Post-nesting movements and submergence patterns of loggerhead marine turtles in the Mediterranean assessed by satellite tracking

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Abstract

Two female loggerhead turtles (*Caretta caretta*) were tracked, following nesting at Alagadi Beach (35°33′N, 33°47′E), Northern Cyprus, eastern Mediterranean for 60 and 82 days, respectively. The two individuals showed marked differences in their behaviour. Individual A was tracked to Syrian coastal waters, whereas individual B travelled around the coast of Northern Cyprus to a foraging site in the waters off the east coast of Northern Cyprus. Submergence durations varied markedly during different phases of the migration, suggesting coastal foraging/resting at certain stages en route with sustained directed travelling movements during initial coastal movements and open ocean crossing. Both turtles showed fidelity to foraging grounds for the duration of transmissions (Turtle A: 36 days; Turtle B: 58 days). In both cases, locations were centred in inshore waters although the two individuals exhibited quite different submergence patterns. Individual A carried out very short dives of typical duration < 10 min, whereas Individual B carried out longer dives with typical duration >20 min. Diel differences in submergence duration at the foraging grounds suggested longer dives at night/early morning for both turtles. For Turtle A, there was a general reduction in submergence duration as the period of residence increased; a pattern that may have been related to increasing temperature experienced. The total distance travelled by the two turtles (320 and 227 km) was relatively short when compared to satellite tracking studies of conspecifics following nesting in South Africa and USA and tagging studies of nesting loggerhead turtles in Greece and Australia. It is hypothesized that short migratory distance may be correlated with both the small body size and the relatively high frequency of remigration in this population.
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1. Introduction

One of the major obstacles in understanding the ecology of many marine vertebrates is the lack of adequate information regarding their distribution, migratory patterns and habitat utilisation. Marine turtles are particularly enigmatic. For decades, the main tool used to gain insights into the distribution and movements in sea turtles was flipper tagging (Hedrickson, 1958) and a great deal of information has been obtained using this method. Flipper tagging of nesting adults has provided an understanding of reproductive behaviour (reviewed by Miller, 1997), pre- and post-breeding migrations (Carr et al., 1978; Balazs, 1980; Meylan et al., 1983; Limpus et al., 1992) and growth rates (Bjorndal et al., 1983). Tagging of juveniles has given preliminary insights into habitat utilisation (Schmid, 1994) and ontogenetic migrations (reviewed by Musick and Limpus, 1997). In recent years, the increased performance and reduction in size of satellite tracking units has allowed them to become of great utility in turtle tracking studies. Using satellite transmitters, it has been possible to ascertain the routes used by post-nesting females to foraging grounds and gain insights into their foraging behaviour (Balazs, 1994; Balazs et al., 1994; Godley et al., 2002; Hatase et al., 2002b) even when these are in the open ocean (Morreale et al., 1996; Hughes et al., 1998; Nichols et al., 2000). The post-reproductive migration routes of males have also been described (Sakamoto et al., 1997; Balazs and Ellis, 2000; Hays et al., 2001b; Hatase et al., 2002a) and the remote assessment of habitat utilisation by juveniles has been demonstrated (Renaud and Carpenter, 1994; Polovina et al., 2000; Bentivegna, 2002). Perhaps more significantly, onboard data-logging and transmission have given detailed insights into behaviour upon migration and in the foraging grounds (Hays et al., 1999; Godley et al., 2002).

The loggerhead turtle (*Caretta caretta*) is widely distributed and extends into the Mediterranean. Although there are no nesting sites in the western Mediterranean, a large number of juvenile loggerheads are caught incidentally in pelagic fisheries (Aguilar et al., 1995). Carr (1987) hypothesized that loggerheads originating from beaches in the western Atlantic undertake a transatlantic migration with some of them entering the Mediterranean. This has been corroborated by Mediterranean recoveries of loggerheads tagged in the western Atlantic (Bolten et al., 1992) and molecular studies (Laurent et al., 1998).

All major nesting sites for the loggerhead turtle are in the eastern basin: Cyprus, Greece, Libya and Turkey (Laurent et al., 1998; Margaritoulis et al., in press). The regional annual nesting population, excluding the large, and as yet unquantified population in Libya (Laurent et al., 1997) is estimated as 2280–2787 females (Broderick et al., 2002) and is considered regionally endangered (Groombridge, 1990). Despite several decades of study, very little is known about the detailed at-sea distribution and behaviour of adult loggerhead turtles in the Mediterranean. Post-nesting movements of turtles tagged in Greece show a wide dispersion predominantly in the eastern basin although two females have been recovered in the western basin (Margaritoulis, 1988; Margaritoulis et al., in press). Analysis of fishery by-catch has suggested that demersal habitats are mainly found in the eastern basin (Laurent et al., 1998) and this is consistent with studies of tag recoveries. Important foraging areas identified to date include the Gulf of Gabès, Tunisia (Laurent and Lescure, 1994) the Adriatic Sea (Lazar and

Tvrtkovic, 1995), the bays of Mersin and Iskenderun in Turkey (Laurent et al., 1996), and the Nile delta in Egypt (Laurent et al., 1996, 1998).

The in-water studies of Mediterranean loggerhead turtles are relatively few. One of the earliest marine turtle satellite tracking projects was carried out in the Mediterranean by Hays et al. (1991) revealing patterns of movement during the internesting period of a loggerhead turtle at the Greek island of Kephalonia. This study was complimented by a detailed study of diving behaviour in the internesting period of two adult loggerhead turtles nesting in Northern Cyprus (Houghton et al., 2002) and an analysis of direct observations of the behaviour of four adult male loggerhead turtles in a nearshore foraging ground (Houghton et al., 2000). Most recently, Bentivegna (2002) has described the extended satellite tracking of a four loggerhead turtles (three females, one male; maturity status not assessed in all animals) after incidental capture in Italian trawl fisheries, rehabilitation and release. This study has shown how these turtles make far-ranging movements and show plasticity of behaviour; moving between the pelagic and neritic environment. Against this relatively data deficient background, we set out to gain insights into the post-nesting behaviour of adult female loggerhead turtles after nesting in Northern Cyprus, Eastern Mediterranean. By utilising transmitters with limited datalogging capabilities, we hoped not only to discover patterns of movement but also correlate these with patterns of submergence.

2. Materials and methods

We attached satellite transmitters to the carapaces of two female loggerhead turtles (Individuals A and B) at Alagadi (35°33′N, 33°47′E) in Northern Cyprus. For more details of the study site, see Broderick and Godley (1996). Turtles were typical in size for the study population: Individual A had a curved carapace length (CCL) of 71 cm; Individual B had CCL of 72.5 cm. To stop turtles moving to the sea during the attachment procedure, a portable 2×2-m wooden corral was erected around the turtles immediately after the completion of egg-laying. The carapace was cleaned thoroughly using domestic pot-scrubbers, which consisted of steel wool and detergent, then lightly abraded with sandpaper and wiped with acetone soaked tissue paper to degrease. The fixative used was a two-part epoxy resin (Foilfast, SFS Stadler, Cheltenham, UK). The methodology was similar to that used for carapace attachments in a previous study of green turtles nesting at this site (Godley et al., 2002) with the transmitting units being centred on the second central carapace scute. Care was taken to ensure that the resin was carefully fared into a hydrodynamic shape in fitting with general contours of the carapace to help reduce drag (Watson and Granger, 1998).

Transmitters (ST-14 A2400 Telonics, Mesa, AZ, USA) measured $16.5 \times 9.8 \times 3.0$ cm; weight 750 g ($<1\%$ of bodyweight). In addition to location, these transmitters provided temperature and basic submergence statistics. Temperature (accuracy 2 °C, Brenda Burger, Telonics, personal communication; precision 0.4 °C) was recorded at the surface during transmission and transmitted during the successive transmission. A count of submergences and mean submergence duration in predetermined 6-h integration periods set by the switching on of the unit were transmitted during the successive 6-h period. The "real dive time", i.e. the minimum threshold to be considered a dive was 60 s. Turtles

Table 1
Performance of the transmitters used

	Individual A	Individual B
Duration (days)	60	82
Number of 6-h data sets	219 (91%)	238 (73%)
Location class		
3	0	0
2	3 (1%)	0
1	20 (8%)	0
0	63 (24%)	17 (21%)
A	73 (28%)	18 (23%)
B	99 (38%)	45 (56%)
Total locations	258	80

Data are presented regarding: duration of transmissions, the number of 6-h integrated submergence duration data sets received and the number of locations of each of the Argos location classes received. Numbers in parentheses indicate percentage of total.

were located using the Argos system (Argos, 1996) where fixes were categorised into six classes (Table 1). Routes were reconstructed using fixes of location classes (LC) 1,2 and A after data presented by Argos (1996) and recent work by the authors (Hays et al., 2001a) has shown these to be the most reliable (no LC 3 (most reliable) were received). The distance between successive fixes was calculated using a great circle route equation. The different phases of movement were classified as coastal travelling and pelagic crossing and the movements in these stages were delineated by the first or last fix in coastal waters or within the area subsequently demonstrated as the foraging site. Overall mean speed values during each phase were calculated using the time taken to complete the whole phase assuming minimum straight-line movements between successive fixes of that phase (LC 2,1, A). For the whole study period in the study area, the time of sunrise ranged from 02:30 to 03:45 GMT and time of sunset ranged from 15:30 to 16:30 GMT.

3. Results

3.1. Duration of transmissions and quality of locations

Transmitters were attached on the June 13 and July 11, 2001 and transmissions were received for 60 and 82 days, for Individuals A and B, respectively. There was considerable difference in the number and relative quality of the locations obtained from the two turtles (Table 1), with the transmitter on Turtle B yielding fewer locations per day and none of higher location classes. The proportion of 6-h integration periods obtained was high for both turtles but again, less for Turtle B (Table 1).

3.2. Internesting habitat and post nesting movements of Individual A

Insufficient locations were received to reconstruct the route of Individual A during the first 12 days after deployment, but showed her to be in the vicinity of Northern Cyprus. She then returned to the same nesting beach where she successfully laid another clutch and

upon returning to the sea headed east closely following the coast of Northern Cyprus (Fig. 1a) before rounding the tip of the easternmost peninsula and crossing the open Mediterranean to the Syrian coast. Once reaching the coast, the turtle headed south, before stopping in Syrian coastal waters. Minimum duration and distance covered during
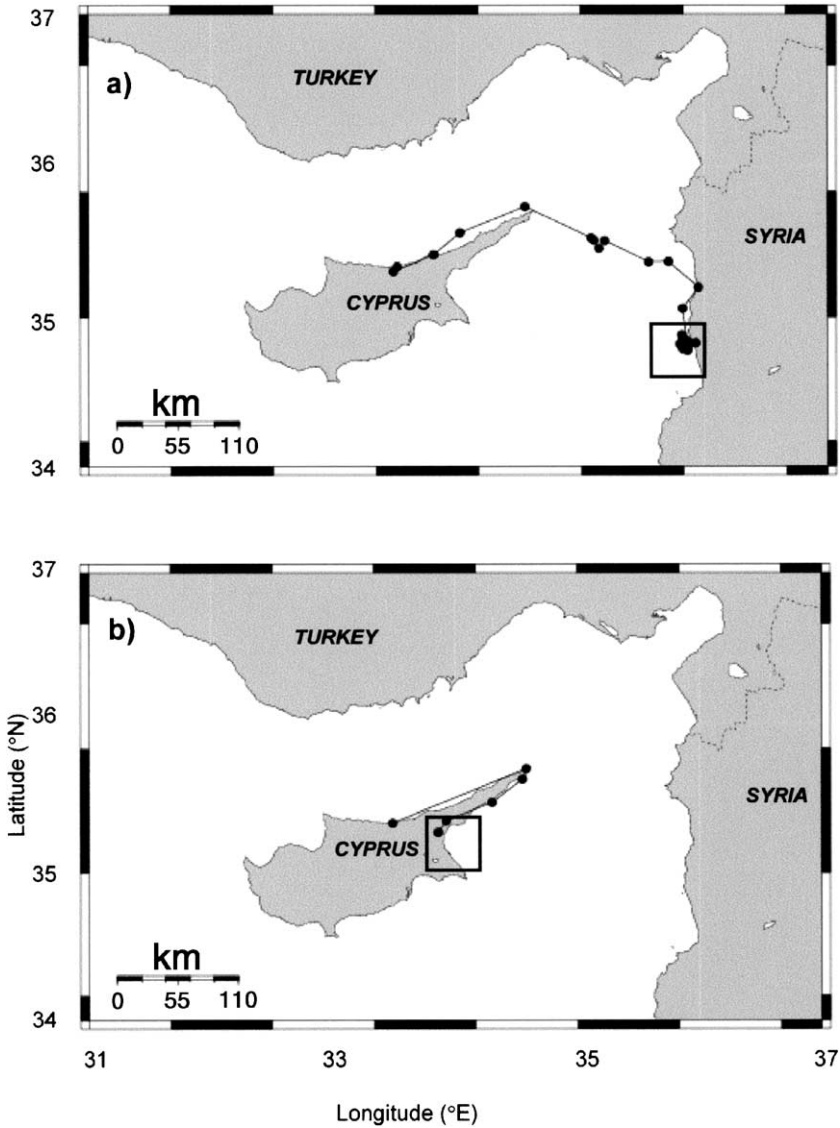

Fig. 1. The tracks of loggerhead turtles migrating away from Alagadi, Northern Cyprus at the end of their nesting season using all fixes of LC 2, 1 and A. (a) Individual A migrating to a foraging ground off Syria and (b) Individual B migrating to a foraging ground off Cyprus. Squares indicate approximate area shown in close up in Fig. 3.

each of the migratory stages is shown in Table 2. The mean minimum speed of travel for the first two stages of the route along the Cyprus coast (1.7 km h^{-1}) and during the pelagic crossing (1.3 km h^{-1}) are very much higher than that undertaken along the Syrian coast (0.5 km h^{-1}). It is worthy of note that the pelagic crossing phase of the journey was both very straight and not specifically directed towards the final destination. The pelagic crossing taken in conjunction with the final coastal phase of the journey meant that the resultant journey was some 50 km (ca. 25%) longer than if the turtle had made a straight beeline journey from the tip of the easternmost peninsula of Cyprus to the final destination.

3.3. Post-nesting movements of Individual B

Individual B headed east from the nesting beach before rounding the easternmost peninsula of Cyprus and progressing approximately southwest along the coast to a foraging site in the waters of a large bay off the east of Northern Cyprus (Fig. 1b). The duration, minimum distance and speed of travel during this journey are shown in Table 2. In comparison with Turtle A, it is obvious that Turtle B travelled much more slowly en route to the foraging ground with her mean minimum speed of travel for the route being only 0.4 km h^{-1}. It should be noted that the track of this individual apparently crosses land in the latter stages. This is a result of the track being recreated using fixes of relatively poor accuracy.

3.4. Submergence behaviour during internesting period and different phases of migration

Given that there is a threshold of 60 s before a submergence is counted, it is interesting to look at the proportion of time that is attributable as having been spent undertaking submergences in each 6-h integration window discounting any 6-h periods which involved time on the nesting beach (number of minutes submerged = mean submergence duration (min) × number of submergences). For Individual A, the vast majority of time was accounted for by submergences of greater than the threshold submergence duration of 1 min (Mean ± S.D.: internesting period: 339.6 ± 6.8 min, $n = 30$; first coastal phase: 334.8 ± 6.7 min, $n = 11$; pelagic crossing: 321.0 ± 22.0 min, $n = 21$; second coastal phase 308.5 ± 33.8 min, $n = 12$; residence in foraging area: 244.1 ± 3.6 min, $n = 143$). There

Table 2
Summary statistics of movements to foraging areas

Stage	Individual A			Individual B		
	Duration (h)	Distance (km)	Speed (km h^{-1})	Duration (h)	Distance (km)	Speed (km h^{-1})
First coastal	67	113	1.7	556	227	0.4
Pelagic	127	163	1.3			
Second coastal	89	44	0.5			
Total	283	320	1.1	556	227	0.4

For each individual summary statistics (duration (hours), minimum distance (km) and resultant average speed (km h^{-1})) are given for each of the stages of movement: first coastal movement through Cyprus coastal waters, across pelagic waters and during the second bout of coastal travelling. Routes used involve connection of fixes of LC 2,1 and A.

was a significant difference among these levels (ANOVA $F_{4,212} = 48.3$, $p < 0.001$), with a post-hoc Tukey test demonstrating that significantly more time was spent at the surface or undertaking submergences of less than 60-s duration at the foraging ground than during any other stage. Individual B showed no significant difference (*t*-test: $t_{214} = 1.2$, NS) in the mean number of minutes accounted for on submergences greater than 1-min duration in 6-h integration periods in the two phases of activity (coastal migration: 326.8 ± 12.3 min, $n = 67$; foraging ground: 324.0 ± 23.0 min; $n = 170$).

Submergence durations varied markedly at different points of the tracking of Individual A. Fig. 2 illustrates the mean submergence duration in all recorded 6-h integration periods in the first 40 days after deployment of this transmitter on Individual A. There were significant differences among the mean submergence durations for the different stages (ANOVA $F_{4,214} = 18.6$, $p < 0.001$; interesting period: 11.0 ± 5.1 min ($n = 32$); first coastal phase: 6.7 ± 8.3 min ($n = 11$); pelagic crossing: 3.1 ± 0.5 min ($n = 21$); second coastal phase 9.5 ± 8.1 min ($n = 12$); residence in foraging area: 4.5 ± 3.6 min ($n = 143$)). A post-hoc Tukey test demonstrated that submergence duration was significantly longer in the interesting period than during all subsequent stages other than the second coastal phase of travelling. In addition, submergence duration during the pelagic crossing was shorter than durations during the subsequent coastal phase that was in turn significantly longer than recorded in the foraging area.

Individual B showed a significant difference (*t*-test: $t_{215} = 11.2$, $p < 0.01$) in submergence duration with mean duration during coastal migration (15.2 ± 4.5 min, $n = 68$) being shorter than that on the foraging grounds (22.6 ± 5.1 min; $n = 170$).

3.5. Fidelity to foraging areas

The number and quality of locations do not allow detailed reconstruction of the movements of turtles in the foraging areas but do allow the two general patterns to be ascertained. Firstly, both turtles showed fidelity to relatively discrete foraging areas within
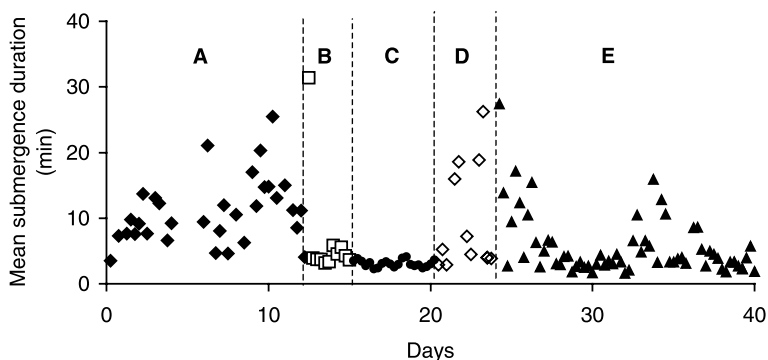

Fig. 2. Mean submergence duration in all 6-h data sets obtained in the first 40 days after attachment of transmitter on Individual A. The different stages are clearly delineated: (A) interesting interval (filled diamonds); (B) first coastal movement (open squares); (C) pelagic crossing (filled circles); (D) second coastal movement (open diamonds); (E) residence in the foraging area (filled triangles).

the duration of transmissions (Turtle A: 36 days; Turtle B: 58 days). Secondly, despite the low number of high quality fixes, the foraging range for both individuals seemed to be centred on inshore waters (Fig. 3a,b) close to some offshore islands in Individual A (islands not shown on map) and being close to the mainland in Individual B.
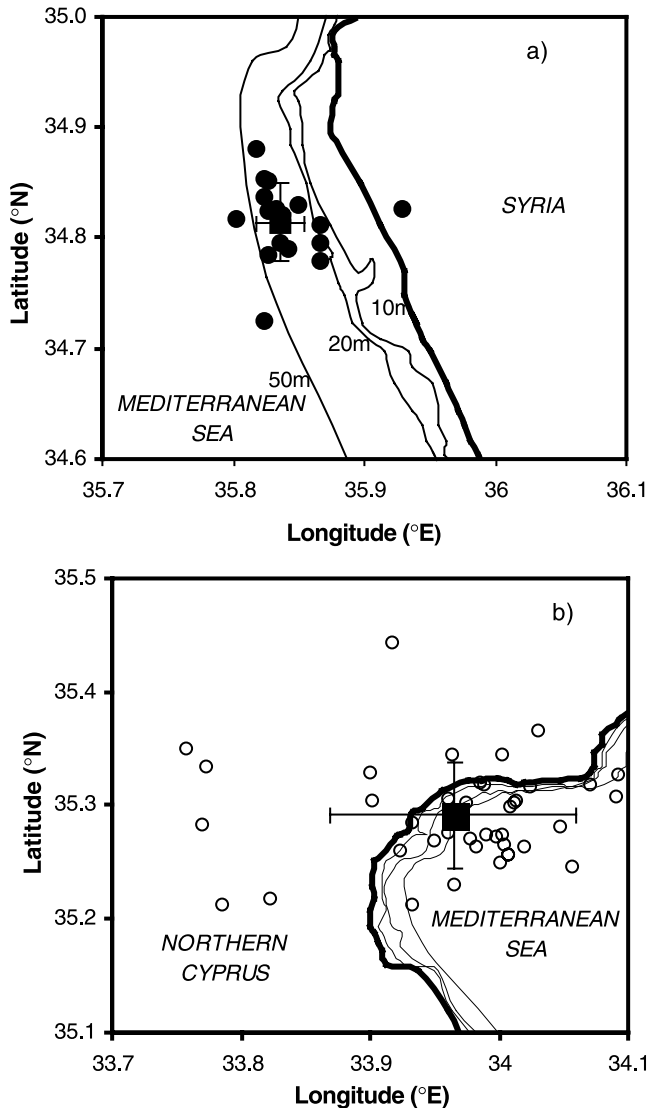

Fig. 3. Locations in the foraging grounds in relation to coastline and the 10-, 20- and 50-m isobath. (a) Individual A: Solid circles show locations of classes 2, 1 and A. (b) Individual B: Open circles show locations of all classes. As only class B locations were obtained, in order to define the centre of the foraging range, we omitted 35% of locations, retaining those that were closest to one another (after Hays et al., 1999). Square represents mean location ± S.D. of all points shown. On both figures, 0.1° of latitude or longitude corresponds to ca. 10 km.

3.6. Diel patterns in submergence duration

Individual A showed no obvious diel patterns in submergence duration in either the interesting period or the three phases of travel (ANOVA, $p>0.05$), however, a clear difference among 6-h integration periods was observed during the residence in the foraging ground (ANOVA $F_{3,139}=3.29$, $p<0.05$) with a post-hoc Tukey test showing mean submergence duration during the period 02:00–08: 00 GMT (5.7 ± 2.8 min; $n=35$) to be longer than mean duration in the period 14:00–20:00 GMT (3.0 ± 2.0 min; $n=33$). Thus, this individual was undertaking generally longer dives in the late night/early morning and shorter dives in the late afternoon/early evening.

Individual B showed clear diel patterns in submergence durations during its extended coastal migration (ANOVA $F_{3,64}=3.66$ $p<0.05$) and comparison using post-hoc Tukey test showed submergence duration in the two categories encompassing 22:00–10:00 GMT (22:00–0400 GMT: 16.5 ± 4.3 min, $n=17$; 04:00–10:00 GMT: 17.1 ± 5.0 min, $n=18$) were significantly longer than those encompassing 10:00–22:00 GMT (10:00–1600 GMT: 13.5 ± 3.9 min, $n=14$; 16:00–22:00 GMT: 13.4 ± 3.6 min, $n=19$). Thus, during migration, this individual was, on average, undertaking longer dives at night/early morning. Once
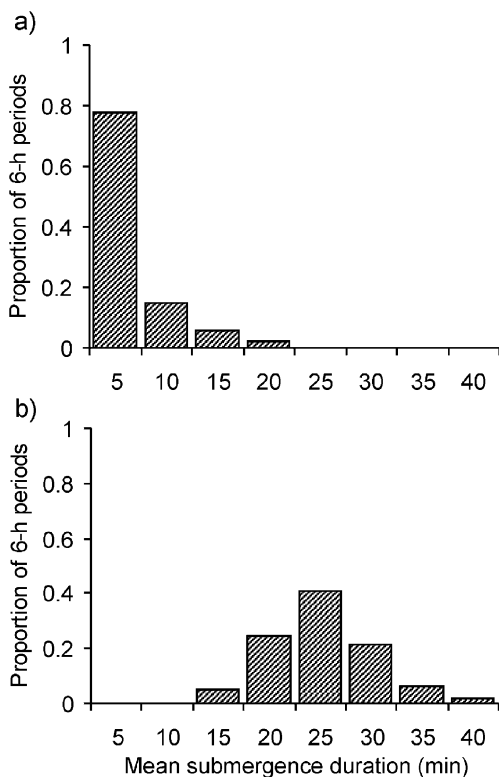

Fig. 4. Relative frequency of 6-h mean submergence durations in 5-min classes from each of (a) Individual A and (b) Individual B.

reaching the foraging ground, Individual B showed a similar diel pattern in submergence as Individual A (ANOVA $F_{3,166} = 18.35$, $p < 0.001$) with a post-hoc Tukey test showing mean submergence duration 22:00–0400 GMT (26.3 ± 5.0 min; $n = 43$) to be longer than mean duration in any of the other temporal categories (04:00–10:00 GMT: 22.9 ± 3.7 min; $n = 48$; 10:00–16:00 GMT: 19.0 ± 4.0 min; $n = 31$; 16:00–22:00 GMT: 21.3 ± 4.8 min; $n = 48$). Thus, this individual was also undertaking longer dives at night.

3.7. Individual differences and seasonal patterns in submergence duration

It is pass-remarkable that both turtles, although present in inshore waters at similar latitudes and time of year, carried out quite different submergence patterns (Fig. 4). Individual A carried out very short dives with more than 90% of integration periods having a mean duration < 10 min (Fig. 4a), whereas Individual B carried out longer
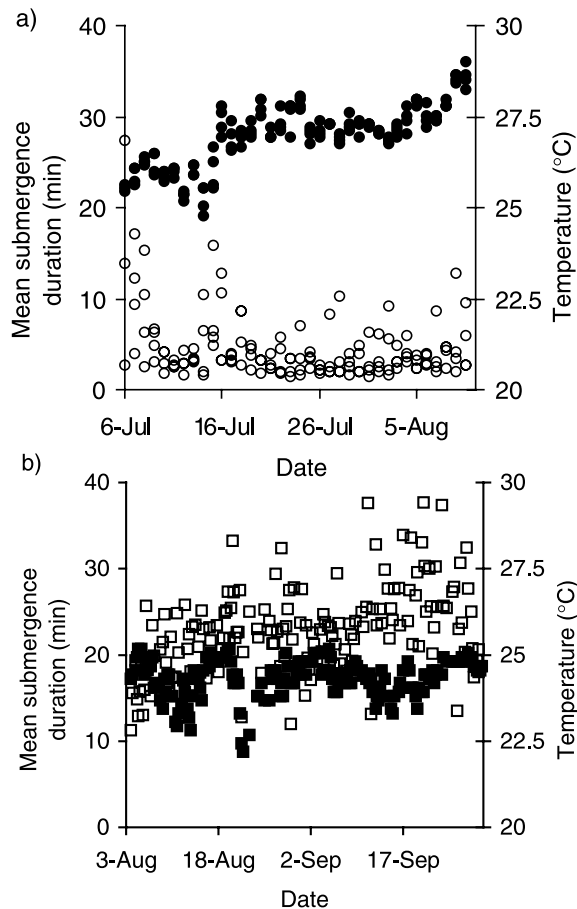

Fig. 5. Variation of mean dive duration (open symbols; primary *y*-axis) and temperature (filled symbols; secondary y-axis) with date in each of (a) Turtle A and (b) Turtle B. Only data from the foraging areas are shown.

dives with more than 95% of integration windows having mean submergence duration
>20 min (Fig. 4b). Fig. 5 shows submergence duration and temperature as recorded by
an onboard thermistor in both transmitters during the periods of residence at the foraging
grounds. The temperature recorded by the transmitter on Individual A is generally higher
(Fig. 5a) and demonstrates a clear increasing trend during residence at the foraging
grounds. Temperature recorded by the transmitter on Individual B is generally lower and
demonstrates no apparent trend during the period of residence at the foraging ground
(Fig. 5b). For Turtle A, there appeared to be a general reduction in submergence
duration as the period of residence increased (Fig. 5a). In two of four 6-h categories,
there was statistically significant correlation between temperature and submergence
duration (14:00–20:00 GMT: Regression $F_{1,31} = 13.0$, $r = 0.55$, $p < 0.001$; 20:00–02:00
GMT $F_{1,36} = 9.7$, $r = 0.46$, $p < 0.005$). Despite the lack of correlation between submer-
gence duration and temperature recorded in Individual B, there was still a seasonal
increase in submergence duration and this was statistically significant (Regression
$p < 0.05$) for all of the 6-h categories except 10:00–16:00 GMT.

4. Discussion

4.1. Pattern of post nesting movements

We have shown that as well as hosting nesting for the loggerhead turtle (Kasparek,
1995; Broderick and Godley, 1996) the waters of Cyprus and Syria serve as previously
unconfirmed foraging grounds. The actual minimum distance covered by the two study
individuals (320 and 227 km) was not large given the wide dispersal of female green
turtles from the same nesting site (Godley et al., 2002; Mean distance travelled to foraging
grounds 1076 km, range 274–1730, $n = 6$). Qualitative data of recaptures of nesting turtles
tagged in Greece suggest a wider dispersion (Margaritoulis et al., in press). When
compared with the complete satellite tracking of three female loggerhead turtles from
nesting grounds in South Africa to foraging grounds in Mozambique (Papi et al., 1997;
Mean minimum distance travelled 738 km, range 545–1000, $n = 3$) and Wassaw Island,
GA, USA (Plotkin and Spotila, 2002: Mean minimum distance travelled 1043 km, range
157–1458, $n = 5$), it shows that the distances travelled by the turtles in this study were
generally shorter than conspecifics elsewhere. Limpus et al. (1992) reviewed the
information gained from recaptures of flipper tagged loggerhead turtles nesting at
Australian rookeries and found that the mean distance travelled by females from mainland
nesting beaches (564 km; $n = 74$) was significantly less than the mean distance travelled by
females from Capricorn Bunker and Swain Reef Cays (1028 km; $n = 44$). However the
range of distances between tagging and recapture of these Australian turtles had a large
range (11–2620 km) highlighting the fact that female loggerhead turtles may undertake a
variety of migratory strategies.

Although caution should be exercised not to over-interpret our small sample size of two
tracks, it is worthy of note at this preliminary stage that loggerhead turtles nesting in
Northern Cyprus are unusual in two respects which may have some bearing on migratory
strategies. Firstly, although Mediterranean loggerhead turtles are, on average, smaller than

those in the wider Atlantic (Broderick and Godley, 1996), the females nesting in Northern Cyprus are the smallest in the Mediterranean (Range of mean CCL: 71.1–77.9 cm; Range of *n*: 6–39; eight seasons 1992–1999; Margaritoulis et al., in press). Secondly, many female loggerhead turtles nesting in Northern Cyprus remigrate with unusually high frequency with approximately equal numbers returning after 1, 2 and 3 years (Broderick et al., 2002). We hypothesize here that there may be links between migratory distance, reproductive frequency and body size in marine turtles.

A major finding of this study is that both females showed fidelity to relatively discrete inshore foraging areas during the period of study. Direct observation of green turtles has suggested that they may maintain distinct sea grass gardens that they serially crop to encourage new and energetically rich growth (Bjorndal, 1980, 1997). As a generalist carnivore, marked foraging site fidelity is not something which would been an a priori prediction unless the home range is centred on a locus of abundance of a patchy food resource and/or other factors such as presence of resting sites play an important role in defining the movements of this species in the foraging areas. Additionally, in the Mediterranean, individuals of this species (maturity status not assessed but possibly approaching adult size) have shown plasticity in foraging behaviour; moving between pelagic and neritic habitats (Bentivegna, 2002). Adult loggerheads breeding in Japan have also been shown to have the capacity for neritic and pelagic feeding (Hatase et al., 2002a,b) with a tendency for smaller individuals to feed in the pelagic (Hatase et al., 2002b).

4.2. Mode of movement and patterns of submergence

The loggerhead turtles in this study have demonstrated homologies in their mode of movement with previous studies of conspecifics and other marine turtle species moving through coastal waters (Papi et al., 1997; Cheng, 2000) and undertaking oceanic crossings with relatively straight headings (Luschi et al., 1996, 1998; Godley et al., 2002). The combination of open ocean and coastal routes, which provide foraging opportunities at the expense of increasing the length and duration of travel, may suggest that the time away from food source is an important factor shaping the routes of migrating turtles. Turtle A undertook a route that, despite having a relatively straight open ocean crossing, was 25% longer than the beeline route.

Turtles showed a diversity of speeds of movements in the different stages of their migratory journeys. Turtle A travelled at $1.3–1.7$ km h^{-1} between the nesting site and the Syrian coast, which is within the range for migrating turtles of this species reviewed by Papi et al. (1997). However, along the Syrian coast, she slowed to some 0.5 km h^{-1} suggesting that this turtle undertook extensive foraging or resting upon reaching these coastal waters. Our submergence data corroborate this suggestion, with generally very short mean submergence durations being recorded during the first two phases of the migratory journey. This is consistent with the findings in other studies (Papi et al., 1997; Hays et al., 1999, 2001c; Godley et al., 2002) when, during open ocean movements, most of the time was spent conducting short and shallow dives to help minimise drag and cost of transport (Hertel, 1966). Some animals, such as seals, can dive to 10s or even 100s of metres while travelling, but such dives probably also serve to survey the

water column for potential prey (Thompson et al., 1991). Given that carnivorous loggerhead turtles can feed pelagically even as adults (Nichols et al., 2000; Hatase et al., 2002a,b), it is possible that they could also survey for prey while making open ocean crossings. The limited evidence presented by the tracking of Individual A suggests that loggerhead turtles in the Mediterranean may undertake the same strategy as green turtles to minimise the cost of transport in ocean crossings as part of post-nesting migration (Godley et al., 2002).

We observed diel patterns in submergence duration where turtles appeared to have undertaken longer dives at night/early morning and shorter dives in the middle of the day. Interpretation of these findings is constrained by the nature of the data; however, we suggest that this may be resulting from increased resting at night and more active foraging by day. Although these patterns contrast with those of loggerhead turtles migrating from South Africa (Papi et al., 1997), they are in broad agreement with the findings of Renaud and Carpenter (1994) for loggerhead turtles and those regarding other marine turtle species (Brill et al., 1995; Renaud et al., 1995; Beavers and Cassano, 1996).

Despite the fact that both turtles foraged in inshore waters at similar latitudes, they showed markedly different submergence durations. Given the relatively small difference between the temperatures recorded by the two transmitters (typically $<5\,^{\circ}C$), the contrasting submergence patterns are most likely to reflect differences in foraging strategies rather than metabolic effects of ambient temperature differences. Indeed, it may be that Individual B undertook longer dives to cooler deeper water thus cooling the transmitter to below that of surface waters and, as a result of thermal inertia, consistently yielded data cooler than surface temperature. The consistently short mean submergence durations of Turtle A are broadly similar to those observed by male loggerhead turtles feeding in shallow inshore waters in Greece (Houghton et al., 2000). We suggest that this individual was either feeding in the subsurface midwater environment or benthically in shallow water around the nearby small offshore islands. Although our duration of tracking was quite short, we demonstrated a seasonal effect in submergence duration consistent with that shown in this species by Renaud and Carpenter (1994).

We have demonstrated the effectiveness of satellite tracking, although relatively expensive on a per animal basis, yields otherwise unattainable information and avoids some of the pitfalls of conventional marking such as capture and reporting biases. With simple transmitting units and careful interpretation, significant insights have been obtained into the behaviour of the enigmatic loggerhead turtle in the Mediterranean, highlighting marked inter-individual differences in movements and submergence patterns.

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