} = 28$, $n_{2012} = 7$, $n_{2013} = 13$, $n_{2014} = 13$; $F_{ST} < 0.071$, p > 0.145*, exact p > 0.060 *except 2008 vs 2013: $F_{ST} = 0.040$, p = 0.04; 2009 vs 2011: $F_{ST} = 0.035$, p = 0.025; 2011 vs 2013: p = 0.030, ns after SB
EP n = 22							
Haplotypes	16	6	0.693	0.005	N/A	N/A	$n_{2007} = 4$, $n_{2008} = 7$, $n_{2011} = 4$, $n_{2013} = 2$, $n_{2014} = 2$; $F_{ST} < 0.724$, p > 0.065; exact p > 0.066
Subhaplotypes	25	6	0.732	0.005	N/A	N/A	$n_{2007} = 4$, $n_{2008} = 7$, $n_{2011} = 4$, $n_{2013} = 2$, $n_{2014} = 2$; $F_{ST} < 0.822$, p > 0.068; exact p > 0.065
STRs	22	8	0.810	0.053	N/A	N/A	$n_{2007} = 4$, $n_{2008} = 7$, $n_{2011} = 4$, $n_{2013} = 2$, $n_{2014} = 2$; $F_{ST} < 0.147$, p > 0.266; exact p > 0.272
STRs + Subhaplotypes	47	10	0.840	0.009	N/A	N/A	$n_{2007} = 4$, $n_{2008} = 7$, $n_{2011} = 4$, $n_{2013} = 2$, $n_{2014} = 2$; $F_{ST} < 0.147$, p > 0.274; exact p > 0.270

shared history (Naro-Maciel et al. 2014a) rather than single stock origins. Several rookeries were also undifferentiated from each other: AV, SU, and BI, as well as most pairwise combinations within the South Atlantic. In exact tests, AV and SU were not differentiated, nor were several South Atlantic combinations. In all tests DT + EP was significantly differentiated from each of the RMUs, and the RMUs from each other ($F_{ST} > 0.038$, p = 0.000; exact p = 0.000). Pairwise comparisons of STRs and/or longer CR sequences to available published data revealed expected results. DT + EP was significantly differentiated from Mediterranean (STR: $F_{ST} = 0.151$, p = 0.000; exact p = 0.000) and Brazilian rookeries (LS + STR: $F_{ST} > 0.068$, p < 0.001; exact p = 0.000).

Mixed stock analysis

Genetic connectivity of DT + EP to Mediterranean, and southern or eastern Atlantic, natal beaches was negligible. Costa Rica, Mexico, Cuba, and Florida each contributed about one quarter of the mean natal origins, although in contrast to the remaining rookeries, their 95% probability intervals were fairly broad. MSA_2 (with weighted priors) had the narrowest intervals. In all analyses, Gelman and Rubin diagnostics confirmed chain convergence to the posterior density, with all shrink factors ≤ 1.2. The lack of temporal variation satisfied the MSA assumption of constancy. In all MSAs (Table 5), Pearson's correlations tests revealed that ocean connectivity and mean MSA estimates were correlated ($R \geq 0.643$, p ≤ 0.010). The range of particle tracking estimates overlapped the MSA probability intervals in all comparisons except for Cuba (Table 5A). However, there were pronounced differences between mean ocean and genetic connectivity with respect to the northeast Florida, Mexico, Cuba, Costa Rica, and Surinam rookeries.

Particle tracking

Ocean connectivity

Virtual backtracking experiments indicated that broad oceanic connectivity is possible between major green turtle rookeries and the DT + EP area (Fig. 2). Though numerous potential source populations were identified as potentially contributing turtles to this area, the highest estimates came from Mexico and Costa Rica, followed by Surinam (Table 5A). Whether transport was more likely from Costa Rica or Mexico depended on simulation parameters. If particles could immediately recruit, more were predicted to come from Mexico. If they were restricted to a year of drift, more arrived from Costa Rica. Annual variation was apparent in contributions from these three rookeries. For instance, when particles could only recruit after 1 yr, predicted contributions ranged from 9–32% for Mexico, 43–78% for Costa Rica, and 1–33% for Surinam. Contributions from other rookeries averaged less than 5% for the modeled period. No significant contributions were predicted to this FG from eastern Florida or the Mediterranean, and only minor contributions were predicted from the southwestern or eastern Atlantic rookeries.

Table 4. Mitochondrial control region diversity at the two study FGs (in bold), as compared to other Atlantic FGs from the published literature (references in Fig. 1). These measures were based on ~ 481 bp segments, and recalculated for published FGs.

FG	Type of FG	Haplotypes	Haplotype diversity (h)	Nucleotide diversity (π)	Sample size
NC	juvenile	12	0.729+/–0.030	0.005+/–0.003	106
ECF	juvenile	16	0.643+/–0.018	0.004+/–0.002	300
HI	juvenile	6	0.486+/–0.067	0.003+/–0.002	62
DT	**juvenile, adult**	**14**	**0.716+/–0.033**	**0.005+/–0.003**	**116**
EP	**juvenile**	**6**	**0.693+/–0.080**	**0.005+/–0.003**	**22**
SJ	juvenile	13	0.711+/–0.022	0.004+/–0.003	255
TX	juvenile	15	0.606+/–0.019	0.002+/–0.002	282
BH	juvenile	22	0.612+/–0.021	0.006+/–0.003	560
BB	juvenile	8	0.773+/–0.028	0.010+/–0.006	60
NI	adult	3	0.208+/–0.061	0.004+/–0.003	70
AF	juvenile	13	0.717+/–0.031	0.007+/–0.004	117
$RA_{juveniles}$	juvenile	8	0.688+/–0.036	0.005+/–0.003	101
RA_{males}	adult	6	0.414+/–0.111	0.003+/–0.002	30
FN	juvenile	12	0.650+/–0.028	0.004+/–0.003	117
BA	juvenile	6	0.648+/–0.053	0.002+/–0.002	45
ES	juvenile	9	0.595+/–0.031	0.003+/–0.002	157
UB	juvenile	10	0.446+/–0.056	0.002+/–0.002	113
AD	juvenile	12	0.583+/–0.045	0.002+/–0.002	115
CA	juvenile	12	0.586+/–0.050	0.003+/–0.002	101
AG	juvenile	9	0.553+/–0.051	0.002+/–0.002	93
CV	juvenile	5	0.588+/–0.045	0.004+/–0.003	44
Average		10	0.602	0.004	136

Discussion

The comparative genetics and modeling approaches revealed constrained green turtle movements within the northwestern Atlantic despite highly migratory potential, and can serve as models for other marine taxa. The overarching consistency of particle modeling, genetic, and published tag and satellite connectivity estimates highlights the key role of ocean currents in DT + EP green turtle dispersal. The mismatches we found between ocean and genetic connectivity, however, indicate that, although ocean circulation is a key factor in marine population structure (Cowen et al. 2007), it represents only one aspect of the complex scenario in our study.

These discrepancies offer insight into the 'lost years', and suggest that directional swimming during this stage may significantly influence emergent population-level distribution (Putman et al. 2012, Putman and Mansfield 2015). Moreover, our results point to juvenile natal homing as a key driver of population structure, and substantiate hypothesized historical impacts on dispersal of Surinam turtles, for example (Shamblin et al. 2012b, Naro-Maciel et al. 2014a). DT and EP were genetically similar to FGs in the area, but highly differentiated from most other Atlantic groups. Similarly, the DT courtship area was characterized by local movements and male philopatry despite highly migratory potential. Deeper genomic coverage revealed new sequences and may improve resolution in future studies. The numerous political boundaries across which turtles migrate highlight the importance of international and interstate cooperation to counter threats and implement conservation strategies.

Ocean and genetic connectivity to rookeries

Despite the highly migratory potential of green turtles, barriers to dispersal were evident between Florida and the southwestern Atlantic, eastern Atlantic, and the Mediterranean. Restricted movement between the North Atlantic, South Atlantic, and Mediterranean was highlighted in a recent green turtle review (Seminoff et al. 2015), and genetics and ocean transport simulation data support these findings. Modeled particles from Mediterranean rookeries remain in that Sea (Putman and Naro-Maciel 2013), and mitochondrial haplotypes there are near-endemic (Fig. 1 and references therein, Tikochinski et al. 2012). Within the Atlantic, a strong historical barrier to north-south dispersal, related to population expansion from distinct northern and southern glacial refugia during the most recent glacial–interglacial cycle, was detected (Naro-Maciel et al. 2014a). These barriers are mirrored by present ocean conditions: virtual particles do not cross the Equator from northwestern Atlantic rookeries to the south Atlantic (Putman and Naro-Maciel 2013).

Thus, all major DT + EP natal sources were restricted to the northwestern Atlantic, although some rookery estimates differed between models. Mean ocean and genetic connectivity to DT+ EP were highest from Costa Rica and Mexico. Satellite and tag data also support links between our study sites and Mexico (KH unpubl.). Tortuguero, Costa Rica, is the largest area rookery by an order of magnitude or more (Supplementary material Appendix 1, Table A1) but its estimated genetic contribution to DT + EP does not dwarf the others, suggesting limits to population size effects. Most nesters tagged or satellite-tracked at Tortuguero were recaptured foraging in Nicaragua and the Caribbean, rather than at DT + EP (Carr et al. 1978, Meylan 1995, Bass et al. 1998, Bjorndal et al. 2005, Bolker et al. 2007). This apparent discordance can be explained if juveniles hatched at Tortuguero recruit to DT + EP, or other FGs, after their 'lost years' and then migrate to Nicaragua and closer to their natal site. Juvenile natal homing has been reported throughout the

Table 5. Independent estimates from particle modeling and mixed stock analysis of DT + EP origins among: A) regional rookeries; B) Regional Management Units (RMUs). Mean estimates and range are given for the particle data. The MSA used Bayesian methods with equal priors (MSA_1) and priors weighted to reflect nester abundance (MSA_2). Parameters of the posterior density are given as summary statistics. Bayes mean values (marginal means of the posterior distribution) are shown with standard deviation (SD). The 2.5 and 97.5% values indicate the upper and lower bounds of the 95% probability interval. Rookeries as in Fig. 1; FN was modeled together with RA with respect to ocean connectivity.

A)

Rookery	Particles	MSA	Mean	SD	2.5%	Median	97.5%
Northeast Florida	0.000	MSA_1	0.238	0.137	0.000	0.254	0.478
	(0.000–0.000)	MSA_2	0.227	0.127	0.000	0.241	0.451
Southeast + west Florida	0.045	MSA_1	0.029	0.073	0.000	0.000	0.269
	(0.037–0.064)	MSA_2	0.009	0.041	0.000	0.000	0.134
Mexico	0.485	MSA_1	0.242	0.134	0.011	0.222	0.539
	(0.425–0.599)	MSA_2	0.269	0.127	0.072	0.250	0.550
Costa Rica	0.374	MSA_1	0.241	0.103	0.031	0.247	0.428
	(0.265–0.453)	MSA_2	0.292	0.094	0.093	0.300	0.462
Cuba	0.001	MSA_1	0.223	0.098	0.075	0.208	0.454
	(<0.001–0.003)	MSA_2	0.195	0.092	0.009	0.185	0.405
Buck Island	<0.001	MSA_1	0.012	0.024	0.000	0.000	0.085
	(0.000–<0.001)	MSA_2	0.000	0.002	0.000	0.000	0.000
Aves Island	0.002	MSA_1	0.006	0.015	0.000	0.000	0.054
	(0.001–0.005)	MSA_2	0.002	0.008	0.000	0.000	0.024
Surinam	0.084	MSA_1	0.005	0.012	0.000	0.000	0.045
	(0.017–0.143)	MSA_2	0.005	0.013	0.000	0.000	0.049
Rocas Atoll	0.001	MSA_1	0.001	0.002	0.000	0.000	0.005
	(<0.001–0.002)	MSA_2	0.000	0.000	0.000	0.000	0.000
Fernando de Noronha	*with RA	MSA_1	0.001	0.002	0.000	0.000	0.006
		MSA_2	0.000	0.000	0.000	0.000	0.000
Trindade Island	0.000	MSA_1	0.001	0.002	0.000	0.000	0.005
	(0.000–0.000)	MSA_2	0.000	0.001	0.000	0.000	0.000
Ascension Island	0.002	MSA_1	0.001	0.002	0.000	0.000	0.006
	(<0.001–0.004)	MSA_2	0.001	0.002	0.000	0.000	0.005
Guinea Bissau	<0.001	MSA_1	0.001	0.002	0.000	0.000	0.005
	(0.000–0.001)	MSA_2	0.001	0.003	0.000	0.000	0.009
Bioko	<0.001	MSA_1	0.001	0.002	0.000	0.000	0.005
	(0.000–<0.001)	MSA_2	0.000	0.001	0.000	0.000	0.000
Sao Tome e Principe	<0.001	MSA_1	0.001	0.002	0.000	0.000	0.006
	(0.000–<0.001)	MSA_2	0.000	0.000	0.000	0.000	0.000
Mediterranean	0.000	MSA_1	0.001	0.002	0.000	0.000	0.005
	(0.000–0.000)	MSA_2	0.000	0.000	0.000	0.000	0.000

B)

Region	Particles	MSA	Mean	SD	2.5%	Median	97.5%
Atlantic North West	0.905	MSA_1	0.973	0.026	0.909	0.980	1.000
		MSA_2	0.988	0.020	0.931	0.998	1.000
South Caribbean	0.086	MSA_1	0.023	0.025	0.000	0.015	0.086
		MSA_2	0.010	0.019	0.000	0.000	0.068
South Atlantic	0.003	MSA_1	0.002	0.004	0.000	0.000	0.014
		MSA_2	0.002	0.004	0.000	0.000	0.012
Mediterranean	0.000	MSA_1	0.002	0.004	0.000	0.000	0.014
		MSA_2	0.000	0.000	0.000	0.000	0.000

Atlantic in various marine turtles (Bowen et al. 2004, Naro-Maciel et al. 2007, 2012), and the limited mark–recapture data available support this hypothesis; juveniles tagged in eastern central Florida depart at ~ 60–70 SCL, with most recaptures reported from Nicaragua (Witherington et al. 2006).

Significant discrepancies between ocean and genetic connectivity estimates were evident for Florida and Cuba, likely due to behavioral factors not included in the ocean transport models. Although virtually no particles reached DT+ EP from these beaches, their mean combined genetic contributions were ~ 45%. The 95% MSA probability intervals do span much lower estimates, including 0% from Florida, but this contradicts satellite and tag data showing that DT, Florida, and Caribbean females use Florida FGs. Florida juveniles have been recaptured nesting in the state, and yearlings from Florida rookeries forage along its coast (Bagley 2003). Limited swimming during the 'lost years', including navigation into counter currents flowing towards the Gulf of Mexico from the Atlantic, and not considered in the ocean transport model, may bring these turtles to the DT + EP area. Indeed, pelagic Gulf green turtles are not limited to passive drifting (Putman and Mansfield 2015), and young loggerheads can swim towards favorable currents (Putman et al. 2012). In the Pacific, even slight behavioral modifications, such as swimming northwards in response to westward drift, is thought to prevent Galapagos green turtles from reaching the Central Pacific, instead transporting them back

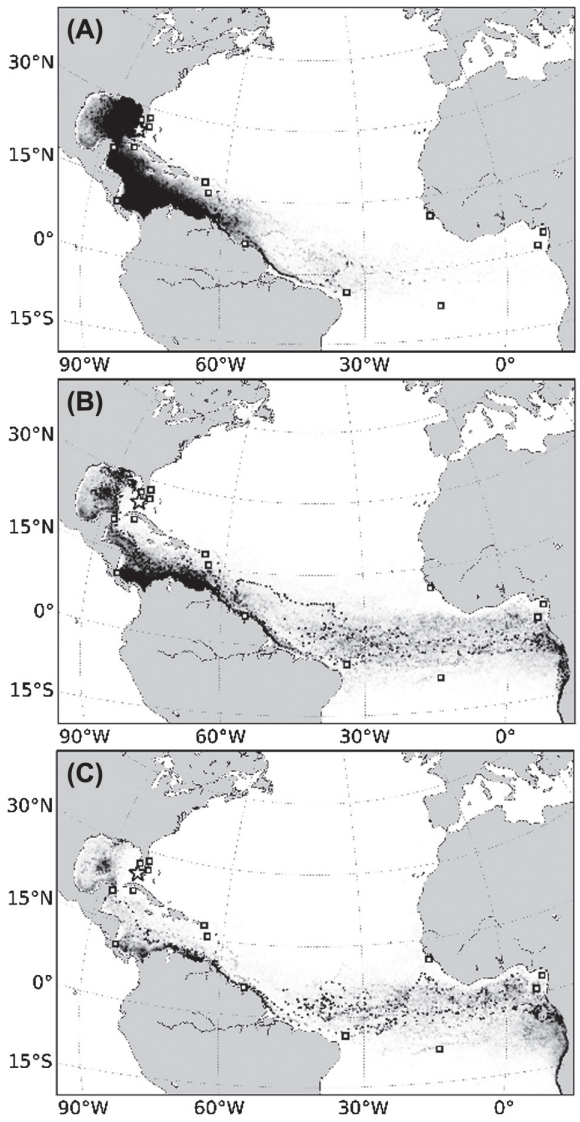

Figure 2. Results of particle tracking experiments (map projection: Lambert Azimuthal Equal Area). (A) Particle distribution plotted every 5th day during the first year of backtracking from the Dry Tortugas and Everglades National Park study sites (star) relative to major green turtle rookeries (squares) in Table 5. Darker coloration indicates oceanic areas where transport to the DT and EP via surface currents is more likely. Results for the release years 2008, 2009, 2010, 2011, and 2012 are shown together. (B) Same as in (A), but showing particle distribution during the second year of backtracking. (C) Same as in (A), but showing particle distribution during the third year of backtracking.

to South America on the North Equatorial Countercurrent (Naro-Maciel et al. 2014b).

Another significant discrepancy between ocean and genetic connectivity estimates, that may highlight 'lost years' retention and population history effects, was found for Surinam and the South Caribbean RMU. Mean particle estimates of Surinam's contribution to DT + EP are higher than the 95% MSA probability intervals, and become increasingly so if recruitment is limited to >1 yr. All of the modeled particles flow northwards to Florida from Surinam. Further, very few particles approach Cape Verde while none reach Brazil (Putman and Naro-Maciel 2013), in contrast to genetic and classic tagging data showing that turtles from Surinam commonly forage in Brazil and Cape Verde (Bowen and Karl 2007, Monzón-Argüello et al. 2010, Naro-Maciel et al. 2012). The historical roots of this discrepancy were initially noted in a phylogeographic analysis that reported genetic mixing of otherwise separate northern and southern lineages in the South Caribbean. Despite being located in the northern hemisphere, Surinam is thought to have been colonized from a southeastern Atlantic refugium (Naro-Maciel et al. 2014a). We propose that, to reach Brazil or Cape Verde from Surinam, these 'lost years' turtles attain favorable currents or counter currents leading to Cape Verde or Brazil. Thus, although marine connectivity is strongly influenced by population size and oceanographic processes, behavior and population history must also be invoked to more completely explain turtle movements to DT + EP.

Dry Tortugas courtship area

Although evidence increasingly supports male philopatry in various marine turtles (FitzSimmons et al. 1997a, b, Hays et al. 2010, Naro-Maciel et al. 2012, 2014a, Schofield et al. 2013), very few CAs have been studied due to the cryptic marine mating habitat. At DT, we detected no significant differentiation between males and females, or adults and juveniles, despite deeper mitogenomic coverage. To date, no study comparing green male to female turtles has detected significant differences where the sexes spatially overlap (FitzSimmons et al. 1997a, Bass et al. 1998, Naro-Maciel et al. 2012, 2014b). In Australia, genetic differentiation among males at different CAs was similar to that of females, confirming male philopatry (FitzSimmons et al. 1997a). Here, we compared DT to Rocas Atoll in Brazil, the only other sequenced CA in the Atlantic (Naro-Maciel et al. 2012). Genetic differentiation values between DT and Rocas Atoll were similar for males and females, supporting male philopatry in the Atlantic as well.

DT however, was unique in that Rocas juveniles were differentiated from adults, suggesting that the latter transited through the FG for breeding and then departed (Naro-Maciel et al. 2012). In contrast, satellite tracks of DT females revealed post-nesting use of local FGs at DT, outside EP, and in the Florida Keys (Hart et al. 2013). Genetic data support this unusual finding, because there was no significant differentiation between the DT rookery and the DT + EP feeding area. DT nesters could thus forage locally and constitute a rare non-migratory breeding stock similar to Cocos Keeling, Indian Ocean (Whiting et al. 2007, Hart et al. 2013). While the DT rookery is also undifferentiated from sequenced FGs from North Carolina to Florida and further south into the Caribbean, DT nesters do not forage at these juvenile developmental habitats (Bagley 2003, Blumenthal et al. 2006), and with an estimated 138 nests or ~ 30 females yr^{-1} (Shamblin et al. 2015a, b), the rookery is too small to be the single source of eventual juvenile recruits to all of these FGs. Thus, this first genetic analysis of a North Atlantic green turtle courtship area points to constrained, local movements and male philopatry.

Florida National Parks and other feeding grounds

Genetic analysis indicates that foraging turtles appear to move around US southeastern coastal FGs sufficiently to achieve homogeneity. The limited tag data available support this finding; most juvenile turtles tagged in East Central Florida FGs were recaptured within and among three local FGs (Bagley 2003). The lack of temporal variation suggests mixing is ongoing, and was also reported from other sites (Bass et al. 2004, Naro-Maciel et al. 2007, 2012, 2014b), except the Bahamas (Bjorndal and Bolten 2008). Limited temporal variation, however, contrasts with observed ocean current variability. Recent modeling studies suggest that directional swimming can significantly dampen effects of variable ocean currents on animal trajectories (Putman et al. 2015), further supporting our hypothesis that swimming behavior is responsible for discordance between genetic and ocean modeling connectivity estimates.

Although satellite-tracked EP turtles remained within the Park, relatively brief tracking durations (27–62 d) may have precluded observation of long-distance movement (Hart and Fujisaki 2010). Most juvenile turtles must depart at some point to mature and breed, as there are few green turtles nesting within EP. These turtles may distribute to other FGs outside of parks, as well as to protected areas in the Florida Keys such as the DT, where the lack of genetic differentiation between adults and juveniles suggests that incoming juveniles may become residents (or return) at older life-stages. Indeed Dry Tortugas is unique regionally because adult turtles forage there, and should thus be considered relevant to conservation. Joining protected areas into a network may be productive, as turtles sheltered in parks are subject to threats when moving through less protected areas. This research advances knowledge of green turtles with conservation applications, and highlights the utility of multidisciplinary approaches for identifying mechanisms responsible for organismal distributions and studying cryptic life stages.

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Supplementary material (Appendix ECOG-02056 at <www.ecography.org/appendix/ecog-02056>). Appendix 1.