

Evidence for an asymmetrical size exchange of loggerhead sea turtles between the Mediterranean and the Atlantic through the Straits of Gibraltar

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Abstract

The permanent eastward current at the Straits of Gibraltar may trap small Atlantic loggerhead sea turtles (*Caretta caretta*) inside the western Mediterranean until their swimming and diving skills improve enough to allow them counter-current swimming abilities through the current. A captivity experiment with twelve loggerhead sea turtles (straight carapace length or SCL range: 25.3–48.0 cm) revealed that the average critical velocity of this species within the considered length range was $0.38 \pm 0.16 \text{ m s}^{-1}$ or $1.01 \pm 0.24 \text{ bl s}^{-1}$. As a consequence, loggerhead sea turtles are predicted to require a minimum SCL of 36.0 cm to swim counter-current through the Straits of Gibraltar, where the water velocity ranges $0.31\text{--}0.37 \text{ m s}^{-1}$. Genetic analysis of 105 specimens using one mitochondrial marker and seven microsatellites, as well as the recapture of three tagged individuals, support this conclusion; all Mediterranean individuals found in the Atlantic side of the Straits were not smaller than 36.0 cm SCL and the average length (47.3 cm SCL) was significantly higher than that of the Mediterranean turtles in the Mediterranean side of the Straits (31.6 cm SCL). Furthermore, the average length of the turtles of any origin moving from the Mediterranean to the Atlantic was much larger than 36.0 cm (SCL: 54.5 cm SCL), which may indicate the intervention of a different, yet unidentified mechanism restricting east–westward movement. The Algerian current, running along northern Africa, may at least partially explain the delayed departure of loggerhead sea turtles from the Mediterranean Sea to the Atlantic Ocean, as it would force the eastward drift of loggerheads occupying the southwestern Mediterranean. Exchange through the Straits is asymmetrical, and Atlantic turtles are found to enter the Mediterranean at a length of about 20.5 cm. However, once in the Mediterranean they would be retained there for up to 7.9 years, due to the surface circulation pattern. This increases the time span at which turtles are exposed to a high mortality rate, caused by fishing.

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1. Introduction

Young loggerhead sea turtles (*Caretta caretta*) are positively buoyant (Milsom, 1975) and since drag is higher at the water surface than at depths deeper than three times the animal's greatest body diameter (Berta and Sumich, 1999), they are poor swimmers. As a consequence, they spend most of their time at the water surface, at least in captivity (Davenport and Clough, 1986). As they grow and gain control over buoyancy (Milsom, 1975; Wyneken, 1997; Minamikawa et al., 2000; Bolten, 2003a; Hochscheid et al., 2003), the time spent submerged increases, both in captivity (Bentivegna et al., 2003) and in the wild (Renaud and Carpenter, 1994; Dellinger and Freitas, 1999; Minamikawa et al., 2000; Godley et al., 2003; Luschi et al., 2003; Cardona et al., 2005; Revelles et al., 2007), probably to reduce drag while swimming; hence, currents are thought to restrict their distribution while young, becoming less important as individuals grow (Luschi et al., 2003). The transition between the juvenile oceanic stage, where passive drifting prevails and the immature-adult neritic stage, where active swimming dominates, appears to occur when individuals reach a straight carapace length (SCL) of 40–60 cm (Bolten, 2003a). Specimens in this size range are competent swimmers, can travel against weak currents (Wyneken, 1997; Dellinger and Freitas, 1999; Polovina et al., 2000) and may exhibit strong homing behaviour (Renaud and Carpenter, 1994; Avens et al., 2003).

One of the best documented migrations undertaken by loggerhead sea turtles is the eastward drift of juveniles across the northern Atlantic Ocean along the Gulf Stream and the subsequent return of late immature individuals after several years of remaining in the feeding grounds of the eastern Atlantic Ocean and the Mediterranean Sea (Bolten, 2003a). Genetic data demonstrate that juveniles from the rookeries of northern America and the Caribbean gain access to the western Mediterranean through the Straits of Gibraltar, where they share feeding grounds with the juvenile loggerhead turtles from the eastern Mediterranean rookeries (Laurent et al., 1998; Carreras et al., 2006a). Passive external tagging has revealed that, after several years, some of the loggerhead sea turtles of western Atlantic origin return to their natal region (Camiñas, 2005; Camiñas, personal communication).

Gaining access to the western Mediterranean through the Straits of Gibraltar is easy because the water column is permanently stratified: a top layer of less saline, Atlantic water flows eastward at $0.31\text{--}0.37\text{ m s}^{-1}$ (assuming a mean instantaneous inflow of 0.78 Sv in

agreement with Tsimplis and Bryden, 2000), while a deeper layer of more saline, Mediterranean water flows westward (Bryden et al., 1994; Delgado et al., 2001). The thickness of the top layer is variable, but measures about 147 m (Tsimplis and Bryden, 2000). As juvenile loggerhead turtles are positively buoyant (Milsom, 1975) and seldom dive deeper than 50 m (Polovina et al., 2003), such stratification facilitates their passing from the Atlantic to the Mediterranean. However, the passage from the Mediterranean to the Atlantic can only be made by turtles of comparatively larger body size, which can swim against the surface eastward current or swim deep enough to reach the deeper westward current. This suggests that the Straits of Gibraltar may trap small Atlantic loggerhead sea turtles inside the western Mediterranean until their swimming and diving skills develop enough to escape. Although genetic studies have demonstrated that Mediterranean turtles cross to the eastern Atlantic (Carreras et al., 2006a), passing is likely to be size biased for this reason.

The hypothesis of an asymmetrical size exchange across the Straits of Gibraltar can be tested in a number of ways. The use of capture-tagging-recapture data are the most obvious of these, but despite substantial tagging effort (Margaritoulis et al., 2003; Camiñas, 2005), only four loggerhead turtles tagged in the Mediterranean have so far been recaptured in the Atlantic (Argano et al., 1992 quoted by Margaritoulis et al., 2003; Camiñas, 2005; Camiñas, personal communication). Length analysis of turtles of known origin in the eastern Atlantic and the western Mediterranean is an alternative approach, but the length composition studies so far undertaken did not assess the origin of the analyzed individuals (Mayol et al., 1988; Hays and Marsh, 1997) or attempted to do it only through mitochondrial markers, which are useful to assess the composition of mixed stocks (Bolten et al., 1998; Laurent et al., 1998; Carreras et al., 2006a), but not to determine the exact origin of individuals (Laurent et al., 1998; Carreras et al., 2006b).

This paper presents the results of a study addressed to test the hypothesis of an asymmetrical size exchange of loggerhead sea turtles across the Straits of Gibraltar that combines two alternative approaches: the study in laboratory conditions of the swimming performance of loggerhead sea turtles subject to the conditions prevailing in the Straits of Gibraltar to accurately determine their ability to swim against surface currents, and the use of nuclear DNA microsatellites that have distinct alleles for the North Atlantic and Mediterranean populations, and thus permit exact affiliation (Carreras et al., 2006b).

2. Materials and methods

2.1. Swimming performance of turtles

A laboratory experiment in a flow chamber was conducted from June to August 2005 at the Turtle Point of the Anton Dorhn Zoological Station (Naples, Italy) to assess the swimming performance of 12 wild loggerhead sea turtles caught off southern Italy. All individuals were considered healthy because feed voraciously, had not external injury and did not exhibit any abnormal behaviour. The SCL of the turtles ranged 25.3–48.0 cm (Table 1). Two variable flow pumps were used to generate the current within a channel constructed by fixing a central 3.1 m long, 1.2 m wide, 0.7 m high, oval island with silicone to the floor of a 5 m long, 3 m wide, 0.7 m deep, oval tank. The swimming chamber was 1.6 m long, 0.6 m wide, 0.7 m deep. To obtain a flow as straight as possible, a flow straightener was built with PVC pipes of 8 cm in diameter and 40 cm in length and situated at the front of the experimental chamber (Fig. 1). The back of the experimental chamber was a 1 cm² mesh-size plastic screen. Water temperature fluctuated in agreement with that of the sea surface and ranged between 24.3–27.9 °C.

The swimming performance of each turtle was measured at four water velocities: 0.2, 0.4, 0.6 and 0.8 m s⁻¹. This range of velocities matches the range recorded in the western Mediterranean, including the Straits of Gibraltar and the Algerian current, where it can be as high as 0.8 m s⁻¹ (Millot, 1999; Obaton et al., 2000). Water velocity was measured at three points across the experimental chamber and the average figure was taken as the experimental velocity experienced by the turtle. Three trials were conducted with each turtle. The water temperature and the mean velocity of the flow in the

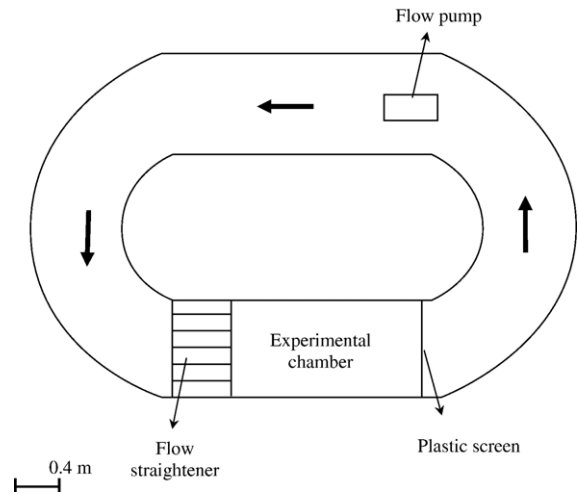


Fig. 1. Tank where the experiment was carried out.

experimental chamber were measured at the beginning of every trial. The trial began with a water velocity of 0.2 m s⁻¹ and after 20 min, the velocity was increased by 0.2 m s⁻¹. This rate of increase was maintained until the turtle was exhausted and could no longer maintain its position in the chamber. Every 20 min, the flipper beat frequency (FBF), calculated as the number of times the turtle beat the flippers per time unit, and the respiratory frequency, calculated as the number of times the turtle emerged for breath per time unit, were recorded. The time span the animal swam counter current was also recorded. Each trial was separated by an interval of 3 days, during which the turtles rested and fed.

To assess swimming performance, we calculated for each turtle its critical velocity, U_{crit} , a parameter that relates the maximum cruise speed that an aquatic animal could sustain without resulting in muscular fatigue (Reidy et al., 2000) and is a convenient descriptor of swimming skills in aquatic animals. It was calculated by means of the following equation (Lowe, 1996):

$$U_{crit} = U_f + [(T_f/T_i)U_i] \quad (1)$$

where U_f is the highest speed that the turtle was able to maintain for the entire 20 minute interval, T_f is the time (<20 min) the turtle was able to swim at the final (next highest) speed, T_i is the time interval (20 min) and U_i is the speed increment by which the velocity was increased (0.2 m s⁻¹). The U_{crit} is called $U_{crit-bl}$ when expressed in terms of body lengths per unit time (bl s⁻¹) and the latter was obtained by dividing the U_{crit} of the turtle by its size. Length and not weight were used since length was easier to measure in the field and a strong correlation

Table 1

Length (SCL), experimental water temperature and critical swimming speed calculated for the ten immature loggerhead sea turtles involved in the experiment

SCL (cm)	Water temperature (°C)	Mean U_{crit} (m s ⁻¹)	Mean U_{crit} (bl s ⁻¹)
26	24.3–26.6	0.20	0.78
28	25.0–26.8	0.21	0.73
29	27.1–27.9	0.23	0.81
30	24.9–26.4	0.30	1.00
36	25.6–26.8	0.27	0.77
37	25.7–25.9	0.41	1.10
41	25.1–26.5	0.52	1.27
44	24.4–26.4	0.63	1.43
46	24.8–27.1	0.56	1.22
48	24.5–26.7	0.46	0.96

exists for both parameters ($r^2=0.899$ in agreement with Mayol, 1990).

2.2. Genetic analysis

Tissue samples (muscle or skin) for genetic analysis were collected from 105 turtles stranded or captured alive from 2003 to 2005 in the foraging grounds located at both sides of the Straits of Gibraltar (Gulf of Cadiz: $n=40$, Alboran Sea: $n=65$) (Fig. 2). The same fishing gears are used at both sides, so no size bias is expected due to differences in the way the turtles were captured. To avoid pseudo-replication, turtles that were subsequently released were tagged with external flipper tags. The SCL was measured, and the minimum size of the turtles genetically associated with the Mediterranean rookeries, collected in the eastern Atlantic Ocean, was considered to be the minimum size required to move westward across the Straits. This value was used as a threshold to test the reliability of the results of the swimming experiment.

For the mitochondrial analysis, a fragment of the D-loop control region was amplified by polymerase chain reaction (PCR) using the primer pairs TCR1–TCR2 (Norman et al., 1994) and the PCR protocol described in Carreras et al. (2006a). PCR products were visualized in a 1% agarose gel and purified with the QIAquick kit (QIAGEN®). Purified products were sequenced with the BigDye™ Primer Cycle Sequencing Kit (Applied

Biosystems) or the DYEnamic™ ET Terminator Cycle Sequencing Kit (Amersham). Sequences were aligned by eye using the program BioEdit version 5.0.9 (Hall, 1999) and compared with haplotypes previously described (Bolten et al., 1998; Encalada et al., 1998; Carreras et al., 2006a) and contained in the Archie Carr Center for Sea Turtle Research database (<http://accstr.ufl.edu/>).

Additionally, we analyzed 7 microsatellites previously used in the species: Cm84, Cc117, Cm72 and Ei8 (FitzSimmons et al., 1995); Cc141 and Cc7 (FitzSimmons et al., 1996); and Ccar176 (Moore and Ball, 2002 re-designed by Carreras et al., 2006b). One primer for each microsatellite pair was fluorescently labeled with NED, PET, VIC or 6-FAM and each locus was amplified using the PCR protocol described in Carreras et al. (2006b). The allele length was determined on an ABI 3730 automated DNA Analyzer (Applied Biosystems) and assigned using the Genemapper package (ABI PRISM® GeneMapper™ Software ver. 3.0.).

2.3. Statistical analyses

Normality and homoscedasticity were tested by means of the Lilliefors' and Levene's tests, respectively. The Pearson's correlation coefficient was calculated to determine the relationship between SCL and U_{crit} , FBF and the respiratory frequency, and that between FBF and the respiratory frequency. The relationship between

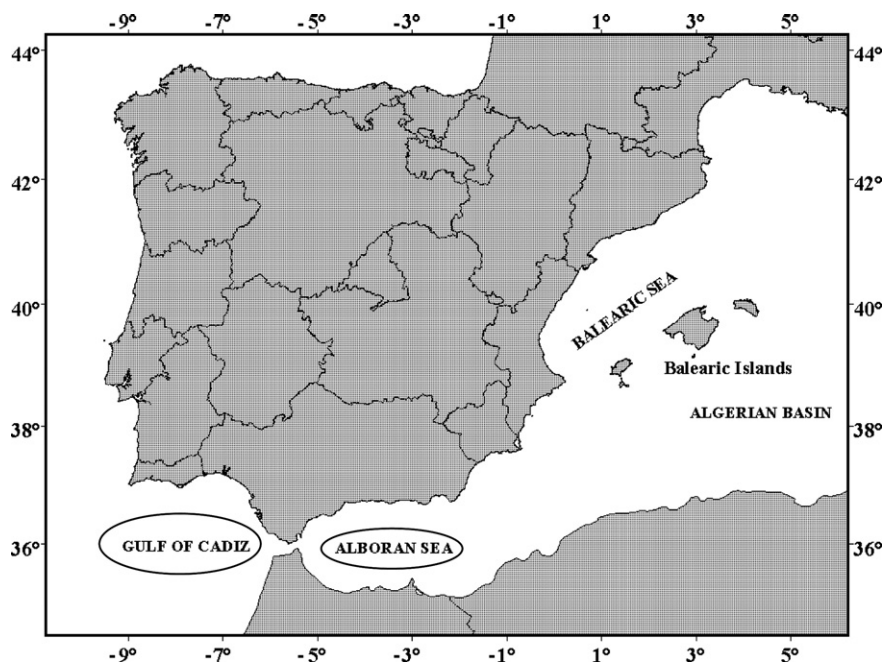


Fig. 2. Sampling locations for the genetic studies.

temperature and $U_{\text{crit-bl}}$ was analysed through the non-parametric Spearman's correlation coefficient, as the data were not normally distributed. For this analysis, the U_{crit} was not used to avoid bias due to the size of the turtles, since the aim was to assess any effect of the temperature on the U_{crit} regardless of turtles size. The Student's t test was used to compare the SCL of both groups of turtles (Atlantic and Mediterranean) from both sides of the Straits of Gibraltar. The Chi-square test (Zaykin and Pudovkin, 1993) was used to check differences in the frequency of mtDNA haplotypes in the considered feeding grounds. Actual frequencies were compared to the distributions generated by randomizing the sampled individuals between the two feeding grounds using Monte-Carlo resampling (Rolf and Bentzen, 1989), as implemented in the CHIRXC program (Zaykin and Pudovkin, 1993). With this method, haplotypes occurring at low absolute frequencies did not have to be grouped. The Zs test was used to compare the haplotype frequencies between both groups of turtles, as implemented in the DNAsp program version 4.0 (Rozas et al., 2003), because it incorporates sequence divergence information to the analysis. Genetic distance (Γ_{st} ; γ_{st} ; Nei, 1982) between foraging grounds was calculated using the DNAsp programme.

Genepop v3.4 (Raymond and Rousset, 1995) was used for comparing the two groups of turtles using microsatellite data. Differentiation tests were conducted for the microsatellites (F_{st}) and linkage disequilibrium between loci pairs was also assessed. P -values for population differentiation were calculated with a Markov chain randomization (Guo and Thompson, 1992). The Fisher's method, which assumes statistical independence across loci, was used to combine test results for allelic counts among the populations for all seven loci (Raymond and Rousset, 1995). The Hardy–Weinberg disequilibrium was not investigated because the units treated were not populations, but feeding aggregations of juveniles at both sides of the Straits of Gibraltar (Gulf of Cadiz and Alboran Sea), and both of them were probably composed of individuals from different populations.

Microsatellites were used to obtain individual assignments through the program STRUCTURE v2.1 (Pritchard et al., 2000), which implements a Bayesian clustering method to determine the probability that each individual belongs to each putative origin area. The combined probability is always 1.00, as no other sources are considered for the Mediterranean feeding grounds. As a baseline for these calculations we used the dataset produced by Carreras et al. (unpublished data). Only specimens with an assignment probability higher than 80% were used to calculate the minimum size that

loggerhead sea turtles must reach to have a chance to migrate westward across the Straits of Gibraltar.

3. Results

3.1. Swimming performance of turtles

After a few trials, the smallest individual (SCL: 25.3 cm) used in the experiment was unable to swim against the lowest current speed (0.2 m s^{-1}) and was therefore excluded from the study. Another turtle (SCL: 47.5 cm) did not become exhausted after swimming for 20 min at the highest current speed (0.8 m s^{-1}) and, hence,

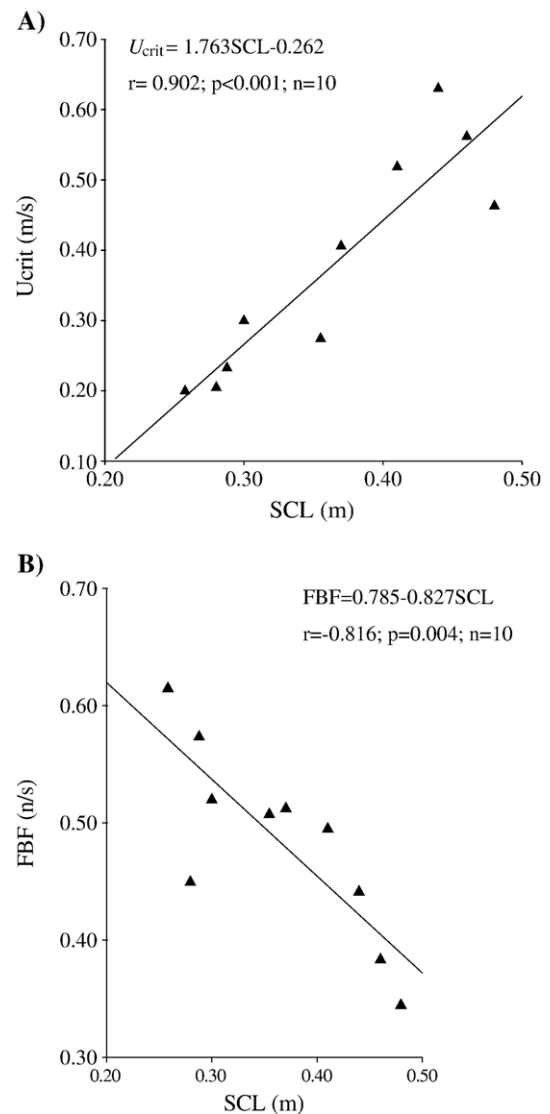


Fig. 3. Correlation observed between: (A) U_{crit} and SCL and (B) FBF and SCL (with a water velocity of 0.2 m s^{-1}), for the ten turtles used in the experiment.

U_{crit} could not be calculated for that specimen. For the remaining ten turtles, the average U_{crit} was $0.38 \pm 0.16 \text{ m s}^{-1}$, and the $U_{crit-bl}$ was $1.01 \pm 0.24 \text{ bl s}^{-1}$ (Table 1). No correlation was found between water temperature and $U_{crit-bl}$ (Spearman's $\rho = -0.198$, $P = 0.295$, $n = 30$). Conversely, a significant positive correlation was found between U_{crit} (m s^{-1}) and SCL (m) ($r = 0.902$, $P < 0.001$, $n = 10$, Fig. 3A). The velocity of the surface current flowing eastward across the Straits of Gibraltar over the sill is expected to range from $0.31\text{--}0.37 \text{ m s}^{-1}$, assuming the following: a Atlantic mean instantaneous inflow of 0.78 Sv, a top layer thickness of 147 m at the Straits of Gibraltar (Tsimplis and Bryden, 2000) and a channel width over the sill ranging from 17.4 km off Algeciras and 14.2 km off Tarifa. Thus, turtles must be able to reach a minimum U_{crit} of at least 0.37 m s^{-1} to sustain counter-current swimming through the Straits of Gibraltar, which is expected to occur for turtles with a mean SCL of 36.0 cm (95% CI = 26.2–45.8 cm).

Whereas a negative correlation between SCL and FBF was found at 0.2 m s^{-1} ($r = -0.816$, $P = 0.004$, $n = 10$, Fig. 3B), no correlation was found at 0.4 m s^{-1} ($r = 0.391$, $P = 0.299$, $n = 9$) or at 0.6 m s^{-1} ($r = 0.428$, $P = 0.472$, $n = 5$). When the experimental velocity was expressed as body length per time unit (bl s^{-1}) to avoid the scatter in the measured values, FBF increased as a logarithmic function of the experimental velocity (Fig. 4), with the highest FBF for any individual turtle ranging from 0.64 to $0.86 \text{ beats s}^{-1}$.

The respiratory frequency and the SCL were not correlated at any of the experimental velocities (at 0.2 m s^{-1} :

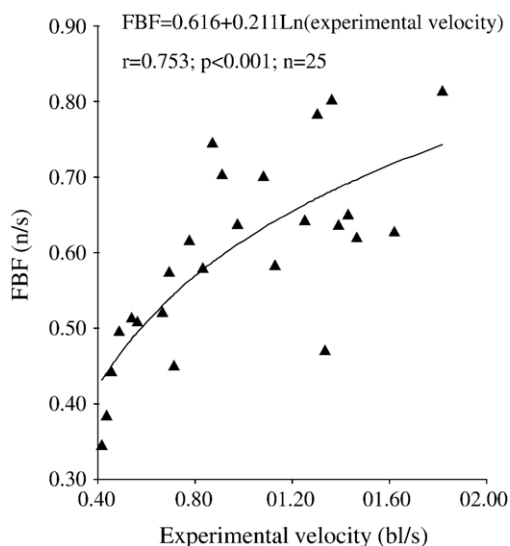


Fig. 4. FBF as a function of experimental velocity for the ten turtles involved in the experiment at every trial.

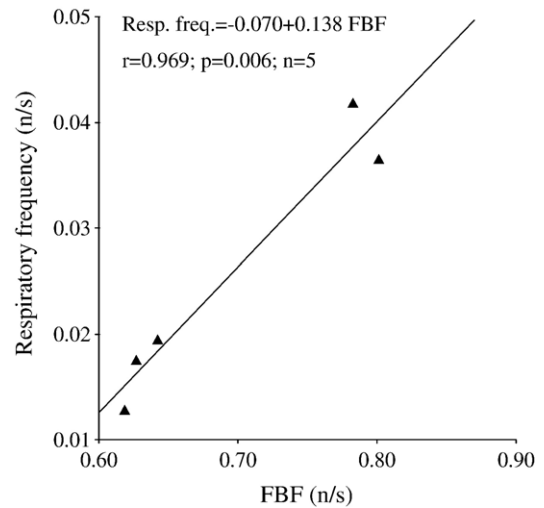


Fig. 5. Correlation observed between FBF and respiratory frequency for the five turtles used in the experiment at a water velocity of 0.6 m s^{-1} .

$r = -0.163$, $P = 0.653$, $n = 10$, at 0.4 m s^{-1} : $r = 0.208$, $P = 0.591$, $n = 9$, at 0.6 m s^{-1} : $r = 0.716$, $P = 0.173$, $n = 5$). However, the respiratory frequency and the FBF were positively correlated at 0.6 m s^{-1} ($r = 0.969$, $P = 0.006$, $n = 5$, Fig. 5), but not at 0.2 m s^{-1} ($r = 0.074$, $P = 0.840$, $n = 10$) nor at 0.4 m s^{-1} ($r = 0.351$, $P = 0.355$, $n = 9$) despite a larger sample size with the latter experimental velocities.

3.2. Genetic analysis

A total of 11 haplotypes were found in the Gulf of Cadiz and the Alboran Sea (Table 2), one of them not

Table 2

Haplotype composition found at the eastern side (Alboran Sea) and the western side (Gulf of Cadiz) of the Straits of Gibraltar

Haplotype	Alboran Sea	%	Gulf of Cadiz	%	Total	%
CCA1	26	40	19	47.5	45	42.9
CCA2	31	47.7	15	37.5	46	43.8
CCA3	2	3.08	0	0	2	1.9
CCA9	0	1.54	2	5	2	1.9
CCA10	1	1.54	0	0	1	1
CCA11	2	3.08	0	0	2	1.9
CCA12	0	0	1	2.5	1	1
CCA14	1	1.54	1	2.5	2	1.9
CCA17	0	0	1	2.5	1	1
CCA21	1	1.54	1	2.5	2	1.9
CCA42	1	1.54	0	0	1	1
Total	65		40		105	
Mean SCL (cm)	43		39		42	
SCL Range (cm)	(15–79)		(13–76)		(13–79)	

Table 3
SCL and calculated U_{crit} of Mediterranean loggerhead sea turtles found at both sides of the Straits of Gibraltar

Individual code	Feeding ground	Probability of being Mediterranean	SCL (cm)	U_{crit} ($m s^{-1}$)
A11	Alboran Sea	83.4	34	0.34
A47	Alboran Sea	91.8	21	0.11
A08	Alboran Sea	94.5	33	0.32
A12	Alboran Sea	93.0	31	0.28
A45	Alboran Sea	82.0	39	0.43
AA08	Gulf of Cadiz	99.1	36	0.37
AA02	Gulf of Cadiz	91.9	53	0.67
AA06	Gulf of Cadiz	91.8	38	0.41
AA07	Gulf of Cadiz	99.2	62	0.83

Hydrographic data indicate that only the turtles that achieve a U_{crit} of $0.37 m s^{-1}$ have a chance to migrate westward across the Straits of Gibraltar. The probability of turtles originating from the Mediterranean rookeries was calculated by the STRUCTURE software on the basis of microsatellite analysis.

previously described (CCA42, Genbank accession number no EF397612). No significant genetic differences were observed between both feeding grounds, neither for the mitochondrial DNA ($\gamma_{st}=0.0079$, Chi-Square test and Zs test $P>0.05$) nor for the nuclear DNA ($F_{st}=0.0027$, $P>0.05$). Moreover, specimens from the two areas did not differ in average SCL (Student's $t=1.080$, $df=94$, $P=0.142$) despite specimens in the western side of the Straits were slightly smaller (Table 2). Assignment tests found 4 Mediterranean individuals in the Gulf of Cadiz and 5 in the Alboran Sea (Table 3). Mediterranean specimens shorter than 36.0 cm, the SCL required to migrate westward across the Straits of Gibraltar according to the swimming experiment, were only found in the Alboran Sea (Table 3). The average SCL of Mediterranean immature loggerhead sea turtles from the Gulf of Cadiz (Mean = 47.3 cm, $SD=\pm 12.4$ cm, $n=4$) was higher than that of turtles from the Alboran Sea (Mean = 31.6 cm, $SD=\pm 6.6$ cm, $n=5$) (Student's $t=2.442$, $df=7$, $P=0.022$).

4. Discussion

Among aquatic animals, fish are the group in which swimming performance and kinematics are best studied. The velocity achieved by fish depends on size and FBF, both in sharks (Lowe, 1996) and teleosts with anguilliform (Liao, 2002), pseudocarangiform–carangiform (Bainbridge, 1958; Dewar and Graham, 1994; Peake et al., 2000) or labriform (Drucker and Jensen, 1996; Mussi et al., 2002) swimming modes. Although a physiological limit should exist for FBF in fish, it is seldom reached in laboratory experiments and hence a positive linear relationship between swimming velocity

and FBF is usually reported to occur in this group of organisms (Bainbridge, 1958; Dewar and Graham, 1994; Drucker and Jensen, 1996; Lowe, 1996; Liao, 2002). Besides this relationship, FBF decreases with size in all fish groups, independently of swimming mode (Bainbridge, 1958; Dewar and Graham, 1994; Drucker and Jensen, 1996; Mussi et al., 2002).

Comparatively, the swimming performance of marine turtles has been less studied (Prange, 1976; Butler et al., 1984; Davenport and Clough, 1986; Davenport and Pearson, 1994). The U_{crit} has been determined in the laboratory for juvenile green turtles (*Chelonia mydas*) (Prange, 1976), but extrapolation to other species and size classes would not be reliable due to differences in anatomy (Bolten, 2003b; Wyneken, 1997). Sea turtles differ from most teleosts in that propulsion is gained by describing an elliptical movement with the foreflippers (Wyneken, 1997), a swimming mode approached only by labriform-type swimming (Drucker and Jensen, 1996).

A negative correlation between FBF and SCL was expected, as power per stroke may depend on muscle mass and hence SCL. However, such a negative correlation was observed only at $0.2 m s^{-1}$. This is because a physiological limit for FBF in loggerhead turtles about $0.7 beats s^{-1}$ exists. Interestingly, the FBF physiological limit found for juveniles loggerhead turtles here was within the range of FBF measured for green turtles while diving in the wild (Hays et al., 2004; Hays et al., 2007), but higher than that reported for the more morphologically distinct leatherbacks during the inter-nesting interval (Reina et al., 2005). That limit is reached by loggerhead sea turtles at experimental velocities ranging from 0.4 to $0.8 m s^{-1}$, thus generating a logarithmic relationship between swimming velocity and FBF, opposite to the linear one typically found in fishes, including those with labriform-type swimming. A physiological limit has also been described for fish with the labriform-type swimming, but they may use their caudal fin for propulsion once pectoral fins reach the FBF physiological limit (Drucker and Jensen, 1996; Mussi et al., 2002); for sea turtles, this is not a possibility. Another limitation for sea turtles is that they have to surface for breathing, increasing drag.

Previous studies have reported an increase in the respiratory frequency of marine turtles with an increase in activity level (Prange, 1976; Prange and Jackson, 1976; Butler and Woakes, 1980; Butler et al., 1984; Lutz et al., 1989; Southwood et al., 2003) and FBF (Hays et al., 2004; Reina et al., 2005) and that the maximal rate of activity is likely to be ultimately restricted by how often the turtle must ventilate its lungs (Lutcavage et al., 1987). However, in our experiment, a correlation between the rate of

respiratory frequency and the experimental velocity was only observed at an experimental velocity of 0.6 m s^{-1} . This is probably due to the scattering in turtle lengths at lower velocity values, as small turtles reach their maximum respiratory frequency at low experimental velocities due to a smaller lung volume and the negative correlation between oxygen consumption per body mass unit and turtle length (Prange and Jackson, 1976).

Prange (1976) reported a U_{crit} of 1.5 bl s^{-1} for young green turtles measuring about 24.0 cm, a higher value than that here reported for larger loggerhead sea turtles (1.01 bl s^{-1}). These differences match observations by Davenport and Pearson (1994), who reported that green turtles appeared to be faster swimmers and made greater use of their fore-flippers than loggerhead sea turtles. On the other hand, Davenport and Clough (1986) mentioned that the limbs of loggerhead sea turtles are more unspecialized than those of green turtles, as the fore-flippers of the former are relatively smaller, less streamlined and more flexible than those of the latter.

Satellite telemetry has provided a wealth of data about the speed of travel of loggerhead sea turtles in the wild (Stoneburner, 1982; Byles and Dodd, 1989; Renaud and Carpenter, 1994; Sakamoto et al., 1997; Balazs et al., 1999; Nichols et al., 2000; Polovina et al., 2000; Bolten, 2003a; Godley et al., 2003; Cardona et al., 2005; Polovina et al., 2006; Revelles et al., 2007). However, this technique is useless for assessing the actual U_{crit} of the tracked animals because satellite-derived measurements bring inherent errors due to satellite location errors, the assumption of continuous straight line movements and the fact that sea turtles do not swim continuously between satellite locations (Renaud and Carpenter, 1994); moreover, they cannot dissociate the actual swimming speed of the turtle from the effect of the currents (Polovina et al., 2006). Despite the above reported shortcomings, the mean speed of travel of loggerhead sea turtles in the wild, as measured by satellite telemetry, ranges from 0.08 to 0.40 bl s^{-1} (Byles and Dodd, 1989; Renaud and Carpenter, 1994; Sakamoto et al., 1997; Balazs et al., 1999; Nichols et al., 2000; Polovina et al., 2000; Bolten, 2003a; Godley et al., 2003; Cardona et al., 2005; Polovina et al., 2006; Revelles et al., 2007). These values are well below the average $U_{\text{crit-bl}}$ reported here. This indicates that in the wild, turtles probably spend most of their time swimming at a velocity lower than one they could sustain without resulting in muscular fatigue.

Measuring water velocity in the top layer of the Straits of Gibraltar is difficult due to the existence of tidal currents and strong winds but, taking into consideration the amount of water exchanged, the thickness

of the top layer and the average width of the sill, it is estimated to range from 0.31 to 0.37 m s^{-1} (Tsimplis and Bryden, 2000). The laboratory experiment reported here indicates that turtles should reach 36.0 cm SCL before being able to achieve a U_{crit} of 0.37 m s^{-1} and thus, to migrate westward through the Straits of Gibraltar. The westward migration may become even more difficult in winter, as the experiment was conducted within the summer range of sea surface temperature and hence the above reported U_{crit} values are thought to be the highest reached throughout the seasonal cycle.

However, a cautionary note is needed. The turtles used in the experiment had spent several months in captivity and hence they did not exhibit the same feeding condition and training than freshly caught wild turtles. Furthermore, they were caught in a region where Mediterranean turtles prevail (Carreras et al., 2006a) and differences in the swimming skills of Atlantic and Mediterranean loggerhead sea turtles might exist. Finally, sample size is not too large and, for this reason, the confidence interval is so wide.

Despite all those shortcomings, the genetic analysis supports the conclusions from the laboratory experiment, as Mediterranean turtles smaller than 36.0 cm have not been found on the western side of the Straits, yet they are present on the eastern side; tagging also supports this conclusion, as the SCL of the only three turtles tagged in the Mediterranean and recaptured in the Atlantic ranged from 60.2–68.0 cm, although the 789 tagged turtles ranged in size from 21 to 71 cm SCL (Camiñas, 2005; Camiñas, personal communication). Finally, Atlantic turtles smaller than 36.0 cm SCL occur in both areas, thus demonstrating that no restriction exists to the eastward dispersal through the Straits.

Atlantic loggerhead sea turtles are thought to drift eastward with the Gulf Stream and as a consequence, the average length of immature turtles increases eastward from central Atlantic to Europe (Carr, 1987; Hays and Marsh, 1997; Bolten et al., 1998). Hays and Marsh (1997) reported a length range of 15.5–104.1 cm off the United Kingdom and concluded that the modal carapace length of juveniles reaching Europe was 20.5 cm, equivalent to an age of 1.6 years according to the growth model of Bjorndal et al. (2000). As the Straits of Gibraltar are roughly at the same longitude as the United Kingdom, and loggerhead sea turtles 36.0 cm long (SCL) are thought to be 5.0 years old (Bjorndal et al., 2000), Atlantic immature turtles entering the Mediterranean Sea are expected to spend at least 3.4 years in that sea before being able to return to the Atlantic Ocean. An alternative way to come back to the Atlantic earlier is approaching the coast to benefit from a lower

current velocity (Luschi et al., 2006), although genetic evidence suggests that they do not do this. Indeed, available data from genetic markers (this study) and passive tags (Camiñas, 2005; Camiñas, personal communication) indicate that they leave the Mediterranean at a much larger size (54.5 cm SCL) and older age (9.5 years). Obviously, the exactitude of these calculations depends on the actual growth curve of the Atlantic loggerhead sea turtles while in the Mediterranean, that has not yet been calculated to our knowledge.

Once in the western Mediterranean, most immature turtles from the Atlantic rookeries concentrate in the Algerian basin (Cardona et al., 2005; Carreras et al., 2006a; Revelles et al., 2007), although some may reach the Adriatic Sea (Carreras et al., 2006a; Maffucci et al., 2006). The Algerian basin is one of the most oligotrophic regions in the western Mediterranean (Longhurst, 1998; Bosc et al., 2004), but its average productivity is higher than that of the North Atlantic Subtropical Gyral province (Longhurst, 1998) where turtles are expected to remain if they do not enter the Mediterranean Sea. This may suggest that immature loggerheads remain in the western Mediterranean for a period longer than expected to take advantage of the higher food availability present locally. However, this hypothesis would require that turtles must be able to integrate changes in food availability with time and remember them for at least 3.4 years. An alternative hypothesis is that turtles are retained inside the western Mediterranean by some physical process other than the currents at the Straits of Gibraltar (Cardona et al., 2005; Revelles et al., 2007).

The circulation of surface water in the Algerian basin is ruled by the Algerian current, a strong eastward coastal current that may reach a velocity of about 0.80 m s^{-1} at the surface (Millot, 1999; Obaton et al., 2000). Satellite tracking of immature loggerhead sea turtles (SCL range: 37.1–61.1 cm) in the Algerian basin has shown an extremely limited use of the Alboran Sea because most turtles approaching northern Africa are swept eastward by the Algerian current (Cardona et al., 2005; Revelles et al., 2007). Furthermore, the swimming experiment reported here indicates that only turtles larger than approximately 60.2 cm SCL should be able to swim against the Algerian current.

Whatever the reason Atlantic loggerhead sea turtles remain on average, eight years in the Mediterranean before returning to the Atlantic Ocean, they are exposed for a long period to the fisheries that operate in the Mediterranean, a significant cause of mortality (Margaitoulis et al., 2003). Besides, the catch per unit of effort is much higher in the western Mediterranean (Camiñas et al., 2006) than in the western north Atlantic Ocean

(Witzell and Cramer, 1995). Unfortunately, the actual number of turtles killed annually due to incidental catch is unknown and the assessment of the relevance of that source of mortality to the Atlantic stock is unfeasible until the actual number of Atlantic turtles inhabiting the western Mediterranean and the mortality rate caused by the long-line fishery are properly assessed.

A final point that deserves discussion is the presence of Mediterranean turtles in the eastern Atlantic, as demonstrated by microsatellite individual assignment. Previous mixed stock analysis on the basis of mitochondrial markers have suggested that turtles of this origin may be found as far as the Azores and Madeira (Carreras et al., 2006a), but hard evidence in the form of endemic Mediterranean markers is missing. This study demonstrates that Mediterranean turtles actually reach the Atlantic and hence that occurrence throughout the Atlantic is possible. Clearly, further research is needed to assess the relevance of this phenomenon.

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