RESEARCH ARTICLE

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Western Mediterranean immature loggerhead turtles: habitat use in spring and summer assessed through satellite tracking and aerial surveys

Abstract An aerial survey was conducted in early spring 2002 over the continental shelf of the Balearic Archipelago to study the distribution of neritic loggerhead turtles. Furthermore, five juvenile loggerhead turtles [straight carapace length (SCL) range 37.1–48.7 cm], were instrumented with transmitters and monitored during 2003 by satellite tracking to study habitat use over a broader geographical range. The distribution of the turtles over the continental shelf matched habitat availability, as defined by depth. However, those tracked by satellite spent most of the time in the oceanic waters of the Algerian basin and generally avoided continental shelf areas. In these turtles, average speed of travel and mean cosine of turning angle did not significantly differ between habitats, indicating that avoidance of shelf areas is not due to active habitat selection. On average, tracked turtles spent $35.1 \pm 19.7\%$ of the time at the surface, although surface time was much greater in the turtle with the shortest carapace length, suggesting that this individual had limited swimming capacity. We conclude that the transition between passive drifting and active habitat selection occurs at an SCL of about 40 cm. The turtles followed tracks that matched prevailing currents, but on some occasions they also swam upstream. Hence, the distribution of late juvenile loggerhead turtles in the southern and central western Mediterranean may reflect a combination of passive drifting and active habitat selection.

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Introduction

The lifecycle of sea turtles is fundamentally influenced by marine currents at all ontogenic stages (Luschi et al. 2003a). The loggerhead turtle *Caretta caretta* is widely distributed in the subtropical regions of all oceans (Pritchard 1997). Juveniles have an oceanic distribution but move to neritic habitats before sexual maturation, whereas adults migrate periodically between neritic foraging sites and rookeries (Bolten 2003). The western Mediterranean is an important feeding ground for juvenile loggerhead turtles from rookeries located in two areas: the eastern Mediterranean and the north-western Atlantic (Laurent et al. 1998). Although population size in the western Mediterranean is unknown, a recent survey calculated that 29,000 loggerhead turtles were caught accidentally by fishing operations in 2000 (Camiñas and Valeiras 2003). This figure indicates that interaction with fisheries is a major threat for the species in this area (Carreras et al. 2004). Detailed information about habitat use by the loggerhead turtles subject to this catch is urgently required to regulate fisheries and to reduce their impact on this species (Polovina et al. 2000, 2002).

The distribution of hatchlings and early juveniles is considered the consequence of passive drifting along prevailing currents (Milsom 1975; Davenport and Clough 1986; Hays and Marsh 1997; Witherington 2002), although active swimming has also been recorded (Bolten 2003). Adults, on the other hand, are vigorous swimmers and their distribution reflects active habitat selection (Sakamoto et al. 1997; Godley et al. 2003; Luschi et al. 2003b). The transition between the juvenile oceanic stage, where passive drifting prevails, and the immature-adult neritic stage, where active swimming

dominates, occurs when individuals reach a straight carapace length (SCL) of 40–60 cm (Bolten 2003). Specimens in this size range are competent swimmers, can travel against weak currents (Wyneken 1997; Dellinguer and Freitas 1999; Polovina et al. 2000), and may exhibit strong homing behaviour (Renaud and Carpenter 1994; Avens et al. 2003).

Specimens in the western Mediterranean are within this size range (Mayol et al. 1988) and hence might be in a transitional stage between passive drifting and active habitat selection. Unfortunately, current information about habitat use by juvenile and immature loggerhead turtles in the western Mediterranean is scarce and based only on the incidental catch of long-liners (Camiñas and de la Serna 1995; Camiñas and Valeiras 2003). As the fishing fleet does not target turtles, the fleet is not sampling all the habitat types that might be exploited by turtles and hence these data are strongly biased. Furthermore, turtles are more vulnerable to long-lines targeting small tuna species than to those targeting swordfish and larger tuna species (Camiñas et al. 2003) The aims of this article are (1) to describe the patterns of habitat use by loggerhead turtles in the western Mediterranean and (2) to investigate whether turtles use habitat types in agreement with availability (passive habitat selection) or concentrate in some habitat types (active habitat selection).

Materials and methods

Aerial surveys

An aerial survey was conducted off the Balearic Archipelago from 7 to 12 March 2002. The transect followed a systematic saw-tooth pattern, with a maximal perpendicular distance to the coastline of 20 nautical miles (36 km), thereby limiting the survey to the continental shelf (depth < 200 m) (Fig. 1).

The survey was carried out by two observers from a high-wing aircraft (Cessna 172) that allowed side viewing. Survey altitude was maintained at 500 feet, and transects were flown at a groundspeed ranging between 140 and 156 km h^{-1}. Six days were needed to survey the considered area, because bad weather is thought to reduce possible sightings and thus surveys were conducted only in Beaufort (wind scale) < 3. Each area was surveyed only once.

Once a turtle was observed, the location of the plane (obtained from a global position system, GPS) and the vertical angle of the sighting line (obtained from an inclinometre) were recorded. This angle was then used to calculate the perpendicular distance from the turtle to the survey transect. Turtles located more than 200 m beyond the survey track were not considered. Sightability is invariant when the probability of seeing a turtle (or any other object) does not change with distance. In aerial surveys, sightability is thought to decrease for objects located 200 m or more away (Marsh and Sinclair
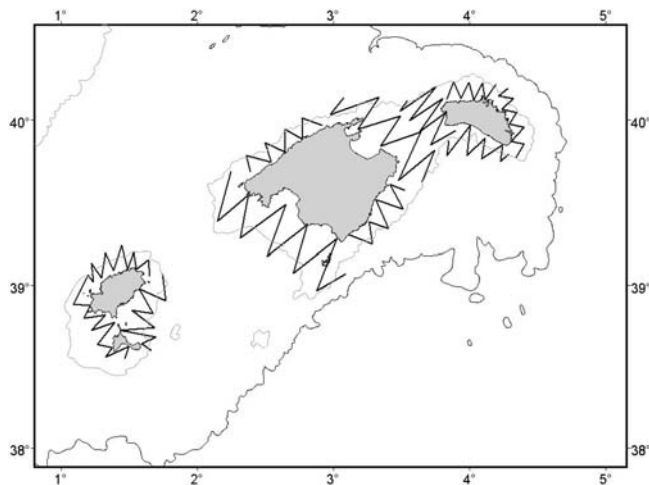
Fig. 1 Line transects for the aerial surveys conducted in March 2002 over the continental shelf of the Balearic Archipelago. The *light grey contour* refers to the 200-m isobath and the *black contour* to the 1,400 isobath

1989; Marsh and Saalfeld 1990; Preen et al. 1997). The aircraft did not have a glass floor; consequently, a band from 0 to 20° was missing on each side, thus reducing the survey strip to 145 m at each side of the plane. The surface covered by the survey was calculated as the distance flown multiplied by twice the survey strip. An ArcView 3.1 geographic information system (GIS) was also used to assess the depth of the water column beneath the turtle at each position.

Satellite tracking

Telonics ST-18 satellite transmitters (referred to as tags) were attached to five juvenile loggerhead turtles collected in April 2003 off the island of Formentera (Balearic Archipelago, western Mediterranean). These instrumented individuals were located while basking over the continental shelf in areas shallower than 200 m. They were then caught by a diver and transferred to land to attach the tag. Average SCL was 41.36 cm (range 37.1–48.7 cm), which is slightly shorter than the average for the turtles by-caught in the area by long-liner (50.21 cm SCL; Mayol et al. 1988). In addition to location, the transmitters provided information on surfacing behaviour as they were equipped with a counter that activated when the top of the tag was exposed to the air. The tags weighed 275 g (< 3% of the turtle's approximate weight) and measured 14×4.8×2.3 cm. Tagging procedures were as described by Balazs et al. (1996). After tagging, turtles were placed in 400-l fibreglass containers with seawater for at least 24 h to ensure that attachment was correct. Animals were released at the same site where they had been caught, which was determined using GPS.

Tag duty cycles (hours on/off) were 8/24. Position data were received and processed by Service Argos

(Argos 2000). Argos assigns a quality index (location class, or LC) to each location. The estimated accuracy in latitude and longitude was < 150 m for LC 3, between 150 and 350 m for LC 2, between 350 and 1,000 m for LC 1, and > 1,000 m for LC 0. Argos does not provide an accuracy estimate for LC A, LC B, and LC Z but Hays et al. (2001) demonstrated that LC A is as accurate as LC 1, and more reliable than LC 0 or LC B. The accuracy of the five units used in the present study was assessed by comparing the positional data supplied by them before being deployed with those supplied by a GPS. Table 1 gives details on the performance of the transmitters used, the total number of locations of each of the Argos classes, and the number of locations monitored (see below).

Correlated random walks provide the conceptual framework for quantifying the movement of individual organisms and for relating movement patterns to the distribution of the organism (Turchin 1991). Although turtles may have moved continuously, satellite tracking supplied only a limited number of fixes and the actual paths were reconstructed by connecting the successive fixes with straight lines. Positional data were screened to select the "high-quality" fix (positional accuracy less than 1 km, that is, LC 3–1 and A and velocity lower than 5 km h^{-1}; Luschi et al. 1998; Argos 2000; Hays et al. 2001) within each 32-h duty cycle, although an occasional fix with a lower accuracy was used when there were multiple days without "high-quality" (LC 3–1 or A) data and the velocity to and from the low-accuracy fix was < 5 km h^{-1} (Luschi et al. 1998). Inland locations were never used. Once data had been screened, each path was reconstructed using GIS to recreate the straight path between successive positions. The velocity, direction, and turning angle, that is, direction of the current heading measured relative to the direction of the previous heading, were calculated for each movement.

GIS was also used to assess the depth of the water column at each turtle position, from a bathymetric dataset with a resolution of 1×1′ (latitude x longitude; Smith and Sandwell 1997). A depth scale, coarser than that used to analyse the aerial surveys, was used to classify fixes by bathymetric domain: neritic when shallower than 200 m, on the slope when between 200 and 1,400 m, and oceanic when deeper than 1,400 m. The maximum diving depth reported in loggerhead turtles is 233 m (Lutcavage and Lutz 1997); therefore, individuals

may reach the sea floor only while on the continental shelf (neritic habitat). The continental slope and the open oceanic waters were considered as distinct habitats because they are characterised by water masses of water different in productivity, origin, and stability (Pinot et al. 1994; Estrada 1996). GIS was also used to calculate areal extent of the surface of each bathymetric domain in the two regions exploited by the tagged turtles: the Algerian basin and the Balearic sea.

Time data were classified into three categories for analysis: morning (from sunrise to noon), afternoon (from noon to sunset), and night (from sunset to sunrise). For the whole study period, sunrise ranged from 05:22 to 04:34 GMT and sunset from 18:11 to 19:06, in agreement with the data supplied by the Balearic Island Meteorological Station (Carreras, personal communication). Each fix was classified as morning, afternoon, or night and a track may expand over these three categories.

Statistics

Two independent analyses of habitat use were performed. The continental shelf around the Balearic Archipelago, covered by the aerial surveys, was divided into three bathymetric domains in agreement with water depth: < 50 m, 50–100 m, > 100–200 m. The region exploited by the satellite-tracked turtles was divided into three habitat types: continental shelf (< 200 m), continental slope (200–1,400 m), and oceanic waters (> 1,400 m). For both analyses, the chi-square test (Zar 1984) was used to check whether habitat use matched habitat availability. Habitat availability was quantified as percent areal extent using GIS. Habitat use was computed as the frequency of sightings/fixes from each habitat type.

When the chi-square test detected that habitat use did not match availability, Ivlev's electivity index (Ivlev 1961, quoted by Crowder 1990) was calculated to identify the habitat type in which turtle occurrence was higher or lower than expected. Ivlev's index (*I*) was calculated for each bathymetric domain as

$$I = (p_o - p_e)/(p_o + p_e)$$

where p_o is the observed percentage of fixes recorded in a given habitat and p_e is the proportional cover of that

Table 1 Tracking performance of the five tagged loggerhead turtles

Specimen number	Fixes	Proportion of messages by location class (%)						Tracking period	
		3	2	1	0	A	B	Months	Days
103	248	6.0	21.0	23.0	5.7	16.5	23.8	April–June	62
203	613	4.9	13.1	15.7	10.0	22.0	34.4	April–September	159
303	310	9.4	15.2	18.4	8.1	24.5	24.5	April–July	75
403	309	7.4	12.3	24.0	11.7	17.5	27.2	April–July	80
503	135	9.0	17.0	15.0	8.1	20.0	29.6	April–June	48
All	1,615	6.8	14.9	18.9	9.7	20.6	29.1	April–September	424

habitat. Confidence intervals were calculated following Strauss (1979) as

$$E_c = \left(2 - \left(\frac{2p_e}{(p_e + p_o)}\right)\right) \times \left[1 \pm 1.96\sqrt{\left[2n_o * p_o * (1 - p_o) * (p_o + p_e)^2 + p_o * (1 - p_o) * n_e + p_e * \frac{(1 - p_e)}{n_o n_e (p_o + p_e)^2}\right]}\right] - 1$$

where E_c is the limit of the confidence interval, n_o is the number of fixes, and n_e is the total number of depth points used to generate the bathymetric chart in the GIS (Smith and Sandwell 1997).

Uniformity of bearing angles and turning angles for each turtle was checked with the Rayleigh test (Zar 1984) and the mean angles were computed in agreement with Zar (1984). Spearman rank correlation coefficient (Zar 1984) was calculated to test whether the absolute value of turning angle and the movement rate were correlated. Two-way analysis of variance (ANOVA; Zar 1984) was used to assess whether individual turtles (factor 1) and bathymetric domain (factor 2) influenced speed of travel and cosine of turning angle. As the data were not normally distributed, the Kruskal–Wallis test (Zar 1984) was used to assess differences in the time spent at the surface in the distinct day intervals: morning, afternoon, and night.

Results

The aerial survey covered 477.01 km^2 or 6.14% of the total surface of the continental shelf of the Balearic archipelago (7,773.7 km^2). Most turtles were observed in areas of intermediate depth (Table 2), but this was also the most abundant habitat type and hence habitat use matched availability ($\chi^2 = 3.064$; $df = 2$; $P = 0.081$).

The five turtles with satellite tags were released from 8 to 26 April 2003 (Table 1). The tracking period lasted from 48 to 159 days, with an average of 84.8 ± 38.7 days. Good-quality fixes were obtained from all the animals (Table 1), although roughly half the duty cycles failed to produce good-quality fixes (52.2% for turtle no. 103, 50.0% for turtle no. 203, 56.3% for turtle no. 303, 39.4% for turtle no. 403, and 51.64% for turtle no. 503). Thereby the routes followed by the turtles were reconstructed using only the best fix for each duty cycle that fulfilled the requirements stated above (Table 2 and

Fig. 2). Turtles spent most of the time in the oceanic waters of the Algerian basin, and only one (203) remained for a significant period in the Balearic sea after release (Fig. 2).

The bearing angles of turtles 103, 203, and 503 did not distribute evenly, but concentrated in the second quadrant (Table 3); that is, the general direction of movement was towards the south-east. However, the routes followed varied greatly. Turtle 103 swam eastwards immediately after release, then turned southwards, but resumed the eastwards movement when approaching the shores of northern Africa. After a few days of swimming parallel to the coastline, it moved offshore and turned westwards. The route of turtle 203 was more complex. After being released, it moved towards the Iberian Peninsula and then southwards, but after a few days turned northwards and swam along the western slope of the Balearic Archipelago. When it reached the north of Mallorca, it turned westwards and then southwards, returning to the release point; then, the route became similar to that of turtle 103, although more convoluted. The route of turtle 403 was similar to the second half of that followed by turtle 203, that is, southwards to the shores of northern Africa and then eastwards close to the coastline, until it moved offshore and described a small anticyclonic gyre; however, as this turtle moved several times northwards and southwards before reaching the shores of northern Africa, the distribution of the bearing angles did not differ from that expected by chance (Table 3). For the first days, the route of turtle 503 resembled that of 203, that is, it approached the Iberian Peninsula and then swam southwards; however, it showed half a cyclonic gyre, with a radius of 147 km. Finally, the route followed by turtle 303 was similar to that of 503, although the gyre was almost completed and hence the bearing angles distributed randomly (Table 3); the diameter of the gyre was 195 km.

Turning angles were not randomly distributed for any of the five turtles tracked (Table 3). Turtles 103 and 303 turned slightly to the left more often that expected, whereas the opposite was true for 203, 403, and 503. The absolute values of the turning angles and the speed of travel were negatively correlated for turtles 303 (Spearman $\rho = -0.298$; $P = 0.034$; $n = 51$), 505 (Spearman $\rho = -0.460$; $P = 0.018$; $n = 26$), 103 (Spearman $\rho = -0.378$;

Table 2 Habitat availability on the section of the continental shelf of the Balearic Archipelago covered by the aerial survey and loggerhead turtles distribution ($\chi^2 = 3.064$; $df = 2$; $P = 0.081$)

Habitat type	Searched area (km^2)	Observed turtles
Depth < 50 m	73.09	6
Depth from 50 to 100 m	202.60	13
Depth from >100 to 200 m	150.92	3

Fig. 2 Turtle tracks (panels *103* to *503*) and prevailing currents in agreement with Millot (1987) (*bottom-right panel*). The *light grey contour* refers to the 200-m isobath and the *black contour* to the 1,400 isobath

$P = 0.015$; $n = 41$), and 203 (Spearman $\rho = -0.222$; $p = 0.021$; $n = 108$), but not for turtle 403 (Spearman $\rho = -0.080$; $P = 0.570$; $n = 53$).

None of the five turtles used the three considered bathymetric domains in accordance with their availability (Table 4). Four strongly avoided the continental shelf (Table 4) and the electivity values for slope and oceanic waters ranged from slightly positive to slightly negative. However, neither individual turtle nor bathymetric domain had significant effects on average speed of travel (two-way ANOVA; $F = 1.481$; $df = 12$; $P = 0.131$; Table 5) or mean cosine of turning angle (two-way ANOVA; $F = 0.330$; $df = 12$; $P = 0.0983$; Table 5).
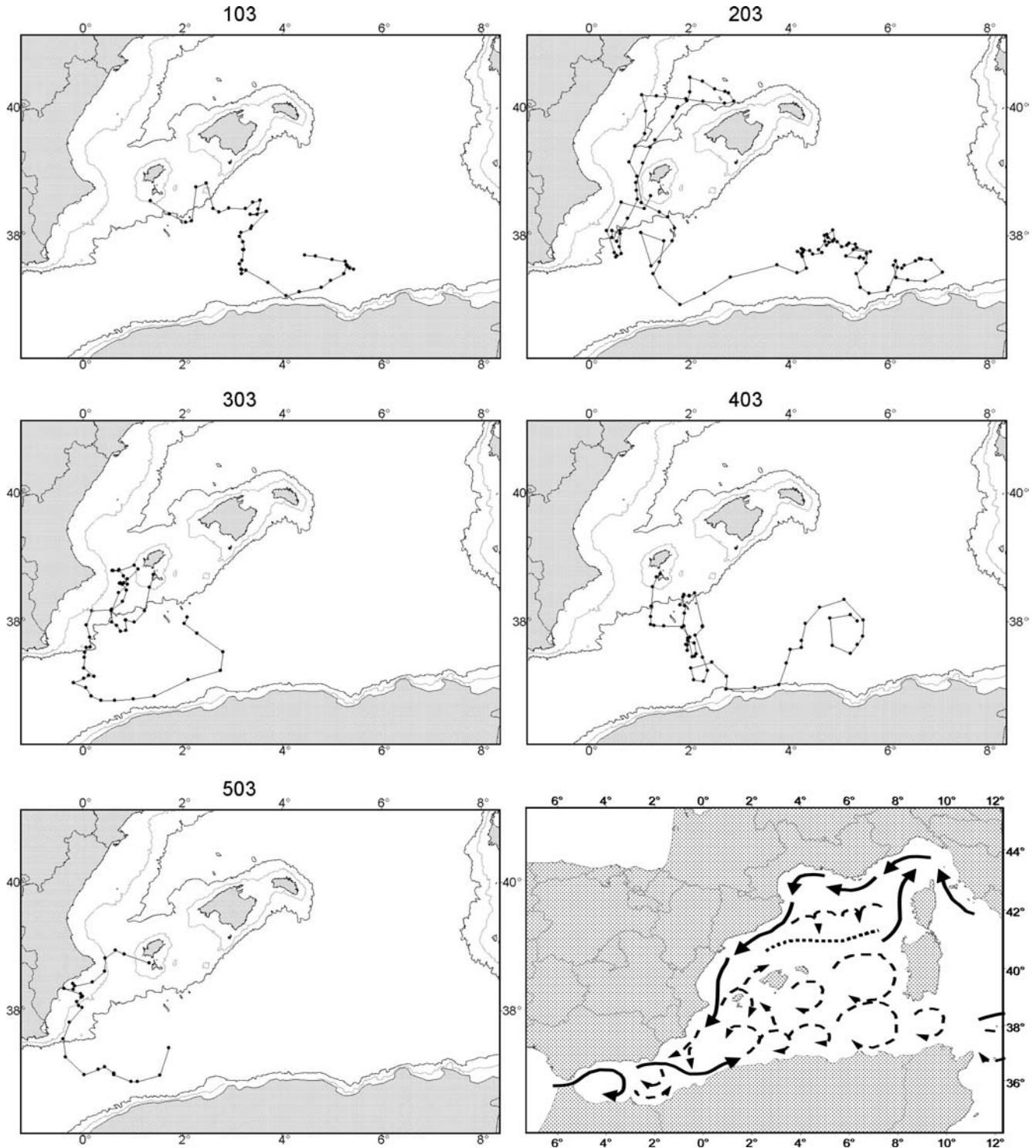
Table 3 Average bearing and turning angles of the five loggerhead turtles tracked

Specimen	Number of moves	Average bearing of move	Direction	Rayleigh's z	Average turning angle	Rayleigh's z
103	42	146.88	SE	4.529*	353.20	3.908*
203	109	97.26	SE	4.115*	14.93	20.86***
303	50	205.756	SW	1.970	355.988	17.221***
403	54	104.14	SE	1.938	10.35	17.59***
503	27	163.127	SE	4.087*	4.832	5.285**

* $P < 0.05$; ** $P < 0.01$; ***$P < 0.001$

Table 4 Habitat use by the five tracked loggerhead turtles and Ivlev's electivity. Habitat availability within the regions visited by the turtles (Fig. 1) was as follows: oceanic 307,574.4 km², slope 94,972.1 km², and continental shelf 66,741.2 km²

Turtle	Chi-square statistic	Habitat type	Number of fixes	Ivlev's electivity	95% CI
103	7.01***	Oceanic	38	0.15	0.23, 0.06
		Slope	4	−0.37	−0.18, −0.56
		Shelf	1	−0.72	−0.64, −0.80
203	12.13***	Oceanic	86	0.09	0.16, 0.01
		Slope	22	−0.01	0.18, −0.19
		Shelf	2	−0.77	−0.74, −0.81
303	6.72***	Oceanic	28	−0.11	0.0006, −0.22
		Slope	22	0.34	0.64, 0.05
		Shelf	3	−0.43	−0.25, −0.61
403	4.6*	Oceanic	44	0.10	0.19, 0.01
		Slope	9	−0.11	0.14, −0.35
		Shelf	2	−0.59	−0.48, −0.71
503	6.62***	Oceanic	10	−0.29	−0.17, −0.42
		Slope	7	0.11	0.50, −0.29
		Shelf	11	0.47	0.97, −0.03

* $P < 0.05$; ** $P < 0.01$; ***$P < 0.001$; $df = 2$ for all the turtles

Table 5 Average speed of travel and mean cosine of turning angle (ψ) of the five tracked loggerhead turtles in the three habitat types available

Turtle	Habitat type	Speed of travel (m s^{-1})	ψ
103	Oceanic	0.47	0.995
	Slope	0.79	0.589
	Shelf	1.08	−
203	Oceanic	0.55	0.333
	Slope	0.82	0.779
	Shelf	0.78	0.586
303	Oceanic	0.67	0.567
	Slope	0.44	0.543
	Shelf	0.39	0.954
403	Oceanic	0.61	0.532
	Slope	0.62	0.712
	Shelf	0.33	0.931
503	Oceanic	0.77	0.666
	Slope	0.74	0.597
	Shelf	0.38	0.292

The tracked animals spent on average $35.1 \pm 19.7\%$ of their time at the surface, with no significant differences between day periods (morning: $31.5 \pm 24.6\%$; afternoon: $39.2 \pm 17.3\%$; night: $34.9 \pm 20.4\%$; Kruskal–Wallis test; Hstat $= 1.289$; $df = 2$; $P = 0.525$). However, turtles 103 and 503 spent 98.8 and 93.0% of their last duty cycle on the surface before the connection with Argos was lost. This behaviour was not exhibited by any of the five turtles in the previous duty cycles. Indeed, the other three turtles spent 18.6% (203), 7.3% (303), and 3.9% (403) of the last duty cycle before the loss of connection with Argos on the surface.

Discussion and conclusions

In an animal that swims, drag is higher at the water surface than at depths deeper than three times the animal's greatest body diameter (Berta and Sumich 1999) and hence positive buoyancy is thought to reduce the capacity for active swimming. Small juvenile loggerhead turtles are positively buoyant (Milsom 1975), and in captivity they spend most of the time at the water surface (Davenport and Clough 1986). As they grow, they gain control over buoyancy (Minamikawa et al. 2000;

Hochscheid et al. 2003) and the time spent submerged increases, both in captivity (Bentivegna et al. 2003) and in the wild (Renaud and Carpenter 1994; Dellinguer and Freitas 1999; Minamikawa et al. 2000; Luschi et al. 2003b; Godley et al. 2003). The turtles tracked by satellite here studied spent most of the time underwater, which suggests that they had already achieved some control over buoyancy and a flipper stroke strong enough to descend to a depth where they reached neutral buoyancy. The only exception was the smallest specimen (turtle 103; SCL = 37.1 cm), which spent 67% of the time at the surface. This observation indicates that this individual was positively buoyant and therefore had limited diving capacity, which increases drag while swimming at the surface and hence limits the capability for swimming against prevailing currents. This supports the hypothesis that the transition between passive drifting and active habitat selection takes place at an SCL of about 40 cm. Thus, turtles with a greater SCL can migrate towards neritic foraging grounds.

Immature loggerhead turtles that inhabit cool-temperate areas in the western Atlantic avoid zones with low temperatures (Coles and Musick 2000) and usually migrate seasonally (Musick and Limpus 1997) to avoid cold stunning at temperatures lower than 12°C (Lutz et al. 1989). A similar latitudinal migration has also been reported along the Italian coast (Bentivegna and Paglialonga 1998; Bentivegna 2002), although winter water temperature is always higher than 14°C (Bentivegna et al. 2003). Around the Balearic Archipelago, immature loggerhead turtles occur year round, but fishermen claim that turtle sightings and by-catch increase in summer (Carreras et al. 2004). On the basis of by-catch data from long-liners, Camiñas and de la Serna (1995) concluded that the population off the Balearic Archipelago mostly moves southwards in autumn, returning to the islands in spring. A similar seasonal pattern has also been reported in the neighbouring Iberian Peninsula on the basis of stranding occurrence (Tomas et al. 2003).

The movement of the five tagged turtles released in April 2003 south of the Balearic Archipelago did not confirm a northwards spring migration, as none exhibited a consistent northwards movement. On the contrary, although they had been released at the beginning of the warm season and were therefore about to start their theoretical northwards migration, three of these turtles exhibited a statistically significant preference to move south-eastwards, and they ended up far away from the archipelago. These results are consistent with the absence of seasonality observed in turtle abundance off the nearby Columbretes islands (Gómez de Segura et al. 2003) and indicate that the increase in strandings, sightings, and by-catch reported during the summer may be the result of the seasonal increase in mortality caused by drifting long-lines and lobster trammel nets, fishing gear used only during the summer (Carreras et al. 2004).

Although each of the five tagged turtles followed a different route, their movements had two common features: (1) the two animals that approached the Iberian Peninsula afterwards headed south and turned counterclockwise, and (2) all five animals that approached the shore of northern Africa moved eastwards until they were deflected offshore. The two individuals tracked for the largest duration seemed to be entrained in an eddy and turned clockwise. According to Millot (1987), the area used by the tagged turtles is dominated by two major permanent surface currents (Fig. 1). The Algerian jet flows eastwards along the coast of northern Africa, although much of the movement is highly convoluted because of a large number of anticyclonic gyres located east of the latitude 0°E. Some of these gyres leave the main current and reach the southern Balearic Archipelago (López-Jurado 1990). The Catalan current flows southwards parallel to the Iberian Peninsula, although a branch is deflected at Cape la Nao and then flows along the west coast of Ibiza and Majorca. A second branching is produced at Cape Palos, where the deflected current moves southwards to meet the Algerian jet.

Comparison of turtle tracks with the routes followed by the prevailing currents indicates that the animals turning counterclockwise in the western Algerian basin entered the Catalan current, followed the branch deflected at Cape Palos, joined the Algerian jet, and were finally deflected. The eastwards movement of animals that approached the African shore, which is usually followed by deflection and often clockwise turning, indicates that the turtles may have entered the Algerian jet. Finally, the only turtle that entered the Balearic sea moved northwards along the west coast of the archipelago and probably swam along the branch of the Catalan current, which deflects at Cape la Nao. On the basis of our observations by satellite tracking, we conclude that the turtle movement is partially due to passive drifting, thus stressing the relevance of currents and associated frontal systems for understanding turtle distribution (Luschi et al. 2003a).

Our conclusion is supported by the absence of differences in the speed of travel and in the mean cosine of the turning angles between turtles when on the shelf, on the slope, or in the open ocean. If the lower than expected occurrence of turtles over the continental shelf was due to active habitat selection, the correlated random-walk theory predicts that both the speed of travel and the mean cosine of turning angles increase while animals are over the continental shelf (Turchin 1991). Although location inaccuracies by Argos may lead to erroneous measures of speed of travel and mean cosine, the screening of the data and the long time between two adjoining fixes (roughly 72 h) had probably improved the quality of the measurement. Furthermore, habitat use by turtles on the continental shelf matched availability, again supporting the notion of the absence of active habitat selection. Although the speed of the plane prevented the determination of turtle body size, stranding data (University of Barcelona, unpublished information) and incidental catch data (Mayol et al. 1988) indicate that most of the turtles in the area were also juvenile or immature.

However, passive drifting alone is not enough to explain the movements of the five tagged turtles, as some of them moved westwards along the shore of northern Africa and southwards along the west shore of the Balearic Archipelago, that is, against prevailing currents. In both situations, the turtles were far offshore. Since prevailing currents flow over the continental slope (Millot 1987; Salat 1995), turtles were not in the main stream but at the edges, where water velocity is thought to be not as high. A similar pattern has been reported in the North Pacific (Polovina et al. 2000), where turtles swim upstream along the edge of prevailing currents, a strategy that increases the rate of seston intercept. Similar swimming against prevailing currents in the Northern Atlantic has also been reported (Dellinguer and Freitas 1999). Indeed, previous research in other oceans suggested that the movements of juvenile loggerhead turtles with an SCL of about 40–50 cm may be tightly linked to frontal systems, along the continental slope (Witzel 1999) or in the open ocean (Polovina et al. 2000). The existence of a weak but significant negative correlation between the movement rate and the absolute value of the turning angle for four of the five turtles shows that they combined two different swimming strategies, that is, fast and direct swimming across unsuitable habitats and slow and convoluted swimming at suitable patches. A similar pattern has been reported for albatrosses that concentrated at hydrographic fronts and in the vicinity of productive continental shelfs (Hyrenbrach et al. 2002).

Although the turtles studied here used the continental slope proportionally to its availability and for most of the time remained far away from the permanent frontal systems (dashed lines in Fig. 1) that occur between the Balearic Archipelago and the Iberian Peninsula (Pinot et al. 1994; Salat 1995), they occupied the area of strong meso-scale activity associated with the eddies generated by the Algerian current, which are frontal systems of enhanced productivity (Estrada 1996). This association with a turbulent system also explains why the turtles tracked in the Mediterranean exhibited more convoluted routes and frequent changes in bearing than those tracked in the North Pacific (Polovina et al. 2000) and in the North Atlantic (Dellinguer and Freitas 1999). Further research combining satellite tracking and simultaneous measurement of geostrophic currents will clarify how turtles exploit hydrographic structures (Luschi et al. 2003a).

The area exploited by the turtles tracked in this study overlaps with the fishing grounds used by the Spanish drifting long-line fleet (Camiñas and de la Serna 1995), thereby leading to high by-catch rates (Mayol et al. 1988; Aguilar et al. 1995; Camiñas and de la Serna 1995). Interestingly, the transmitters of turtles 103 and 503 were exposed continuously to the air throughout the final active period of the duty cycle (8 h). This was not observed in any of the other turtles. Hays et al. (2003) interpreted this type of behaviour as evidence of capture, which is a plausible explanation. Although we cannot assess whether the animals were slaughtered or released again once the transmitters were removed, it is likely that these turtles interacted with fisheries. The tracking of more instrumented turtles will help estimate the habitats of loggerhead sea turtles in the Mediterranean and their probability of being taken in fisheries.

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