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ORIGINAL ARTICLE

Evidence from genetic and Lagrangian drifter data for transatlantic transport of small juvenile green turtles

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ABSTRACT

Aim A key life-history component for many animals is the need for movement between different geographical locations at particular times. Green turtle (*Chelonia mydas*) hatchlings disperse from their natal location to spend an early pelagic stage in the ocean, followed by a neritic stage where small juveniles settle in coastal areas. In this study, we combined genetic and Lagrangian drifter data to investigate the connectivity between natal and foraging locations. In particular we focus on the evidence for transatlantic transport.

Location Atlantic Ocean.

Methods We used mitochondrial DNA (mtDNA) sequences (n = 1567) from foraging groups (n = 8) and nesting populations (n = 12) on both sides of the Atlantic. Genetic data were obtained for Cape Verde juvenile turtles, a foraging group not previously sampled for genetic study. Various statistical methods were used to explore spatial genetics and population genetic structure (e.g. exact tests of differentiation, GENELAND and analysis of molecular variance). Many-to-many mixed stock analysis estimated the connectivity between nesting and foraging groups.

Results Our key new finding is robust evidence for connectivity between a nesting population on the South American coast (25% of the Surinam nesting population are estimated to go to Cape Verde) and a foraging group off the coast of West Africa (38% of Cape Verde juveniles are estimated to originate from Surinam), thus extending the results of previous investigations by confirming that there is substantial transatlantic dispersal in both directions. Lagrangian drifter data demonstrated that transport by drift across the Atlantic within a few years is possible.

Main conclusions Small juvenile green turtles seem capable of dispersing extensively, and can drop out of the pelagic phase on a transatlantic scale (the average distance between natal and foraging locations was 3048 km). Nevertheless, we also find support for the 'closest-to-home' hypothesis in that the degree of contribution from a nesting population to a foraging group is correlated with proximity. Larger-sized turtles appear to feed closer to their natal breeding grounds (the average distance was 1133 km), indicating that those that have been initially transported to far-flung foraging grounds may still be able to move nearer to home as they grow larger.

Keywords

Atlantic Ocean, buoy trajectory data, *Chelonia mydas*, foraging grounds, geographical connectivity, landscape genetics, mitochondrial DNA, mixed stock analysis.

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INTRODUCTION

Understanding how organisms are distributed and dispersed in space and time, and how they achieve this, are key objectives in biogeography. Evolutionary models and empirical studies show that multiple factors influence the costs and benefits of dispersal (Bowler & Benton, 2005; Dawson & Hamner, 2008). In the sea, the pelagic juvenile stage represents an important dispersal mechanism, but dispersal could be affected by oceanographic factors or life-history traits (Palumbi, 2004). Some of the most remarkable movements are by marine animals, with some species migrating thousands of kilometres while returning to their natal areas to reproduce (Bowen *et al.*, 1992; Lohmann *et al.*, 1999; Putman & Lohmann, 2008). Green turtles, *Chelonia mydas* (Linnaeus, 1758), constitute such an example, exhibiting a complex life-history pattern with weak migratory connectivity (Bolten, 2003; Bolker *et al.*, 2007; Bjorndal & Bolten, 2008). Their life begins in specific geographical areas, followed by dispersal across vast expanses of sea (Lohmann *et al.*, 1999, 2008a,b). This first stage is spent in the open ocean for 3 to 5 years (Carr & Meylan, 1980; Reich *et al.*, 2007), although this period could be longer (Zug *et al.*, 2002; McClellan & Read, 2007). After that, juveniles of approximately 20–40 cm in curve carapace length (CCL) (or 18–37 cm in straight carapace length, SCL) settle into neritic benthic habitats as herbivores (Bjorndal, 1980; Balazs, 1982; Musick & Limpus, 1997). This habitat shift is relatively rapid and direct, although variation in temperature, diet quality and/or food availability could affect recruitment size (Reich *et al.*, 2007). Following settlement, green sea turtles may undertake further developmental migrations among neritic foraging grounds, but after several decades sexual maturity is attained and adults migrate back to their natal areas to reproduce (Lohmann *et al.*, 1999, 2008a,b; Bjorndal & Bolten, 2008).

Previous studies indicate that a variety of factors may influence the composition of a neritic foraging group (FG), including: nesting population (NP) size (Bass *et al.*, 1998; Lahanas *et al.*, 1998), geographical distance (Bass & Witzell, 2000), oceanic currents (Luke *et al.*, 2004; Bass *et al.*, 2006; Naro-Maciel *et al.*, 2007) and homing behaviour (Bowen *et al.*, 2004; Bass *et al.*, 2006; Bolker *et al.*, 2007). Of these, currents and homing behaviour have been the key focus for formulating hypotheses.

Recently, genetic studies have looked at sampling gaps in the western coast of Africa (Formia *et al.*, 2006), and these have enabled larger-scaled mixed stock analyses (MSAs) to better resolve the movements of green turtles in the Atlantic Ocean (Bolker *et al.*, 2007; Naro-Maciel *et al.*, 2007). In an important advance, Bolker *et al.* (2007) developed a Bayesian hierarchical model ('many-to-many' MSA) that simultaneously estimates the origins ('foraging group-centric' perspective) and destinations ('nesting population-centric' perspective) of individuals in a metapopulation with several source populations ('rookeries' or NPs) and many mixed stocks, with rookery size as a constraint in the analysis. This resulted in novel insights, for example that there were greater contributions than previously thought to distant FGs, with extensive connectivity among NPs and FGs within three broad regions. The authors suggested that the latter pattern could be caused by the tendency of immature turtles to settle in FGs closest to their natal beach, but noted that within regions the 'closest-to-home' hypothesis did not always hold. One of the most important outcomes was the observation that transatlantic dispersal was possible. They showed that the Guinea Bissau (West Africa) NP was an important contributor to foraging assemblages on the north-east Brazilian coast. There was also an indication of connectivity in the other direction, between a north-east Brazilian NP and a West African FG, but this was not supported by the 'many-to-many' analysis.

Here, we extend the study of Bolker *et al.* (2007) by adding new data for a West African FG not previously studied, with the aim of establishing further evidence for transatlantic dispersal of early juvenile green turtles. Additionally, we mined Lagrangian drifter data to find out whether ocean currents would allow for such transport. Finally, we attempt to compare the average distances between natal and foraging locations for small-sized juveniles versus larger-sized turtles.

MATERIALS AND METHODS

Sampling, data collection and DNA sequencing

We focus on the shift from pelagic to benthic habitats by examining coastal areas where juveniles of approximately 20–40 cm CCL (18–37 cm SCL; hereafter called *small juveniles*) can be found. As size data for each individual sampled for genetic study were not available, we used size range information and found eight FGs that include these body sizes (SCL size range 24.0–78.7 cm; Table 1). These are considered to be FGs where small juveniles are likely to first drop out of the pelagic phase (hereafter called *small-sized foraging groups*, ssFGs) because they include individuals of the sizes that are expected of such turtles (i.e. below 40 cm CCL, or 37 cm SCL). We also employed one FG with turtles of larger body sizes (hereafter called the *large-sized foraging group*, lsFG) that did not overlap with the sizes of those in ssFGs (Nicaragua; Table 1), and must therefore represent later life stages. We used 1567 mitochondrial DNA (mtDNA) control region sequences of green turtles in the Atlantic, incorporating data published up to 2008 for NPs and FGs (Fig. 1, Tables 1 & 2). Most of the locations (Fig. 1, Table 1) are as named by Bolker *et al.* (2007), with the exception of: (1) Rocas Atoll, previously called north-east Brazil; (2) Bioko and São Tomé and Príncipe, formerly grouped as the Gulf of Guinea; and (3) the Rocas Atoll foraging group, previously called north-east Brazil. We added data for Ubatuba and Almofala (Brazil; Fig. 1) that had been subsequently published (Naro-Maciel *et al.*, 2007). Although the genetic data for the Corisco Bay FG were reported in a thesis (Formia, 2002), they were not included here since they were not formally published by the author at the time of our analysis. We added new genetic data for the FG of the Cape Verde Islands, a location off the West African coast not previously studied.

Table 1 References for the dataset used in this study. Size information for the analysed green turtles (*Chelonia mydas*) is given by the straight carapace length (SCL) in centimetres.

Location	Area	SCL	Type of FG	Pop. size	*h*	π	References
Nicaragua	Foraging	88.3–105.7	lsFG	–	0.183 ± 0.062	0.0038 ± 0.0025	Bass *et al.* (1998)
Florida	Foraging	25.0–70.0	ssFG	–	0.485 ± 0.067	0.0031 ± 0.0021	Bass & Witzell (2000)
N. Carolina	Foraging	24.0–74.0	ssFG	–	0.678 ± 0.031	0.0051 ± 0.0031	Bass *et al.* (2006)
Bahamas	Foraging	31.0–67.0	ssFG	–	0.370 ± 0.065	0.0064 ± 0.0037	Lahanas *et al.* (1998)
Barbados	Foraging	31.0–70.0	ssFG	–	0.773 ± 0.028	0.0103 ± 0.0056	Luke *et al.* (2004)
Ubatuba	Foraging	*30.7–73.7	ssFG	–	0.446 ± 0.056	0.0020 ± 0.0015	Naro-Maciel *et al.* (2007)
Almofala	Foraging	*27.7–78.7	ssFG	–	0.717 ± 0.031	0.0068 ± 0.0039	Naro-Maciel *et al.* (2007)
Rocas Atoll	Foraging	No data	ssFG	–	0.644 ± 0.092	0.0022 ± 0.0017	Bjorndal *et al.* (2006)
Cape Verde	Foraging	25.5–58.3	ssFG	–	0.587 ± 0.045	0.0042 ± 0.0027	Present study
Mexico	Nesting	–	–	1587	0.816 ± 0.057	0.0051 ± 0.0032	Encalada *et al.* (1996)
Florida	Nesting	–	–	779	0.562 ± 0.047	0.0012 ± 0.0011	Encalada *et al.* (1996)
Costa Rica	Nesting	–	–	26535	0.163 ± 0.023	0.0033 ± 0.0021	Bjorndal *et al.* (2005)
Aves	Nesting	–	–	267	0.186 ± 0.088	0.0039 ± 0.0025	Lahanas *et al.* (1998)
Surinam	Nesting	–	–	1814	0.257 ± 0.142	0.0030 ± 0.0021	Encalada *et al.* (1996)
Rocas Atoll	Nesting	–	–	115	0.537 ± 0.075	0.0026 ± 0.0018	Encalada *et al.* (1996), Bjorndal *et al.* (2006)
Trindade Is.	Nesting	–	–	3000	0.505 ± 0.052	0.0012 ± 0.0011	Bjorndal *et al.* (2006)
Guinea Bissau	Nesting	–	–	2523	0.000 ± 0.000	0.0000 ± 0.0000	Encalada *et al.* (1996), Formia *et al.* (2006)
Ascension Is.	Nesting	–	–	3709	0.289 ± 0.071	0.0007 ± 0.0008	Encalada *et al.* (1996), Formia *et al.* (2006)
Sâo Tomé and Príncipe	Nesting	–	–	90	0.569 ± 0.110	0.0026 ± 0.0019	Formia *et al.* (2006)
Bioko	Nesting	–	–	407	0.184 ± 0.068	0.0004 ± 0.0005	Formia *et al.* (2006)
Cyprus	Nesting	–	–	100	0.077 ± 0.070	0.0002 ± 0.0003	Encalada *et al.* (1996), Kaska (2000)

*Data originally collected as curved carapace length (CCL) (McClellan & Read, 2007) were transformed to SCL using the equation CCL = 1.388 + (1.053) SCL (Bjorndal *et al.*, 2000).

Population size data were obtained from Bellini *et al.* (1995), Seminoff (2002, 2004) and Formia *et al.* (2006). Haplotype (*h*) and nucleotide (π) diversities detected at each location are shown. Type of foraging group (FG) is shown: small-sized foraging group (ssFG) and large-sized foraging group (lsFG).

Forty-four tissue samples from Boavista Island (Cape Verde) were collected in a 20% DMSO (dimethyl sulfoxide) solution or 96% ethanol during 2001, 2007 and 2008. Genomic DNA was isolated using the DNeasy Tissue Kit (Qiagen, Hamburg, Germany). A 760-base pair (bp) fragment of the mtDNA control region was amplified by polymerase chain reaction (PCR) (Abreu-Grobois *et al.*, 2006). Up to 2 μL of extracted DNA (60 ng) was used in 20 μL PCR mixes containing 0.5 μM of each primer, 0.25 mM dNTPs (deoxyribonucleoside triphosphates), 0.6 U of *Taq* DNA polymerase (Bioline, London, UK), 1 × PCR buffer (Bioline), 0.2 μg μL^{-1} bovine serum albumin (BSA) and 2 mM $MgCl_2$ (Bioline). The thermal conditions were an initial denaturation step at 94 °C for 2 min, followed by 40 cycles of 94 °C for 1 min, 55 °C for 1 min and 72 °C for 1 min, with a final extension at 72 °C for 5 min. Cycle sequencing was with the Big Dye fluorescent dye-terminator and the fragments analysed on model 3100 or 3730 automated sequencers (Applied Biosystems Inc., Foster City, CA, USA). Chromatograms were aligned using Bioedit Sequence Alignment Editor v.7.0.9 (http://www.mbio.ncsu.edu/BioEdit/bioedit.html) or Sequencher v.3.1.2 (Gene Codes Corporation, Ann Arbor, MI, USA).

Sequence data analyses

Our control region sequence alignment was trimmed to 486 bp and classified according to standardized nomenclature (Archie Carr Center for Sea Turtle Research, ACCSTR; http://accstr.ufl.edu/ccmtdna.html). Haplotype frequencies, Nei's (1987) haplotype diversity (*h*) and nucleotide diversity (π) of mtDNA sequences were measured using Arlequin v.3.11 (Excoffier *et al.*, 2005). FindModel (http://www.hiv.lanl.gov/content/sequence/findmodel/findmodel.html) determined the best model of nucleotide substitution that fits the data. Exact tests of population differentiation (Raymond & Rousset, 1995) used a Markov chain length of 10,000 steps with 1000 dememorization steps.

Bayesian clustering algorithms (http://www2.imm.dtu.dk/~gigu/Geneland/) were applied to infer population structure (number of clusters, *K*) and assign individuals to clusters (Guillot *et al.*, 2005). Sequences were recoded as instructed in the Geneland v. 3.1.4 program documentation and a model with multinomial distribution of genotypes conditional on uncorrelated allele frequencies and population memberships together with linkage equilibrium was assumed. Spatial

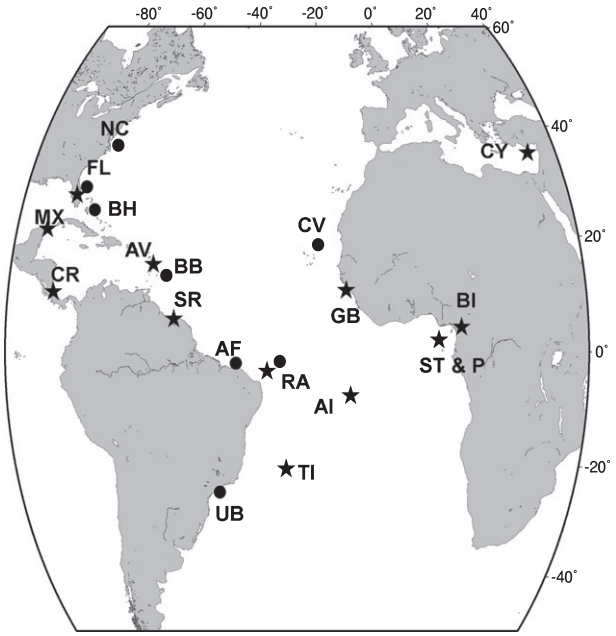

Figure 1 Map of the Atlantic Ocean and Mediterranean Sea showing locations for green turtle (*Chelonia mydas*) nesting populations (stars) and small-sized foraging groups (circles) with abbreviated names using a Mollweide projection: NC, North Carolina; FL, Florida; MX, Mexico; BH, Bahamas; CR, Costa Rica; AV, Aves Island; BB, Barbados; SR, Surinam; AF, Almofala; RA, Rocas Atoll; UB, Ubatuba; TI, Trindade Island; AI, Ascension Island; CV, Cape Verde; GB, Guinea Bissau; BI, Bioko; ST & P, Sâo Tomé and Príncipe; CY, Cyprus.

coordinates for NP and FG locations were entered into Geneland, which uses models based on free Voronoi tessellation where spatial domains of inferred clusters are approximated by polygons constructed independently of sampling locations. Spatial clustering models potentially achieve more accurate results than non-spatial models for datasets characterized by low levels of genetic differentiation and/or a small number of loci (Guillot *et al.*, 2009). Individual-based Bayesian clustering used by Geneland means that the georeferenced haplotypes are assigned to the inferred clusters without any prior knowledge of the population units and limits (Guillot *et al.*, 2005), which is different from the more traditional method of using predefined populations (Waples & Gaggiotti, 2006). NPs and ssFGs were analysed separately. The first run inferred *K*, and the second run, with *K* fixed at the modal value, assigned individuals to inferred populations. The first step was replicated 10 times to check for convergence, allowing *K* to vary from 1 to 10 clusters and using 200,000 Markov chain Monte Carlo (MCMC) iterations, a burn-in of 200 and an uncertainty associated with the spatial coordinates of 0.1. The number of clusters (*K*) was inferred from the modal value of *K* for these runs. Runs were then sorted according to mean posterior density and only the best run was post-processed to obtain posterior probabilities of population membership for each individual and each pixel of the spatial domain. With the NPs, Geneland estimated a clear mode at $K = 5$ across 10 replicates. To further support these results, analysis of molecular variance (AMOVA; Arlequin v.3.11) employing Φ_{ST} distances and 10,000 permutations (Excoffier *et al.*, 2005) was performed. This examined how the differentiation was partitioned among the groups; the first using the clusters identified for NPs by Bayesian clustering analysis, and the other with individual ssFGs.

When Bolker *et al.* (2007) compared their new 'many-to-many' MSA method with the classic 'many-to-one' MSA (Pella & Masuda, 2001), they obtained qualitatively similar results but with increased precision (lower coefficients of variation). We tested both methodologies with the new Cape Verde samples and obtained similar mean estimates but much lower standard deviation (SD) values with the new approach (the average SD decreases from 0.097 'many-to-one' to 0.048 'many-to-many'). Consequently, we proceeded with the 'many-to-many' MSA (Bolker *et al.*, 2007) using the software winbugs (Spiegelhalter *et al.*, 2004). This excludes 'orphan' haplotypes (haplotypes found in FGs but not in NPs), and all sets of haplotypes found only in a single NP are lumped together. Sources need to be reasonably well characterized, including their relative population sizes, while the mixed stocks allow for an 'unknown' category (Bolker *et al.*, 2007). We used all published NP sizes (Table 1) (Bellini *et al.*, 1995; Seminoff, 2002, 2004; Formia *et al.*, 2006) as prior information and the analyses were performed until Gelman and Rubin diagnostics confirmed convergence of the chains to the posterior distribution, with values close to 1.0 and less than 1.2 (Pella & Masuda, 2001). The results are presented in two ways: first a 'nesting population-centric' MSA that estimates the proportion of individuals from each NP that go to each FG; then a 'foraging group-centric' MSA that gives the proportion of individuals in each FG that originates from each NP.

Estimating average distances travelled between nesting and foraging locations

As it is not possible to tag or track small hatchlings, the MSA results were used to estimate the average distances of FGs from NPs. However, genetic data for the larger size class of green turtles (lsFG) were only available from one location, Nicaragua. Therefore, we used information from tagging and satellite-tracking studies of adult turtles to estimate distances for further lsFGs. Satellite tracking data came from females equipped on nesting beaches. Females remain in residence close to the nesting beaches during an extended breeding season that may last several months, during which time they lay several clutches of eggs. The movements made by females between clutches within the breeding season are generally small, both for green turtles (Hays *et al.*, 1999) and several other species (e.g. Hays *et al.*, 1991; Schofield *et al.*, 2007, 2009). At the end of the nesting season female green turtles, along with other species, generally travel to specific foraging sites to which they generally maintain long-term fidelity (e.g. Godley *et al.*, 2003a; Lohmann *et al.*, 2008a). These foraging

Table 2 Green turtle (*Chelonia mydas*) mitochondrial DNA (mtDNA) control region haplotypes detected at Cape Verde (CV) and other Atlantic groups from the published literature. Absolute frequencies are shown for foraging groups and nesting populations. Abbreviations for each site, except for NI (Nicaragua), are defined in Fig. 1.

	Foraging groups									Nesting populations										
	CV	FL	NC	NI	BB	BH	RA	UB	AF	FL	MX	CR	AV	SR	RA	TI	AI	GB	CY	BI	ST&P
Total	44	62	97	60	60	80	23	114	117	24	20	433	30	15	3	99	70	70	26	50	20
CM-A1	0.02	0.19	0.35		0.12	0.03				0.46	0.35										
CM-A2		0.02	0.02							0.04											
CM-A3	0.05	0.69	0.44	0.90	0.35	0.78		0.02	0.15	0.50	0.25	0.91	0.10								
CM-A4												0.002									
CM-A5	0.52	0.05	0.05	0.10	0.22	0.13	0.22	0.12	0.24		0.05	0.07	0.90	0.87							0.05
CM-A6	0.02						0.09		0.03					0.07			0.04			0.10	0.05
CM-A7														0.07							
CM-A8	0.39		0.07		0.23	0.01	0.57	0.73	0.45						0.68	0.68	0.84	1.00		0.90	0.65
CM-A9					0.02		0.09	0.04	0.03						0.13	0.19	0.01				
CM-A10					0.03			0.03	0.03						0.04		0.04				
CM-A11															0.02	0.01					
CM-A12															0.09						
CM-A13																			0.96		
CM-A14																			0.04		
CM-A15			0.01								0.05										
CM-A16			0.02						0.01		0.05										
CM-A17					0.02						0.10										
CM-A18		0.03	0.03								0.15										
CM-A20						0.01						0.005									
CM-A21						0.04			0.01			0.01									
CM-A22		0.02			0.02																
CM-A23																0.06					
CM-A24								0.02	0.01							0.01	0.01				
CM-A25															0.02						
CM-A32								0.02	0.01						0.02	0.04					
CM-A33																0.01					
CM-A35																					0.05
CM-A36																					0.05
CM-A37																					0.05
CM-A38																					0.10
CM-A39																	0.01				
CM-A42									0.02												
CM-A44								0.01	0.01												
CM-A45									0.01								0.01				
CM-A46							0.04	0.01									0.01				
CM-A55								0.01													
Hetero-plasmy								0.01													

sites can therefore be accurately assessed by satellite tracking, and we are confident that our definition of the foraging areas, and hence migration distance, for turtles was accurate. Distances between NPs and ssFGs, and those between NPs and the lsFG consisting of older and larger turtles were then compared. Although some large animals can also be found at ssFGs and were consequently pooled in the analysis, the overall comparison is relevant because we know that adults are certainly able to home to natal areas to breed (Bowen & Karl, 2007) and larger juveniles and adults in the lsFG may therefore forage closer to breeding areas in accordance to the 'closest-to-home' hypothesis.

Geographical coordinates and distances were obtained using Google Earth v. 4.3. The average distances travelled by individuals were calculated in two ways. First, the average distance travelled by individuals from each NP was estimated using the 'nesting population-centric' MSA results. Second, the average distances travelled by individuals that are feeding in a particular FG was calculated, but using 'foraging group-centric' MSA results. This provided distance data for all ssFGs and a single lsFG. Published data of satellite transmitters or mark–recapture studies provided further distance estimates for other adult-sized FGs. In satellite tracking studies turtles are equipped with transmitters that relay data via the Argos

satellite system, which provides locations with a typical accuracy of a few kilometres (Bradshaw *et al.*, 2007). However, multiple locations are obtained, and so despite the poor accuracy of individual locations the overall position of the FGs is relatively well resolved. For Costa Rican adult turtles, the average of direct distances for 10 individuals (Troëng *et al.*, 2005) was 512 km (range 130–1250 km). For Ascension turtles, we used satellite tracking data for 10 of 11 tracked turtles (Luschi *et al.*, 1998; Hays *et al.*, 2002). After discarding data for one turtle due to its short tracking duration (Luschi *et al.*, 1998), the average direct distance was 2455 km (range 1793–3025 km). For Guinea Bissau, the average direct distance of 1016 km was estimated from the reported foraging location (Godley *et al.*, 2003b). Finally, the average direct distance for the Bioko population was 548 km (130–1250 km) based on mark–recapture results (Tomas *et al.*, 2001).

Lagrangian drifter data

Data on satellite-tracked buoys were obtained from the National Oceanic and Atmospheric Administration (NOAA, USA). These buoys are released throughout the year. To minimize the impact of wind on the trajectories, either a 25-m^2 window shade drogue or a 50-kg weight are attached to each buoy via a long (up to 100 m) rope and chain tether. The locations of these buoys are determined using various satellite tracking systems (RAMS, Argos, EOLE) which provided several position fixes per day with a high degree of accuracy (0.1–2.0 km), and the data are reported on the NOAA web site (http://www.aoml.noaa.gov/). Buoy trajectory data have been used to estimate the age of juvenile loggerheads by estimating their transatlantic drift time from the eastern USA (Hays & Marsh, 1997). Here we searched the data for satellite-tracked near surface (0–100 m) buoys that have drifted near the main Atlantic green turtle NPs between 1979 to the present, selecting a particular window with an amplitude of ±1° for longitude and latitude.

RESULTS

Population genetic structure of nesting populations and foraging groups

FindModel showed that the best model of nucleotide substitution was the Tamura–Nei model (Tamura & Nei, 1993). The global test of differentiation among Atlantic and Mediterranean NPs revealed significant differences (exact $P < 0.001$). Four spatially coherent clusters (K) were identified with Geneland analysis: the first were the central western Atlantic NPs (Aves and Surinam; CWA cluster); the second was unequivocally composed of the samples from the Mediterranean Sea (Cyprus; MED cluster); the third consisted of the north-western Atlantic NPs (Florida, Mexico and Costa Rica; NWA cluster); and the fourth included the south-western and eastern Atlantic populations together (Rocas Atoll, Trindade Island, Ascension Island, Guinea Bissau, Bioko and São Tomé and Príncipe; SWEA cluster). The Atlantic clusters correspond to the three broad regions of connectivity identified by Bolker *et al.* (2007). AMOVA showed that the great majority of the variation derived from differences among the clusters (83.66%), with only a small amount due to differences among and within NPs (1.27 and 15.07%, respectively; $\Phi_{ST} = 0.849$, $P < 0.001$), thus corroborating the results of the Bayesian analysis.

Table 3 Results of pairwise comparisons of small-sized neritic foraging groups of green turtles (*Chelonia mydas*). Abbreviations for each site are defined in Fig. 1.

	CV	FL	NC	BB	BH	RA	UB	AF
CV	–	0.768	0.688	0.291	0.632	0.069	0.199	0.063
FL	<0.001	–	0.033	0.324	0.051	0.829	0.846	0.640
NC	<0.001	0.011	–	0.226	0.046	0.712	0.757	0.560
BB	<0.001	<0.001	<0.001	–	0.178	0.301	0.413	0.168
BH	<0.001	<0.001	<0.001	<0.001	–	0.657	0.727	0.514
RA	0.019	<0.001	<0.001	<0.001	<0.001	–	**0.016**	**0.043**
UB	<0.001	<0.001	<0.001	<0.001	<0.001	**0.106**	–	0.077
AF	**0.090**	<0.001	<0.001	<0.001	<0.001	**0.196**	<0.001	–

Φ_{ST} values are shown above the diagonal, and the P-values for exact tests of differentiation, as derived from observed haplotype frequencies, are shown below the diagonal. Values not significant at 0.05 are in bold.

The global test of differentiation among ssFGs was also significant (exact $P < 0.001$), and for pairwise exact tests of differentiation there were only three non-significant comparisons (Cape Verde and Almofala exact $P = 0.090$; and Rocas Atoll with Ubatuba and Almofala exact $P = 0.106$ and 0.196, respectively; Table 3). However, the Bayesian cluster analysis applied to ssFGs failed to produce any consistent clustering. AMOVA found that the variation was equally derived from differences within (49.32%) and among the ssFGs (50.68%; $\Phi_{ST} = 0.507$, $P < 0.001$), which is consistent with the Bayesian analysis not being able to find clear clusters among the ssFGs.

Genetic connectivity among nesting populations and foraging groups

Generally, the 'foraging group-centric' MSA, that estimates the origin of juveniles that are feeding in a particular Atlantic ssFG, are broadly consistent with results found by Bolker *et al.* (2007) (Fig. 2, Table 4). The key novel finding of our study is that the individuals that feed in Cape Verde were estimated to be from NPs on both sides of the Atlantic as well as the middle of the ocean (e.g. Surinam, Ascension and Guinea Bissau; Fig. 2, Table 4), with this being the first report from a 'many-to-many' MSA of a substantial (>30%) contribution of a rookery on the coast of South America to a FG on the coast of West Africa.

In contrast, individuals from the Mediterranean NPs (Cyprus) were rare or absent in the Atlantic FGs studied, with contributions to these areas always less than 1%. Consequently, we excluded the Cyprus NP from the 'nesting population-

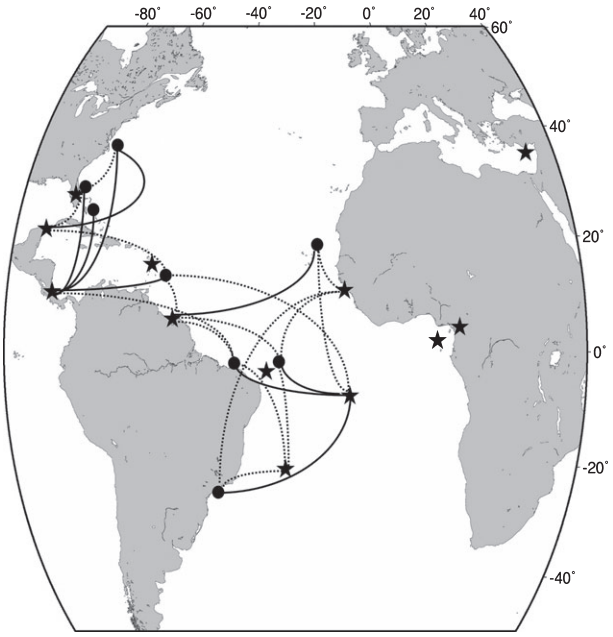

Figure 2 Major genetic connectivity between small-sized foraging groups and nesting populations of green turtles (*Chelonia mydas*). Based on the results of the foraging group-centric mixed stock analysis, black solid lines indicate contributions greater than 30% and dashed lines show connections between 10 and 30%. Other contributions <10% are excluded for clarity. Lines were curved to increase clarity and are not meant to indicate routes of travel. Stars and circles show nesting populations and foraging grounds, respectively. For names of each location see Fig. 1.

centric' MSA analysis. We also excluded the Nicaraguan samples because they represent a lsFG rather than a ssFG (see relatively large body sizes in Table 1). The 'nesting population-centric' MSA showed that small green turtle juveniles from one NP generally end up in many widely dispersed ssFGs (Table 5); again, broadly consistent with Bolker *et al.* (2007). There was an overall negative correlation between distance from the NP to the ssFG and the proportion of individuals of that NP that feed in this ssFG ($r = -0.462$, $P < 0.001$). However, this correlation was not always evident when analysing each cluster (CWA cluster: $r = -0.165$, $P = 0.543$; NWA cluster: $r = -0.732$, $P < 0.001$; and SWEA cluster: $r = -0.426$, $P = 0.003$; Table 5). This corresponds with the observation by Bolker *et al.* (2007) that the 'closest-to-home' pattern did not always apply within regions.

Distances travelled by small juveniles and adults

We estimated the average distance travelled by individuals from a particular NP to reach their ssFGs using 'nesting population-centric' MSA data. The comparison with four NPs with tagging or tracking data for adults (Costa Rica, Ascension, Guinea Bissau and Bioko) revealed that in all cases adults were foraging closer to their NPs than were small juveniles (Table 6). Furthermore, the average distance travelled by individuals of a particular feeding aggregation were found to

Table 4 'Foraging group-centric' mixed stock analysis showing the origin of juveniles in each foraging group (FG) of green turtles (*Chelonia mydas*), including mean proportions and standard deviation (SD).

	Nicaragua	Florida	N Carolina	Bahamas	Barbados	Ubatuba	Almofala	Rocas Atoll	Cape Verde
NWA									
Mexico	0.006 (0.006)	**0.160 (0.054)**	**0.353 (0.084)**	0.015 (0.011)	**0.117 (0.050)**	0.009 (0.009)	0.019 (0.014)	0.024 (0.025)	0.033 (0.028)
Florida	0.005 (0.005)	0.070 (0.046)	**0.176 (0.089)**	0.010 (0.008)	0.043 (0.038)	0.009 (0.009)	0.010 (0.010)	0.018 (0.020)	0.030 (0.026)
Costa Rica	**0.933 (0.027)**	**0.678 (0.071)**	**0.316 (0.090)**	**0.908 (0.032)**	**0.368 (0.081)**	0.024 (0.017)	**0.183 (0.040)**	0.053 (0.048)	0.056 (0.039)
CWA									
Aves	0.002 (0.002)	0.008 (0.008)	0.014 (0.013)	0.003 (0.004)	0.019 (0.020)	0.013 (0.012)	0.016 (0.017)	0.014 (0.014)	0.030 (0.030)
Surinam	0.007 (0.007)	0.016 (0.015)	0.020 (0.017)	0.011 (0.011)	**0.114 (0.046)**	0.088 (0.027)	**0.179 (0.038)**	**0.103 (0.049)**	**0.382 (0.071)**
SWEA									
Rocas Atoll	0.001 (0.001)	0.004 (0.004)	0.007 (0.006)	0.001 (0.001)	0.007 (0.008)	0.005 (0.005)	0.006 (0.006)	0.006 (0.006)	0.010 (0.011)
Trindade Is.	0.014 (0.014)	0.016 (0.017)	0.022 (0.020)	0.015 (0.014)	0.074 (0.055)	**0.229 (0.086)**	**0.119 (0.057)**	**0.261 (0.123)**	0.073 (0.068)
Guinea Bissau	0.012 (0.011)	0.014 (0.014)	0.033 (0.025)	0.014 (0.010)	0.073 (0.058)	**0.288 (0.114)**	0.099 (0.069)	**0.136 (0.101)**	**0.194 (0.106)**
Ascension Is.	0.013 (0.015)	0.016 (0.015)	0.026 (0.023)	0.014 (0.010)	**0.149 (0.068)**	**0.309 (0.112)**	**0.330 (0.088)**	**0.339 (0.139)**	**0.120 (0.096)**
São Tomé and Príncipe	0.002 (0.002)	0.005 (0.004)	0.010 (0.009)	0.002 (0.002)	0.011 (0.010)	0.007 (0.007)	0.009 (0.008)	0.010 (0.010)	0.016 (0.016)
Bioko	0.003 (0.003)	0.009 (0.008)	0.017 (0.016)	0.004 (0.004)	0.020 (0.020)	0.017 (0.016)	0.025 (0.023)	0.029 (0.029)	0.048 (0.043)
MED									
Cyprus	0.001 (0.001)	0.004 (0.004)	0.005 (0.005)	0.001 (0.001)	0.005 (0.005)	0.003 (0.003)	0.004 (0.004)	0.006 (0.006)	0.008 (0.008)

Locations (nesting populations in rows and FGs in columns) are listed west to east. Nesting populations are clustered according to genetic analysis (see text for details of analysis): NWA (north-western Atlantic nesting populations), CWA (central western Atlantic nesting populations), SWEA (south-western and eastern Atlantic nesting populations) and MED (Mediterranean Sea nesting population). Values of 10% or more are shown in bold.

Table 5 'Nesting population-centric' mixed stock analysis showing the proportion of juveniles of green turtles (*Chelonia mydas*) from a nesting population going to each foraging group.

	Florida	N Carolina	Bahamas	Barbados	Ubatuba	Almofala	Rocas Atoll	Cape Verde	Unknown
NWA									
Mexico	**0.293 (0.121)**	**0.281 (0.115)**	**0.111 (0.080)**	**0.145 (0.134)**	0.016 (0.018)	0.025 (0.021)	0.035 (0.036)	0.025 (0.023)	0.068 (0.061)
Florida	**0.231 (0.129)**	**0.310 (0.130)**	**0.112 (0.092)**	**0.107 (0.085)**	0.031 (0.033)	0.028 (0.030)	0.050 (0.050)	0.045 (0.041)	0.085 (0.078)
Costa Rica	0.083 (0.041)	0.016 (0.008)	**0.599 (0.166)**	0.030 (0.016)	0.002 (0.002)	0.015 (0.007)	0.005 (0.006)	0.003 (0.002)	**0.246 (0.165)**
CWA									
Aves	0.077 (0.075)	0.069 (0.063)	**0.107 (0.100)**	**0.137 (0.116)**	**0.133 (0.114)**	**0.132 (0.115)**	**0.118 (0.102)**	**0.130 (0.112)**	0.096 (0.086)
Surinam	0.025 (0.024)	0.014 (0.012)	0.052 (0.049)	**0.127 (0.062)**	**0.138 (0.060)**	**0.219 (0.076)**	**0.135 (0.066)**	**0.246 (0.082)**	0.044 (0.041)
SWEA									
Rocas Atoll	0.099 (0.092)	0.082 (0.081)	**0.123 (0.109)**	**0.121 (0.109)**	**0.114 (0.101)**	**0.116 (0.105)**	**0.121 (0.103)**	**0.100 (0.092)**	**0.122 (0.108)**
Trindade	0.018 (0.021)	0.010 (0.010)	0.080 (0.080)	0.054 (0.049)	**0.219 (0.121)**	0.091 (0.061)	**0.204 (0.131)**	0.026 (0.029)	**0.298 (0.171)**
Guinea Bissau	0.019 (0.021)	0.017 (0.015)	0.083 (0.076)	0.065 (0.062)	**0.315 (0.157)**	0.085 (0.071)	**0.128 (0.109)**	0.096 (0.069)	**0.188 (0.146)**
Ascension	0.012 (0.015)	0.009 (0.009)	0.053 (0.050)	0.080 (0.049)	**0.241 (0.114)**	**0.197 (0.088)**	**0.219 (0.117)**	0.038 (0.035)	**0.148 (0.117)**
São Tomé and Príncipe	0.088 (0.084)	0.074 (0.069)	**0.126 (0.108)**	**0.117 (0.104)**	**0.116 (0.101)**	**0.101 (0.092)**	**0.125 (0.111)**	**0.115 (0.100)**	**0.138 (0.120)**
Bioko	0.065 (0.063)	0.056 (0.053)	**0.114 (0.099)**	**0.104 (0.094)**	**0.120 (0.106)**	**0.130 (0.106)**	**0.155 (0.125)**	**0.123 (0.106)**	**0.132 (0.113)**

Nesting populations (rows) are clustered according to genetic analysis (see text for details of analysis): NWA (north-western Atlantic nesting populations), CWA (central western Atlantic nesting populations), SWEA (south-western and eastern Atlantic nesting populations) and MED (Mediterranean Sea nesting population). Foraging groups (columns) are arranged from west to east. Unknown are unsampled feeding groups. Values of 10% or more are shown in bold.

Table 6 Comparison of average distances travelled by the small juveniles and adults of each nesting population of green turtles (*Chelonia mydas*). Small juvenile distances were calculated using the results of the 'nesting population-centric' mixed stock analysis. Adult distances were obtained from published satellite transmitter and mark–recapture studies.

	Distance travelled (km)	
Nesting population	Juveniles	Adults
Florida	1575	–
Mexico	2063	–
Costa Rica	1435	512
Aves	2683	–
Surinam	2608	–
Rocas Atoll	2812	–
Trindade	2084	–
Ascension	3055	2455
Guinea Bissau	3360	1016
Bioko	6067	548
Sâo Tomé and Príncipe	5793	–
Mean	3048	1133
SD	1543	911

be smaller for the single lsFG for which genetic data were available (Nicaragua FG, 722 km) than for the rest of the ssFGs (average distance 2919 km; range 2007–3801 km). Perhaps it is more relevant to compare Nicaragua with nearby ssFGs, as these may recruit from similar NPs. For these, average distances were still greater (Florida 2080 km, North Carolina 2811 km, Bahamas 2007 km, Barbados 3340 km). All these results must be taken with some caution as they are based on comparisons with a single lsFG sampled for genetic data, and with distance data for other large-sized turtle foraging groups based on non-genetic approaches. On the other hand, all comparisons were consistent in that average distances away from natal locations were always less for FGs consisting of larger-sized turtles.

Lagrangian drifter data

Finally, we looked at observations of drift trajectories of released buoys to assess if drift is likely between NPs and ssFGs. Eleven buoys released close to NPs in the Atlantic (Fig. 3a,b) indicated that the presence of turtles at the various ssFGs could be achieved by passive drift (see Appendix S1 in Supporting Information). For example, Buoy 1 (Fig. 3a) released close to Surinam and Aves passed the Bahamas, Barbados and Florida, drifting with the strong North Atlantic Gyre. This is consistent with dispersal from Surinam and Aves to Barbados and the Bahamas, and with the high proportions of juveniles from Florida in the Florida and North Carolina ssFGs. Interestingly, the buoy then swung eastwards, crossed the Atlantic and then drifted southwards, with its final trajectory heading towards Cape Verde. This is consistent with the genetic finding that large proportions of juveniles from Surinam (0.246, SD 0.082) and Aves (0.130, SD 0.112) reached Cape Verde, and also with

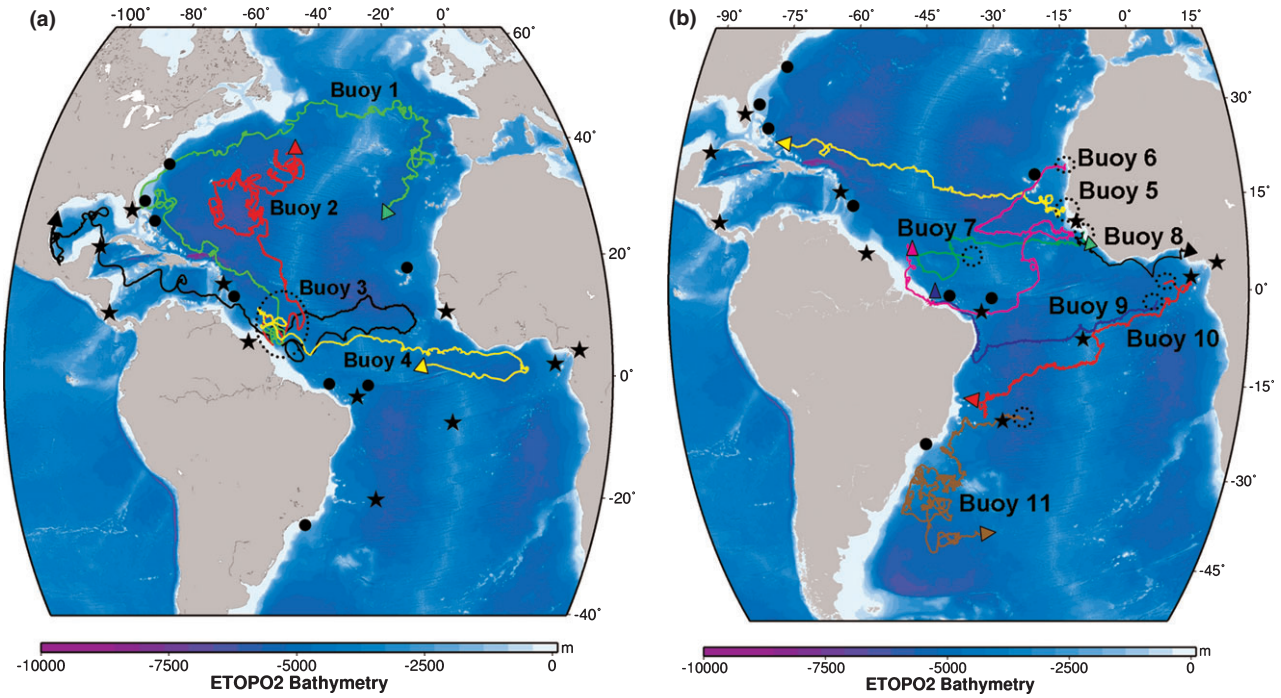

Figure 3 Map (Mollweide projection) of trajectories for buoys released in the vicinity of green turtle (*Chelonia mydas*) nesting populations. Stars and circles show the location of nesting populations and foraging grounds, respectively. Dotted circles show the release area for buoys. Triangles mark the end point for each trajectory. (a) Four buoys released near the central western Atlantic (CWA) and north-western Atlantic (NWA) nesting populations. The drift times and release location for the buoys were 1395 days, 50°41′ W and 5°31′ N (Buoy 1); 1507 days, 50°18′ W and 5°02′ N (Buoy 2); 618 days, 50°41′ W and 5°19′ N (Buoy 3); and 401 days, 52°62′ W and 8°34′ N (Buoy 4). (b) Seven buoys released in the vicinity of the south-western and eastern Atlantic (SWEA) cluster. The drift times and release locations for the buoys were 564 days, 17°75′ W and 11°89′ N (Buoy 5); 494 days, 17°01′ W and 19°47′ N (Buoy 6); 236 days, 35°14′ W and 4°78′ N (Buoy 7); 160 days, 14°44′ W and 8°74′ N (Buoy 8); 426 days, 0°25′ W and 1°64′ S (Buoy 9); 1011 days, 0°85′ E and 0°10′ N (Buoy 10), and 1235 days, 25°00′ W and 20°01′ S (Buoy 11). See also Appendix S1 in Supporting Information.

the surprisingly large proportion of the Cape Verde aggregation consisting of Surinam turtles (0.382, SD 0.071). The buoy took 1395 days (3.8 years) to make this journey, well within the 3–5-year period that small juveniles would typically spend in the pelagic developmental phase.

Another interesting transatlantic route was displayed by Buoys 3 and 4 (Fig. 3a), which were released close to Surinam and drifted east reaching the African coastline. This showed that turtles from Surinam could reach Cape Verde following an equatorial trajectory. These buoys then turned around and were transported back in the opposite direction, towards South America. Buoys 5 (released near Guinea Bissau) and 6 (released near Cape Verde) (Fig. 3b) also showed transatlantic transport in this direction, and demonstrated how turtles from African sites could reach locations such as the Bahamas, Rocas Atoll and Almofala. Not all drifters were transported across the Atlantic. Some travelled to relatively close locations (Buoys 8 and 11), and some had circuitous routes that kept them in the same area (Buoys 2 and 11).

DISCUSSION

Dispersal allows exploitation of spatially and/or temporally variable resources and is also an effective means of attaining different resources at different life stages. Our study extends the current understanding of the early developmental stages of green turtles at a period when they shift from pelagic to benthic habitats.

Population genetic structure of nesting populations and foraging groups

As expected, there was significant population genetic structure among NPs, consistent with the hypothesis of homing to natal breeding locations by adults. Bolker *et al.* (2007) suggested three main Atlantic regions where the FGs were primarily recruited from NPs within the regions – connectivity thus being influenced by spatial proximity. Here, we confirm the genetic similarity of the NPs within these regions. Our observation of a broad correlation between geographical distances between NPs and ssFGs and the proportion of small juveniles that had travelled to the ssFGs also supports the idea that connectivity is generally stronger for closer locations. However, we found that this correlation did not always apply within regions. Indeed, the genetic structure for ssFGs was far less defined than for NPs. The genetic differences among ssFGs based on the exact test of population differentiation confirmed the non-random distribution of animals among these loca-

tions, as has been shown in previous studies (Luke *et al.*, 2004; Bass *et al.*, 2006; Bolker *et al.*, 2007; Naro-Maciel *et al.*, 2007). However, these could not be grouped into distinct genetic clusters. The lack of genetic similarity between most neighbouring ssFGs (Table 3) indicates that NP sources of recruitment for each FG are quite variable, resulting in high diversity both within and between the ssFGs. AMOVA showed lower levels of population structure for ssFGs than for NPs (Φ_{ST} = 0.51 vs. Φ_{ST} = 0.85). This pattern is probably a result of the 'weak migratory connectivity' typical for the green turtle (Bolker *et al.*, 2007), where there are no strong links between individual foraging grounds and individual natal populations and individuals from the same natal population disperse to many foraging locations (Webster *et al.*, 2002).

Genetic connectivity among nesting populations and foraging grounds

Overall, the key patterns of connectivity were broadly similar to those found by Bolker *et al.* (2007), even though there were differences in datasets used by the two studies. The 'many-to-many' MSA results therefore appear robust, but one should still be cautious when interpreting the results, since point estimates had large SDs, and not all NPs and ssFGs have necessarily been adequately sampled. The 'nesting population-centric' MSA revealed higher SD values for smaller populations ($n < 1000$ compared with $n > 1000$; Mann–Whitney *U*-test, $P = 0.021$), showing that there is less confidence in estimating where individuals from very small rookeries end up [coefficient of variation (CV) = standard deviation/mean; average CV = 0.881 and 0.751 for populations of smaller and larger sizes, respectively].

As previously observed (Bolker *et al.*, 2007), we also find regional geographical association among NPs and ssFGs in some cases, such as those of the north-western Atlantic, whereas juveniles of other NPs distribute to areas that are more widely separated (Fig. 2, Table 5). Previous studies have interpreted this connectivity between NPs and ssFGs as evidence for juvenile natal homing (Bolker *et al.*, 2007), where turtles prefer to settle in foraging areas close to natal locations ('closest-to-home' hypothesis). There are also other factors that may influence the distribution of small juvenile turtles, such as passive drift with ocean currents (Hughes, 1974; Carr & Meylan, 1980; Luke *et al.*, 2004; Bass *et al.*, 2006; Bolker *et al.*, 2007; Naro-Maciel *et al.*, 2007). If an object is drifting, it is more likely to first encounter locations closer to the release point than further away, so an association between distance and the probability of drifting to a location may be expected. Juvenile turtles may in fact by-pass the closest suitable neritic habitats during the pelagic phase of their life cycle, and end up in the vicinity of locations further away, depending on their pattern of drift. Several authors have suggested the importance of currents in marine turtle life cycles, and considered that these played the major role in determining the dispersal of hatchlings and early juveniles (Hughes, 1974; Carr & Meylan, 1980; Witham, 1980; Hirth, 1997). Certainly for other marine organisms, swimming ability and the strength of waves and currents may determine distribution and choice of habitat (e.g. Fulton & Bellwood, 2004). Bolker *et al.* (2007) suggested that future green turtle MSA studies should also consider the impact of ocean currents. Here, we used Lagrangian drifter data to show that there were buoys released in the Atlantic that had drifted between many of the NPs and ssFGs linked by genetic connectivity (Fig. 3), thereby confirming that transport by ocean currents between these locations is possible. Most importantly, Lagrangian drifter data provided independent evidence that transatlantic transport is feasible.

New evidence for transport across the Atlantic

Evidence for transatlantic movement of small juvenile green turtles from Africa to South America has previously been provided by genetic data, for example demonstrating that the Guinea Bissau NP is an important contributor to foraging assemblages around the Brazilian coast (north-east Brazil, Bolker *et al.*, 2007; Rocas Atoll and Ubatuba, this study). Surface drifters released off the West African coast show that drift towards Brazil is possible (Fig. 3b), supporting the genetic evidence. The major novel finding of this study is genetic evidence for significant dispersal of small juvenile green turtles in the opposite direction, and that transport across the North Atlantic is likely. This is an important finding, as it finally confirms that transatlantic travel in either direction is possible and indeed commonly achieved by small juvenile turtles, extending the conclusions of Bass *et al.* (2006), Bolker *et al.* (2007) and Reich *et al.* (2007). Our finding is based on new genetic data for a juvenile FG on the West African coast (Cape Verde) that had not been previously studied. A large proportion of the Cape Verde FG (38%) was estimated by 'many-to-many' MSA of mtDNA data to have originated from Surinam in South America. The analysis also indicated that the Cape Verde contingent represents a large proportion of the Surinam population (25%). Bolker *et al.* (2007) also included a West African FG (Corisco Bay) in their MSA. Many-to-one analysis showed a strong contribution from small north-east Brazilian rookeries ($n = 125$), indicating that eastwards transport across the Atlantic is likely – however, this was no longer the case with the more sophisticated 'many-to-many' analysis, which takes population sizes into account (Fig. 2 of Bolker *et al.*, 2007). In contrast, the Surinam NP is large ($n = 1814$) and the 'many-to-many' analysis of this study finally provides firm evidence for transatlantic migration in an easterly direction.

The trajectory of Buoy 1 (Fig. 3a) encapsulates one possible scenario of transatlantic transport from the coast of Surinam to the coast of West Africa. After being released close to Surinam, the buoy drifted north with the Gulf Stream, then east with the North Atlantic Drift, then south with the Canary Current. How typical is this transport trajectory? Along the east coast of North America the Gulf Stream is a significant current, and the conventional view of it is as a well-defined transport system and a strong barrier to near-surface cross-frontal exchange (Bower *et al.*, 1985). However, instead of

being transported towards the Grand Banks by the Gulf Stream and taken further north as would be expected, surface drifters in the Gulf Stream off the east coast of the USA are observed to almost always end up in the Sargasso Sea (T. Rossby, University of Rhode Island, pers. comm.). In fact, there is virtually no movement of surface drifters between North Atlantic subtropical and subpolar gyres (Brambilla & Talley, 2006). Instead, surface drifters have a tendency for expulsion out of the Gulf Stream to the south. A recent study of data from over a thousand drifters indicates that southward exits are aggregated in specific locations off the coast of New England and Newfoundland, and indicate the most likely mechanism to be wind-driven Ekman drift (T. Rossby, pers. comm.). Thus, small juvenile turtles that have entered the Gulf Stream are unlikely to be taken far north into subpolar regions. Rather they are more likely to be ejected southwards into the Sargasso Sea. Once there, it is possible to drift with the North Atlantic Oscillation and cross the Atlantic in a few years. For example, particle-tracking models for eels (*Anguilla anguilla*) estimate an average migration duration of less than 2 years to cross the North Atlantic from the Sargasso Sea (Kettle & Haines, 2006; Bonhommeau *et al.*, 2009). The entire journey of Buoy 1 from Surinam to the West coast of Africa (Fig. 3a) took 1395 days (3.8 years). Another possible route across the Atlantic is via the equator. The trajectories of Buoys 3 and 4 (Fig. 3a) shows transatlantic transport from Surinam to the eastern Atlantic coasts with the Equatorial Counter Current. Notably, this demonstrates that drift in the opposite direction, from the African coasts to the western Atlantic, is also possible with the South Equatorial Current.

Lagrangian drifter data and particle tracking models therefore confirm that marine organisms can be transported across the Atlantic Ocean by passive means, and that the journey time can be within the estimated oceanic developmental phase of green turtles. Drift with ocean currents is not the only factor determining the post-natal dispersal of small juvenile green turtles, but it may be an important facilitator for long-distance transoceanic journeys.

Distances travelled by small juveniles compared with those of larger-sized juveniles and adults

According to the 'closest-to-home' hypothesis, turtles tend to settle in foraging areas close to their natal origin. In all cases, we found that larger turtles foraged closer to their NPs than did smaller juveniles. This implies that even if turtles initially recruit to neritic locations far away, they may eventually move closer to 'home'. Lagrangian drifter data (Fig. 3, Appendix S1) showed that most of the FGs indicated by 'many-to-many' analysis as being connected to particular natal locations can indeed be reached by drift, even for transatlantic locations. We do not suggest that turtles *only* get there by drift, but rather that ocean currents may play a role in explaining how turtles reach distant foraging locations. We refine the 'closest-to-home' hypothesis in suggesting that while it is true in general, and particularly for certain NPs (e.g. the NWA cluster), for cases where some juveniles may be transported to far-flung locations by external factors such as strong currents (e.g. the CWA and SWEA clusters) it seems that the turtles may still try to return closer to 'home' via further developmental migrations when they become larger. This would explain the observation first made by Bolker *et al.* (2007) that the 'closest-to-home' hypothesis did not always apply within regions of connectivity. We caution though that our attempt to compare the average distances between NPs and FGs for small- versus large-sized turtles remains tentative. Future studies could improve on this, with further genetic sampling of lsFGs and by obtaining individual size measurements linked with genetic information when sampling ssFGs and lsFGs.

Comparison with other sea turtle species: size and navigation

Loggerhead (*Caretta caretta*) and green turtles diverged more than 50 million years ago (Bowen *et al.*, 1993; Naro-Maciel *et al.*, 2008); however, there may still be similarities in their biology. During the pelagic stage, hatchling loggerheads exhibit directional swimming in relation to the Earth's magnetic field (Lohmann *et al.*, 2001, 2008a). However, juvenile sizes may be a limitation on swimming capacity (Revelles *et al.*, 2007; Eckert *et al.*, 2008; Monzón-Argüello *et al.*, 2009). The pelagic stage of green turtles is shorter than for loggerheads (Bjorndal *et al.*, 2000; Reich *et al.*, 2007), so it is not unreasonable to suspect that active navigation is constrained for the smaller-sized green sea turtles during their pelagic stage.

The population genetic structure of loggerhead turtles becomes progressively more distinct as they advance in age and development. The pelagic juvenile aggregations have no genetic structure (Bolten *et al.*, 1998; Bowen *et al.*, 2004; Bowen & Karl, 2007), although there could be spatial variation in their composition (Monzón-Argüello *et al.*, 2009). More advanced benthic juveniles migrate from oceanic habitat to coastal habitat in the vicinity of their natal rookery, showing juvenile natal homing behaviour (Maffucci *et al.*, 2006). MSA of benthic juvenile FGs showed significant mtDNA haplotype frequency shift and a significant correlation between haplotype frequencies in coastal feeding populations and haplotype composition of adjacent NPs. Thus, as juveniles grow they exhibit more natal homing behaviour (Bowen *et al.*, 2004; Bowen & Karl, 2007). However, other species may show different patterns. For the hawksbill sea turtle (*Eretmochelys imbricata*) in Puerto Rico, new recruits as well as resident juveniles appeared to be largely composed of individuals originating from other rookeries, showing that recruitment into feeding areas appears to be largely influenced by oceanic mixing during the pelagic stage (Velez-Zuazo *et al.*, 2008).

CONCLUSIONS

We extend the scenario initially proposed by Carr & Meylan (1980) for green turtles in the Atlantic Ocean. Small early

juveniles from the same NP reach many different foraging locations, and dispersal may in some cases be affected by strong ocean currents, because at the pelagic stage they may be too small to swim effectively against the current, although it is possible that they maintain their position using navigational senses. Many will indeed recruit to locations close to their natal beach, perhaps aided by navigation senses, but a proportion will travel across the Atlantic, perhaps facilitated by strong prevailing currents. Transatlantic transport can occur in either direction. If the locations reached by the small juveniles represent a suitable habitat for development, they will leave the pelagic habitat to become benthic feeders and become larger (data on body sizes show turtles in some of the ssFGs to be quite large; Table 1). Advanced juveniles attaining larger sizes may then swim more effectively against currents and use their navigation and homing abilities to find their way towards foraging areas that are closer to their natal NPs. As adults, turtles of nearly all species migrate intermittently to and from their FGs to their nesting beaches (Miller, 1997; Bowen & Karl, 2007), using their homing and sensory abilities to navigate to their final destination (Luschi *et al.*, 2001; Hays *et al.*, 2002; Lohmann *et al.*, 2008a,b). Finally, it is important to note that the switch from pelagic to benthic habitat is not immutable, and both advanced juveniles and adults can switch back to pelagic feeding, as has been shown in other species (Hatase *et al.*, 2002; Witzell *et al.*, 2002; Hawkes *et al.*, 2006; McClellan & Read, 2007). Hence, there must be some degree of flexibility in feeding and in dispersal behaviour.

FUTURE DIRECTIONS

Continuing advances in the development of new markers, sequencing methods and increasingly more sophisticated analytical approaches (Riddle *et al.*, 2008) mean that sea turtle phylogeography and population genetics should continue to progress. Currently, the MSA of green turtles is based on a single linked marker (mtDNA sequences), but in future multilocus genotypes could be useful (Lee, 2008). Furthermore, we recommend expanding the genetic analysis throughout Macaronesia, the western coast of Africa and the Mediterranean Sea. This will complete the necessary framework for a fuller understanding of the life history of green turtles in the Atlantic. We know that the current dataset does not include all FGs because of the high proportion juveniles of some breeding populations dispersing to still unknown destinations (Table 5). A further direction that promises to be fruitful would be the inclusion of oceanographic particle tracking models (Hays & Marsh, 1997) in attempting to predict more accurately the dispersal of small juvenile turtles. Particle tracking models are becoming more biologically realistic, allowing the incorporation of parameters such as behaviour and mortality (Kettle & Haines, 2006; Bonhommeau *et al.*, 2009). Such investigation would require sophisticated modelling that is beyond the scope of the current study, but this may be the future route towards delivering accurate predictions concerning the relative importance of various ssFGs for particular NPs.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Comparison of the trajectories of individual buoys with movements of juvenile green turtles inferred from genetic data.

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BIOSKETCH

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