Variation in spatial distribution of juvenile loggerhead turtles in the eastern Atlantic and western Mediterranean Sea

Catalina Monzón-Argüello [a,b,*], Ciro Rico [b], Carlos Carreras [b], Pascual Calabuig [c],
Adolfo Marco [c], Luis Felipe López-Jurado [d]

[a] Instituto Canario de Ciencias Marinas. Crta. de Taliarte s/n, 35200 Telde, Gran Canaria, Spain
[b] Estación Biológica de Doñana, CSIC, Avda. María Luisa s/n, 41013 Sevilla, Spain
[c] Centro de Recuperación de Fauna Silvestre de Tafira. Crta. del Centro Km. 7, 35017, Las Palmas de G.C., Spain
[d] Departamento de Biología. Universidad de Las Palmas de Gran Canaria, Campus de Tafira. 35017 Las Palmas de G.C., Spain

Keywords:
Loggerhead
Mitochondrial DNA
Oceanic juveniles
Atlantic Ocean
Mixed stock analysis

abstract

Loggerhead sea turtles (Caretta caretta) originating from the Western Atlantic carry out one of the largest marine migrations, reaching the eastern Atlantic and Mediterranean Sea. It has been proposed that this transatlantic journey is simply a consequence of drifting, with the lack of a target destination and a passive dispersal with oceanic currents. This predicts that the size of the source populations and geographic distance to the feeding grounds should play important roles in defining stock composition in the eastern Atlantic and Mediterranean Sea. Under this scenario, near pelagic stocks would have no genetic structure, and would be composed of similar cohorts from regional rookeries. To address this question, we sampled individuals from one important eastern Atlantic feeding ground, the Canary Islands, and sequenced a fragment of the mitochondrial DNA control region. We compared the composition of this feeding stock with published data of other proximal areas: Madeira, Azores and Andalusia. "Rookery-centric" mixed stock analysis showed that the distribution of loggerhead sea turtles along the eastern Atlantic feeding grounds was in latitudinal accordance to their natal origin: loggerhead turtles from Florida were significantly more abundant in Azores (30%) than in Canary Islands (13%), while those from Mexico had a poor representation in Azores (13%) but were more prevalent in Canary Islands (34%). Also, genetic stability in temporal and size analyses of the Canary Island aggregation was found, showing a long period of residency. These results indicate a non-random distribution of loggerhead juveniles in oceanic foraging grounds. We discuss possible explanations to this latitudinal variation.

.

1. Introduction

Previous studies, many using genetic data, have demonstrated that various species of sea turtles may undertake long journeys between natal and foraging areas, and even between different foraging locations (e.g. see studies listed in Bowen and Karl, 2007; Lee, 2008). The globally endangered loggerhead sea turtle (Caretta caretta) is one such species, carrying out some of the greatest known migrations. The life history is characterized by a first developmental stage in the open ocean followed by later development in the neritic zone (Bolten, 2003). Western Atlantic loggerhead turtles spend the oceanic stage inhabiting the north Atlantic gyre between 6.5 and 11.5 years (Bjorndal et al., 2000) until they return to neritic zones in the western Atlantic (Carr, 1986; Bolten et al., 1998; Bowen et al., 2004). The transatlantic journey is only carried out during the juvenile stage (Bolten et al., 1993; Bolten et al., 1998). A similar pattern occurs in the Pacific, where juveniles from Japan cross the entire Pacific Ocean to the vicinity of Baja California (Bowen et al., 1995). During the neritic stage, loggerhead juveniles often show fidelity to specific feeding grounds, returning to them after long seasonal migrations (Avens and Lohmann, 2004). Furthermore, experimental displacements have shown that these have navigational abilities based, at least partly, on magnetic information (Ireland, 1980; Avens and Lohmann, 2003, 2004; Avens et al., 2003).

The eastern Atlantic harbours juveniles of loggerhead sea turtles, distributed in different foraging grounds of the Azores, Madeira, and Canary Islands as well as Andalusia, the westernmost portion of the Mediterranean Sea surrounding the Gibraltar Straits (Bolten et al., 1993; Bjorndal et al., 2000; Casale et al., 2002; López-Jurado and Mateo, 1997; Revelles et al., 2007). Although the loggerhead sea turtle is threatened around the world, every year, about twenty thousand turtles are incidentally captured in the Mediterranean Sea (Camiñas, 1988; Camiñas and de la Serna, 1995; Camiñas et al., 2006) and no data of mortality rates for the turtles of the Azores, Madeira and

---

[*] Corresponding author. Instituto Canario de Ciencias Marinas. Crta. de Taliarte s/n, 35200 Telde, Gran Canaria, Spain. Fax: +34 928 13 29 08.
E-mail address: catalinama@iccm.rcanaria.es (C. Monzón-Argüello).

Canary Islands exist. Therefore, knowledge of the origin of these feeding aggregations may contribute to conservation efforts.

Studies using length-frequency (Carr, 1986; Bolten et al., 1993), tag returns (Bolten, 2003) and genetic markers (Bolten et al., 1998; Casale et al., 2002; Carreras et al., 2006) have confirmed the relationships between juveniles of the eastern Atlantic, mainly with the rookeries of the western Atlantic. Nevertheless, the variation in the distribution of different rookeries in these areas has been poorly studied with only a single survey in the Mediterranean Sea showing structure among feeding grounds explained by the pattern of sea surface currents and water masses (Carreras et al., 2006). During the early stage of juveniles, the lack of a target destination and a passive dispersal movement with the current as a consequence of drifting has been proposed as a migration mechanism (Luschi et al., 2003). In this context, proximal feeding areas, like Canary Islands, Madeira, Azores and Andalusia that are all affected by the Gulf Stream System, should present similar rookery compositions.

However, studies tracking individuals produce results different from those expected from the passive dispersal hypothesis. The tracked oceanic juveniles in different foraging grounds were found to make long-distance movements in different directions, often swimming against the prevailing currents (Dellinger and Freitas, 2000; Polovina et al., 2000, 2006). This shows that juveniles are not totally passive drifters and can perform active movements because of foraging needs (Polovina et al., 2000) and/or environmental factors (Bentivegna, 2002). This, together with the long period that turtles remain in the pelagic feeding areas where they congregate (Dellinger and Freitas, 2000; Polovina et al., 2004, 2006; Casale et al., 2007; López-Jurado unpublished data), suggest that juveniles are not passively dispersed and thus, are not randomly distributed in the oceanic areas. Instead, they may be using orientation mechanisms that enable them to stay in such areas as it occurs in later stages of their lives.

In this paper, we examine the distribution of oceanic juvenile loggerhead sea turtles that forage in the eastern Atlantic and Mediterranean Sea to test the general hypothesis of non-random distribution during oceanic stage. With this aim, we assessed the origin of 329 oceanic-feeding juveniles of four proximal areas, using sequence data of the mitochondrial DNA (mtDNA) control region and many-to-many mixed stock analysis (MSA; Bolker et al., 2007). We analyzed samples from Canary Islands, and incorporated previous published surveys from Madeira, Azores and Andalusia (Bolten et al., 1998; Revelles et al., 2007) along with complementary surveys of regional nesting females (Encalada et al., 1998; Laurent et al., 1998; Kaska, 2000; Bowen et al., 2004; Carreras et al., 2007) to take into account the entire metapopulation. Also, we incorporate new data for 186 samples from the Cape Verde rookery, a previously unstudied nesting population. This population is important for our study area due to its size, as is the second largest nesting rookery in the Atlantic and Mediterranean Sea (López-Jurado and Liria, 2007; Marco et al., 2008) and its geographic location as it is expected that a proportion of juveniles from these feeding ground come from this rookery (Fig. 1).

Comparisons of population composition and the body sizes of the individuals among feeding grounds were used to test the following specific predictions under the general hypothesis of non-random distribution:

(1) If oceanic juveniles born in different rookeries present spatial variation in their distribution, then population composition of foraging grounds would be different, even when closely located areas are compared. (2) If there is a fidelity to specific feeding areas for each rookery, then juveniles would stay there during long periods resulting in a temporal genetic stability in the foraging stock and their size range should be similar irrespective of the location. (3) If animal movements against prevailing currents are related to body sizes, then differences in haplotype frequencies between these areas would increase if we considered larger animals. (4) If there are differences among feeding ground composition due to geographic distance between nesting populations and feeding grounds, then a correlation would be found. Furthermore, we will discuss several biological aspects of the dispersal capabilities of juvenile loggerhead sea turtles that may have conservation implications for successful management plans.

2. Materials and methods

2.1. Sample and data collection

Stranded juveniles recovered from 2000 to 2004 in the Canary Islands ($n = 93$) were analyzed. These animals are assumed to represent a local juvenile cohort because stranded juveniles in the Canary Islands usually come from incidental captures in fishing nets or hook from small vessels that fish only locally. These juveniles are thus expected to be part of the Canary Islands foraging ground. Blood samples or tissue samples were taken and stored in 96% ethanol at 4 °C. Straight carapace length (SCL) was taken for 82 of these 93 samples. The SCL data was used to establish different size classes to test haplotype variation between size classes, as well as differences in sizes found. Haplotype frequencies from Azores and Madeira turtles were directly obtained from published studies (Bolten et al., 1998) and no individual data on SCL were available for these. Further, haplotype frequencies from Andalusia were also obtained from published data (Revelles et al., 2007). SCL measures were available from the authors for 96 samples and thus they were also used to establish different size classes as for the Canarian samples. The Andalusian samples were obtained from stranded turtles from local fishing vessels in the Gulf of Cadiz ($n = 40$) and the Alboran Sea ($n = 65$). No difference in haplotype frequencies between them was found (χ^2-test, $p = 0.71$) and thus, the two areas were considered as a single sample.

Since the loggerhead turtle's capability to swim against local currents is size dependent (Revelles et al., 2007), we established two size groups in the Canary Islands and Andalusian stocks in order to compare genetic structure of turtles that are able to swim actively in the area with those that might be more influenced by currents. Hence, we used the regression formula $U_{crit} = 1.763\text{SCL} - 0.262$ (Revelles et al., 2007), where U_{crit} is a parameter that determines the maximum cruise speed that an aquatic animal could sustain without resulting in muscular fatigue (Reidy et al., 2000). Mean velocities of the Canarian (Batten et al., 2000) and Andalusian (Tsimplis and Bryden, 2000) currents were used as U_{crit} values to calculate the size threshold for independent swimming capacity (32 cm for Canarian loggerheads and 36 cm of SCL for Andalusian juveniles). Juveniles at this size or larger are expected to be able to move, as least partly, independently of currents.

2.2. Laboratory procedures and genetic analysis

Genomic DNA was isolated using DNeasy Tissue Kit (QIAGEN®) following the manufacturer's protocol. A 391 base pair (bp) fragment of the mtDNA control region was amplified by the polymerase chain reaction (PCR) using the primers TCR5 (5′-TTGTACATCTACTTATTTACCAC-3′) and TCR6 (5′-GTACGTACAAGTAAAACTACCGTATGCC-3′) (Norman et al., 1994). PCR reactions were typically performed in 20 μl volumes under the following conditions: 94 °C for 5 min; followed by 30 cycles at 94 °C for 1 min, 55 °C for 1 min, 72 °C; with a final extension at 72 °C for 5 min. PCR products were purified using Montage-PCR Kit (Millipore®). Cycle sequencing reactions were conducted with Big Dye fluorescent dye-terminator (Applied Biosystems) and fragments were analyzed on an automated sequencer (Applied Biosystems Inc. model 3100). Each sample was sequenced in both forward and reverse directions to ensure accuracy. Chromatograms were aligned using Bioedit Sequence Alignment Editor vers. 7.0.9 (http://www.mbio.ncsu.edu/BioEdit/bioedit.html, Hall, 1999).

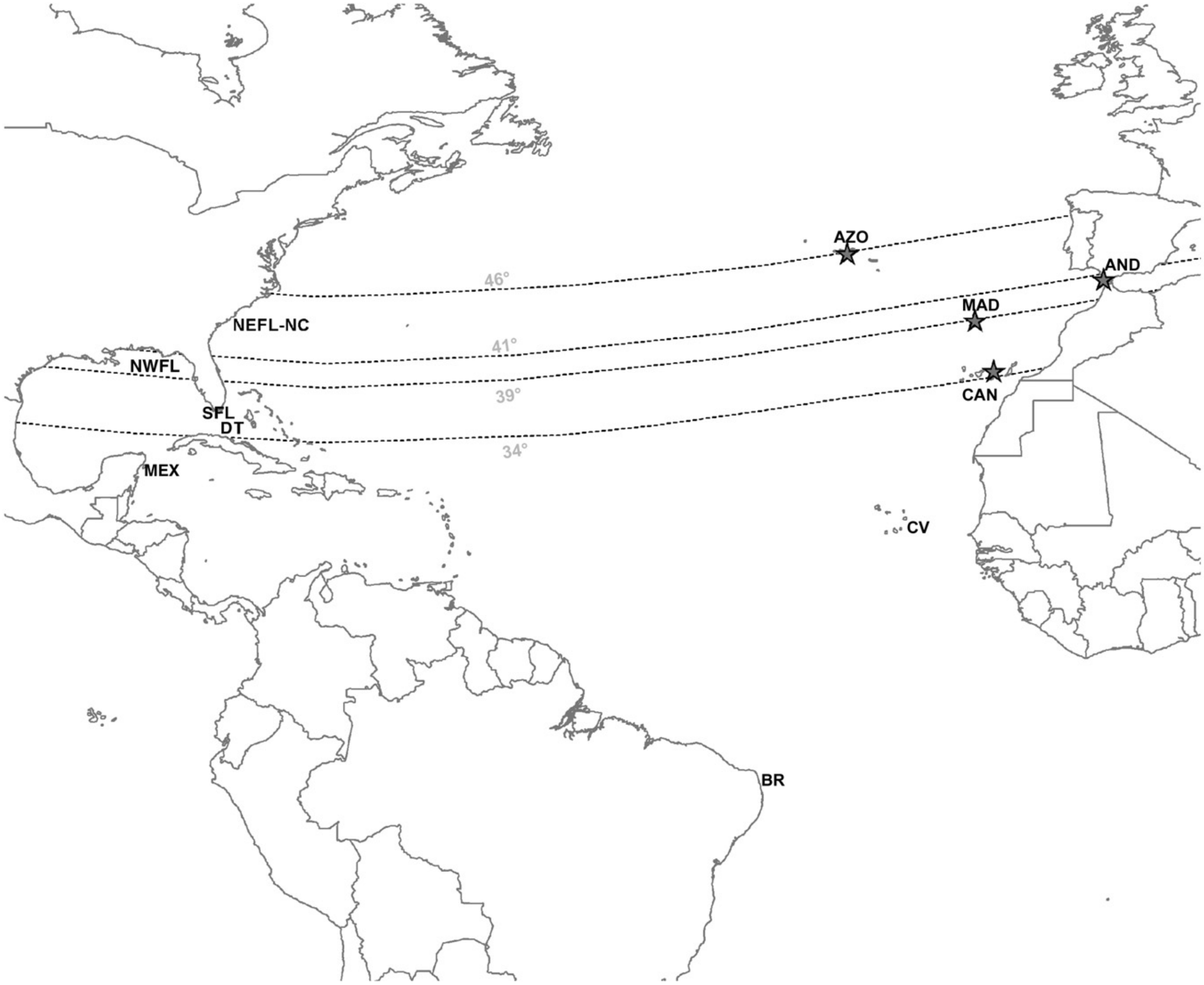

Fig. 1. Map of study locations. Atlantic nesting populations and in-water groups are symbolized by circles and stars, respectively. Rookeries: NEFL-NC, Northeastern Florida–North Carolina; NWFL, Northwestern Florida; SFL, South Florida; DT, Dry Tortugas; MEX, Mexico; BR, Brasil; CV, Cape Verde. Feeding grounds: CI, Canary Islands; MAD, Madeira; AND, Andalusia; and AZO, Azores. Isoclinics (lines of equal magnetic inclination angle) are represented by dashed lines. Isoclinics are adapted from Skiles (1985).

Sequences were compared with existing haplotypes from nesting and foraging locations (http://accstr.ufl.edu/ccmtdna.html). Whenever possible, a haplotype identification was assigned based on the web site maintained by the Archie Carr Center for Sea Turtle Research (ACCSTR) (http://accstr.ufl.edu/ccmtdna.html). New haplotype sequences were submitted to ACCSTR and deposited in GenBank. Throughout this paper we used standardized haplotypes nomenclature established by ACCSTR.

2.3. Statistical analysis

Haplotype frequencies, haplotype diversity (hd) and nucleotide diversity (π) were estimated for each feeding ground using Arlequin vers. 3.0 (Excoffier et al., 2005). To determine the best model of nucleotide substitution that better fits our data, we used FindModel (http://www.hiv.lanl.gov).

2.3.1. Spatial variation in juvenile distribution

To determine if the Canarian foraging stock is indeed a mixed stock, haplotype frequencies were compared with that found in all analyzed loggerhead nesting populations using the χ^2-test of independence (Sokal and Rohlf, 1981). We used a Bayesian approach method for "many-to-many" MSA that simultaneously estimates the origins and destinations of individuals in a metapopulation (Bolker et al., 2007; WINBUGS, Spiegelhalter et al., 2003). Firstly, we used the "foraging ground-centric" approach to determine the proportion of juveniles found in each foraging ground originated in the different rookeries. Next, to determine the contribution of each rookery relative to its size to each foraging ground, we conducted a "rookery-centric" analysis. This analysis allowed us to determine the proportion of individuals from each rookery that select a particular feeding area. We conducted these analyses with rookery sizes as prior information, assuming that the overall contribution of a rookery is proportional to its size. Rookery sizes were taken from Ehrhart et al. (2003) and Margaritoulis et al. (2003). Finally, the Gelman–Rubin diagnostic test was used to confirm convergence of the chains to the posterior distribution, with values less than 1.2 (Gelman and Rubin, 1992).

2.3.2. Fidelity to specific feeding areas

To test whether there is temporal variation in the genetic structure of the Canarian feeding ground, we took the years with the largest samples sizes, 2001 ($n=18$), 2002 ($n=16$) and 2004 ($n=54$) and used χ^2-test of independence (Sokal and Rohlf, 1981). This analysis could not be performed with the other areas because we have no data from them. Further, to determine whether there are differences in the range of sizes of juveniles from Andalusia and the Canary Islands'

Table 1

Genetic analysis of eastern Atlantic feeding grounds.

	CC-A1	CC-A2	CC-A3	CC-A4	CC-A7	CC-A8	CC-A9	CC-A10	CC-A11	CC-A12	CC-A13	CC-A14	CC-A15	CC-A16	CC-A17	CC-A21	CC-A42	CC-A46	Total	SCL (cm)
CI	40	33	8	1	2	1		5				1			1			1	93	15–67 (37.85)
CI_{01}	7	7	1	1				2											18	20–47 (36.28)
CI_{02}	6	7	2															1	16	27.5–58 (40.21)
CI_{04}	25	17	4		2	1		3				1			1				54	15–67 (37.42)
MAD	24	19	2					3	1	1		1			1				52	7–66□
AND	45	46	2				2	1	2	1		2			1	2	1		105	13–76 (40.47)
AZO	36	31	5			1					2	2	1	1					79	18–51□
Total	145	129	17	1	2	2	2	9	3	2	2	6	1	1	3	2	1	1	329	

Absolute frequencies of haplotypes found in different eastern Atlantic foraging grounds. Size information of the analyzed sea turtles is given by the Straight Carapace Length (SCL) in centimetres (range and mean values). CI, Canary Islands; CI_{01}, Canary Islands in 2001; CI_{02}, Canary Islands in 2002; CI_{04}, Canary Islands in 2004; MAD, Madeira Island; AND, Andalusia; AZO, Azores Islands. □Data originally collected as Curved Carapace Length (CCL) and transformed to SCL using the equation $CCL = 1.388 + (1.053)$ SCL (Bjorndal et al., 2000).

stocks, we computed a non parametric U Mann–Whitney test (Statistica 7.0, StatSoft Inc., 2001).

2.3.3. Swimming capacity of larger animals

To determine whether there are differences between sizes in the Canary Island and Andalusian stocks, two groups of sizes were established as previously described by carrying two χ^2-test of independence (Sokal and Rohlf, 1981) with the Monte Carlo randomization method with the program CHIRXC (Zaykin and Pudovkin, 1993). The first using all observed haplotype frequencies and the second using haplotypes frequencies from juveniles larger than 36 or 32 cm depending if the samples were from Andalusia or Canary Islands (see above). To test if differences in foraging grounds' composition increase as juveniles are larger, we conducted two additional “rookery-centric” MSAs with juveniles shorter and larger than 36 cm (Andalusia) and 32 cm (Canary Islands) respectively.

2.3.4. Effect of geographic distance

To examine the potential effects of the distance from a nesting site on the turtles that go to a foraging area a correlation test between the contribution of a rookery to a particular feeding ground and geographic distance between them was established. Because it is impossible to realistically determine the distances actually travelled by the turtles, the only way to standardise this type of analysis is to use the shortest swimming distance between potentially contributing nesting populations and juvenile foraging areas. This approach however, might be inaccurate.

3. Results

We found eighteen haplotypes, seventeen already described and one novel (Table 1) in the foraging areas studied. This new haplotype was found in a single sample and consisted of point transition of haplotype CC-A2 in position 96. It was named CC-A46 (GenBank accession number: EF687771) following the nomenclature proposed by the ACCSTR. Most of the studied animals had either haplotypes CC-A1 (44%) or CC-A2 (39%). Both haplotypes are found in several rookeries in the Atlantic. Other previously observed haplotypes in nesting populations were CC-A3 (5%), CC-A4 (0.3%), CC-A7 (0.6%), CC-A8 (0.6%), CC-A9 (0.6%), CC-A10 (3%), CC-A11 (1%) and CC-A14 (2%). We found eight haplotypes not assignable to any rookery in very low frequencies (4% of the total). The online application FindModel showed that the model of nucleotide substitution that better fits the data was Tamura-Nei (Tamura and Nei, 1993). The haplotype (hd) and nucleotide (π) diversities were very similar in all foraging ground and ranged between 0.628–0.685 and 0.025–0.033 respectively. As expected, all haplotype frequencies of nesting populations (Table 2) were significantly different from those found in the Canarian feeding ground (p b 0.01) confirming that this foraging assemblage, as the other three, Madeira, Azores and Andalusia previously described, constituted mixed stocks. Furthermore, a total of five haplotypes were found in Cape Verde Islands, four previously described CC-A1, CC-A2, CC-A11, CC-A17; and one new CC-A47 (GenBank accession number EU091309; Table 2). These data were included to complete the baseline for the MSA of the foraging grounds.

Table 2

Relative frequencies of mtDNA control region haplotypes in Atlantic and Mediterranean nesting populations.

	NEFL-NC	NWFL	SFL	DT	MEX	BR	CV	GRE	CYP	LEB	CRE	ISR	ETU	WTU
CC-A1	0.990	0.775	0.477	0.069	–	–	0.683	–	–	–	–	–	–	–
CC-A2	0.009	0.143	0.413	0.862	0.55	–	0.011	0.90	1	1	1	0.85	0.594	0.937
CC-A3	–	0.041	0.036	–	0.1	–	–	–	–	–	–	–	0.406	0.062
CC-A4	–	–	–	–	–	1	–	–	–	–	–	–	–	–
CC-A5	–	–	0,009	–	–	–	–	–	–	–	–	–	–	–
CC-A6	–	–	–	–	–	–	–	0.083	–	–	–	–	–	–
CC-A7	–	0.041	0.027	–	–	–	–	–	–	–	–	–	–	–
CC-A8	–	–	–	–	0.05	–	–	–	–	–	–	–	–	–
CC-A9	–	–	–	0.034	0.05	–	–	–	–	–	–	–	–	–
CC-A10	–	–	–	0.034	0.25	–	–	–	–	–	–	–	–	–
CC-A11	–	–	0.009	–	–	–	0.005	–	–	–	–	–	–	–
CC-A14	–	–	0.018	–	–	–	–	–	–	–	–	–	–	–
CC-A17	–	–	–	–	–	–	0.285	–	–	–	–	–	–	–
CC-A20	–	–	0.009	–	–	–	–	–	–	–	–	–	–	–
CC-A29	–	–	–	–	–	–	–	–	–	–	–	0.15	–	–
CC-A32	–	–	–	–	–	–	–	0.016	–	–	–	–	–	–
CC-A47	–	–	–	–	–	–	0.016	–	–	–	–	–	–	–
Sample sizes	105	49	105	58	20	11	186	60	35	9	19	20	32	16
Pop size	6200	600	67100	217	1800	2400	14000	2073	572	35	387	33	100	124

NEFL-NC, Northeast Florida–North Carolina; NWFL, Northwest Florida; SFL, South Florida; DT, Dry Tortugas; MEX, Mexico; BR, Brazil; CV, Cape Verde; GRE, Greece; CYP, Cyprus; LEB, Lebanon; CRE, Crete; ISR, Israel; ETU, Eastern Turkey; and WTU, Western Turkey. Pop size represents number of nest/year in each population.

Table 3
"Foraging ground-centric" many-to-many results of four oceanic feeding grounds; includes mean and standard deviation (SD).

	CI	MAD	AND	AZO
NEFL-NC	0.085 (0.066)	0.086 (0.072)	0.067 (0.057)	0.063 (0.051)
NWFL	0.015 (0.018)	0.009 (0.011)	0.008 (0.009)	0.005 (0.006)
SFL	0.687 (0.122)	0.666 (0.126)	0.769 (0.099)	0.828 (0.079)
DT	0.005 (0.005)	0.003 (0.004)	0.003 (0.004)	0.002 (0.002)
MEX	0.065 (0.038)	0.033 (0.025)	0.023 (0.018)	0.011 (0.011)
BR	0.022 (0.015)	0.020 (0.018)	0.010 (0.010)	0.013 (0.012)
CV	0.068 (0.046)	0.132 (0.078)	0.068 (0.045)	0.048 (0.044)
GRE	0.028 (0.028)	0.030 (0.030)	0.033 (0.031)	0.018 (0.017)
CYP	0.011 (0.012)	0.009 (0.010)	0.009 (0.019)	0.005 (0.006)
LEB	0.001 (0.001)	0.001 (0.001)	0.000 (0.001)	0.000 (0.000)
CRE	0.008 (0.009)	0.006 (0.006)	0.006 (0.006)	0.004 (0.005)
ISR	0.001 (0.001)	0.001 (0.001)	0.000 (0.001)	0.000 (0.000)
ETU	0.002 (0.003)	0.002 (0.002)	0.001 (0.002)	0.001 (0.001)
WTU	0.003 (0.003)	0.002 (0.002)	0.002 (0.002)	0.001 (0.001)

SFL, South Florida; NWFL, Northwest Florida; NEFL-NC, Northeast Florida–North Carolina; DT, Dry Tortugas; MEX, Mexico; BR, Brazil; CV, Cape Verde; GRE, Greece; CYP, Cyprus; LEB, Lebanon; CRE, Crete; ISR, Israel; ETU, Eastern Turkey; and WTU, Western Turkey; CI, Canary Islands; MAD, Madeira Island; AND, Andalusia and AZO, Azores Islands.

3.1. Spatial variation in juvenile distribution

There was no significant difference in the comparison of overall haplotype frequencies between foraging grounds (p N 0.24) except for the pairs Andalusia and the Canary Islands ($p = 0.02$). The "foraging ground-centric" MSA for the four foraging areas revealed that the vast majority of the eastern Atlantic juveniles come from the South Florida rookery (67–83%) while the rest of juveniles originated from Northeast Florida–North Carolina (6–9%), Mexico (1–7%) and Cape Verde (5–13%). The analysis also confirmed that Mediterranean juveniles are rare or absent in Atlantic waters (Table 3). Revelles et al. (2007) found that only 9 out of 105 turtles (8%) collected in the Strait of Gibraltar area were born in the Mediterranean Sea and similar results were obtained by Bolten et al. (1998). They found no contribution of Mediterranean nesting populations to Azores and Madeira foraging areas. Consequently, we conducted the "rookery-centric" MSA for the Atlantic populations only.

The "rookery-centric" MSA, which takes into account the size of the rookeries to establish the relative contribution of each of them to the foraging grounds, showed latitudinal significant differences in the distribution of the North American source populations ($\chi^2 = 698.30$; p b 0.05): there was a latitudinal equivalence between the major foraging ground selected by juveniles and the rookery of origin. The contribution of the Mexican rookery from the Caribbean coast of Quintana Roo to the Canary Islands is a good example to illustrate the results of this type of analysis. This is very small rookery with less than 2000 nests per year while the South Florida rookery is the largest in the Atlantic with over 60,000 nests per year. Thus, despite the fact that up to 69% of the Canarian juveniles originated in South Florida, the relative contribution of this rookery to this foraging ground is as small as 13%. Likewise, only 7% of the Canarian juveniles originated in Mexico but the relative contribution of this rookery to this foraging ground is as big as 34%. Interestingly, according to this analysis a large proportion of the juveniles from Cape Verde (61%) and Brazil (49%) rookeries seem to go to unknown feeding areas, while the remaining samples were clearly distributed among the four studied sites (Fig. 2; Table 4).

3.2. Fidelity to specific feeding areas

Haplotypes used for temporal analysis are shown in Table 1. No significant differences in haplotype frequencies were found for Canarian turtles samples from different years (p N 0.54), and the Mann–Whitney U test revealed no significant differences between the mean sizes present in Canary Islands and Andalusia samples ($p = 0.49$). This sizes ranged between 15–67 cm ($\text{mean} = 37.8$, $n = 82$) and 13–79 cm ($\text{mean} = 41.7$, $n = 96$) for Canary Islands and Andalusia samples respectively.

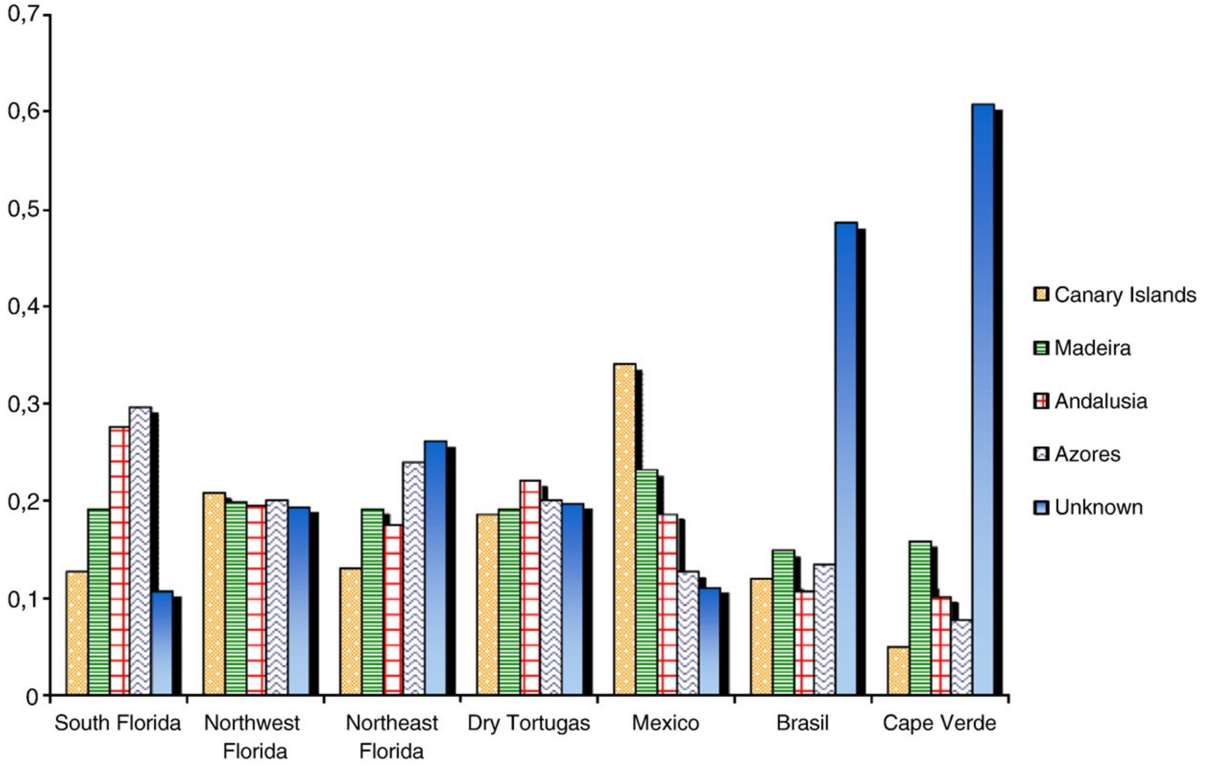

Fig. 2. "Rookery-centric" many-to-many results. Bars represent mean estimation. Results include unknown areas where juveniles of a particular population are feeding.

Table 4
"Rookery-centric" many-to-many results.

	Latitude		CI 28°06′	MAD 32°66′	AND 36°53′	AZO 38°45′	Unknown –
NEFL-NC	31°40′	Mean	0.131	0.193	0.175	0.239	0.261
		SD	0.114	0.152	0.145	0.170	0.186
		2.5%	0.005	0.006	0.0526	0.010	0.012
		97.5%	0.429	0.556	0.005	0.622	0.688
NWFL	29°44′	Mean	0.209	0.200	0.196	0.200	0.195
		SD	0.170	0.163	0.156	0.165	0.155
		2.5%	0.008	0.005	0.006	0.005	0.005
		97.5%	0.631	0.595	0.569	0.609	0.556
SFL	25°47′	Mean	0.127	0.193	0.276	0.296	0.107
		SD	0.090	0.111	0.132	0.131	0.092
		2.5%	0.021	0.041	0.076	0.087	0.003
		97.5%	0.353	0.468	0.555	0.587	0.331
DT	24°37′	Mean	0.186	0.192	0.222	0.201	0.198
		SD	0.158	0.152	0.176	0.169	0.162
		2.5%	0.004	0.007	0.006	0.006	0.006
		97.5%	0.563	0.554	0.669	0.632	0.587
MEX	21°17′	Mean	0.342	0.232	0.187	0.127	0.112
		SD	0.148	0.141	0.128	0.103	0.104
		2.5%	0.082	0.012	0.008	0.005	0.002
		97.5%	0.645	0.544	0.493	0.385	0.385
BR	−24°00′	Mean	0.120	0.149	0.107	0.135	0.488
		SD	0.125	0.152	0.117	0.138	0.232
		2.5%	0.007	0.003	0.002	0.002	0.033
		97.5%	0.476	0.556	0.430	0.527	0.193
CV	16°00′	Mean	0.051	0.159	0.102	0.078	0.610
		SD	0.053	0.145	0.096	0.088	0.186
		2.5%	0.003	0.012	0.006	0.002	0.168
		97.5%	0.193	0.566	0.355	0.169	0.880

NEFL-NC, Northeast Florida–North Carolina; SFL, South Florida; NWFL, Northwest Florida; DT, Dry Tortugas; MEX, Mexico; BR, Brazil; CV, Cape Verde; CI, Canary Islands; MAD, Madeira Island; AND, Andalusia; AZO, Azores Islands. Latitude values of each area are shown in italics. Values include mean contribution, standard deviation (SD), and lower (2.5%) and upper (97.5%) bounds of the 95% confidence interval.

3.3. Swimming capacity of larger animals and effect of geographic distance

A comparison of haplotype frequencies between the two size classes established within the Canarian or the Andalusian samples revealed no significant differences (p N 0.41). Interestingly however, we found significant differences between Canary Islands ($n = 59$) and the Andalusia ($n = 48$) samples when we compared haplotypes frequencies only from larger juveniles (N32 and 36 cm respectively, $p = 0.02$), but no differences were found between smaller Canarian ($n = 18$) and Andalusian ($n = 49$) animals ($p = 0.73$). Furthermore, the "rookery-centric" MSA considering only smaller ($n = 67$) or bigger animals ($n = 107$) revealed differences in their distribution (χ^2; Canary Islands, $p = 0.00$ and Andalusia, $p = 0.04$). Results showed that distribution of larger juveniles fitted better to the latitudinal equivalence between the major foraging ground selected by juveniles and the rookery of origin (Table 5). Finally, we found no significant correlation between the percentage of individuals that go to a foraging area and the geographic distance that separates their natal rookeries to the different feeding ground ($p = 0.23$).

4. Discussion

Of the four predictions analysed in this study under the general hypothesis of non-random distribution during the oceanic stage, three were supported by the data. First, there is a clear latitudinal variation in the juvenile distribution in all studied areas; second, there is sufficient evidence of site fidelity of juveniles to their oceanic feeding areas and the size ranges within areas are also similar; and third, the size of the turtles appeared to influence their distribution among the foraging grounds. Finally, our last prediction was not supported as there is no correlation between the percentage of individuals that go to a foraging area and the geographic distance that separates their natal rookeries to the different feeding grounds.

4.1. Spatial variation in juvenile distribution

In 1986, Carr proposed a model of loggerheads' migration from western Atlantic populations during their developmental stage: After hatching, loggerhead turtles enter the ocean, swim to leave the waters of the continental shelf, and become entrained in the Gulf Stream. They are carried by the North Atlantic gyre to the Azores and past Madeira and the Canary Islands during several years of growth at sea. In this context, the mixture of hatchlings of distinct populations and their random distribution in the eastern oceanic environment due to passive dispersal with the currents were assumed. However, our results indicate that there is a non-random distribution of juveniles in the eastern Atlantic foraging grounds. The MSA of the eastern Atlantic foraging grounds indicated that there are differences in composition among areas, and there appears to be a latitudinal pattern for this distribution.

According to Carr (1986), if animals cross the Atlantic Ocean carried by the Gulf Stream current, a mixture of different populations would be expected when they arrive to the eastern and proximal areas. Also, early stages, where size limits free movements, should be more affected by oceanic currents. Once juveniles are able to move more independently from the currents, they could select a foraging area to stay for several years. In our study, we have shown that southern rookeries, such as Mexican population, prefer southern latitudes to feed. Northern populations such as south Florida population are more common in Azores than in Madeira or Canary Islands (Fig. 2). Rookeries of an intermediate latitude geographic position, like Dry Tortugas or Northwest Florida, distribute in similar frequencies in all studied areas. Two potential causes could explain the observed structure: (1) segregation throughout the Gulf Stream, under a drift passive dispersion, and/or (2) selection of specific feeding area for each rookery. Below we discuss the evidence for each of these possible scenarios that are not mutually exclusive.

1. Segregation throughout the Gulf Stream: Once entering the water, hatchlings drift passively in ocean currents (Carr, 1986) and drift scenarios can be predicted using oceanographic particle tracking models (Hays and Marsh, 1997). A segregation of animal movements throughout the Gulf Stream according to their natal location results in a latitudinal distribution pattern. Animals from South Florida would enter, and therefore, be swept further north than Mexican turtles and will arrive more to northern areas like Azores, and less to southern latitudes like Canary Islands. This hypothesis is extremely difficult to test as it would require samples of stranded turtles in northern latitudes which are not readily available from fishing vessels. In this scenario, it would be expected that turtles born in Mexico, for example, would be absent in these northern

Table 5
"Rookery-centric" many-to-many results of Canary Islands and Andalusia, considering only larger (N32 cm and 36 respectively) or smaller (≤32 cm and 36 respectively) animals; includes mean and standard deviation (SD).

	Canary Islands		Andalusia	
	Smaller	Larger	Smaller	Larger
NEFL-NC	0.326 (0.232)	0.273 (0.206)	0.313 (0.229)	0.326 (0.225
NWFL	0.333 (0.231)	0.340 (0.236)	0.343 (0.244)	0.326 (0.231
SFL	0.287 (0.187)	0.245 (0.153)	0.357 (0.211)	0.553 (0.189
DT	0.323 (0.235)	0.323 (0.230)	0.332 (0.239)	0.354 (0.235
MEX	0.361 (0.218)	0.575 (0.207)	0.419 (0.228)	0.228 (0.176
BR	0.323 (0.240)	0.244 (0.196)	0.263 (0.221)	0.246 (0.205
CV	0.389 (0.215)	0.083 (0.101)	0.289 (0.192)	0.173 (0.173)

SFL, South Florida; NWFL, Northwest Florida; NEFL-NC, Northeast Florida–North Carolina; DT, Dry Tortugas; MEX, Mexico; BR, Brazil; CV, Cape Verde; CI, Canary Islands and AND, Andalusia.

latitudes or be occurring at an even lower frequency than in the Azores. The analysis of other feeding areas in the North Atlantic may provide more data for understanding the juveniles' distribution during the oceanic stage. Also, the use of oceanographic particle models to compare drift scenarios of hatchlings from Florida versus Mexico could be used to test this hypothesis.

2. Selection of specific feeding areas: Carreras et al. (2006) found that immature loggerheads entering the Mediterranean from the Atlantic remain linked to particular water masses, with a limited exchange of turtles between water masses. A number of different cues could be used to reach and stay in a particular area (e.g. chemical trails in the currents or provided by winds, geomagnetic parameters, water temperature or landmark-based orientation along the coast) and to feed in similar ambient conditions to the natal areas (Carr and Hirth, 1962; Koch et al., 1969; Luschi et al., 1996, 1998; Papi et al., 2000; Lohmann and Lohmann, 2006; Lohmann et al., 2008). In 1994, Lohmann showed that hatchlings are capable of detecting different magnetic inclination angles and that could be used to identify latitudes (Lohmann and Lohmann, 1994). Several features of the earth's magnetic field vary in a predictable way across the surface of the earth, like the intensity (strength) of the total field, intensity of the horizontal and vertical fields and the inclination angle. Among these, field line inclination is the most reliably correlated with latitude (Skiles, 1985). We found that most of the juveniles were in areas with the same isoclines of their natal rookeries (Fig. 1). The current knowledge of the loggerhead turtle's orientation capabilities, based on experimental test in tanks as well as field telemetry studies, suggest that the data here presented could be explained equally by the turtles' selection of specific foraging areas, or the segregation throughout the Gulf Stream or both.

On the other hand, we have not found a significant contribution of the Mediterranean nesting areas to the eastern Atlantic feeding grounds despite being geographically close. The Strait of Gibraltar may be acting as a barrier, or the dominant currents in the Mediterranean Sea could prevent a higher presence of Mediterranean juveniles in the eastern Atlantic (Carreras et al., 2006; Revelles et al., 2007). Also, the sizes of Mediterranean populations are quite small compared to the number of turtles breeding in Atlantic rookeries (Broderick et al., 2002; Margaritoulis et al., 2003). This also decreases the probability of finding Mediterranean juveniles in Atlantic waters. Hence, the number of juveniles found in different areas of the Atlantic would be a consequence of both, (1) the numbers coming out of those different rookeries and (2) how they move from rookeries. Finally it is important to note the high frequency of juveniles from Cape Verde and Brazil that go to unknown areas during their pelagic stages (Fig. 2). These results are also confirmed by the low frequencies of haplotypes CC-A17 (Cape Verde) and CC-A4 (Brazil) (Tables 1 and 2) which are unique to each rookery. The geographic location of these two rookeries, Cape Verde in the southeastern edge of the Gulf Stream and Brazil in the South Atlantic, could cause that Cape Verdean and Brazilian juveniles are rare in our studied areas. Further studies need to investigate other possible causes such as hatchling mortality or unknown juvenile feeding areas (e.g. the western and eastern South Atlantic).

4.2. Fidelity to specific feeding areas

There is a temporal stability in size and genetic composition of each area, suggesting that once a juvenile reaches a stock, it stays there for a long period. Sizes found in each area are similar; hence we can discard the idea of a size dependent distribution. These results are in accordance with satellite telemetry studies and flipper tag returns in other areas (Bolten, 2003; Polovina et al., 2006; López-Jurado pers comm). However, variation in stock recruitment could alter this stability (Bjorndal and Bolten, 2008). We did not find significant temporal variation but this may have resulted from the short temporal interval of our sampling or the relatively small annual sample size.

4.3. Effects of the geographic distance and of the swimming capacity of larger animals

No correlation between rookeries' dispersion and geographic distance to foraging grounds was found. Therefore, other factors, such as population sizes segregation through oceanographic currents and/or selection of specific feeding area, may determine the population composition of a mixed stock. Other studies have obtained similar results, concluding that distance is not a determinant factor in feeding ground composition (Lahanas et al., 1998; Luke et al., 2004). The genetic differences among Canary Islands and Andalusian feeding grounds are found only in the size class that is able to swim independently of the sea currents of the area, suggesting that active area selection should be higher in larger animals. Also, the comparison of the mixed stock analyses using smaller and larger individuals show statistically significant differences in the composition of mixed stocks further substantiating this hypothesis.

In conclusion, our study supports the model proposed by Carr (1986) about the mysterious and little known “lost years” where hatchling and young loggerhead sea turtles were supposed to wander around the Atlantic gyre. However, our data also substantiates the hypothesis that juveniles do not distribute randomly, providing some evidence that juveniles distribute in order to forage in areas of similar latitude to their original rookery.

Acknowledgements

We would like to thank the following people for their contributions and for critically reviewing the manuscript: Ana Belén Casal, Nuria Varo, Ana Liria and Joaquín Muñoz. David Aragonés helps us with the map. B. Bolker and X. Vélez-Zuazo helped us in many to many mixed stock analysis using R2WinBugs. We also thank P.L.M. Lee, G. Hays and two anonymous referees for their helpful review and comments. We are also grateful to the following institutions: Centro de Recuperación de Fauna Silvestre de Tafira, Instituto Canario de Ciencias Marinas, Estación Biológica de Doñana and Centro de Recuperación de Especies Marinas Amenazadas (CREMA). The study was partially funded by the Fundación BBVA. The first author was supported by a PhD grant from the Canary Islands government. [RH]

References

Avens, L., Lohmann, K.J., 2003. Use of multiple orientation cues by juvenile loggerhead sea turtles Caretta caretta. J. Exp. Biol. 206, 4317–4325.

Avens, L., Lohmann, K.J., 2004. Navigation and seasonal migratory orientation in juvenile sea turtles. J. Exp. Biol. 13, 1771–1778.

Avens, L., Braun-McNeill, S.E., Lohmann, K.J., 2003. Site fidelity and homing behaviour in juvenile loggerhead sea turtles (Caretta caretta). Mar. Biol. 143, 211–220.

Batten, M.L., Martinez, J.R., Bryan, D.W., Buch, E.J., 2000. A modeling study of the coastal eastern boundary current system off Iberia and Morocco. J. Geophys. Res. 105, 14173–14195.

Bentivegna, F., 2002. Intra-Mediterranean migrations of loggerhead sea turtles (Caretta caretta) monitored by satellite telemetry. Mar. Biol. 141, 795–800.

Bjorndal, K.A., Bolten, A.B., 2008. Annual variation in source contributions to a mixed stock: implications for quantifying connectivity. Mol. Ecol. 17, 2185–2193.

Bjorndal, K.A., Bolten, A.B., Martins, H.R., 2000. Somatic growth model of juvenile loggerhead sea turtle Caretta caretta: duration of pelagic stage. Mar. Ecol. Prog. Ser. 202, 265–272.

Bolker, B.M., Okuyama, T., Bjorndal, K.A., Bolten, A.B., 2007. Incorporating multiple mixed stocks in mixed stock analysis: “many -to-many” analyses. Mol. Ecol. 16, 685–695.

Bolten, A.B., 2003. Active swimmers–passive drifters: the oceanic juvenile stage of loggerheads in the Atlantic system. In: Bolten, A.B., Witherington, B.E. (Eds.), Loggerhead Sea Turtles. Smithsonian Institution, Washington, D.C., pp. 63–78.

Bolten, A.B., Martins, H.R., Bjorndal, K.A., Gordon, J., 1993. Size distribution of pelagic-stage loggerhead sea turtles (Caretta caretta) in the waters around the Azores and Madeira. Arquipélago. Life Mar. Sci. 11 (A), 49–54.

Bolten, A.B., Bjorndal, K.A., Martins, H.R., Dellinger, T., Biscoito, M.J., Encalada, S.E., Bowen, B.W., 1998. Transatlantic developmental migrations of loggerhead sea turtles demonstrated by mtDNA sequence analysis. Ecol. Appl. 8, 1–7.

Bowen, B.W., Karl, S.A., 2007. Population genetics and phylogeography of sea turtles. Mol. Ecol. 16, 4886–4907.

Bowen, B.W., Abreu-Grobois, F.A., Balazs, G.H., Kamezaki, N., Limpus, C.J., Ferl, R.J., 1995. Trans-Pacific migrations of the loggerhead sea turtle demonstrated with mitochondrial DNA markers. Proc. Natl. Acad. Sci. U.S.A 92, 3731–3734.

Bowen, B.W., Bass, A.L., Chow, S.-M., Bostrom, M., Bjordal, K.A., Bolten, A.B., Okuyama, T., Bolker, B.M., Epperly, S., Lacasella, E., Shaver, D., Dodd, M., Hopkins-Murphy, S.R., Musick, J.A., Swingle, M., Rankin-Baransky, K., Teas, W., Witzell, W.N., Dutton, P.H., 2004. Natal homing in juvenile loggerhead turtles (Caretta caretta). Mol. Ecol. 13, 3797–3808.

Broderick, A.C., Glen, F., Godley, B.J., Hays, G.C., 2002. Estimating the size of nesting green and loggerhead turtle populations in the Mediterranean. Oryx 36, 227–253.

Camiñas, J.A., 1988. Incidental Captures of Caretta caretta (L.) with surface longlines in the Western Mediterranean. Rapports et Procés-Verbaux des Réunions du la Commission Internationale Pour l'Exploration Scientifique de la Mer Méditerranée, vol. 231 (2). CIESM, Montecarlo, p. 285.

Camiñas, J.A., de la Serna, J.M., 1995. The loggerhead distribution in the western Mediterranean Sea as deducted from captures by the Spanish Long Line Fishery. In: LLorente, G.A., Martin, A., Santos, X., Carretero, M.A. (Eds.), Scientia Herpetologica, pp. 316–323.

Camiñas, J.A., Báez, J.C., Valeiras, X., Real, R., 2006. Differential loggerhead bycatch and direct mortality due to surface longlines according to boat strata and gear type. Sci. Mar. 70 (4), 661–665.

Carr, A., 1986. Rips, FADS and little loggerheads. Bioscience 36, 92–100.

Carr, A., Hirth, H., 1962. The ecology and migrations of sea turtles, 5. Comparative features of isolated green turtles colonies. Am. Mus. Novit. 2091, 1–42.

Carreras, C., Pascual, M., Cardona, L., Aguilar, A., Margaritoulis, D., Rees, A., Türkozan, O., Levy, Y., Gasith, A., Aureggi, M., Khalil, M., 2007. The genetic structure of the loggerhead sea turtle (Caretta caretta) in the Mediterranean as revealed by nuclear and mitochondrial DNA and its conservation implications. Conserv. Genet. 8, 761–775.

Carreras, C., Pon, S., Maffucci, F., Pascual, M., Barceló, A., Bentivegna, F., Cardona, L., Alegre, F., SanFélix, M., Fernández, G., Aguilar, A., 2006. Genetic structuring of immature loggerhead sea turtles (Caretta caretta) in the Mediterranean Sea reflects water circulation patterns. Mar. Biol. 149 (5), 1269–1279.

Casale, P., Laurent, L., Gerosa, G., Argano, R., 2002. Molecular evidence of male-biased dispersal in loggerhead turtle juveniles. J. Exp. Mar. Biol. Ecol. 267, 139–145.

Casale, P., Mazaris, A.D., Freggi, D., Basso, R., Argano, R., 2007. A model of area fidelity, nomadism, and distribution patterns of loggerhead sea turtles (Caretta caretta) in the Mediterranean Sea. Mar. Biol. 152, 1039–1049.

Dellinger, T., Freitas, C., 2000. Movements and diving behaviour of pelagic stage loggerhead sea turtle in the north Atlantic: preliminary results obtained through satellite telemetry. 19th annual sea turtle symposium, 1999. South Padre Islands, Texas, USA.

Encalada, S.E., Bjorndal, K.A., Bolten, A.B., Zurita, J.C., Schroeder, B., Possardt, E., Sears, C.J., Bowen, B.W., 1998. Population structure of loggerhead turtle (Caretta caretta) nesting colonies in the Atlantic and Mediterranean as inferred from mitochondrial DNA control region sequences. Mar. Biol. 130, 567-557.

Ehrhart, L.M., Bagley, D.A., Redfoot, W.E., 2003. Loggerhead turtles in the Atlantic Ocean: geographic distribution, abundance, and population status. In: Bolten, A.B., Witherington, B.E. (Eds.), Loggerhead Sea Turtles. Smithsonian Institution, Washington, D.C., pp. 157–174.

Excoffier, L., Laval, G., Schneider, S., 2005. Arlequin (version 3.0): an integrated software package for population genetics data analysis. Evol. Bioinform. Online 1, 47–50.

Gelman, A., Rubin, D.B., 1992. Inference from iterative simulation using multiple sequences (with discussion). Satistical Sci. 7, 457–511.

Hall, T.A., 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucl. Acids. Symp. Ser. 41, 95–98.

Hays, G.C., Marsh, R., 1997. Estimating the age of juvenile loggerhead sea turtles in the North Atlantic. Can. J. Zool. 75, 40–46.

Ireland, L.C., 1980. Homing behavior of juvenile green turtles, Chelonia mydas. In: AmlanerJr. Jr., J.D., MacDonald, D.W. (Eds.), A Handbook on Biotelemetry and Radio Tracking. Pergamon Press, Oxford, pp. 761–764.

Kaska, Y., 2000. Genetic structure of Mediterranean sea turtle populations. Turk. J. Zool. 24, 191–197.

Koch, A.L., Carr, A., Ehrenfeld, D.W., 1969. The problem of open-sea navigation: the migration of the green turtle to Ascension Island. J. Theor. Biol. 22, 163–179.

Lahanas, P.N., Bjorndal, K.A., Bolten, A.B., Encalada, S.E., Miyamoto, M.M., Valverde, R.A., Bowen, B.W., 1998. Genetic composition of a green turtle feeding ground population: evidence for multiple origins. Mar. Biol. 130, 345–352.

Laurent, L., Casale, P., Bradai, M.N., Godley, B.J., Gerosa, G., Broderick, A.C., Schroth, W., Scierwater, B., Levy, A.M., Freggi, D., Abd El-Mawla, E.M., Hadoud, D.A., Gomati, H.E., Domingo, M., Hadjichristophorou, M., Kornaraky, L., Demirayak, F., Gautier, C.H., 1998. Molecular resolution of marine turtle stock composition in fishery by-catch: a case study in the Mediterranean. Mol. Ecol. 7, 1529–1542.

Lee, P.L.M., 2008. Molecular ecology of marine turtles: new approaches and future directions. J. Exp. Mar. Biol. Ecol. 356, 25–42.

Lohmann, K.J., Lohmann, C.M.F., 1994. Detecting of magnetic inclination angle by sea turtles: a possible mechanism for determining latitude. J. exp. Biol. 194, 23–32.

Lohmann, K.J., Lohmann, C.M.F., 2006. Sea turtles, lobsters, and oceanic magnetic maps. Mar. Freshw. Behav. Physiol. 39, 49–64.

Lohmann, K.J., Luschi, P., Hays, G.C., 2008. Goal navigation and island-finding in sea turtles. J. Exp. Mar. Biol. Ecol. 356, 83–95.

López-Jurado, L.F., Mateo, J.A., 1997. Conservation status of reptiles in the Canary Islands. Bonn Zool. Beitr. 36, 585–606.

López-Jurado, L.F., Liria, A., 2007. Programa de reintroducción de la tortuga boba en Canarias. Quercus 255 (supp.), 20–25 (In Spanish).

Luke, K., Horrocks, J.A., LeRoux, R.A., Dutton, P.H., 2004. Origins of green turtle (Chelonia mydas) feeding aggregations around Barbados, West Indies. Mar. Biol. 144, 799–805.

Luschi, P., Hays, G.C., Del Seppia, C., Marsh, R., Papi, F., 1998. The navigational feats of green sea turtles migrating from Ascension Island investigated by satellite telemetry. Proc. Royal Soc. Lond. B 265, 2279–2284.

Luschi, P., Hays, G.C., Papi, F., 2003. A review of long-distance movements by marine turtles, and the possible role of ocean currents. Oikos 103, 293–302.

Luschi, P., Papi, F., Liew, H.C., Chan, E.H., Bonadonna, F., 1996. Long-distance migration and homing after displacement in the green turtle (Chelonia mydas): a satellite tracking study. J. Comp. Physiol. A 178, 447–452.

Margaritoulis, D., Argano, R., Baran, I., Bentivegna, F., Bradai, M.N., Camiñas, J.A., Casale, P., de Metrio, G., Demetropoulos, A., Gerosa, G., Godley, B.J., Haddoud, D.A., Houghton, J., Laurent, L., Lazar, B., 2003. Loggerhead turtles in the Mediterranean Sea: present knowledge and conservation perspectives. In: Bolten, A.B., Witherington, B.E. (Eds.), Loggerhead Sea Turtles. Smithsonian Institution Press, Washington D.C., pp. 175–198.

Marco, A., López, O., Abella, E., Varo, N., Martins, S., Gaona, P., Sanz, P., López-Jurado, L.F., 2008. Massive capture of nesting females in severely threatening the CaboVerdian loggerhead population. 28th Annual Symposium on Sea Turtle Biology and Conservation, Loreto, Baja California Sur, Mexico 19–26 January 2008.

Norman, J.A., Moritz, C., Limpus, C.J., 1994. Mitochondrial DNA control region polymorphisms: genetic markers for ecological studies of marine turtles. Mol. Ecol. 3, 363–373.

Papi, F., Luschi, P., Akesson, S., Capogrossi, S., Hays, G.C., 2000. Open-sea migration of magnetically disturbed sea turtles. J. Exp. Biol. 203, 3435–3443.

Polovina, J.J., Balazs, G.H., Howell, E.A., Parker, D.M., Seki, M.P., Dutton, P.H., 2004. Forage and migration habitat of loggerhead (Caretta caretta) and olive ridley (Lepidochelys olivacea) sea turtles in the central North Pacific Ocean. Fisheries Oceanogr. 13 (1), 36–51.

Polovina, J.J., Kobayashi, D.R., Ellis, D.M., Seki, M.P., Balazs, G.H., 2000. Turtles on the edge: movement of loggerhead turtles (Caretta caretta) along oceanic fronts in the central North Pacific, 1997–1998. Fisheries Oceanogr. 9, 71–82.

Polovina, J.J., Uchida, I., Balazsm, G., Howell, E.A., Parker, D., Dutton, P., 2006. The Kuroshio Extension Bifurcation Region: a pelagic hotspot for juvenile loggerhead sea turtles. Deep-Sea Res. II 53, 326–339.

Revelles, M., Carreras, C., Cardona, L., Marco, A., Bentivegna, F., Castillo, J.J., de Martino, G., Mons, J.L., Smith, M.B., Rico, C., Pascual, M., Aguilar, A., 2007. Evidence for an asymmetrical size exchange of loggerhead sea turtles between the Mediterranean and the Atlantic through the Straits of Gibraltar. J. Exp. Biol. Ecol. 349, 261–271.

Reidy, S.P., Kerr, S.R., Nelson, J.A., 2000. Aerobic and anaerobic swimming performance of individual Atlantic cod. J. Exp. Biol. 203, 347–357.

Skiles, D.D., 1985. The geomagnetic field: its nature, history and biological relevance. In: Kirschvink, J.L., Jones, D.S., Macfadden, B.J. (Eds.), Magnetite biomineralization and magnetoreception by living organisms: A new biomagnetism. Plenum Publishing corporation, New York, pp. 43–102.

Sokal, R.R., Rohlf, F.J., 1981. Biometry, Second Edition. W.H. Freeman and Company, San Francisco, California, U.S.A.

Spiegelhalter, D., Thomas, A., Best, N., Lunn, D., 2003. WINBUGS, version 1.4 user manual. MRC Biostatistics Unit, Cambridge, UK.

StatSoft Inc., 2001. STATISTICA (data analysis software system), version 6. www.statsoft.com.

Tamura, K., Nei, M., 1993. Estimation of the number of substitutions in the control region of mitochondrial DNA in humans and chimpanzees. Mol. Biol. Evol. 10, 512–526.

Tsimplis, M.N., Bryden, H.L., 2000. Estimation of the transports through the Strait of Gibraltar. Deep-Sea Res. Pt. I 47, 2219–2242.

Zaykin, D.V., Pudovkin, A.I., 1993. Two programs to estimate significance of Chi-square values using pseudo-probability test. J. Heredity 84, 152.