

When surfacers do not dive: multiple significance of extended surface times in marine turtles

S. Hochscheid^{1,*}, F. Bentivegna¹, A. Hamza^{2,3} and G. C. Hays⁴

¹Stazione Zoologica Anton Dohrn, Villa Comunale 1, 80121 Napoli, Italy, ²Nature Conservation Department, Environment General Authority, PO Box 13793, Tripoli, Libya, ³Institute of Estuarine and Coastal Studies, University of Hull, Hull, HU6 7RX, UK and

⁴School of Environment and Society, Swansea University, Swansea, SA2 8PP, UK

*Author for correspondence (sandra.hochscheid@szn.it)

Accepted 29 December 2009

SUMMARY

Marine turtles spend more than 90% of their life underwater and have been termed surfacers as opposed to divers. Nonetheless turtles have been reported occasionally to float motionless at the surface but the reasons for this behaviour are not clear. We investigated the location, timing and duration of extended surface times (ESTs) in 10 free-ranging loggerhead turtles (*Caretta caretta*) and the possible relationship to water temperature and diving activity recorded *via* satellite relay data loggers for 101–450 days. For one turtle that dived only in offshore areas, ESTs contributed 12% of the time whereas for the other turtles ESTs contributed 0.4–1.8% of the time. ESTs lasted on average 90 min but were mostly infrequent and irregular, excluding the involvement of a fundamental regulatory function. However, 82% of the ESTs occurred during daylight, mostly around noon, suggesting a dependence on solar radiation. For three turtles, there was an appreciable (7°C to 10.5°C) temperature decrease with depth for dives during periods when ESTs occurred frequently, suggesting a re-warming function of EST to compensate for decreased body temperatures, possibly to enhance digestive efficiency. A positive correlation between body mass and EST duration supported this explanation. By contrast, night-active turtles that exceeded their calculated aerobic dive limits in 7.6–16% of the dives engaged in nocturnal ESTs, probably for lactate clearance. This is the first evidence that loggerhead turtles may refrain from diving for at least two reasons, either to absorb solar radiation or to recover from anaerobic activity.

Key words: dive behaviour, marine turtle, behavioural thermoregulation, aerobic dive limit, surface time, vessel strike.

INTRODUCTION

Behavioural ecology made an important breakthrough in the study of air-breathing marine animals when Kramer (Kramer, 1988) used the marginal value theorem (Charnov, 1976) to generate predictions as to how diving animals might optimise temporal patterns of diving activity. In essence, oxygen is a resource that is only available at the water surface while many other activities, be they feeding, predator avoidance or mating, take place underwater and the cost of commuting between surface and depths is accounted for by the benefits gained from these underwater activities. Many diving optimality models thereafter have used Kramer's concept to establish how animals organise their behaviour around the necessity to return to the surface to breathe while minimising the time spent at the surface (Houston and Carbone, 1992; Carbone and Houston, 1996; Walton et al., 1998; Halsey et al., 2003). However, across the range of vertebrate taxa that have air-breathing representatives in the marine ecosystems, physiological and behavioural constraints on diving vary considerably and have led to a distinction between 'divers' and 'surfacers', whereby the former spend more than 50% of their time at the water surface and conduct excursions to the depth in bouts that are often diurnal. Surfacers instead are those animals that spend most of their time underwater and surface only briefly for gas exchange (Kooyman, 1989). This latter group includes, among others, Weddell seals, *Leptonychotes weddellii*, elephant seals, *Mirounga leonina* and *Mirounga angustirostris*, and all species of marine turtles.

Indeed, marine turtles often spend >90% of their time underwater (Renaud and Carpenter, 1994; van Dam and Diez, 1996; Lutcavage

and Lutz, 1997; van Dam and Diez, 1997), and generally only adult females leave the water for depositing their eggs during the reproductive season. The only exception reported until today is that some green turtles at Hawaii have been observed to crawl onto the beach during the day apparently to bask (Whittow and Balazs, 1982). However, while basking literally means to bathe in the sun, some behaviours of these green turtles, such as covering themselves with sand and choosing the less sun-exposed beach, indicate that there might actually be other reasons for why these turtles take a break from underwater activities (Whittow and Balazs, 1982). Avoidance of potential predators or aggressive males has been suggested as alternative purposes of this haul-out behaviour but there were no further investigations on this matter (but see Swimmer, 2006). Besides, warming up can also be achieved by basking at the water surface. In particular, a loggerhead turtle was shown to raise its body temperature by more than 3°C above that of the water during floating at the surface and exposing a substantial proportion of the carapace to the sunlight (Sapsford and Van der Riet, 1979). Nonetheless, despite the demonstrated and widely accepted thermoregulatory benefits of basking, either on land or in water, a multiple biological significance of this behaviour has often been assumed, including retardation of algal or fungal infestations, vitamin D synthesis and probably enhancement of immune response in infected turtles (Boyer, 1965; Chessman, 1987; Manning and Grigg, 1997; Swimmer, 2006).

Thus, returning to the above described concept of surfacers, it would be intriguing to learn if and for what reasons animals that are physiologically adapted to reload their oxygen stores in a

minimum time should prevail at the water surface for extended periods. Marine turtles have often been observed floating in the sea with partially exposed carapaces which, when dry, may indicate that the turtle has not been diving for some time. However, to our knowledge no study has dealt with this kind of surfacing behaviour so far, so we aimed at determining the occurrence and possible function of extended surface times in loggerhead turtles *Caretta caretta* Linnaeus.

The above described functions (i.e. thermoregulation, therapeutic and physiological radiation absorption) depend on the sun's radiation, and hence it is expected that they would drive the turtles to stay at the surface only during daytime. In addition, there are benefits from extended surface time (EST) that would not require sunlight. Resting is one likely and simple explanation. However, there are numerous studies that have confirmed that marine turtles usually rest either on the sea floor (Hochscheid et al., 1999; Hays et al., 2000) or, if this is not within reach, at mid-water (Minamikawa et al., 1997). Thus, it needs to be investigated under which conditions a turtle may choose the otherwise so rarely used surface resting site over the relative safety of an underwater resting site. A second possible and also often discussed reason for ESTs in diving animals is the unloading of accumulated lactic acid after anaerobic activity (Chappell et al., 1993; Boyd and Croxall, 1996; Boyd, 1997; Hochachka, 2000; Hochachka and Somero, 2002). Yet, anaerobic metabolism is an inefficient utilisation of energy and may be used only to exploit an extremely rich food resource in an environment with patchy prey distribution (Boyd, 1997).

Finally, it has to be mentioned that buoyancy disorders and disease (e.g. cold stunning) could impact the turtles' diving capacities and constrain them to stay involuntarily at the surface. While it was not possible in the present study to investigate the physiological data related to some of the above described scenarios, we attempted to identify the most likely reasons for ESTs through the combined analysis of behavioural data and temperature profiles with respect to time of day and the turtles' position at sea. In this way we intended to respond to key questions regarding the location, duration and time of ESTs, the activity and experienced temperatures preceding ESTs.

MATERIALS AND METHODS

We used 10 immature loggerhead turtles, which ranged from 19.7 kg to 52 kg (mean \pm s.e.m. = 36.9 ± 3.4 kg) in body mass and from 55 cm to 74.7 cm (mean \pm s.e.m. = 66.0 ± 1.9 cm) in curved carapace length (CCL). The largest turtle could be identified as a male. The animals were originally recovered by Marine Turtle Rescue Centres specialised in the cure and rehabilitation of turtles impacted by human activities, disease or other difficulties. Eight of the turtles [ID 15383, 29359, 4395, A, B, E, G corresponding to the turtles in Hochscheid et al. (Hochscheid et al., 2007a) and ID C06, body mass = 37.2 kg, CCL = 67.7 cm] were housed for convalescent periods ranging from 47 to 366 days at the Rescue Centre of the Stazione Zoologica Anton Dohrn in Naples, Italy. Two further turtles were incidentally caught by bottom trawl in the Gulf of Sirte, Libya, and housed for two weeks in the Rescue Centre of the Tajura Marine Biology Research Centre. During their stay in the Rescue Centres the turtles were kept in individual tanks with circulating seawater, provided with food and received, when necessary, treatment and medication prescribed by a veterinary. The veterinary also confirmed the complete recovery of health prior to the release of the turtles. Both the Naples and the Tajura Rescue Centres are recognised by the Italian Ministry of the Environment and the Libyan Environment General Authority, respectively, and conform to the 'Guidelines to

Improve the Involvement of Marine Rescue Centres for Marine Turtles' (RAC/SPA, 2004).

Just prior to their release turtles were equipped with satellite relay data loggers (SRDL, Sea Mammal Research Unit, University of St Andrews, UK). The units were glued onto the anterior central scutes of the carapace using fast-setting epoxy resin (Power-Fast® Powers Fasteners Inc., New Rochelle, NY, USA). The SRDLs weighed less than 0.6% of the smallest turtle's body mass in water and less than 2% of its body mass in air.

The releases were organised close to where the turtles were originally found. Some of the turtles were released from a boat in the Gulf of Naples, Italy (40°45'N, 14°00'E) in August 2002 (turtle 15383), September 2004 (turtles 29359 and 4395) and October 2006 (turtle C06). In October 2005, releases took place on a beach north of Naples close to the city of Mondragone, SW Italy (41°07'N, 13°53'E) (turtles B, E and G) and on a beach close to Galipoli, SE Italy (40°03'N, 17°59'E) (turtle A). In April 2006, turtles L1 and L2 were released from a beach at Misurata, Libya (32°22'N, 15°5'E).

The SRDLs were fitted with an internal clock, a pressure sensor for dive depth measurements and a temperature sensor (except the SRDL of turtle 15383). Recorded data were processed and compressed onboard prior to transmission *via* the Advanced Research and Global Observation Satellite (ARGOS, <http://www.argos-system.org/>) system. Dive data were recorded with respect to Co-ordinated Universal Time and were delivered as start and end times and date of a dive, maximum dive depth reached during a dive and in some cases also dive profiles were transmitted as the time and depth of the five most significant points of inflection. Temperature profiles over the depth range used by the turtles were provided as 12 selected points of inflection. A more detailed description of the configuration for onboard data processing was given in Hochscheid et al. (Hochscheid et al., 2007a). In addition, information on surface times was derived from the saltwater switch, which is integral part of all marine ARGOS transmitters. The saltwater switch is active when submerged and becomes interrupted when it is dry, and thus the satellite tag 'knows' when it is at the water surface and starts to transmit. As the SRDLs were mounted on top of the carapace, the saltwater switch became dry when the carapace emerged from the water as it occurs during breathing periods and an EST. When the duration of the saltwater switch dry time exceeded 10 min an EST was recorded and transmitted with the corresponding start and end times and geographical location. If no location was available for a particular date when an EST occurred, latitude and longitude were obtained by linear interpolation from adjacent locations. The end of an EST was registered when the saltwater switch was submerged for at least 40 s, so that momentary wetting due to wave action would not interrupt the registration of an EST. All behavioural data were also summarised for 24 h periods that included the proportion of time spent in each of three behavioural states [diving, at the surface (i.e. above 3 m) or in an EST], as well as the number of dives, and the means \pm s.d. and maximum values for both dive duration and maximum dive depth.

To help minimise biases in the transmission of data records caused by the animal's surfacing behaviour, a buffering strategy was used. Each recorded event (individual dive, 24 h summary, EST, etc.) was stored in a buffer where it was made available for transmission for the next 5 days. Data from this 5-day buffer were randomly relayed. A count number was assigned to each EST (in order of occurrence), so that it was possible to determine the number of missed events between those that were recovered *via* Argos. This transmission strategy also meant that data regarding dive behaviour, temperatures

and EST were not necessarily transmitted together and were thus often not available for the same days (i.e. time of day, date).

Turtle G was recaptured 255 days after its release (and two weeks after the last satellite uplink) with the unit still attached but the antennae was damaged. The SRDL was removed together with all remaining glue and the turtle was released back into the sea. After returning the recovered unit to the manufacturer it was possible to download all data for the complete 255 days period contained in the memory of the SRDL.

Data analysis

The proportion of time that turtles allocate to ESTs was estimated using the following equation:

%Time = (Σt_{EST} / t_{track}) × (N_{tot} / N_{rec}) × 100 , (1)

where Σt_{EST} is the sum of all durations of the recorded ESTs, t_{track} is the total time that a turtle was tracked, N_{rec} is the number of recorded ESTs and N_{tot} is the total number of ESTs that a turtle made during the tracking period (retrieved from the ‘count number’, see above).

Time of sunrise and sunset were calculated for each day and geographical position of each EST, based on equations by Schlyter (P. Schlyter – free C source for computing sunrise/sunset times, with comments: <http://stjarnhimlen.se/comp/sunrise.c>, <http://stjarnhimlen.se/english.html>), which determines the time at which the sun reaches the altitude of −0.833° (i.e. when the sun’s upper limb touches the horizon, accounting for atmospheric refraction). We then determined which EST occurred during night (i.e. between sunset of one day and the sunrise of the following day) and day (i.e. between sunrise and sunset of the same day).

Due to a software problem of the SRDLs of turtles 29359 and 4395 the data were not always transmitted with the correct time and date and also summary data were not available. Therefore, for these turtles only duration, location and month of occurrence of an EST could be analysed and presented.

Because of the differences in the availability of data for single turtles and differences in space and time of EST occurrence, it was not possible to summarise dive and temperature data for all turtles. For this reason, periods for dive and temperature analysis were selected individually for each turtle corresponding to the month(s) where turtles allocated relatively more time to ESTs (hereafter referred to as EST periods) (see also Fig. 2).

Aerobic dive limits were calculated (cADL, in minutes) for three turtles (15383, C06, E) that dived in pelagic habitats during EST periods to investigate whether the occurrence of EST may be

connected with anaerobic activity. The calculations were done using the equation:

cADL = (ΣO_{2(B+T,L)} / V̇_{O₂}) = ((6.7 M_b) + (0.174 × 114 M_b^{0.94}) / (−2.87 + 0.168 T_w + 0.353 ln M_b)) , (2)

where ΣO_{2(B+T,L)} is the sum of the blood, tissue and lung oxygen stores, M_b is body mass of the turtle (in kg), V̇_{O₂} is rate of oxygen consumption (ml O₂ min^{−1}) and T_w is the water temperature (in °C) of the upper 2 m surface layer as measured by the SRDL (except for turtle 15383, for which average sea surface temperatures were obtained from the International Comprehensive Ocean-Atmosphere Data Set from <http://www.cdc.noaa.gov/coads/products.html>) (see Hochscheid et al., 2005). The constant used for calculating the blood oxygen content (6.7 ml O₂ kg^{−1}) was derived from a study by Lutz and Bentley (Lutz and Bentley, 1985) on loggerhead turtles, and calculation of the lung oxygen store was based on the non-species-specific relationship between M_b and lung volume published by Hochscheid et al. (Hochscheid et al., 2007b), and assuming that the proportion of oxygen in the inspired air at the start of a dive is 0.174 as in green turtles (Berkson, 1966). The equation for oxygen consumption rates of loggerhead turtles in relation to T_w and M_b was provided by Hochscheid et al. (Hochscheid et al., 2004). cADL were calculated for each variation in T_w during the period that was taken into consideration and compared with the corresponding transmitted dive durations. As shown in Hochscheid et al. (Hochscheid et al., 2007a), the turtles usually experienced less than 1°C differences between temperatures at the water surface (0–2 m) and at the maximum dive depth, so that temperatures from the upper 2 m layer were considered to be representative of the temperatures experienced in general by each turtle during diving. The only exception is turtle E, which sometimes dived through larger temperature differentials, and consequently may have had decreased metabolic rates. In this case cADL would have been underestimated but the results show (see below) that this was of little relevance because this turtle never dived close to its cADL.

RESULTS

The turtles were followed for periods varying between 101 and 450 days, during which they utilised different areas. Turtles 15383, A and B all moved to Greece, although taking different routes (Fig. 1A). Turtle E initially stayed in SW Italian coastal waters but then moved along the coast to northern Italy and went into the Ligurian Sea (Fig. 1B). Turtles 29359, 4395 and G stayed in coastal waters of SW Italy close to the release site for the entire tracking period (Fig. 1C). Turtle C06 left the coastal waters and spent almost

Table 1. Numbers of total extended surface times (ESTs) (N_{tot}) made by each turtle and numbers of recorded ESTs (N_{rec}) for which data were transmitted

Turtle	N _{rec}	N _{tot}	N _{rec} (% total)	f EST [days ^{−1}]	N _{rec} night	N _{rec} day
15383	7	31	22.6	0.14	4	3
29359	26	n.a.		n.a.		
4395	12	n.a.		n.a.		
A	9	36	25	0.12	4	5
B	18	37	48.6	0.15	2	16
C06	104	161	64.6	0.84	20	84
E	35	54	64.8	0.19	2	33
G	25	25	100	0.11	9	16
L1	15	18	83.3	0.18	0	15
L2	20	48	41.7	0.24	0	20

N_{rec} is also expressed as a percentage of the total EST. The frequency f of EST indicates how often this event occurred (N_{tot}/days of tracking). N_{rec} night indicates the numbers of EST that occurred during hours of darkness and N_{rec} day is number of EST during daylight. Note: data for turtles 29359 and 4395 are not included because of unreliable information on date and time (see text for more explanation).

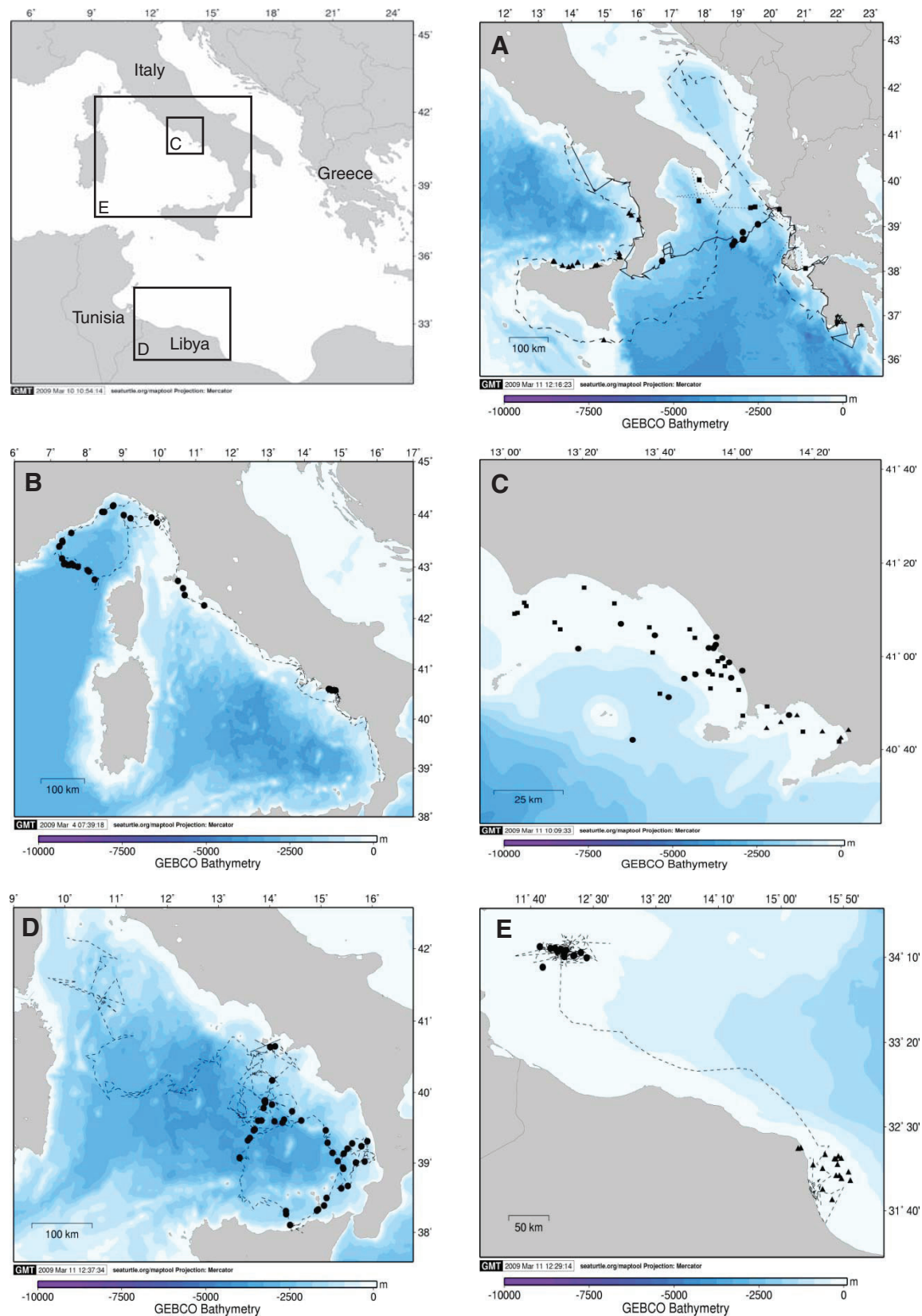


Fig. 1. Maps showing the locations of extended surface times (ESTs) (symbols) along the turtles' movement routes (lines). The first map indicates the location of the geographic region enlarged in panels C, D and E. For those turtles that stayed within a limited area, no movement routes are shown. Legend for the symbols/lines: (A) Turtle 15383: solid line with filled circles; turtle A: dotted line with filled squares; turtle B: broken line with filled triangles; (B) turtle E; (C) turtle 29359: filled circles; turtle G: filled squares; turtle 4395: filled triangles; (D) turtle C06; (E) turtle L1: broken line with filled circles; turtle L2: filled triangles.

the entire tracking period in the Tyrrhenian Sea (Fig. 1D). Finally, the turtles released from Libya (L1 and L2) both stayed in coastal waters close to the release site but L1 left the area around Misurata to settle farther to the west in an offshore shallow water habitat (Fig. 1E).

All turtles conducted ESTs but the total number of occurrences varied considerably between individuals, ranging from 18 to 161 (Table 1). For the different turtles, ESTs occurred on average once every 1.2 to 9.3 days, although intervals between successive ESTs were by no means regular. On average 56% (range 22–100%) of the total number of ESTs were transmitted with detailed data that were used for analysis (Table 1). Fig. 1 demonstrates that the location of ESTs occurred in both coastal and oceanic regions, either along the turtles' movement routes or in their coastal areas of residence. The 24 h summaries on the proportion of time spent either diving or in the upper 3 m surface waters or floating at the surface (i.e. EST) revealed no apparent pattern of EST occurrence with respect to time of year or the time spent diving during a day. For all turtles, there were one to several months of the tracking period during which ESTs occurred more frequently than during the remainder of the tracking period (i.e. EST periods) but there was no correspondence to any specific season (Fig. 2).

Duration and timing of ESTs

There were individual differences in the duration of ESTs with median values between 20 min and 143 min and maximum values ranging from 91 min to 17 h (Kruskal–Wallis test, $H=75.71$, d.f.=9, $P=0.000$, overall $N=271$; Table 2). Median EST duration tended to increase with body mass (Spearman rank correlation, $R_s=0.648$, $P<0.05$).

The majority of ESTs occurred during daytime (82.3%; Table 1), and all turtles (excluding turtles 4395 and 29359 for the above described reasons) engaged in ESTs significantly more often during the day than during the night (paired t -test: $t=-2.51$, $N=8$, $P<0.05$). Of those 191 ESTs that were recorded during the daytime the major part was initiated in the late morning and during the middle of the day (until 2 h after solar noon; Fig. 3). Much less EST occurred during the late afternoon and early evening. There was also a negative correlation between EST duration and the start time with regard to sunrise ($R_s=-0.37$, $P<0.001$); ESTs lasted longer (often several hours) when they were initiated in the early morning hours whereas ESTs towards sunset were of relatively short duration (<2 h; Fig. 4).

Diving activity during EST periods

It was difficult to make an analysis of the correlation between the dive behaviour immediately prior to EST events because of non-continuous data sets. Therefore, dive (and temperature, see following section) data are presented individually for each turtle (except 29359 and 4395) and refer to the turtle's EST periods. Descriptive statistics for dive duration and depth during EST periods are summarised in Table 3.

Three turtles made a majority of their ESTs during periods of diving in the open sea. Turtle C06 made longer ($N=849$, $W=112587.5$, $P<0.001$) and deeper dives ($N=849$, $W=144948.5$, $P<0.001$) at night, during the period when many ESTs were also recorded during the night (November 2006 to January 2007, Table 3). This turtle actually exceeded its cADL in 16% (178 out of 1112) of the dives (Fig. 5A), and all but four of these anaerobic dives occurred during the night.

All recorded ESTs of turtle 15383 were made in August 2002 when the turtle traversed the Ionian Sea. Also this turtle made longer ($N=295$, $W=31573.0$, $P<0.001$) and deeper ($N=295$, $W=144948.5$,

$P<0.001$) dives during the night. 7.6% of the pelagic dives exceeded the cADL of this turtle and all of them occurred during the night (Fig. 5B).

Turtle E made most of the ESTs during June and all occurred during daytime. This turtle showed diurnal activity, with less diving during the night, and dives were longer ($N=357$, $W=9334.5$, $P<0.01$)

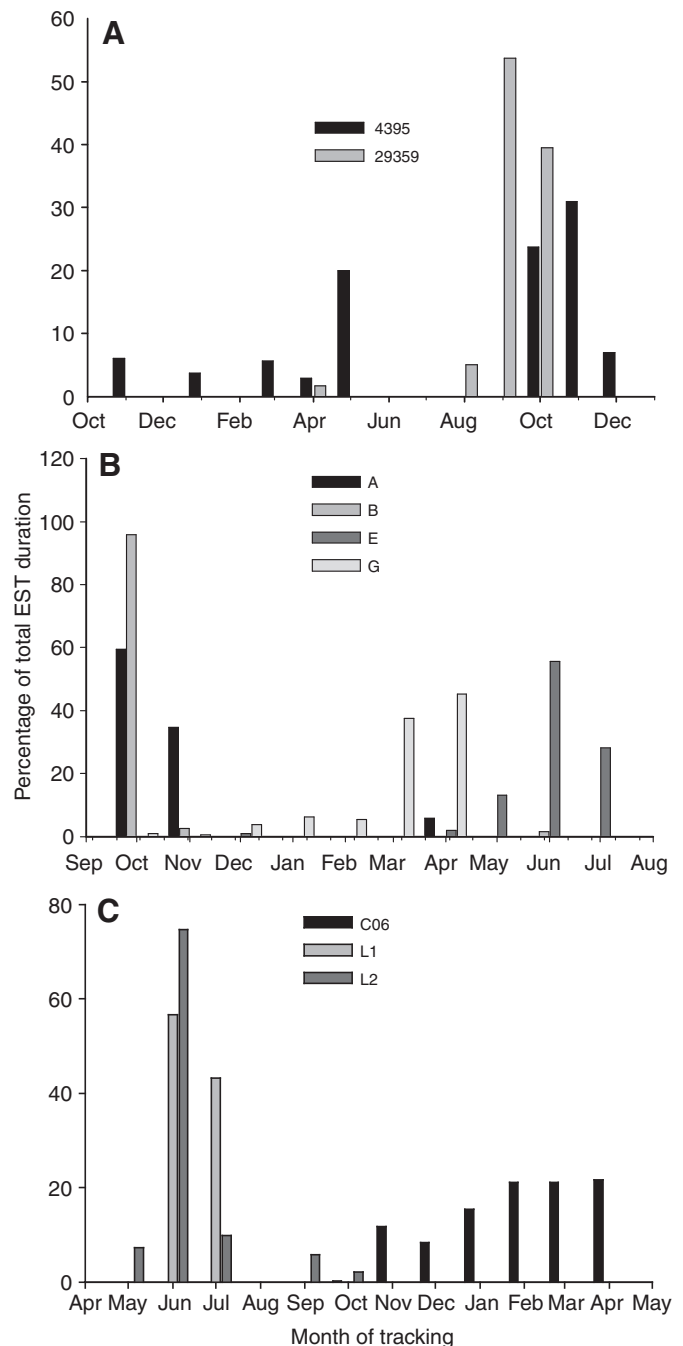


Fig. 2. The time that each turtle allocated each month to extended surface times (ESTs), expressed as the percentage of the total duration of ESTs (see also Table 2). Data for turtle 15383 are not shown because all recorded ESTs occurred only during the month of August. The different panels show data for turtles that were collected during the same tracking periods, and hence the time axes start with different months depending on the time at which turtles were released. (A) Turtles 4395, 29359; (B) turtles A, B, E, G; (C) turtles C06, L1, L2. Colour codes are given in the legends.

Table 2. Statistical summary of extended surface time (EST) duration (min) for 10 loggerhead turtles

Turtle	N_{rec}	Mean (min)	Median	s.d.	s.e.m.	Min	Max	Q1	Q3	Total (min)	% time
15383	7	108.7	60.5	119.5	45.2	13.5	360.3	40.0	148.3	761	1.03
29359	26	34.10	27.43	24.14	4.74	11.07	101.43	15.45	48.43	886.48	
4395	12	36.5	27.18	27.12	7.83	12.57	91.43	17.38	48.93	437.98	
A	9	46.6	38.2	35.0	11.7	10.3	114.4	22.5	64.9	419.55	0.41
B	18	95.5	84.9	71.2	16.8	22.8	293.9	38.7	132.9	1718.18	0.96
C06	104	208	142.9	183.8	18	11.3	779.9	48.2	365.9	21635.5	12.18
E	35	137.2	66.4	153.4	25.9	12.6	515.9	31.7	190.9	4801.45	1.81
G	25	101.6	37.1	209.6	41.1	10.3	1018.3	19.4	73.1	2640.73	0.76
L1	15	50.6	30.2	44.7	11.5	10.6	154.9	15.8	78.4	759.43	0.63
L2	20	46.1	20.6	60.9	13.6	10.3	240.9	10.7	56.7	922.38	0.78
Overall	209	89.21	41.18	125.41	8.67	10.32	1018.3	23.45	98.22		

Total refers to the sum of durations recorded for each individual. % time is an estimate of the proportion of time that turtles spent in EST with respect to the total time that they were tracked, considering also that the total duration is only a part of the actual total EST duration for which no data were transmitted (see Materials and methods for equation).

and deeper ($N=357$, $W=5883.0$, $P<0.001$) during the day. The maximum dive duration of this turtle was 60 min, and hence it never dived for more than 40% of its cADL (145 min).

Turtle A made most of its ESTs in October and November but too few dive data ($N=65$) and locations ($N=28$) were available during the period, and hence no data are presented here for this turtle.

Four turtles (B, G, L1, L2) dived in nearshore waters during EST periods. Turtle B was the only turtle that conducted ESTs during its travel along the northern coast of Sicily in October. Diving during the night was longer ($N=277$, $W=11836.5$, $P<0.001$) and deeper ($N=277$, $W=14474.0$, $P<0.001$) than during the day. The other three turtles were resident in nearshore shallow water habitats during EST periods and all ESTs (except one for turtle G) occurred during daytime. No significant difference between day and night diving was found for turtle L2 whereas turtle L1 made significantly longer ($N=801$, $W=44820.0$, $P<0.001$) and deeper ($N=801$, $W=32652.0$, $P<0.001$) dives during the day. By contrast, dives of turtle G were longer ($N=519$, $W=22811.0$, $P<0.001$) and deeper ($N=519$, $W=24516.0$, $P<0.001$) during the night, as for turtle B.

Water temperatures

For eight turtles (except turtles 15383 and L1) temperatures were available for random days that were however often different from the days for which ESTs were recorded. For turtle L1 the temperature

data were corrupted during transmission and were therefore excluded from the analysis. Three turtles dived through the thermocline during EST periods; turtle B when it travelled along the north Sicilian coast, turtle E during its stay in the Ligurian sea, and turtle L2 diving at the edge of the Libyan continental shelf. These turtles experienced temperature differences between surface waters and the maximum dive depth (ΔT) of up to 10°C (mean \pm s.e.m. = $2.8 \pm 0.5^{\circ}\text{C}$, $N=38$, Fig. 6). Maximum dive depth was significantly positively correlated with ΔT ($R^2=0.833$, $P<0.001$).

For all of the other turtles (29359, 4395, A, C06, G), there was no temperature difference between surface and the maximum dive depth (mean \pm s.e.m. = 0.02 ± 0.01 , $N=425$, $W=-7265.0$, $P>0.05$) over the entire tracking period.

DISCUSSION

Spatial and temporal occurrence of ESTs

The present study has shown that on certain occasions all turtles remained at the surface for periods longer than usual breathing intervals. Yet this does not contradict their categorisation as typical surfacers, i.e. animals that dive continuously and spent only a minimum amount of time at the surface for a quick gas exchange (Kramer, 1988). Quite the opposite, most turtles allocated only a small amount of their time ($<1-2\%$) to EST (Table 2), which may explain why this extraordinary surfacing behaviour has so far been

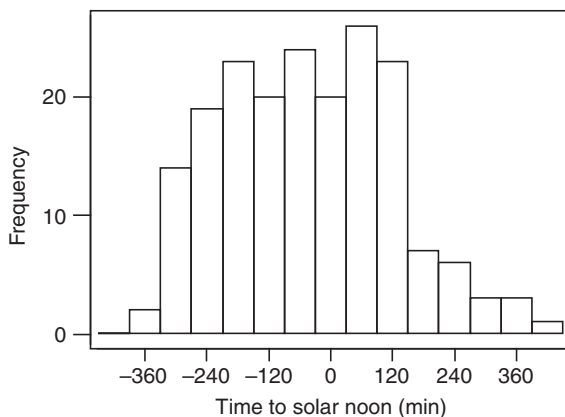


Fig. 3. The occurrence of extended surface times (ESTs) during daylight hours shown as number of ESTs starting within a given 1 h interval. The intervals refer to the time that passed between solar noon (at zero) and the start of each EST. Negative values indicate that the EST started before noon and positive numbers indicate when the EST started after noon.

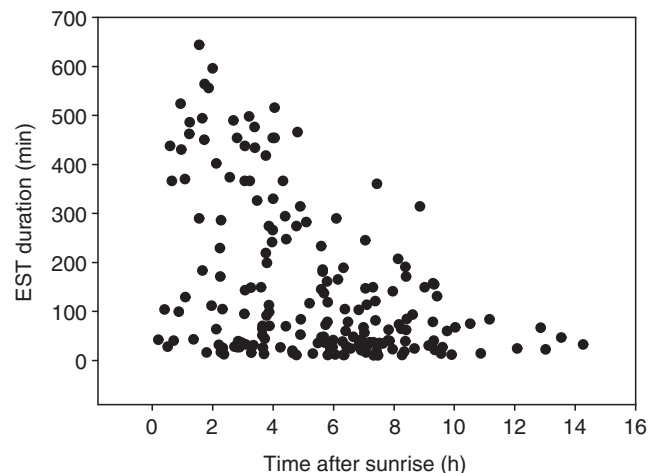


Fig. 4. The relationship between the duration of daytime extended surface times (ESTs) and the time of day at which the EST started, expressed as time (in h) after sunrise.

Table 3. Median (Q1–Q3) dive duration and maximum dive depth (MDD) during extended surface time (EST) periods

Turtle	Duration (min)		MDD (m)		Number of dives		Location
	Day	Night	Day	Night	Day	Night	
15383	6 (2–13)***	34 (11–63)	13.5 (7.5–34.5)***	34 (19.5–34.5)	129	166	Pelagic
B	2.5 (1–6)***	12 (5–22)	16 (10–28)***	24 (10–40)	122	155	Coastal
C06	1.3 (0.7–9)***	80 (12–105)	6 (4–10)***	12 (6–18)	405	444	Pelagic
E	3 (1–10)**	1 (0.8–5)	12 (6–24)***	4 (3–8)	294	63	Pelagic
G	4.3 (1.3–69.6)***	67.5 (3.1–176.5)	7 (3.9–14.1)***	13.2 (5.3–18.2)	313	206	Coastal
L1	9 (1.3–20)***	1.3 (0.7–7)	10 (5–90)***	4 (3–5)	338	464	Coastal
L2	9 (0.8–40)	26 (1–53.8)	5 (3–70)	6 (3–10)	79	63	Coastal

Statistical significant differences between day and night are indicated by asterisks (*** $P<0.001$, ** $P<0.01$).

neglected. Unfortunately, no general temporal or spatial pattern of ESTs could be detected because of the variability in individual behaviour. Indeed, surfacing behaviour occurred in various locations along both coastal and oceanic legs of the turtles' movements (Fig. 1). On a long-term scale there was no discernible seasonal pattern nor did the occurrence of ESTs peak during particular periods (Fig. 2). On a short-term scale instead, turtles showed a clear preference for daylight hours to remain at the surface, particularly when the sun was highest (Fig. 3). Yet sometimes turtles made ESTs also during the night, indicating that there may be multiple functions for this surfacing behaviour. Whatever the function(s) of ESTs, most of them seem to depend on the sun's radiation either as a heat source for thermoregulation or for other physiological needs.

The temporal and individual irregularity of EST occurrences exclude the function of a regulatory mechanism that is essential to the turtles' daily activities. More likely, certain combinations of behavioural patterns and environmental conditions are required for the turtle to gain benefits from prolonged surface periods. In the following we will discuss some scenarios of behaviour–environment relationships that were present in our data set and that may be explanatory for the possible functions of ESTs, in particular with regard to thermoregulation and anaerobic activities.

Light-dependent functions of EST

In some turtles, high frequency of EST occurrence corresponded to periods during which they dived repeatedly into deep waters below the thermocline, thereby experiencing temperatures that were up to 10°C lower than those of surface waters (Fig. 6). It has already been shown that diving activity in cold waters leads to decreases of body temperature (Sakamoto et al., 1990; Southwood et al., 2005). These turtles conducted ESTs exclusively during the day, which strongly suggests that they sought to warm up by basking at the water surface (Sapsford and Van der Riet, 1979). The high number of ESTs during the middle of the day (Fig. 3) indicates that turtles choose the hours when the sun was highest to maximise heat gain whereas turtles that commenced ESTs during early morning hours tended to stay longer (Fig. 4), probably because they did not gain the required heat due to shallow radiation angles and lower air temperatures (Boyer, 1965). Further support for the heating function of some ESTs is given by the correlation between body mass and EST duration, as it would take longer to heat up larger turtles (Boyer, 1965; Standora et al., 1982).

It is also worth considering that despite the evident advantage of heat gain, turtles may not make an endeavour to bask at the surface for thermoconformity reasons, because they would also recover their

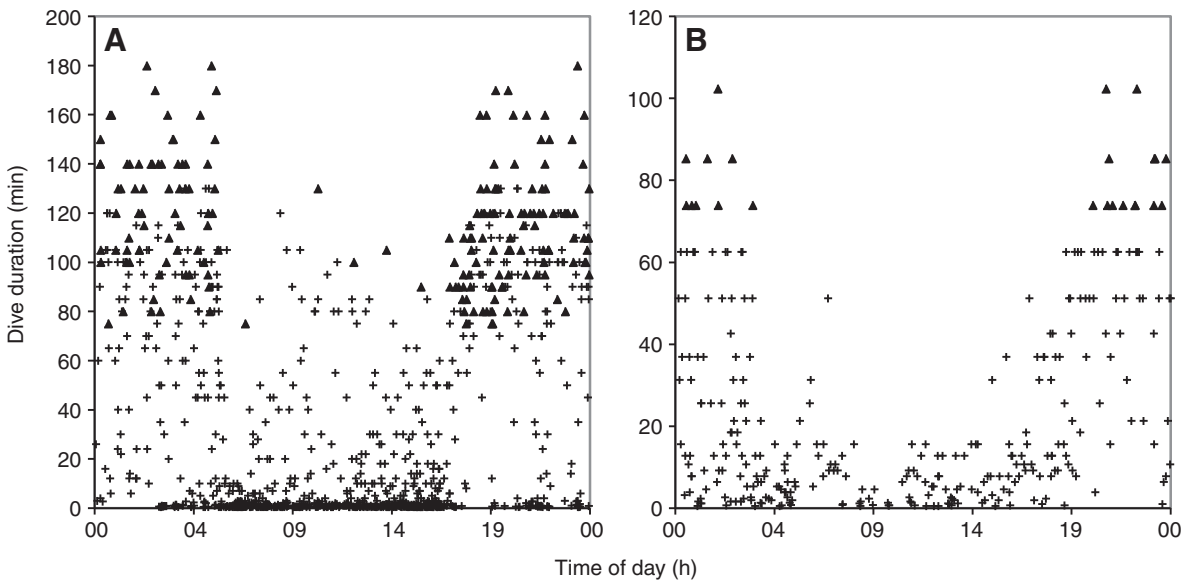


Fig. 5. Dive durations as a function of time of day for dives made during extended surface time (EST) periods by turtles C06 (A) and 15383 (B). Filled triangles indicate dives that exceeded the calculated aerobic dive limit (cADL) and crosses indicate dives that did not exceed cADL. Triangles and crosses may overlap when cADL for these dives was different because of different ambient temperatures experienced during the dives (see Materials and methods for more details on cADL calculations).

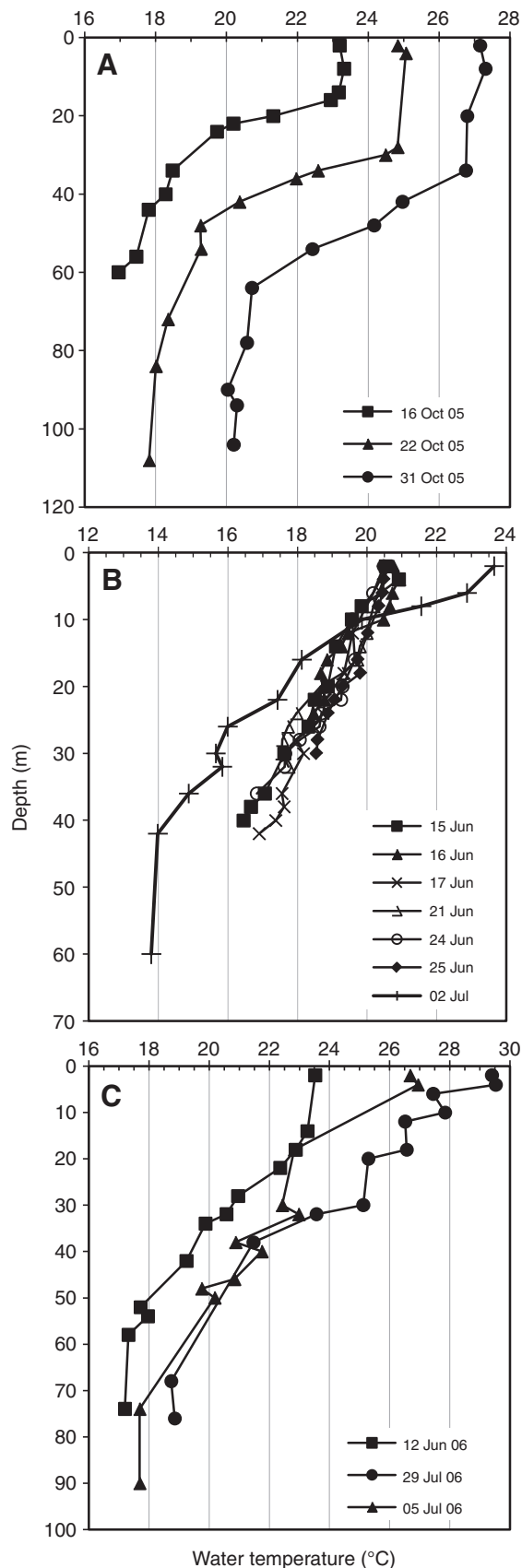


Fig. 6. Profiles of water temperature registered during diving of turtles B (A), E (B) and L2 (C). Please note differences in the scale that were due to the different depths frequented by the turtles and the different ranges of temperatures experienced during these dives.

initial body temperature (i.e. that before diving through the thermocline) by simply staying in the warmer surface layer (Hochscheid et al., 2002). More likely, they seek to accelerate heating rates through surface basking under favourable climatic conditions (Boyer, 1965), which may be beneficial for enhancing digestive processes (Carey et al., 1984; Spencer et al., 1998; Amorcho and Reina, 2008). This makes sense because the turtles dived through the thermocline to exploit prey of deeper water layers, and hence most likely returned to the surface with full stomachs. For ectothermic animals that live in temporally resource-sparse environments, thermoregulation for warmer body temperatures has been discussed as a means to maximise energy production in times when food is abundant (Carey et al., 1984; Waldschmidt et al., 1986; Zimmerman and Tracy, 1989). Also loggerhead turtles, particularly those foraging in pelagic habitats, are subject to patchy food distribution and hence would profit from maximising the rate of food processing by achieving favourable body temperatures when ample food is present.

Temperature decreases at depth were not responsible for ESTs of turtle G, yet it spent long periods at the surface particularly in the months of March and April when it resumed activity, and hence most likely feeding, after winter dormancy (Hochscheid et al., 2008). We can surmise the following scenario where the turtle is in need of refuelling energy stores after a long dormant period and therefore increases its food intake rate quite drastically despite the persistent cool water temperatures (mostly below 14°C in March). It is well known that marine iguanas foraging at Galapagos in waters between 22°C and 27°C spent long periods basking on the lava flows to maintain elevated body temperatures between 35°C and 37°C and thus improve digestion rate (Bartholomew, 1966; Buttemer and Dawson, 1993). Also our turtle G would have profited from thermoregulation by surface basking to periodically increase digestive efficiency. However, unstable climatic conditions during springtime are an inevitable drawback of aquatic basking and would consequently impede the turtle to do so on a regular basis. While these explanations fit well with the observed pattern of ESTs, future studies could further decipher this behaviour by relating it to meteorological parameters.

Behavioural thermoregulation appears important for a number of semi-terrestrial and aquatic turtles (Crawford et al., 1983; Dubois et al., 2009; Schofield et al., 2009). For example, breeding loggerhead turtles in Greece select the warmest water possible in semi-enclosed bays adjacent to their nesting beaches, apparently to maximise egg development rates prior to oviposition (Schofield et al., 2009). However, as well as being important for breeding turtles, our results also show the significance of behavioural thermoregulation for foraging turtles.

It goes without saying that maximum UV absorption for other reasons such as retardation of fungal and algal growth or vitamin D synthesis may also necessitate a coordination between the timing of ESTs and the hours of maximum radiation. It was not possible to investigate the involvement of ESTs in these non-thermoregulatory functions but at least the former is probably of less importance, because anti-fouling behaviour would be effective only for the exposed portion of the carapace. Vitamin D₃ is synthesised in the reptile skin only in the presence of UV light and is essential for calcium absorption from the intestine (Aaron, 1978; Barnes and Lawson, 1978). Therefore, sufficient UV exposure is important especially for young turtles that need calcium for bone growth (Frye, 1991). However, our study animals were already large juveniles and sub-adults and even infrequent ESTs may have been sufficient for Vitamin D₃ synthesis.

It might be argued that the transmitter itself may have affected the desired benefit of ESTs, considering that it was positioned on the top of the carapace, so that the device and the glue covered a large portion of the carapace's surface. Unfortunately, it was not possible to use the head as an alternative body part for the attachment (cf. Papi et al., 2000), because the SRDLs were too big to be fitted on the heads of the juveniles used in the present study. Future studies on surface basking and EST in marine turtles might consider measuring the heat flow through the epoxy glue experimentally and how the presence of the glue on the carapace affects heating rates in basking turtles. Whatever the likely effect may have been, it was equal for all turtles, because they were equipped in the same way.

Light-independent functions of ESTs

Obviously, for those ESTs that occurred during the night the above discussed light-dependent functions can be excluded. On days with calm sea conditions the turtles may have preferred the water surface to rest instead of diving either to the floor, or if not within reach, to a depth in mid water (Minamikawa et al., 2000; Hays et al., 2001). Thereby resting could have occurred at any time during day or night. Besides that, surface resting would be obligatory if the turtles were in need for lactate clearance after anaerobic activity (Hochachka and Somero, 2002). Nitrogen accumulation may also be a problem for air-breathing divers (Kooyman and Ponganis, 1998). However, it is most probably mitigated not by ESTs but by either behavioural (e.g. dive stops during ascent) or physiological (e.g. cardiovascular adjustments) means during diving (Fahlman et al., 2006).

It was striking that nocturnal ESTs were predominantly registered in two turtles diving in the open sea, and that these turtles often exceeded their cADL (Fig. 5A,B). As these turtles were clearly night active (longer and deeper dives), they were most likely foraging in the water column on prey that ascends to shallow depths during diel vertical migrations (Hays et al., 2004; James et al., 2006). Feeding on patchy resources may have led the turtles to extend their time underwater beyond their aerobic capacity to exploit the food patch as much as possible (Chappell et al., 1993; Boyd, 1997). This is actually the first indication for the use of anaerobic pathways in pelagic foraging loggerhead turtles, which have such low metabolic scopes that they are generally considered to dive well within their aerobic dive limit [Wallace and Jones (Wallace and Jones, 2008) and references cited therein].

Conclusions

We have based our analysis and interpretation mainly on correlations between ESTs and available data for water temperature and behaviour. Although correlations do not necessarily mean causality, it is particularly interesting that ESTs almost always occurred when turtles had either (a) conducted dives longer than their cADL, or (b) dived through a strong thermocline. These findings strongly suggest that ESTs serve at least dual functions: (a) to re-oxygenation following lactate accumulation, and (b) to rewarming following dives to cold water. Thus, when loggerhead sea turtles spend prolonged periods at the water surface they do not necessarily bask in the sun to thermoregulate, as confirmed by the lack of a temporal pattern (Sato et al., 1995). Nonetheless, the turtles may sometimes compensate for low body temperatures caused either temporarily by deep diving below the thermocline or more permanently by low winter temperatures, although we postulated that such behaviour may primarily serve digestive requirements. Further investigations using, for example, stomach temperature data loggers (Sato et al., 1994; Southwood et al., 2005) in combination with telemetry

techniques used in this study, are needed to evaluate this possibility. In addition, an integration with physical-meteorological data, in particular wave height, radiation intensity, wind speed and cloud cover, etc. should be foreseen. The low temporal and spatial predictability and the low frequency of occurrence of ESTs in loggerhead turtles makes the reasons for this behaviour difficult to elucidate. In fact, all but one turtle allocated only a small proportion of their time to EST (<2%). Intriguingly, the only turtle that remained in offshore habitats during the entire tracking period spent more than 12% of its time at the surface, in addition to the time required for gas exchange (Table 2). Although any conclusion based on a single individual would be premature, it suggests that ontogenetic shifts in behaviour between oceanic and neritic stage turtles (Bolten et al., 2003) warrant further investigations. ESTs might be of hitherto unrecognised importance for oceanic stage turtles, which forage in deep, often cold waters with patchy prey distribution and which can rest only at the water surface or in mid-water. Our work has also important potential conservation implications. Boat strikes are an important source of mortality for many air-breathing divers, including cetaceans, manatees and turtles (Aipanjiguly et al., 2003; Panigada et al., 2006; Bentivegna et al., 2009). Turtles may be hit by vessels when floating at the surface, and hence information on the location and factors driving ESTs may highlight critical zones in need of regulations on vessel traffic. Shipping has greatly expanded in the Mediterranean over the past half century and is expected to grow further (Dobler, 2002). Hence, it would also be worth investigating how long-term changes in vessel traffic may drive changes in EST behaviour.

ACKNOWLEDGEMENTS

This work was funded by a grant to G.C.H. from the Natural Environment Research Council of the UK (NERC). The missions to Libya were supported by the Environment General Agency (EGA) of Libya and the United Nations Environment Programme-Regional Activity Centre for Specially Protected Areas (UNEP-RAC/SPA, Tunisia), and we are especially grateful to A. Ouerghi from RAC/SPA for his commitment. Logistical support was also provided by the Stazione Zoologica Anton Dohrn in Naples (SZN). We acknowledge the use of the Maptool program (www.seaturtle.org) for Fig. 1. We are thankful to the staff of the SZN, particularly M. Ciampa, G. De Martino, F. Maffucci, G. Mazza, and G. Treglia for their assistance during the releases and the recovery of the turtles. The turtle releases were organized in collaboration with the 'Risorsa Mare' service and the Polizia of the city of Naples, G. Cataldini (Centro Studi Cetacei), S. Panzera (Museo di Calimera), and in a joint collaboration with the General Environment Authority (EGA) of Libya and the Marine Biology Research Centre (MBRC) of Tajura (Libya). Special thanks to the Libya team are due to E. Alsharif, H. Elghmati, A. Abuissa, M. Alshwehdi (MBRC), and to A. Saied and E. Buras (EGA) and the fishermen who caught the turtles. Finally, we would like to express our gratefulness to P. Lovell from Sea Mammal Research Unit for his tireless work and advice on the SRDL's. An earlier version of the manuscript was improved thanks to the valuable contributions of two referees.

REFERENCES

- Aaron, J. E. (1978). Histological aspects of the relationship between vitamin D and bone. In *Vitamin D* (ed. D. E. M. Lawson), pp. 201-265. New York: Academic Press.
- Aipanjiguly, S., Jacobson, S. K. and Flamm, R. (2003). Conserving manatees: knowledge, attitudes, and intentions of boaters in Tampa Bay, Florida. *Conserv. Biol.* **17**, 1098-1105.
- Amorcho, D. F. and Reina, R. D. (2008). Intake passage time, digesta composition and digestibility in east Pacific green turtles (*Chelonia mydas agassizii*) at Gorgona National Park, Colombian Pacific. *J. Exp. Mar. Biol. Ecol.* **360**, 117-124.
- Barnes, M. J. and Lawson, D. E. M. (1978). Biochemistry of bone in relation to the function of vitamin D. In *Vitamin D* (ed. D. E. M. Lawson), pp. 267-302. New York: Academic Press.
- Bartholomew, G. A. (1966). A field study of temperature relations in the Galapagos marine iguana. *Copeia*, 241-250.
- Bentivegna, F., Ciampa, M., De Martino, G., Maffucci, F., Paglialonga, A., Scalesse, R. and Hochscheid, S. (2009). Heavy boat traffic threatens loggerhead turtles in south-west Italian waters. In *Proceedings of the Second Mediterranean Conference on Marine Turtles* (eds A. Demetropoulos and O. Turkozian), pp. 50-52. Kemer, Turkey: Barcelona Convention – Bern Convention – Bonn Convention (CMS).
- Berkson, H. (1966). Physiological adjustments to prolonged diving in the Pacific green turtle (*Chelonia mydas agassizii*). *Comp. Biochem. Physiol.* **18**, 101-119.

- Bolten, A. B., Lutz, P. L., Musick, J. A. and Wyneken, J. (2003). Variation in sea turtle life history patterns: neritic vs. oceanic developmental stages. In *The Biology of Sea Turtles* (ed. P. L. Lutz), pp. 243-257. Boca Raton: CRC Press.
- Boyd, I. L. (1997). The behavioural and physiological ecology of diving. *Trends Ecol. Evol.* **12**, 213-217.
- Boyd, I. L. and Croxall, J. P. (1996). Dive durations in pinnipeds and seabirds. *Can. J. Zool.* **74**, 1696-1705.
- Boyer, D. R. (1965). Ecology of the basking habit in turtles. *Ecology* **46**, 99-118.
- Buttner, W. A. and Dawson, W. R. (1993). Temporal pattern of foraging and microhabitat use by Galapagos marine iguanas, *Amblyrhynchus cristatus*. *Oecologia* **96**, 56-64.
- Carbone, C. and Houston, A. I. (1996). The optimal allocation of time over the dive cycle: an approach based on aerobic and anaerobic respiration. *Anim. Behav.* **51**, 1247-1255.
- Carey, F. G., Kanwisher, J. W. and Stevens, E. D. (1984). Bluefin tuna warm their viscera during digestion. *J. Exp. Biol.* **109**, 1-20.
- Chappell, M. A., Shoemaker, V. H., Jones, D. N., Bucher, T. L. and Maloney, S. K. (1993). Diving behavior during foraging in breeding adie penguins. *Ecology* **74**, 1204-1215.
- Charnov, E. L. (1976). Optimal foraging: the marginal value theorem. *Theor. Popul. Biol.* **9**, 129-136.
- Chessman, B. C. (1987). Atmospheric and aquatic basking of the Australian freshwater turtle *Emydura macquarii* (Gray) (Testudines: Chelidae). *Herpetologica* **43**, 301-306.
- Crawford, K. M., Spotila, J. R. and Standora, E. A. (1983). Operative environmental temperatures and basking behavior of the turtle *Pseudemys scripta*. *Ecology* **64**, 989-999.
- Dobler, J. P. (2002). Analysis of shipping patterns in the Mediterranean and Black seas. In *Alien Marine Organisms Introduced By Ships In The Mediterranean And Black Seas* (ed. F. Briand), pp. 19-28. CIESM Workshop Monographs, No. 20. Monaco: CIESM (The Mediterranean Science Commission).
- Dubois, Y., Blouin-Demers, G., Shipley, B. and Thomas, D. (2009). Thermoregulation and habitat selection in wood turtles *Glyptemys insculpta*: chasing the sun slowly. *J. Anim. Ecol.* **78**, 1023-1032.
- Fahlman, A., Olszowska, A., Bostrom, B. and Jones, D. R. (2006). Deep diving mammals: dive behavior and circulatory adjustments contribute to bends avoidance. *Respir. Physiol. Neurobiol.* **153**, 66-77.
- Frye, F. L. (1991). *Reptile Care-An Atlas Of Diseases And Treatments*. Neptune City, New Jersey: T.H.F. Publications.
- Halsey, L. G., Woakes, A. J. and Butler, P. J. (2003). Testing optimal foraging models for air-breathing divers. *Anim. Behav.* **65**, 641-653.
- Hays, G. C., Adams, C. R., Broderick, A. C., Godley, B. J., Lucas, D. J., Metcalfe, J. D. and Prior, A. A. (2000). The diving behaviour of green turtles at Ascension Island. *Anim. Behav.* **59**, 577-586.
- Hays, G. C., Akesson, S., Broderick, A. C., Glen, F., Godley, B. J., Luschi, P., Martin, C., Metcalfe, J. D. and Papi, F. (2001). The diving behaviour of green turtles undertaking oceanic migration to and from Ascension Island: dive durations, dive profiles and depth distribution. *J. Exp. Biol.* **204**, 4093-4098.
- Hays, G. C., Houghton, J. D. R. and Myers, A. E. (2004). Pan-Atlantic leatherback turtle movements. *Nature* **429**, 522.
- Hochachka, P. W. (2000). Pinniped diving response mechanism and evolution: a window on the paradigm of comparative biochemistry and physiology. *Comp. Biochem. Physiol. A* **126**, 435-458.
- Hochachka, P. W. and Somero, G. N. (2002). *Biochemical Adaptation: Mechanism and Process in Physiological Evolution*. New York: Oxford University Press.
- Hochscheid, S., Godley, B. J., Broderick, A. C. and Wilson, R. P. (1999). Reptilian diving: Highly variable dive patterns in the green turtle, *Chelonia mydas*. *Mar. Ecol. Prog. Ser.* **185**, 101-112.
- Hochscheid, S., Bentivegna, F. and Speakman, J. R. (2002). Regional blood flow in sea turtles: implications for heat exchange in an aquatic ectotherm. *Physiol. Biochem. Zool.* **75**, 66-76.
- Hochscheid, S., Bentivegna, F. and Speakman, J. R. (2004). Long-term cold acclimation leads to high Q10 effects on oxygen consumption of loggerhead sea turtles, *Caretta caretta*. *Physiol. Biochem. Zool.* **77**, 209-222.
- Hochscheid, S., Bentivegna, F. and Hays, G. C. (2005). First records of dive durations for a hibernating sea turtle. *Biol. Lett.* **1**, 82-86.
- Hochscheid, S., Bentivegna, F., Bradai, M. N. and Hays, G. C. (2007a). Overwintering behaviour in sea turtles: dormancy is optional. *Mar. Ecol. Prog. Ser.* **340**, 287-298.
- Hochscheid, S., McMahon, C. R., Bradshaw, C. J. A., Maffucci, F., Bentivegna, F. and Hays, G. C. (2007b). Allometric scaling of lung volume and its consequences for marine turtle diving performance. *Comp. Biochem. Physiol. A* **148**, 360-367.
- Hochscheid, S., Bentivegna, F. and Hays, G. C. (2008). Winter ecology and physiology of sea turtles. In *Hypometabolism In Animals: Hibernation, Torpor And Cryobiology* (eds B. G. Lovegrove and A. E. McKechnie). Pietermaritzburg: University of KwaZulu-Natal.
- Houston, A. I. and Carbone, C. (1992). The optimal allocation of time during the dive cycle. *Behav. Ecol.* **3**, 233-262.
- James, M. C., Ottensmeyer, C. A., Eckert, S. A. and Myers, A. E. (2006). Changes in diel diving patterns accompany shifts between northern foraging and southward migration in leatherback turtles. *Can. J. Zool.* **84**, 754-765.
- Kooyman, G. L. (1989). *Diverse Divers*. Berlin: Springer-Verlag.
- Kooyman, G. L. and Ponganis, P. J. (1998). The physiological basis of diving to depth: birds and mammals. *Annu. Rev. Physiol.* **60**, 19-32.
- Kramer, D. L. (1988). The behavioral ecology of air breathing by aquatic animals. *Can. J. Zool.* **66**, 89-94.
- Lutcavage, M. E. and Lutz, P. L. (1997). Diving physiology. In *The Biology Of Sea Turtles* (ed. P. L. Lutz and J. A. Musick), pp. 277-296. Boca Raton: CRC Press.
- Lutz, P. L. and Bentley, T. B. (1985). Respiratory physiology of diving in the sea turtle. *Copeia*, 671-679.
- Manning, B. and Grigg, G. C. (1997). Basking is not of thermoregulatory significance in the 'basking' freshwater turtle *Emydura signata*. *Copeia*, 579-584.
- Minamikawa, S., Naito, Y. and Uchida, I. (1997). Buoyancy control in diving behaviour of the loggerhead turtle, *Caretta caretta*. *J. Ethol.* **15**, 109-118.
- Minamikawa, S., Naito, Y., Sato, K., Matsuzawa, Y., Bando, T. and Sakamoto, W. (2000). Maintenance of neutral buoyancy by depth selection in the loggerhead turtle *Caretta caretta*. *J. Exp. Biol.* **203**, 2967-2975.
- Panigada, S., Pesante, G., Zanardelli, M., Capoulade, F., Gannier, A. and Weinrich, M. T. (2006). Mediterranean fin whales at risk from fatal ship strikes. *Mar. Pollut. Bull.* **52**, 1287-1298.
- Papi, F., Luschi, P., Akesson, S., Capogrossi, S. and Hays, G. C. (2000). Open-sea migration of magnetically disturbed sea turtles. *J. Exp. Biol.* **203**, 3435-3443.
- RAC/SPA (2004). Guidelines to improve the involvement of marine rescue centres for marine turtles. Tunis: RAC/SPA.
- Renaud, M. L. and Carpenter, J. A. (1994). Movements and submergence patterns of loggerhead turtles (*Caretta caretta*) in the Gulf of Mexico determined through satellite telemetry. *Bull. Mar. Sci.* **55**, 1-15.
- Sakamoto, W., Uchida, I., Naito, Y., Kureha, K., Tujimura, M. and Sato, K. (1990). Deep diving behavior of the loggerhead turtle near the frontal zone. *Nippon Suisan Gakkaishi* **56**, 1435-1443.
- Sapsford, C. W. and Van der Riet, M. (1979). Uptake of solar radiation by the sea turtle, *Caretta caretta*, during voluntary surface basking. *Comp. Biochem. Physiol. A* **63**, 471-474.
- Sato, K., Sakamoto, W., Matsuzawa, Y., Tanaka, H. and Naito, Y. (1994). Correlation between stomach temperatures and ambient water temperatures in free-ranging loggerhead turtles, *Caretta caretta*. *Mar. Biol.* **118**, 343-351.
- Sato, K., Sakamoto, W., Matsuzawa, Y., Tanaka, H., Minamikawa, S. and Naito, Y. (1995). Body temperature independence of solar radiation in free-ranging loggerhead turtles, *Caretta caretta*, during interesting periods. *Mar. Biol.* **123**, 197-205.
- Schofield, G., Bishop, C. M., Katselidis, K. A., Dimopoulos, P., Pantis, J. D. and Hays, G. C. (2009). Microhabitat selection by sea turtles in a dynamic thermal marine environment. *J. Anim. Ecol.* **78**, 14-21.
- Southwood, A. L., Andrews, R. D., Paladino, F. V. and Jones, D. R. (2005). Effects of diving and swimming behavior on body temperatures of Pacific leatherback turtles in tropical seas. *Physiol. Biochem. Zool.* **78**, 285-297.
- Spencer, R.-J., Thompson, M. B. and Hume, I. D. (1998). The diet and digestive energetics of an Australian short-necked turtle, *Emydura macquarii*. *Comp. Biochem. Physiol. A* **121**, 341-349.
- Standora, E. A., Spotila, J. R. and Foley, R. E. (1982). Regional endothermy in the sea turtle, *Chelonia mydas*. *J. Therm. Biol.* **7**, 159-165.
- Swimmer, Y. (2006). Relationship between basking and fibropapillomatosis in captive green turtles (*Chelonia mydas*). *Chel. Conserv. Biol.* **5**, 305-309.
- van Dam, R. P. and Diez, C. E. (1996). Diving behaviour of immature hawksbills (*Eretmochelys imbricata*) in a Caribbean cliff-wall habitat. *Mar. Biol.* **127**, 171-178.
- van Dam, R. P. and Diez, C. E. (1997). Surfacing behaviour of the marine turtle *Eretmochelys imbricata*. *J. Herpetol.* **31**, 313-316.
- Waldschmidt, S. R., Jones, S. M. and Porter, W. P. (1986). The effect of body-temperature and feeding regime on activity, passage time, and digestive coefficient in the lizard *Uta stansburiana*. *Physiol. Zool.* **59**, 376-383.
- Wallace, B. P. and Jones, T. T. (2008). What makes sea turtles go: metabolism and its consequences. *J. Exp. Mar. Biol. Ecol.* **356**, 8-24.
- Walton, P., Ruxton, G. D. and Monaghan, P. (1998). Avian diving, respiratory physiology and the marginal value theorem. *Anim. Behav.* **56**, 165-174.
- Whitrow, G. C. and Balazs, G. H. (1982). Basking behaviour of the Hawaiian green turtle (*Chelonia mydas*). *Pac. Sci.* **36**, 129-139.
- Zimmerman, L. C. and Tracy, C. R. (1989). Interactions between the environment and ectothermy and herbivory in reptiles. *Physiol. Zool.* **62**, 374-409.