

Long-term satellite telemetry of the movements and habitat utilisation by green turtles in the Mediterranean

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There is a relative paucity of data regarding the at-sea distribution and behaviour of marine turtles. This is especially true for the critically endangered green turtle *Chelonia mydas* population in the Mediterranean. Six adult female green turtles were equipped with satellite transmitters and tracked for periods of between 28 and 293 d following their final nesting of the season in northern Cyprus. Data elucidated hitherto unknown migratory pathways and highlighted the importance of North African coastal waters as feeding habitat for adults of this species. For three individuals, instruments transmitted detailed information on dive depth, dive duration and water temperature which afforded novel insights into behaviour during different stages of migration, feeding in the foraging grounds and most remarkably, during a period of midwinter diapause when water temperatures were generally below 25°C. Turtles showed fidelity to specific shallow inshore feeding areas and moved offshore to deeper wintering sites.

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For many animals, long-distance movements are an important component of their life history. One such group is marine turtles that often migrate long distances between feeding and nesting areas (Miller 1997). The fundamental reason for these migrations is thought to be that nesting beaches typically lie in areas where food availability is sub-optimal or absent and hence at the end of the nesting season it is advantageous or essential for turtles to swim to distant foraging zones. Although preliminary work using flipper tagging established the likely endpoints of these post-nesting migrations (Balazs 1976, Pritchard 1976, Meylan 1982, Carr 1984), the advent of satellite tracking technology has started to reveal some aspects of the behaviour of turtles during these long-distance movements. A general dichotomy has emerged with animals undertaking coastal and open-ocean migration. For example, popu-

lations that nest on mainland beaches, such as loggerhead turtles *Caretta caretta* in South Africa, may simply migrate along the coast to their foraging grounds (Papi et al. 1997). On the other hand, populations nesting on islands are forced to conduct open-ocean crossings, such as green turtles *Chelonia mydas* migrating from Ascension Island to Brazil (Luschi et al. 1998) or those which move among Pacific Oceanic Islands (Balazs 1994, Balazs et al. 1994, Balazs and Ellis 2000). Interestingly, open-ocean crossings are accomplished with turtles following very straight-line courses (Papi and Luschi 1996, Morreale et al. 1996, Nicholls et al. 2000). Certainly for green turtles, which are benthic herbivores (Bjørndal 1997), there is very little food in the open-ocean and hence these straight-line tracks are presumably advantageous by facilitating early arrival in neritic environments where foraging

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may be undertaken, allowing individuals to refuel before continuing their journey (Spring 1990, Cheng 2000).

However, as satellite tracks often end before the final destination is reached (Luschi et al. 1998), or fixes from neritic habitats where turtles are in residence can be infrequent and of low accuracy, our knowledge of the behaviour after completing the open-ocean phase of the migrations is relatively scant. However, there is evidence that once they have reached their foraging grounds, green turtles may maintain distinct home ranges, at least over the short periods of time during which observations have been maintained (Limpus et al. 1992, Whiting and Miller 1998). Indeed some authors have suggested that individuals may show fidelity to these sites between multiple successive breeding seasons (Limpus et al. 1992).

In addition to identifying the routes that individuals follow, satellite transmitters have also started to reveal the diving behaviour of migrating turtles. For green turtles during migration most dives are short (3 or 4 min), consistent with near surface travelling, but occasionally longer dives (up to 30 min or more) have been recorded which suggests that turtles may periodically rest beneath the surface (Hays et al. 1999). However, due to the premature failure of transmitters, diving information during coastal migration and from the foraging grounds is again sparse. It might be expected that if an open-ocean crossing is followed by coastal migration, green turtles would be able to start feeding, at least to some extent, once in shallow waters, leading to longer, benthic dives and a reduction in speed before the final destination is reached.

As well as leading to different food availability, long-distance migrations may also effect the thermal biology of turtles. All Cheloniid marine turtles are ectothermic, being unable to raise their body temperature more than a degree or so above the water temperature (Sato et al. 1998) and a tight coupling between water temperature and turtle behaviour is expected and has been confirmed by some empirical evidence. For example, the length of the internesting interval (i.e. the period between successive clutches during the nesting season) increases in colder water, presumably because in colder waters turtles have a lower metabolic rate (Sato et al. 1998). This thermal coupling with green turtle tissue metabolism has been demonstrated *in vitro* (Penick et al. 1996). Similarly, during winter we might predict a decrease in metabolic rate and, indeed, observations of turtles resting passively on the sea bed (Felger et al. 1976) or being dredged from benthic mud (Carr et al. 1980–81) have been used to suggest that at some sites, loggerhead and green turtles may enter a state of midwinter diapause or brumation. Alternatively, a second strategy is for animals to migrate to warmer waters to avoid cold winter temperatures, and, for example, this has also been recorded for loggerhead

turtles on the eastern seaboard of the United States of America (Musick and Limpus 1997).

To help fill in some of the many gaps in our knowledge of the biology of adult turtles once they have left nesting areas, in this study we document the movements and diving behaviour of post-nesting green turtles in the Mediterranean over periods of up to 10 months. This very long duration of successful satellite telemetry allowed us to address the following fundamental questions: 1) do turtles migrate directly to their final foraging destinations or do they include a section of coastal migration? 2) does the speed of travel during different segments of the migration vary in line with a prediction of open-ocean fasting versus coastal feeding? 3) do turtles maintain distinct home-ranges on their foraging grounds? and 4) does the behaviour of turtles change during midwinter?

Methods

In late July and early August 1998 and 1999 we attached satellite transmitters to six female green turtles (1998: turtles A–C; 1999: turtles D–F) at Alagadi (35°33'N, 33°47'E; n = 5) and Esentepe (35°36'N, 33°69'E; n = 1) in northern Cyprus. The fixative used was a two part epoxy resin. Attachment procedure was undertaken while turtles were laying and covering the eggs. They were not restrained in any way and when they had completed the nesting process they were allowed to return to the sea.

Different models of transmitter and sites of attachment were used in the two years, both of which are routinely used in marine turtle research.

In 1998, we used relatively large tracking units (SDR-SSC3, Wildlife Computers Redmond, WA, USA). These measured 20.0 × 15.0 × 4.0 cm; weight 750 g (< 1% of bodyweight). These units were attached to the second central carapace scute and care was taken to ensure the attaching resin was carefully faired into a hydrodynamic shape in fitting with general contours of the carapace to help reduce any drag (Watson and Granger 1998). As well as providing location information, these units supplied dive and temperature data. Depth and temperature were measured by the transmitters every 10 s. For each dive the maximum depth and duration were recorded and assigned into a histogram bin. For maximum dive depth, upper limits of the histograms were 5, 10, 15, 20, 25, 30, 35, 40 and 45 m with a final bin for all dives with a maximum depth of > 45 m. For dive duration the upper limits of the bins were 5, 10, 15, 20, 25, 30, 45, 60 and 90 min with a final bin for all dives of duration > 90 min. Dives were logged when depth was > 2 m. Temperature data were recorded as the proportion of time spent at different temperature ranges with maxima of 4, 8, 12, 16, 20, 24,

Table 1. Performance of satellite transmitters. For each individual (A–F) the date of deployment, the duration of transmissions (d) and the number of locations of each ARGOS location class (LC) received. For more details regarding accuracy of location classes see Anon. (1996) and Hays et al. (2001).

Individual	Start	No. days	Location class						Total
			3	2	1	0	A	B	
A	1 Aug. 1998	289	18	19	33	26	103	213	412
B	30 Jul. 1998	221	12	32	32	30	115	194	415
C	28 Jul. 1998	293	30	50	44	39	156	267	586
D	26 Jul. 1999	169	6	3	18	10	41	53	131
E	20 Jul. 1999	28	1	5	14	7	27	62	116
F	20 Jul. 1999	241	1	6	15	13	23	35	93

28, 32 and 36°C with an upper bin of > 36°C. Data were integrated into 6-h periods beginning at 03:00, 09:00, 15:00 and 21:00 GMT and transmitted in histograms. Due to limited bandwidth, not all data could be transmitted during each uplink and histograms were stored in a buffer memory and overwritten when the capacity of the buffer was reached.

In 1999 we used smaller transmitters (ST-18 Telonics, Mesa, AZ, USA) which provided location information only. These measured 14.0 × 4.8 × 3.3 cm; weight 275 g (< 0.25% of bodyweight) and were attached to the horny plates on the dorsal aspect of the head following a previously described methodology (Luschi et al. 1998, Papi et al. 2000).

Turtles were located using the Argos system (Anon. 1996) and fixes were categorised into 6 classes (Table 1). Routes were reconstructed using fixes of location classes 1, 2, 3 and A after data presented by Argos (Anon. 1996) and recent work by the authors (Hays et al. 2001) has shown these to be the most reliable. The

distance between successive fixes was calculated using a great circle route equation. A straightness index of the open-ocean crossing was calculated as the ratio of the beeline distance and the cumulative sum of all segments of the journey (Butschelet 1981). Speed of travel for the different stages of the route to the foraging grounds was calculated assuming straight-line movements between successive fixes. For comparison with temperature data collected, long term records of sea surface temperature were obtained from the Comprehensive Ocean Atmosphere Data Set (COADS).

Results

Pattern of post-nesting movements

After nesting, all turtles migrated away from Cyprus at the end of the nesting season in a) 1998 (Fig. 1a, b). In 1998 (Fig. 1a), one individual (A) headed NW towards Turkey and along the Turkish

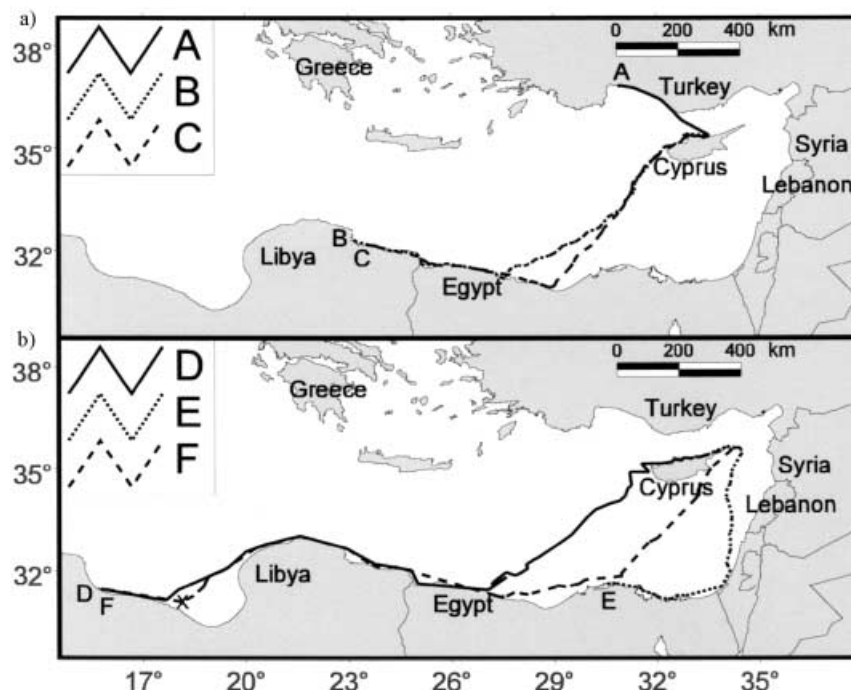


Fig. 1. The tracks of green turtles migrating away from Cyprus at the end of the nesting season in a) 1998 (n = 3; turtles A–C) and b) 1999 (n = 3; turtle D–F). For the tracks of individual F, the end of the initial route is denoted by x with the subsequent part of the line being that necessary to complete the route based upon fixes obtained after 21 d of no fixes.

Table 2. Summary statistics of movements to foraging areas. For each individual (A–F) summary statistics (duration (h), minimum distance (km) and resultant average speed (km h^{-1})) are given for each of the three stages of movement: through Cyprus coastal waters, across the open sea and during subsequent coastal travelling. Numbers in parentheses are the proportion of time and distance constituted by each stage. Routes used involve connection fixes of LC 3,2,1 and A. In addition, the total duration, distance and overall speed for travel is given as well as the minimum distance that the journey would have been should the open-ocean crossing have been direct from Cyprus to the endpoint. The resultant increase in distance (%) over the minimum feasible bee-line route as a result of the coastal phase is given.

Location		Individual					
		A	B	C	D	E	F
Cyprus	Duration (h)	37.0 (18.8)	95.0 (16.1)	82.9 (14.0)	59.1 (5.9)	91.0 (16.8)	95.7 (9.1)
	Distance (km)	21.8 (6.8)	141.1 (11.2)	154.0 (12.2)	149.5 (6.8)	120.8 (11.9)	181.9 (8.6)
	Speed (km h^{-1})	0.6	1.5	1.8	2.5	1.3	1.9
Open sea	Duration (h)	60.1 (30.6)	203.5 (34.4)	173.0 (29.3)	244.8 (24.5)	212.1 (39.1)	179.7 (17.1)
	Distance (km)	162.9 (50.5)	651.3 (51.5)	530.6 (42.2)	802.5 (36.5)	464.1 (45.8)	448.9 (21.1)
	Speed (km h^{-1})	2.7	3.2	3.1	3.3	2.2	2.5
	Straightness index	0.99	0.94	0.977384	0.75	0.89	0.97
Coastal	Duration (h)	99.5 (50.6)	292.6 (49.5)	334.3 (56.6)	694.0 (69.5)	239.7 (44.2)	776.2 (73.8)
	Distance (km)	137.9 (42.7)	471.5 (37.3)	572.9 (45.6)	1247.6 (56.7)	428.1 (42.3)	1494.7 (70.3)
	Speed (km h^{-1})	1.4	1.6	1.7	1.8	1.8	1.9
Overall	Duration (h)	196.6	591.1	590.2	997.9	542.8	1051.6
	Distance (km)	322.6	1263.9	1257.5	2199.6	1013.0	2125.5
	Speed (km h^{-1})	1.6	2.1	2.1	2.2	1.9	2.0
Minimum distance km		274.0	1035.6	1019.7	1704.0	692.0	1730.9
Distance (% increase)		17.7	22.0	23.3	29.1	46.4	22.8

coast before stopping in coastal waters. The other two individuals tracked in the same season (B and C; Fig. 1a) proceeded west, around the coastline of Cyprus before crossing the Mediterranean towards the coast of Egypt; they then moved along the North African coast before stopping in Libyan coastal waters. All three individuals tracked in this season were very clearly tracked for > 6 months in the coastal foraging grounds (Tables 1 and 2).

In 1999 (Fig. 1b), one individual (D) followed a route very similar to that of B and C but proceeded much further along the Libyan coastline. In contrast, the other two individuals left the nesting beaches in an easterly direction, rounding the Karpaz Peninsula of northern Cyprus. Individual E then swam south to enter the coastal waters of Israel, the Gaza Strip and then Egypt with individual F swimming into Egyptian coastal waters and along the North African coast to a location ca 16 km from the endpoint of individual D. The endpoint of the three turtles tracked in 1999 was not as clearly defined as those in the previous year, with fewer transmissions being received in the months following arrival at the foraging grounds. For the purpose of calculating speed of travel in turtle F, the endpoint of the coastal part of the journey was taken as the point where the final transmission before an extended break of 21 d. This is indicated on Fig. 1b.

The distance covered by the turtles ranged from 320 to 2200 km in periods ranging from 8 to 44 d (Table 2). The movements of all six individuals can be delineated into three distinct phases: 1) a period in the coastal

waters of Cyprus; 2) an open-sea crossing; 3) a movement through coastal waters (Table 2). The speed of movement was significantly greater (Kruskal-Wallis, $H_2 = 10.56$, $p < 0.01$) during the open-sea crossing (mean 2.8 km h^{-1} , range $2.2\text{--}3.3 \text{ km h}^{-1}$, $n = 6$) than during the period in Cyprus coastal waters (mean 1.6 km h^{-1} range $0.6\text{--}2.5 \text{ km h}^{-1}$, $n = 6$) or on the movement through Turkish or North African coastal waters (mean 1.7 km h^{-1} , range $1.4\text{--}1.9 \text{ km h}^{-1}$, $n = 6$). During the open-sea crossing, turtles were able to maintain remarkably straight headings as demonstrated by the straightness index of their routes (mean 0.92 , range $0.75\text{--}0.99$, $n = 6$). However, although straight and generally orientated towards the final destination, crossings were never undertaken along the most direct course, shortening the open-sea crossing at the expense of a longer journey through coastal waters leading to an increase in the distance to the endpoint (mean 26.9% , range $17.7\text{--}46.4\%$; Table 2). For clarity it should be noted that further analyses are only based on data from individuals A–C.

Diving during post-nesting movements

During all stages of the journeys of individuals A–C, shallow dives predominated (Fig. 2), particularly during open-ocean migration (Fig. 2A–Cii), although a greater proportion of deeper dives were undertaken during the time in Cyprus coastal waters and in the coastal migration undertaken after the open-sea crossing. Frequency of dive duration was similarly skewed towards shorter

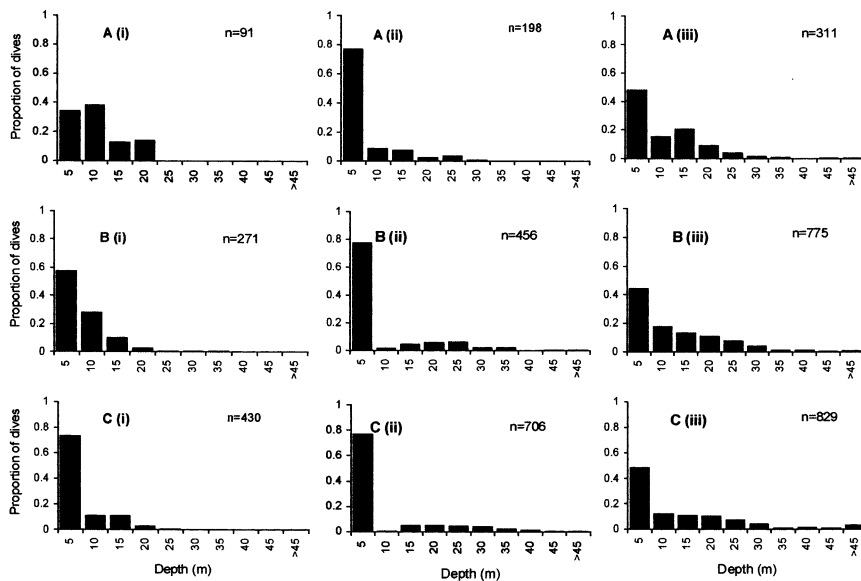


Fig. 2. Dive depth during travelling for individuals A–C. Relative proportion of dives to different depths are shown for periods i) in Cyprus coastal waters; ii) during open-ocean crossing; iii) during movements along the coasts of Turkey (A) and North Africa (B and C). Values shown on x axes are maxima in data range except for the upper bin which includes all values above this threshold.

durations during all migratory phases (data not shown). However, when the proportions of time spent undertaking dives of different durations are viewed (Fig. 3), this bias is less pronounced whilst turtles were in Cyprus coastal waters; during this stage, as well as spending 20–40% of their time conducting short dives of up to 5 min duration, of the order of 5–20% of the time is spent undertaking dives assigned to each of the other four categories encompassing dives of duration up to 25 min. Turtle A, which moved the shortest distance (Table 2), spent the majority of time during both the open-ocean and coastal movements undertaking short dives. This is in marked contrast to individuals B and C which demonstrated a clear bimodality in the propor-

tion of time spent undertaking very short dives (< 5 min) and a smaller peak undertaking dives of 11–25 min in duration (Fig. 3B–Cii). During coastal movements this bimodality was again seen in individuals B and C (Fig. 3B–Ciii).

However, it is important to consider time spent at < 2 m depth which was not logged as diving *per se*. Because no dives of duration > 90 min were recorded during either of the three stages of post-nesting movement, it is possible to estimate the proportion of time in the surface 2 m, by calculating the cumulative duration of dives recorded in each 6-h period assuming median duration in each time bin. These further highlight the skew towards high usage of the surface waters, espe-

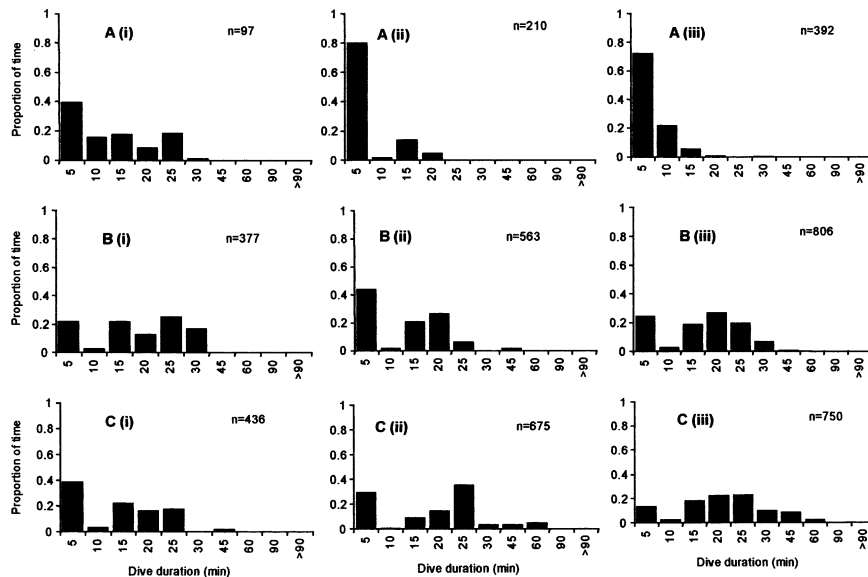
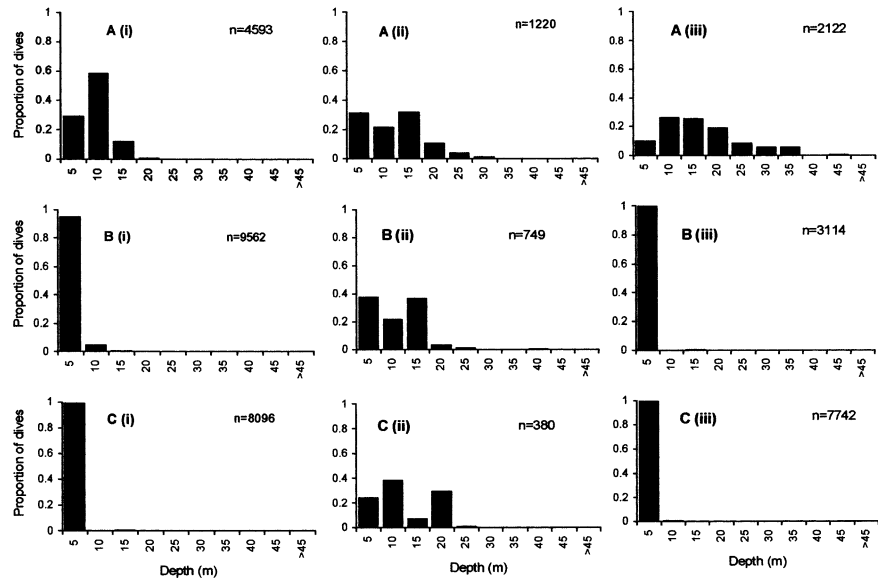


Fig. 3. Dive duration during travelling for individuals A–C. Relative proportion of time spent undertaking dives of different duration are shown for periods i) in Cyprus coastal waters; ii) during open-ocean crossing; iii) during movements along the coasts of Turkey (A) and North Africa (B and C). Values shown on x axes are maxima in data range except for the upper bin which includes all values above this threshold. To calculate the proportion of time, it was assumed that all values in a data range had the median value except for the highest category for which a minimum value was used.

Fig. 4. Dive depth at the foraging grounds for individuals A–C. Relative proportions of dives to different depths are shown for periods i) prior to wintering behaviour; ii) during overwintering behaviour; iii) post wintering. Values shown on x axes are maxima in data range except for the upper bin which includes all values above this threshold.



cially during open-ocean crossings. (Mean proportion time at $<2\text{ m} \pm \text{SD}$; Cyprus coastal waters: turtle A: 0.31 ± 0.41 ($n = 4$), turtle B: 0.20 ± 0.20 ($n = 10$), turtle C: 0.19 ± 0.15 ($n = 8$); open-ocean crossing: turtle A: 0.32 ± 0.09 ($n = 4$), turtle B: 0.74 ± 0.21 ($n = 29$), turtle C: 0.41 ± 0.34 ($n = 21$); movement through coastal waters: turtle A: 0.23 ± 0.17 ($n = 7$), turtle B: 0.13 ± 0.13 ($n = 18$), turtle C: 0.16 ± 0.13 ($n = 24$).

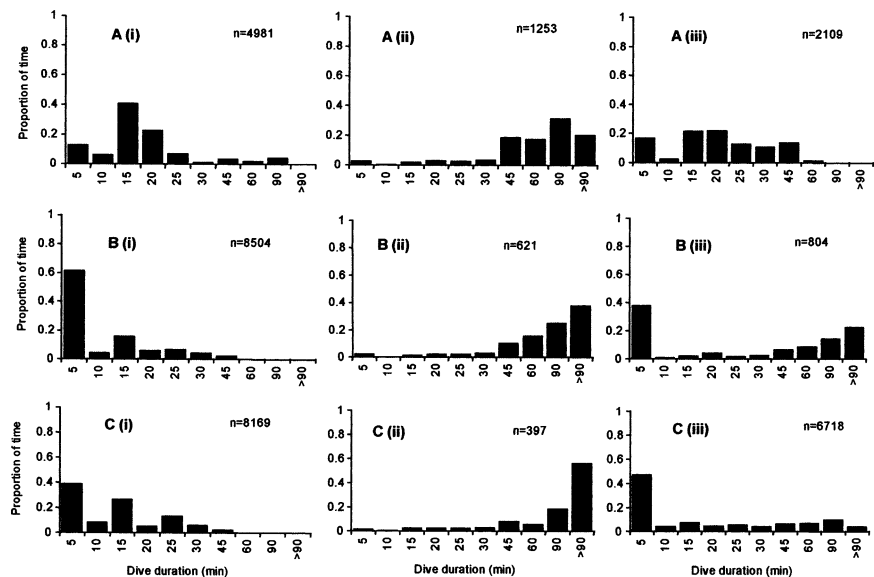
Diving in the foraging grounds

When the animals first reached the foraging grounds, the depths used were highly skewed to the shallow, especially in individuals B and C (Fig. 4A–Ci). How-

ever, a moderate proportion of time was spent conducting dives of longer duration (Fig. 5A–Ci).

Behaviour in the foraging grounds showed a marked seasonality. Figure 6 shows the temporal change in the minimum proportion of time spent undertaking dives of 25 min or more assuming all long dives had minimum possible durations. There is a pronounced seasonal variation in the behaviour with a sudden increase in the proportion of time spent undertaking longer dives for the turtle in Turkey in late September and for the two turtles in Libya in mid-October. While variable, the dive duration stayed relatively long throughout the winter before starting to reduce in the early spring in all three individuals. It is of interest to view the temperature experienced by the turtles during these periods and

Fig. 5. Dive duration at the foraging grounds for individuals A–C. Relative proportions of time spent undertaking dives of different duration are shown for periods i) prior to wintering behaviour; ii) during overwintering behaviour; iii) post wintering. Values shown on x axes are maxima in data range except for the upper bin which includes all values above this threshold. To calculate the proportion of time, it was assumed that all values in a data range had the median value except for the highest category for which a minimum value was used.



the trends in mean temperature recorded by the tracking units are shown on Fig. 6 for comparison. The behavioural shifts in dive duration are largely coinci-

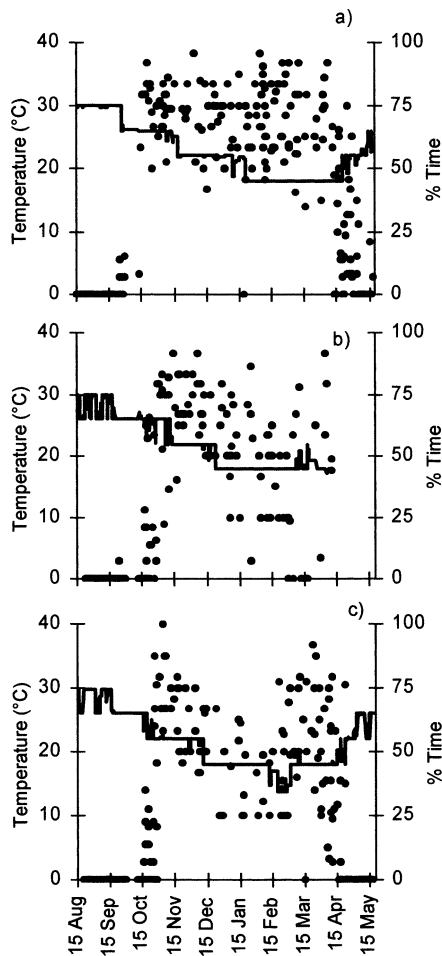


Fig. 6. Influence of temperature on the seasonal pattern of behaviour in individuals A–C. (a–c). Dots represent the minimum proportion of time in any 6 h period spent undertaking dives of duration 25 min (15 August 1998–15 May 1999) shown with the seasonal trend in mean temperature recorded by the satellite transmitter.

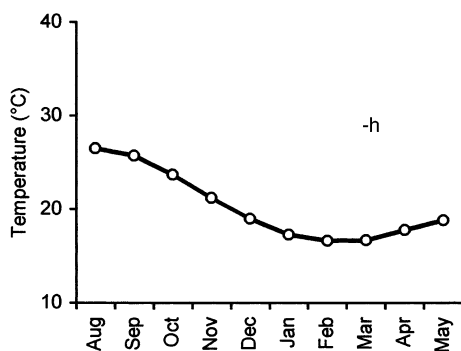


Fig. 7. The mean monthly sea surface temperature as calculated from COADS (1961–1997) data for 30–31°N, 15–20°E (range of monthly sample sizes: 27–108).

dental with a drop in mean sea temperatures $< 25^{\circ}\text{C}$. In addition, the temperature recorded by the transmitters is largely in fitting with the mean sea surface temperature profile that would be expected for the region. Figure 7 shows mean COADS data demonstrating the mean monthly sea surface temperature recorded (1961–1997) for the region 30–31°N, 15–20°E.

These behavioural shifts were largely coincidental with turtle movements within their coastal habitats to different offshore areas as demonstrated by satellite locations. The two turtles in Libya moved offshore to deeper water at approximately the same time (Fig. 8b: turtle B between 26 October and 16 November; turtle C between 26 October and 4 November) and this movement was coincidental with the pronounced shift in dive duration (Fig. 6b, c). Turtle A moved offshore between 28 September and 5 October and a large part of the wintering behaviour was undertaken at a deeper site (Fig. 8a).

We defined three stages at the foraging grounds as 1) autumn: from arrival until the turtles moved to offshore to the deeper site, 2) winter: the period at the deeper offshore site in which long dive durations were undertaken and, 3) spring: once the turtles had moved back into the shallow waters (individuals B and C). The winter/spring delineation was not possible on geographic movements in turtle A but was taken as when the dive duration began to reduce. Figures 4 and 5 show the data on dive depth and duration for the different stages at the foraging grounds. During the wintering phase dives were generally deeper (Fig. 4A–Cii) and there was a pronounced shift in the proportion of time spent undertaking dives of longer durations (Fig. 5A–Cii). Following the wintering phase dive depth was profoundly skewed towards shallow in individuals B and C with individual A showing a mixed depth usage (Fig. 4A–Ciii); however, dive duration (Fig. 5A–Ciii) was greatly reduced, approaching that of the pattern before the winter.

Again it is important to consider time spent at < 2 m depth which was not logged as diving. It is only possible to estimate this in 6 h periods with no dives greater than 90 min duration. We estimated the proportion of time spent at < 2 m during these recording periods, by calculating the cumulative duration of dives recorded in each 6-h period assuming median duration in each time bin. This showed a general pattern of decreased time at or near the surface when animals were wintering rather than during autumn or spring (mean proportion time at < 2 m \pm SD; autumn: turtle A: 0.12 ± 0.06 ($n = 135$), turtle B: 0.17 ± 0.20 ($n = 110$), turtle C: 0.17 ± 0.12 ($n = 137$); winter: turtle A: 0.07 ± 0.08 ($n = 76$), turtle B: 0.07 ± 0.07 ($n = 28$), turtle C: 0.13 ± 0.10 ($n = 10$); spring: turtle A: 0.14 ± 0.14 ($n = 7 = 60$), turtle B: 0.32 ± 0.38 ($n = 10$), turtle C: 0.20 ± 0.18 ($n = 107$)). The method of data collection means that it is not

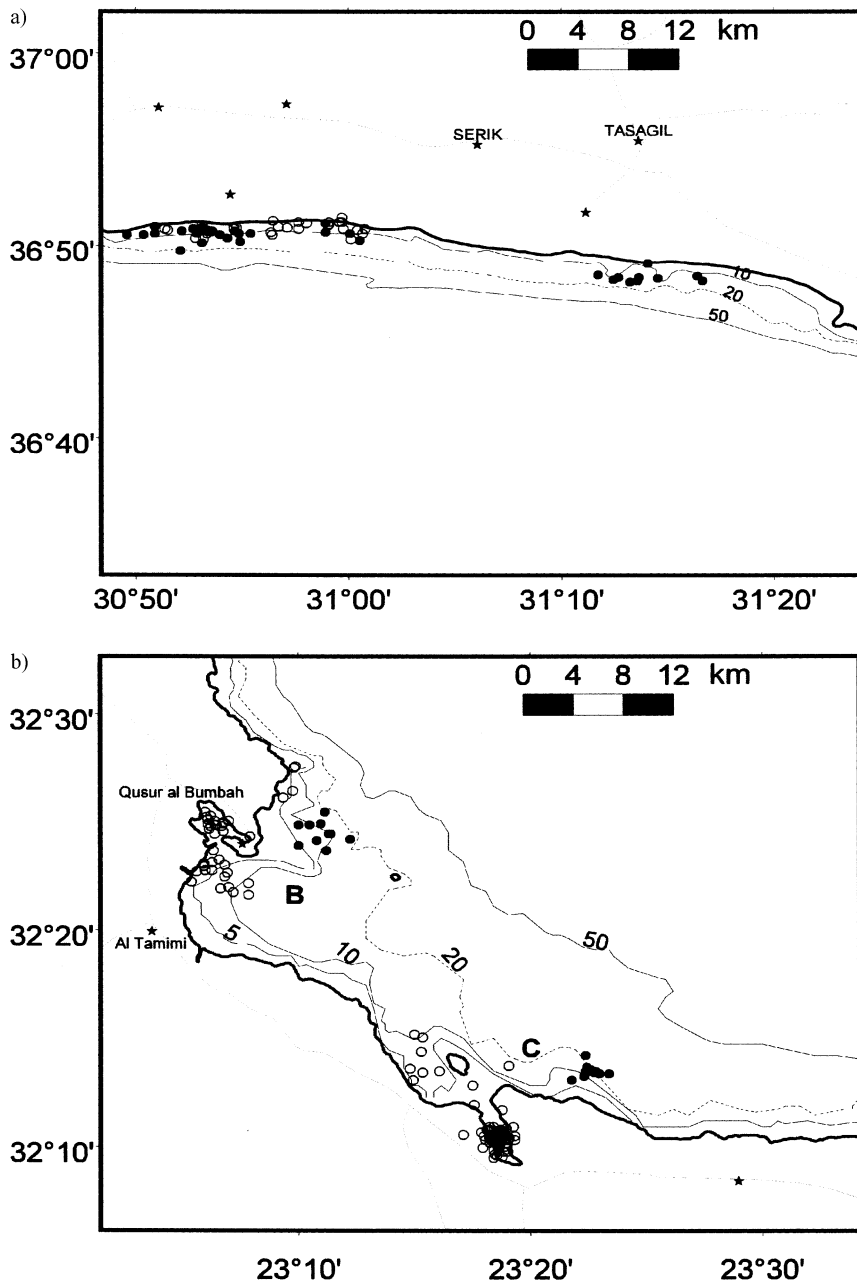


Fig. 8. The locations of 3 turtles at the foraging grounds during 1998/1999. a) Locations for the turtle which migrated to Turkey (turtle A) in relation to 10, 20 and 50 m isobaths. b) Locations for the two turtles that migrated to Libya (turtles B and C) in relation to 5, 10, 20, 50 m isobaths. Solid circles indicate positions during wintering behaviour (n: turtle A: 34, turtle B: 10, turtle C: 17) and open circles indicate positions before and after wintering (n: turtle A: 28, turtle B: 38, turtle C: 89).

possible to accurately assess the length of long dives as we cannot account for both time spent at < 2 m and conducting dives in excess of 90 min. However, for some recording periods the only dive recorded was one of > 90 min duration, suggesting that wintering dives can be up to and possibly exceeding 360 min long. However, the maximum interval between uplinks during the wintering behaviour (mean \pm SD: turtle A: 1.8 ± 3.9 d, range 0–32 d; turtle B: 2.3 ± 3.9 d, range 0–20 d; turtle C: 2.6 ± 2.4 d, range 0–14 d) preclude,

beyond any doubt the possibility of uninterrupted brumation of longer than 32, 20, 14 d in individuals A–C respectively.

Discussion

The patterns of movements demonstrated by adult female green turtles following their nesting in northern

Cyprus are generally in fitting with those previously studied by satellite telemetry. Post-nesting individuals in other populations have been shown to disperse to a diverse set of regional foraging grounds using a combination of open-ocean and coastal routes which provides foraging opportunities at the expense of increasing the length and duration of travel (Luschi et al. 1998, Cheng 2000). However, the novelty of our results is that we have reported the longest set of satellite telemetry observations for the movements and diving behaviour for any species of marine turtle. In terms of the evolution of migration strategies it is axiomatic that turtles, like other migrating animals, will have evolved strategies that minimise their cost of migration. Both the routes followed and the depths utilised by migrating turtles might therefore be expected to be optimised in some way.

During open-ocean movements most of the time was spent conducting short and shallow dives, in common with green turtles elsewhere (Hays et al. 1999). It is known that the drag experienced by swimming animals decreases away from the surface, being minimised once the depth is > 2.5 times the animals diameter (Hertel 1966). While some animals, such as seals, may dive very deeply (10s or even 100s of metres) while travelling, such dives probably also serve to survey the water column for potential prey (Thompson et al. 1991). However, for adult green turtles, being herbivorous, there is little food available in the open-ocean and hence there is no need for animals to dive in search of prey. Therefore, minimisation of the cost of transport is probably the most important objective for a migrating green turtle, which would explain why they swim close to, but not actually at, the surface. A similar pattern of near-surface travelling has been recorded in the analogous situation of penguins commuting from the land out to known offshore foraging sites, where once again their prime objective is to minimise their transport costs (Kooyman et al. 1992).

When there is no possibility of feeding en-route, then the optimum strategy for turtles would be to swim directly to the goal (i.e. the final foraging site). However, the fact that migrating turtles in the Mediterranean did not swim directly to their final foraging grounds, but instead conducted extensive coastal travelling, suggests that there was the possibility of feeding during coastal movements and hence of reducing the overall cost of migration. This conclusion is further supported by the finding that compared to open-ocean travel, during coastal movements the speed of travel was reduced and the depth utilisation more varied with more deep and longer dives. Hence the combination of open-ocean followed by coastal movements is probably another strategy to minimise the costs of migration. Alternatively it might be argued that turtles might simply have a poor navigational ability and so it is easiest for them to reach their destination by crossing

to the mainland as directly as possible and then simply making the correct binomial choice on which way to turn upon meeting the continental shelf. However, the island finding ability of turtles in general points to a good navigational ability (Luschi et al. 1996, Papi et al. 2000). Furthermore, during their coastal movements, not all turtles simply followed the coastline. For example, towards the end of their coastal routes turtles D and F which migrated to western Libya, crossed a bay (19°E, 32°N) with an open-water crossing of only 230 km, as opposed to 360 km if the turtles had followed the coastline. Hence we would argue that turtles combine open-ocean and coastal movements for energetic reasons rather than simply navigational necessity. In short, green turtles in the Mediterranean seem to have been behaving like many long-distance avian migrants which may follow an indirect course to their final destination in order to exploit feeding sites en-route which allow them to refuel (e.g. Gudmundsson et al. 1995).

There is almost nothing known about the movements of adult green turtles in the Mediterranean. Although nesting turtles have been marked with flipper tags for a decade in Cyprus (Broderick and Godley 1999), there are no records of tag returns from foraging grounds. Nevertheless, the capture of green turtles in artisanal fisheries in Egypt (Venizelos and Nada 2000) has shown that at least some individuals do exploit the North Africa coast. Of the six turtles we satellite tracked, five travelled to North Africa suggesting that this is, indeed, the most important foraging area for this species in the Mediterranean.

Upon arrival at their final foraging grounds, the three individuals which were followed for extended periods maintained distinct home ranges. For example, the two turtles that migrated to North Africa in 1998 maintained home ranges that were within 30 km of each other but clearly did not overlap. Direct observations have shown that green turtles may maintain distinct sea grass gardens that they serially crop to encourage new (and energetically rich) growth (Bjornrdal 1980, 1997). Our satellite telemetry observations suggest that fidelity to discrete areas, in line with previous studies, may be maintained for many weeks or even months.

During the middle of winter, both of these turtles simultaneously moved offshore within a few days of each other and showed a profound change in their behaviour, switching from relatively short dives to very long dives. In many animals, the timing of seasonal behaviours may be triggered by day length (Baker 1938), with animals within a population changing their behaviour within a few weeks of each other. However, the offshore movement of the two turtles within a few days of each other suggests that we may have observed a response to a distinct environmental cue, possibly water temperature. Additionally, it is worthy of note

that turtle A in Turkey began conducting the wintering behaviour earlier and continued for longer than turtles B and C in Libya; the expected latitudinal effect.

This extended dive duration in midwinter is consistent with the turtles entering a state of diapause. Midwinter diapause has been widely reported in freshwater turtles with individuals being able to remain submerged for many months and even to stay alive in frozen water (Ultsch et al. 1985, Packard and Packard 1993). However, records of diapause in marine species are less extensive. This dichotomy perhaps partially reflects the fact that while freshwater species remain in the same area throughout the year, marine species may move large distances and so may simply migrate away from seasonally cold water. This strategy of seasonal movements certainly seems to be widely utilised by turtles in the Atlantic (Musick and Limpus 1997). However, the Mediterranean is effectively an enclosed sea, and so turtles in North Africa are unable to migrate further south to avoid cold waters. Hence it is perhaps inevitable that if water temperatures drop too low off North Africa, turtles will be forced into diapause. The midwinter diapause that we recorded for green turtles in 1998/99 is probably not an unusual event (as, for example, is cold water stunning of adult turtles off Florida) since long-term temperature records revealed that 1998/99 had quite normal winter temperatures. We would conclude, therefore, that midwinter diapause is probably a routine strategy for green turtles in the Mediterranean.

Interestingly, the satellite transmitters lasted long enough to record the end of this midwinter state in some turtles, with a springtime movement onshore and a return to shallow and short dives. As in freshwater turtles, the period of mid-water diapause might be expected to be linked to water temperature, with this period being longer when cold winter temperatures persist for longer as demonstrated by the extended period of wintering behaviour of turtle A in Turkey vs B and C in Libya.

In summary, we have reported here the first records of turtle movements and diving behaviour that span both the post-nesting movements and an extended period on foraging grounds. For green turtles in the Mediterranean, a key foraging area appears to be North Africa, with turtles following broadly consistent patterns of open-ocean crossing followed by coastal travelling and then showing a period of midwinter diapause characterised by very long dives.

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References

- Anon. 1996. User's manual. – Argos/CLS, Toulouse.
- Baker, J. R. 1938. The evolution of breeding seasons. – In: De Beer, G. R. (ed.), *Evolution: essays on aspects of evolutionary biology*. Clarendon, Oxford, pp. 161–177.
- Balazs, G. H. 1976. Green turtle migrations in the Hawaiian Archipelago. – *Biol. Conserv.* 9: 125–140.
- Balazs, G. H. 1994. Homeward bound: satellite tracking of Hawaiian green turtles from nesting beaches to foraging pastures. – In: Schroeder, B. A. and Witherington, B. E. (eds), *Proc. 13th Annu. Symp. on Sea Turtle Biology and Conservation*. NOAA Tech. Memo. NMFS-SEFSC-341, pp. 205–208.
- Balazs, G. H. and Ellis, D. M. 2000. Satellite telemetry of migrant male and female green turtles breeding in the Hawaiian islands. – In: Abreu-Grobois, F. A. et al. (eds), *Proc. of the 18th Annu. Symp. on Sea Turtle Biology and Conservation*. NOAA Tech. Memo. NMFS-SEFSC-436, pp. s3–s5.
- Balazs, G. H. et al. 1994. Satellite telemetry of green turtles nesting at French Frigate Shoals, Hawaii, and Rose Atoll, American Samoa. – In: Bjorndal, K. A. et al. (eds), *Proc. 14th Annu. Symp. on the Sea Turtle Biology and Conservation*. NOAA Tech. Memo. NMFS-SEFSC-351, pp. 184–187.
- Bjorndal, K. A. 1980. Nutrition and grazing behavior of the green turtle, *Chelonia mydas*. – *Mar. Biol.* 56: 147–154.
- Bjorndal, K. A. 1997. Foraging ecology and nutrition of sea turtles. – In: Lutz, P. L. and Musick, J. A. (eds), *The biology of sea turtles*. CRC Press, Boca Raton, pp. 199–232.
- Broderick, A. C. and Godley, B. J. 1999. Effect of tagging marine turtles on nesting behaviour and reproductive success. – *Anim. Behav.* 58: 587–591.
- Butschelet, E. 1981. *Circular statistics in biology*. – Academic Press.
- Carr, A. 1984. *The sea turtle. So excellent a fish*, 2nd ed. – Univ. of Texas Press, Austin.
- Carr, A., Olgren, L. and McVea, C. 1980–81. Apparent hibernation of the Atlantic loggerhead turtle (*Caretta caretta*) off Cape Canaveral, Florida. – *Biol. Conserv.* 19: 7–14.
- Cheng, I. J. 2000. Post nesting migrations of green turtles (*Chelonia mydas*) at Wan-An Island, Penghu Archipelago, Taiwan. – *Mar. Biol.* 137: 747–754.
- Felger, R. S., Clifton, K. and Regal, P. J. 1976. Winter dormancy in sea turtles: independent discovery and exploitation in the Gulf of California by two local cultures. – *Science* 191: 283–285.
- Gudmundsson, G. A. et al. 1995. Examining the limits of flight and orientation performance: satellite tracking of brent geese migrating across the Greenland ice-cap. – *Proc. R. Soc. Lond. B* 261: 73–79.
- Hays, G. C. et al. 1999. Changes in behaviour during the inter-nesting period and post-nesting migration for Ascension Island green turtles. – *Mar. Ecol. Prog. Ser.* 189: 263–273.
- Hays, G. C. et al. 2001. The implications of location accuracy for the interpretation of satellite tracking data. – *Anim. Behav.* 61: 1035–1040.

- Hertel, H. 1966. Structure, form and movement. – Reinhold Publishing Corporation, New York.
- Kooyman, G. L. et al. 1992. Diving behaviour and energetics during foraging cycles in king penguins. – *Ecol. Monogr.* 62: 143–163.
- Limpus, C. J. et al. 1992. Migration of green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) turtles to and from eastern Australian Rookeries. – *Wildl. Res.* 19: 347–358.
- Luschi, P. et al. 1996. Long distance migration and homing after displacement in the green turtle (*Chelonia mydas*): a satellite tracking study. – *J. Comp. Physiol.* 178: 447–452.
- Luschi, P. et al. 1998. The navigational feats of green sea turtles migrating from Ascension Island investigated by satellite telemetry. – *Proc. R. Soc. Lond. B* 265: 2279–2284.
- Meylan, A. B. 1982. Sea turtle migration-evidence from tag returns. – In: Bjørndal, K. A. (ed.), *Biology and conservation of sea turtles*. Smithsonian Institution Press, Washington DC, pp. 91–103.
- Miller, J. D. 1997. Reproduction in sea turtles. – In: Lutz, P. L. and Musick, J. A. (eds), *Biology of sea turtles*. CRC Press, Boca Raton, pp. 51–81.
- Morreale, S. J. et al. 1996. Migration corridor for sea turtles. – *Nature* 384: 319–320.
- Musick, J. A. and Limpus, C. J. 1997. Habitat utilisation and migration in juvenile sea turtles. – In: Lutz, P. L. and Musick, J. A. (eds), *The biology of sea turtles*. CRC Press, Boca Raton, pp. 137–165.
- Nicholls, W. J. et al. 2000. Transpacific migration of a loggerhead turtle monitored by satellite telemetry. – *Bull. Mar. Sci.* 67: 937–947.
- Packard, G. C. and Packard, M. J. 1993. Hatchling painted turtles (*Chrysemys picta*) survive exposure to subzero temperatures during hibernation by avoiding freezing. – *J. Comp. Physiol. B* 163: 147–152.
- Papi, F. and Luschi, P. 1996. Pinpointing “Isla Meta”: the case of sea turtles and albatrosses. – *J. Exp. Biol.* 199: 65–71.
- Papi, F. et al. 1997. Satellite tracking experiments on the navigational ability and migratory behaviour of the loggerhead turtle *Caretta caretta*. – *Mar. Biol.* 129: 215–220.
- Papi, F. et al. 2000. Open-sea migration of magnetically disturbed sea turtles. – *J. Exp. Biol.* 203: 3435–3443.
- Penick, D. N. et al. 1996. Thermal dependence of tissue metabolism in the green turtle *Chelonia mydas*. – *Comp. Biochem. Physiol.* 113A: 293–296.
- Pritchard, P. C. H. 1976. Post-nesting movements of marine turtles (Cheloniidae and Dermochelyidae) tagged in the Guianas. – *Copeia* 1976: 749–754.
- Sato, K. et al. 1998. Interesting intervals for loggerhead turtles, *Caretta caretta*, and green turtles, *Chelonia mydas*, are affected by temperature. – *Can. J. Zool.* 76: 1651–1662.
- Spring, S. 1990. Satellite tracking of green turtles in Australia-preliminary results. – In: James, R. (compiler), *Proc. of the Australian marine turtle conservation workshop*. Queensland Dept of the environment, Heritage and Australian Natural Conservation Agency, Queensland, Australia, pp. 192–197.
- Thompson, D. et al. 1991. Movements, diving and foraging behaviour of grey seals (*Halichoerus grypus*). – *J. Zool.* 224: 223–232.
- Ultsch, G. R., Hanley, R. W. and Bauman, T. R. 1985. Responses to anoxia during simulated hibernation in northern and southern painted turtles. – *Ecology* 66: 388–395.
- Venizelos, L. and Nada, M. A. 2000. Exploitation of loggerhead and green turtles in Egypt: good news? – *Mar. Turtle Newsl.* 87: 12–13.
- Watson, K. P. and Granger, R. S. 1998. Hydrodynamic effect of a satellite transmitter on a juvenile green turtle (*Chelonia mydas*). – *J. Exp. Biol.* 201: 2497–2505.
- Whiting, S. D. and Miller, J. D. 1998. Short term foraging ranges of adult green turtles (*Chelonia mydas*). – *J. Herpetol.* 32: 330–337.