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Overwintering behaviour in sea turtles: dormancy is optional

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ABSTRACT: Thirteen loggerhead turtles *Caretta caretta* were released (10 from Naples, Italy, 2 from Monastir, Tunisia, 1 from Gallipoli, South Italy) with satellite relay data loggers (SRDL) to elucidate their overwintering behaviour. Nine turtles were successfully tracked throughout the winter, while 4 SRDLs failed to transmit after short deployment periods. Of these 9, 4 remained within 80 km of the release site, 3 travelled to a distant overwintering site, and 2 continued to move and did not remain within 80 km of a specific site. Apart from these differences, all turtles stayed near the coast and dedicated most of their time to dives lasting 3 h and longer. Maximum dive durations ranged from 270 to 480 min and were highly correlated with water temperatures, which fell below the supposed 15°C threshold for sea turtle hibernation in all overwintering sites. Median dive depths were between 4 and 24 m and were, thus, well within the mixed layer, as revealed by temperature profiles, which also were relayed by the SRDLs. No evidence was found that the turtles preferred warmer temperatures to overwinter in, because the range of temperature was very narrow on both the horizontal and the vertical scale of their movements. Despite the long resting phases and the low temperatures (minimum = 11.8°C) all turtles retained activity to some degree, at least to commute between the depth of resting and the surface to breathe. While the degree of winter dormancy is certainly affected by temperature, turtles were by no means obligatory hibernators, and their ability to move and even forage during the winter may be important for their growth and maturation rates, as well as their reproductive output.

KEY WORDS: *Caretta caretta* · Hibernation · Seasonal · Diving behaviour · Temperature · Satellite tracking

INTRODUCTION

The choice of an appropriate overwintering strategy may be limited in aquatic habitats, in particular for ectothermic animals. Fish or turtles that live in lakes do not have the possibility of moving towards the equator to find warm waters and, hence, they must generally endure a reduction of metabolic rate as a consequence of their inability to keep their body temperature above ambient temperature. Water bodies can also become partially or, in extreme cases, completely frozen, which poses the additional challenge of anoxia for all inhabitants. Both laboratory and field studies on hibernating freshwater turtles have increased our knowledge on the ecology of hibernation in this group of ectotherms. Although it has been widely discussed whether the term hibernation is applicable to the nature of the ectotherm overwintering mode, Ultsch (1989) pointed out that the Latin origin of the word 'hibernation' does not imply any physiological state of the animal. Keeping in mind that metabolic rates as well as many other life functions of ectothermic animals are dictated by ambient temperature rather than by physiological control by the animal itself, it is nonetheless appropriate to use the term 'hibernation' also to describe the

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status of ectotherms that employ a similar overwintering strategy to that of mammalian hibernators.

Underwater hibernation requires the capability of air-breathing vertebrates to tolerate prolonged submergences (Reese et al. 2001). Freshwater turtles that live in habitats with severe cold winters and ice-covered lakes stay submerged for several months at a time (see Ultsch [2006] for a most recent review). However, water under ice may become oxygen depleted and the important respiratory pathway via the skin or the buccopharyngeal area can no longer be effective. Consequently, to avoid life-threatening development of acidosis and lactate accumulation, turtles, which are often buried in the mud, may come out of their burrows and move into better oxygenated water (Ultsch 1989, Reese et al. 2001).

Interestingly, sea turtles, which are confronted with less severe winter conditions than their freshwater relatives, have been reported to seek refuge in underwater hibernacula also by burying in the mud (Felger et al. 1976). However, not all sea turtle species seem to use this strategy, and of those which do only certain populations are known to hibernate, such as green turtles *Chelonia mydas* in the Baia California, Mexico and loggerhead turtles *Caretta caretta* in the Cape Canaveral area, Florida, USA (Ogren & McVea 1995). Felger et al. (1976) suggested that water temperatures below 15°C provoke hibernation in sea turtles that become dormant on the sea floor and do not re-emerge for as long as the low water temperatures persist, even for months. However, so far, studies attempting to experimentally induce hibernation in sea turtles have not been successful (Moon et al. 1997) and only a few recent studies on free-living sea turtles during the winter period have been conducted (Southwood et al. 2003, Hochscheid et al. 2005). By means of satellite relay data loggers (SRDLs) Hochscheid et al. (2005) showed that one loggerhead turtle overwintering in Greece at temperatures below 15°C surfaced regularly after submergences that lasted for several hours. This behaviour did not suggest underwater hibernation, but may not have been much different to the behaviour of freshwater turtles found at the same temperature range.

Knowing the mode of overwintering in sea turtles will contribute to an understanding of their life history patterns. Since periods of dormancy are linked to a net energy loss and, hence, to reduced growth rates and reproductive output, the behavioural choices of sea turtles may have important consequences for their population dynamics. Our study was undertaken to elucidate how loggerhead turtles in the temperate Mediterranean live through periods with seasonally low temperatures, by contemporaneously measuring ambient temperature, turtle movements and dive parameters.

MATERIALS AND METHODS

Study animals. Thirteen loggerhead turtles were equipped with SRDLs (Sea Mammal Research Unit, University of St. Andrews) between July 2002 and October 2005. The units were attached to the anterior central scutes of the carapace using fast setting epoxy resin (Power-Fast®, Power Fasteners). Before the attachment the SRDLs were weighed in air and in water to evaluate the effective weight added to the turtle. In air the transmitters weighed 390 g and in water 110 g, which equalled 0.8% of the body mass of the smallest turtle used in this study (range of body mass 13 to 52 kg, Table 1). All turtles were found in the western Mediterranean Sea, except Turtles A and 15119, which were found on the South coast of Italy bordering the Ionian Sea. As part of a sea turtle rescue and conservation programme all turtles (except 9541 and 9543) were recovered and transferred to the Rescue and Rehabilitation Centre of the Stazione Zoologica Anton Dohrn in Naples, Italy. Turtles 9541 and 9543 were caught by bottom trawl (9541 near Gabès and 9543 just south of Sfax) and were transferred to the Rescue Centre of the Institut National des Sciences et Technologies de la Mer (INSTM) in Monastir, Tunisia. At the Rescue Centre, turtles were kept in individual tanks with circulating sea water, provided with food and received treatment and medication prescribed by a veterinary consultant. Turtles which had no health problems were released after 2 d, others remained in observation for periods of 47 to a maximum of 366 d until the veterinarian confirmed that the turtles had recovered completely (Table 1). Both the Naples and the Monastir Rescue Centre conform to the 'Guidelines to Improve the Involvement of Marine Rescue Centres for Marine Turtles' published by RAC-SPA (2004).

Releases. The turtles were set free from 3 main release sites located in the area where they were first found (except Turtle 15119, Table 1): (1) the Gulf of Naples (40° 45′ N, 14° 00′ E), (2) just outside the Monastir harbour (35° 46′ N, 10° 49′ E), and (3) the Baia Domizia Littoral north of Naples close to the city of Mondragone (41° 07′ N, 13° 53′ E). Turtle A was the only turtle to be released in the Southeast of Italy close to Gallipoli (40° 03′ N, 17° 59′ E). Releases were undertaken either from a boat (Gulf of Naples, Monastir) or from the beach (Baia Domizia, Gallipoli).

Instruments and tracking. The SRDLs were fitted with an internal clock, a pressure sensor for dive depth measurements and a temperature sensor (the latter was not included in the SRDL of Turtle 15383). All recorded data were processed and compressed onboard before being transmitted via the Advanced Research and Global Observation Satellite (ARGOS, www.argosinc.com) system. The SRDLs were also

Table 1. *Caretta caretta*. Turtle identification (ID), body mass (M_b [kg]) and curved carapace length (CCL [cm]) on the day of their release. The table also shows the date when each turtle arrived in the Rescue Centre (Arrival), the date of release, the date of the last uplink to the satellite, which could still have provided dive data but not necessarily a successful location (refers to the last uplink when the turtle was still alive, in cases where the turtle died), the total number of days that each turtle was monitored and the date of the last valid location. n.a.: not applicable, no location available

ID	M_b (kg)	CCL (cm)	Date of arrival	Site of capture	Latitude/Longitude	Release location	Date of release	Date of last uplink	Number of days monitored	Date of last location
15383	52	73.51	08/10/01	Terracina, SW Italy	(41° 17' 24" N, 13° 14' 58" E)	Gulf of Naples	23/07/02	08/03/03	228	12/02/03
15119	49.63	76	28/06/03	Montegiordano, S Italy	(40° 02' 25" N, 16° 36' 28" E)	Gulf of Naples	04/05/04	07/08/04	95	10/05/04
15120	33.33	63.4	31/03/04	Bacoli–Naples, SW Italy	(40° 47' 47" N, 14° 04' 23" E)	Gulf of Naples	24/06/04	08/08/04[a]	45	n.a.
4394	18.8	52.7	25/06/04	Capo Miseno–Naples, SW Italy	(40° 46' 56" N, 14° 05' 05" E)	Gulf of Naples	13/09/04	18/09/04[b]	5	18/09/04
29359	29.46	63.2	19/07/04	Capri, Naples, SW Italy	(40° 33' 10" N, 14° 14' 19" E)	Gulf of Naples	13/09/04	26/10/05	408	25/10/05
4395	30.09	61.5	24/03/04	Montecorice, SW Italy	(40° 13' 09" N, 14° 59' 03" E)	Gulf of Naples	13/09/04	07/12/05	450	07/12/05
9543	13.1	46.5	27/02/05	Sfax, Tunisia	(34° 44' 57" N, 10° 46' 06" E)	Monastir	01/03/05	09/04/06	404	20/02/06
9541	46	75	27/02/05	Gabès, Tunisia	(33° 53' 27" N, 10° 10' 12" E)	Monastir	01/03/05	16/07/05	137	09/07/05
C	17.25	52.5	02/10/04	Gaeta, SW Italy	(41° 12' 55" N, 13° 34' 02" E)	Baia Domizia	03/10/05	08/10/05[c]	5	08/10/05
G	19.65	55	17/08/05	Ostia, SW Italy	(41° 43' 44" N, 12° 16' 29" E)	Baia Domizia	03/10/05	01/06/06[d]	242	01/06/06
E	42.13	70	21/05/05	Positano, SW Italy	(40° 37' 38" N, 14° 29' 13" E)	Baia Domizia	03/10/05	15/07/06	285	15/07/06
B[e]	50.25	67.5	02/10/04	Capri, SW Italy	(40° 33' 10" N, 14° 14' 19" E)	Baia Domizia	03/10/05	14/06/06	255	12/06/06
A	34.5	63	18/02/05	Frassanito, SE Italy	(40° 13' 22" N, 18° 27' 46" E)	Gallipoli	15/10/05	21/08/06	310	17/06/06

[a]recovered alive on 18 January 2005 in the Gulf of Naples
[b]stranded dead on 25 September 2004 on a beach south of Montecorice
[c]stranded dead on 15 October 2005 on a beach north of Gaeta
[d]recovered alive on 14 June 2006 at Castel Volturno
[e]this turtle was first found at Salerno (40°40'47"N, 14°45'19"E) on 28 January 2001, and then again at the island of Capri on 23 March 2003

equipped with a saltwater switch that was interrupted each time the turtle was at the surface and the switch became dry, at which time the SRDL began to transmit immediately.

Animals were tracked with the Argos system. All locations on land and those which indicated track reversals or recorded unnaturally high swim speeds (> 9 km h^{-1}) were removed from further analysis.

Dive parameters. Each SRDL was configured to register a dive when the turtle descended below 3 m for at least 30 s and the end of a dive when the turtle ascended above 3 m or when the saltwater switch was dry at any time. This depth limitation was necessary to capture the highest possible number of dives for transmission, not counting shallow dives close to the surface, which are often difficult to distinguish from short inter-breath submergences and occur when turtles travel. However, this configuration may potentially underestimate the dive ratios for turtles that preferably dived to shallow depths. Information on single dives as well as summary data for 24 h periods was transmitted. Parameters for single dives included the time at the end of the dive, the duration of the dive, the time spent at the surface after the dive and the maximum depth reached during the dive. For some dives, profiles were also transmitted as the time and depth of the 5 most significant points of inflection together with the time at the end of the dive and the dive duration. The 24 h summary data included the proportion of time spent either diving or at the surface (i.e. above 3 m), the number of dives, and the mean ± SD and maximum values for both dive duration and dive depth. The resolution of the transmitted dive parameters are given in Table 2. We had previously validated that these satellite derived dive parameters are of the same quality provided by data loggers (Myers et al. 2006).

Temperature data. Temperature was measured every 4 s between 2 and 200 m in bins of 2 m. Of all temperatures measured, 12 points of inflection were selected to represent the temperature

Table 2. Resolution of dive parameters transmitted by the satellite relay data loggers. na = not available

Depth bin (m)	Resolution (m)
3–6	1
6–30	2
30–50	5
50–100	10
100–220	20
Duration bin (min)	**Resolution (s)**
<1	10
1–3	20
3–10	60
10–30	120
30–120	300
120–180	600
180–240	1200
240–360	1800
360–720	7200
720–1080	10 800
>1080	na

profile over the depth range used by the turtle. The temperatures were transmitted with a resolution of 0.01°C and with an accuracy of 0.1°C. We have validated the long term accuracy (0.1°C) of these satellite relayed temperature data (McMahon et al. 2005). Additionally, monthly average sea surface temperatures (SST) were obtained for each winter site using the Advanced Very High Resolution Radiometer (AVHRR) Global SST colour maps provided by the Maptool (www.seaturtle.org) (as in Fig. 1).

Data analysis. Unless stated otherwise, dive data presented here refer to the period beginning December 21 and ending March 21, which we defined as winter. Dives for which profiles were available were assigned to 4 different dive types, including U-dives, type 3 dives, S-dives and V-dives (Fig. 2). These are typical dive types for sea turtles, described in detail by Hochscheid et al. (1999) and Houghton et al. (2002). In essence, during a U-dive a turtle spends a large proportion of the total dive duration at the maximum dive depth of that dive; during V-dives the turtle dives to the maximum dive depth and ascends without spending time at that depth; during S-dives the turtle dives to the maximum depth and returns immediately with a short and fast ascent, followed by a longer phase (45% of the total dive duration, cf. Hochscheid et al. 1999) with a reduced ascent rate; finally, Type-3 dives are like S-dives without the initial steep ascent, so that the slow ascent starts immediately upon reaching the maximum dive depth.

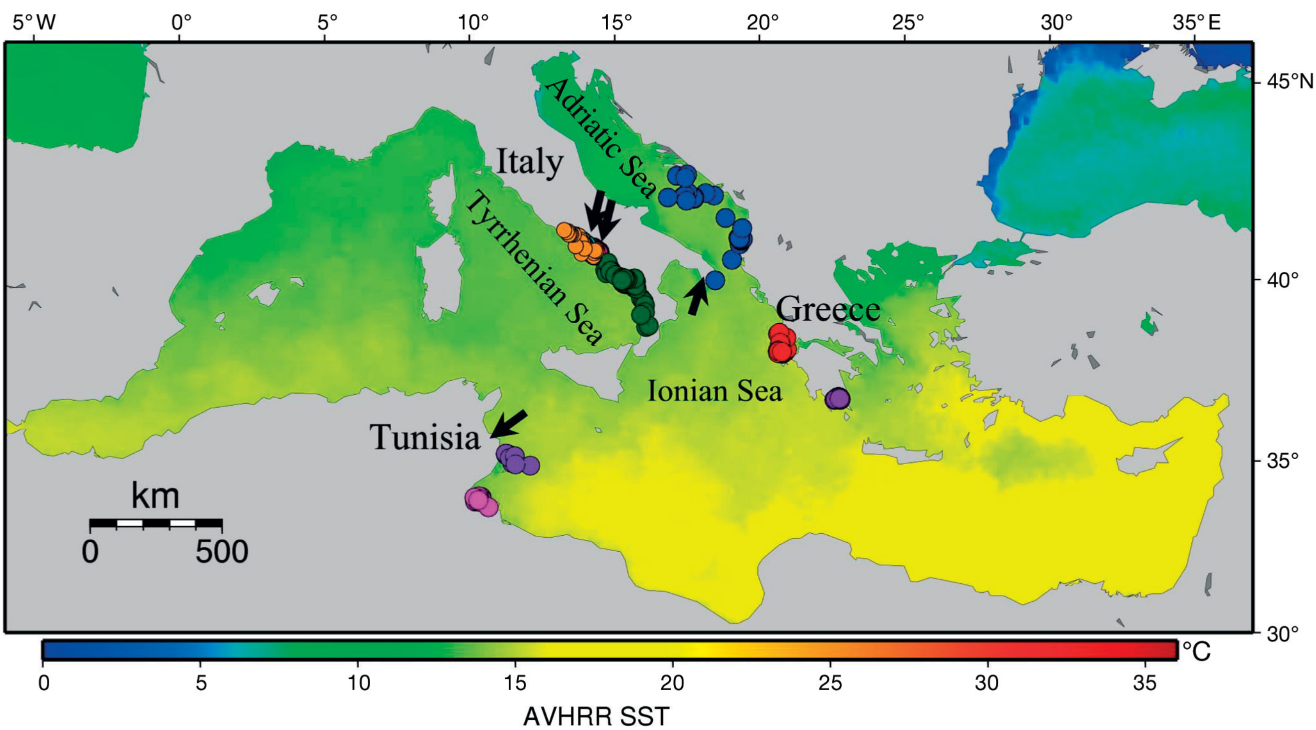

Fig. 1. *Caretta caretta*. Winter sea surface temperature in the Mediterranean Sea and the overwintering locations (coloured circles) of 9 loggerhead turtles monitored in this study. The release sites are indicated by arrows. Background colour shows the average sea surface temperature (AVHRR: Advanced Very High Resolution Radiometer) for February 2006. Colour of circles corresponds to turtle identification codes: orange = G, 29359 and 4395; purple = 15383; pink = 9541; violet = 9543; red = A; blue = B; green = E

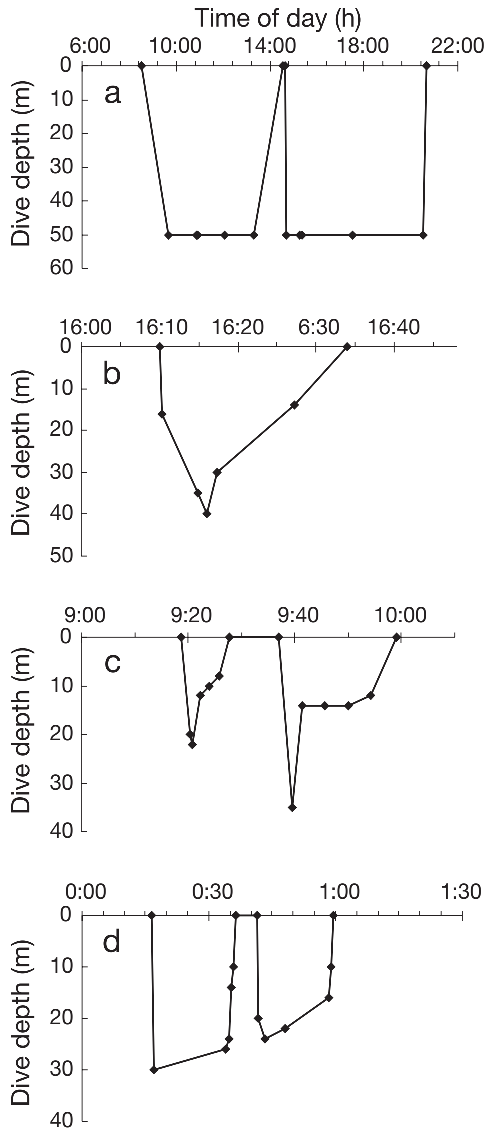

Fig. 2. *Caretta caretta*. Typical dive profiles relayed via satellite as the 5 most significant points of inflection. Note that the scales of the axes of the graphs were chosen to present each dive profile in the best dimension, and hence there are differences in the scales of the 4 panels. (a) 2 U-dives performed by Turtle 4395, (b) a V-dive by Turtle B, (c) 2 S-dives by Turtle A, (d) 2 Type 3 dives by Turtle B

RESULTS

Data volume

Three of the SRDLs worked for a relatively short time of between 5 and 95 d and did not last until the beginning of the winter. The other transmitters worked on average for 262 d, with 3 transmitters working for over 400 d (Table 1). Data were received from all turtles for a total of 8390 dives and winter data were available for 9 of the 13 equipped turtles. Due to a software problem of the SRDLs of Turtles 29359 and 4395 the dive (and temperature) data were not always transmitted with the correct date and time. Therefore, these dives were not included in the analysis since it could not be determined with certainty which dives occurred during the winter period. Summary data for 24 h periods were available for Turtles A, B, E, G, 15383, 9541 and 9543.

Turtle movements and winter habitat

Seven turtles were successfully tracked from the day of release until winter, whereas the 2 turtles from Tunisia (9541 and 9543) were released when it was still winter and continued to transmit data for several months afterwards (one even until the following winter). The turtles showed different movement patterns with respect to their release site and differed in the choice of their overwintering habitat. Four turtles (29359, 4395, 9543, G; Fig. 1) overwintered within 80 km of their release site, 3 turtles (15383, 9541, A) moved to a distant (>80 km) overwintering site and 2 turtles (E, B) continued to move during the winter and did not remain within 80 km of a specific site. Turtle 15383 travelled farthest covering a total distance of 2989 km between the release site and the winter site, followed by Turtles A and 9541 travelling 878 km and 234 km, respectively. Turtles B and E travelled a total of 3190 and 1274 km, respectively; 658 km and 568 km of the total distance were covered during the winter period. Since there was no location for Turtle B after February 10, 2006, the distance covered during the winter period is better expressed as distance travelled per day, which was (13 km d^{-1}) for Turtle B and 6.3 km d^{-1} for Turtle E.

Ambient temperature

Most temperature profiles were received from Turtles B, E and G (n = 35, 46 and 36, respectively), while for Turtles A, 9541 and 9543 n = 7, 4 and 2 temperature profiles, respectively, were available. Because of the software problem of the SRDLs of Turtles 29359 and 4395 mentioned above the temperature data from these units were not considered here. An example of the seasonal change in water temperature in the upper 2 m layer as experienced by Turtles E and G is found in Fig. 3. The difference in water temperature between the release date and the coldest temperature measured in February 2006 was 10°C in the Tyrrhennian Sea, with minimum temperatures between 12.5°C and 13.4°C. Winter water temperatures were colder in the

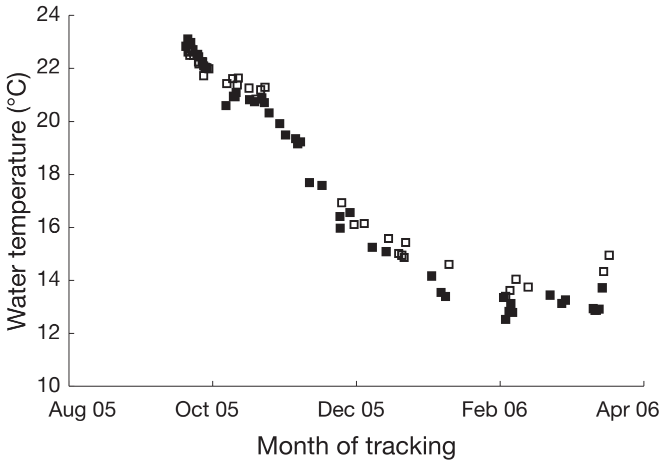

Fig. 3. *Caretta caretta*. Seasonal variation in water temperature in the upper 2 m layer, measured by satellite relay data loggers attached to the carapace of Turtles E (□) and G (■)

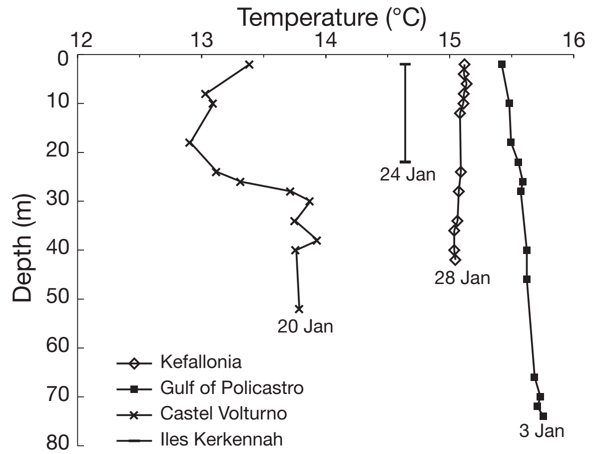

Fig. 4. Vertical temperature profiles for 4 coastal loggerhead turtle overwintering sites in the Mediterranean (Kefallonia, Greece; Gulf of Policastro, Italy; Castel Volturno, Italy; Iles Kerkennah, Tunisia)

western Mediterranean and increased towards the Eastern basin (Fig. 1). Because of the strong seasonal character of the temperature regime in the Mediterranean, all turtles monitored in this study were subject to temperatures below 15°C, whether they stayed close to the release site or left the area to overwinter elsewhere (Fig. 1). None of the turtles moved into the far eastern sector or to the Libyan coast, where they could have encountered warmer temperatures (Fig. 1). Average SST in December was 18 to 18.5°C in all overwintering sites, but in January SST dropped to average values between 13.5°C and 15.6°C in all sites except the Gulf of Laconia (Greece) where SST remained around 18°C. February was the coldest month and temperatures differed slightly between the winter sites. The turtles overwintering in Greece experienced average SST of 14.6 to 14.9°C, while Turtle B was subject to 13.5°C, and turtles in the South Tyrrhenian between 12.8 and 13.7°C. There was a 2°C difference between the SST in the Tunisian wintering sites, where Turtle 9541 experienced the coldest mean water temperature of 11.8°C.

Vertical temperature profiles showed that the water column at the different wintering sites was well mixed, so that the turtles experienced usually less than 1°C differences between surface water temperature and temperature at depth (Fig. 4, mean ± SE temperature difference for Turtles A [n = 3], E [n = 10], and G [n = 13] was 0.008 ± 0.04, −0.11 ± 0.06, and −0.1 ± 0.05°C, respectively). For this reason, temperatures from the upper 2 m layer were considered to be representative of the temperatures experienced in general by each turtle during diving and used in subsequent tests of correlation between temperature and diving behaviour.

Diving behaviour

There was a strong seasonal pattern in the dive duration of all turtles with an increase in dive duration at the beginning of the winter period, long dives all through the winter and shorter dives in the summer months (Fig. 5). Variation in temperature explained 56% of the increase in logarithmically transformed daily maximum dive durations (ln [maximum duration] = 6.944 − 0.116 × SST), $F_{1,88}$ = 110.5, $p < 0.001$; Fig. 6).

All turtles that remained resident at a specific site during the winter, either in the vicinity of the release site or at a distant location, stayed close to the coast in shallow water (Fig. 7). Also, Turtle E which travelled along the southwestern Italian coast during the winter

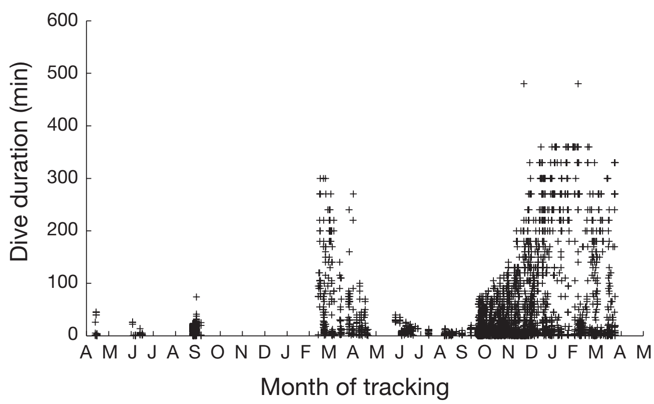

Fig. 5. *Caretta caretta*. Seasonal variation in dive duration of 8 loggerhead turtles monitored during the winter 2004–2005 and 2005–2006 in the Mediterranean. Months with missing data points are periods where turtles were not tracked and/ or transmissions of previously tracked turtles had ceased

remained close to the coast. Although the turtles had different depth utilisations ($H = 102.4$, df = 6, $p < 0.001$), all except Turtle B spent most of their time at depths shallower than 30 m (Fig. 8, Table 3). Turtle B, which utilised deeper water ≥40 km offshore for part of the winter period (Fig.1), spent most of its time at depth between 75 and 80 m (Fig. 8e). Seventy-seven percent of the dive profiles were U-dives, while Type 3 dives,

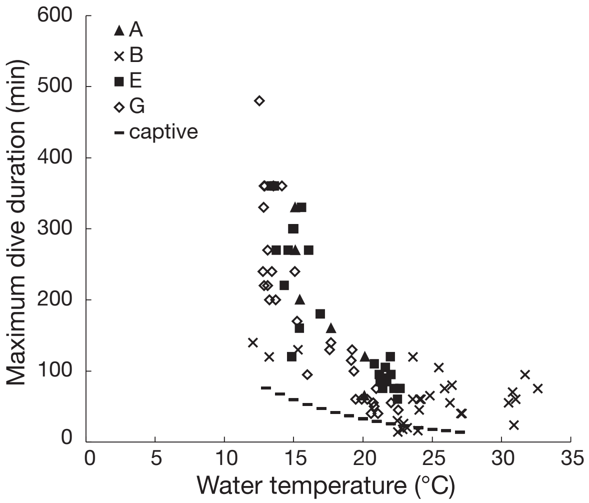

Fig. 6. *Caretta caretta*. Correlation between water temperature and daily maximum dive duration for 4 free-ranging loggerhead turtles.The relationship for captive turtles (**–** captive), established by Bentivegna et al. (2003), was inserted into the graph for comparative purposes

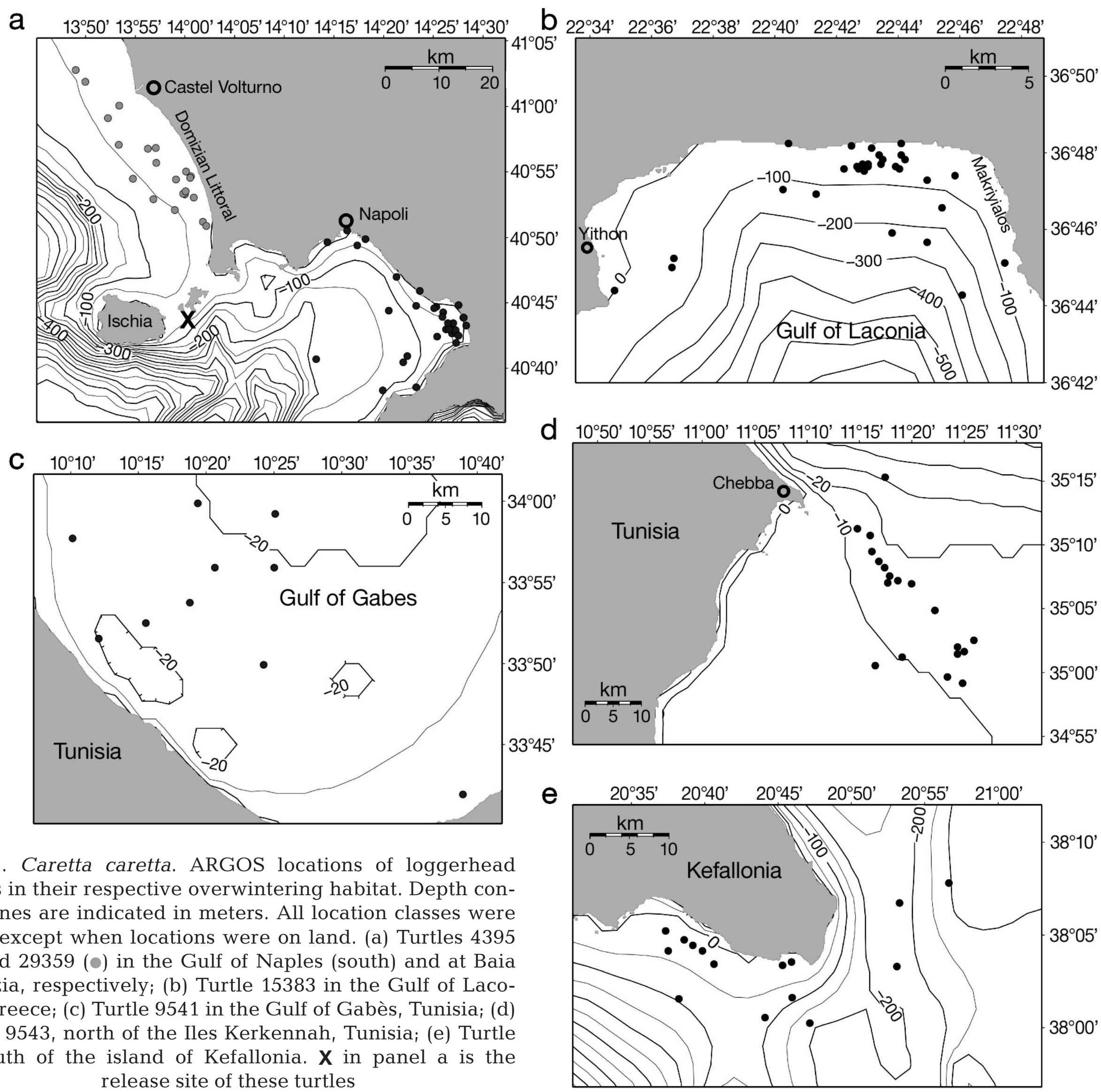

Fig. 7. *Caretta caretta*. ARGOS locations of loggerhead turtles in their respective overwintering habitat. Depth contour lines are indicated in meters. All location classes were used, except when locations were on land. (a) Turtles 4395 (●) and 29359 (●) in the Gulf of Naples (south) and at Baia Domizia, respectively; (b) Turtle 15383 in the Gulf of Laconia, Greece; (c) Turtle 9541 in the Gulf of Gabès, Tunisia; (d) Turtle 9543, north of the Iles Kerkennah, Tunisia; (e) Turtle A, south of the island of Kefallonia. **X** in panel a is the release site of these turtles

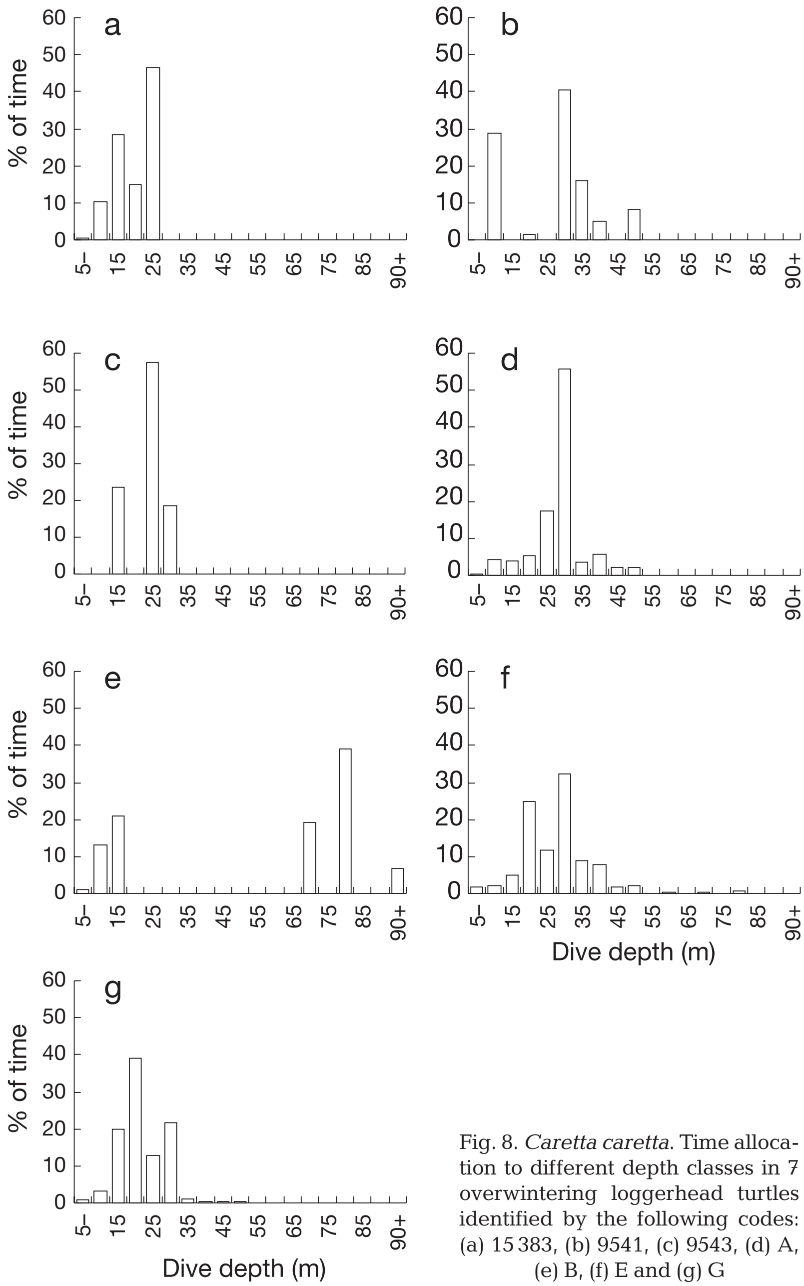

Fig. 8. *Caretta caretta*. Time allocation to different depth classes in 7 overwintering loggerhead turtles identified by the following codes: (a) 15383, (b) 9541, (c) 9543, (d) A, (e) B, (f) E and (g) G

S-dives and V-dives accounted for 11%, 7% and 5%, respectively, of all dive profiles. Although dive data from Turtles 29359 and 4395 were not included in the analysis, some of the dive profiles transmitted for these turtles showed the same pattern as those in the other turtles. An example of this is shown in Fig. 2a. There were rarely profiles for more than 2 consecutive dives, but information on the duration of single dives also revealed a very regular dive pattern where the turtles repeatedly dived to the same depth and stayed there for several hours with short surface times in between dives. For example, from February 26 to 28 successive dives were relayed from Turtle 15383 with durations of 410 min and depths of 24.5 m. This type of pattern was frequently seen in the data and suggests bouts of resting dives. All turtles allocated a substantial proportion of their time to these long dives, whereby 85 to 92% of the time was spent in dives lasting 3 h and longer (Fig. 9). The time spent at the surface after each dive increased initially with increasing dive duration and peaked at dive durations between 180 and 209 min with median surface time of 478 s (Kruskal-Wallis test for differences in surface time between duration categories < 210 min: $H_{503,6}$ = 133.3, p < 0.001; Fig. 10). After this, for all dives longer than 210 min there was no further increase in surface time and no difference was found for surface times in the duration categories > 210 min (Kruskal-Wallis $H_{231,5}$ = 8.72, p = 0.12).

Table 3. *Caretta caretta*. Descriptive dive statistics during the winter (21 Dec to 21 Mar). Dive ratio is the proportion of a 24 h period spent diving (below 3 m). Q_1 and Q_3 are the 25th and 75th quartiles, respectively

ID	No. of dives	Depth (m) Median (Q_1–Q_3)	Duration (min) Median (Q_1–Q_3)	Maximum depth (m)	Maximum duration (min)	Mean dive ratio (no. of days)
15383	108	11.5 (9.5–15.4)	28.4 (2.7–204.8)	24.5	410	93.9% (12)
9541	38	9.0 (6.0–30.0)	9.0 (5.0–180.0)	50	270	75.8% (4)
9543	37	24.0 (12.0–24.0)	200.0 (45.0–240.0)	28	360	94.6% (5)
A	85	24.0 (10.0–28.0)	120.0 (18.0–240.0)	50	300	86.4% (18)
B	35	4.0 (3.0–12.0)	0.8 (0.8–100.0)	100	330	43.8% (10)
E	276	20.0 (12.0–30.0)	26.0 (6.0–240.0)	90	360	77.9% (46)
G	273	16.0 (8.0–20.0)	115.0 (7.5–200.0)	50	480	84.4% (65)

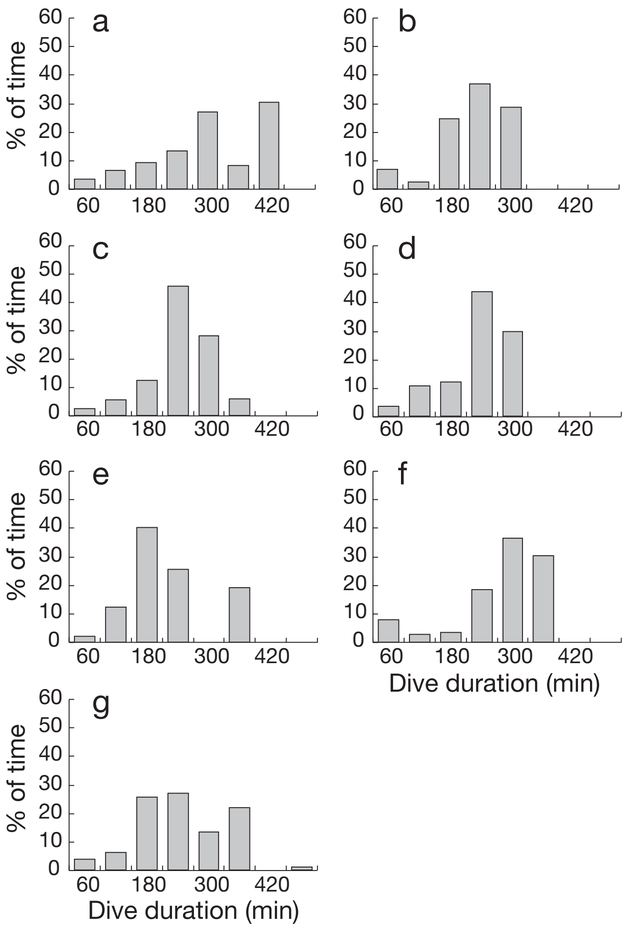

Fig. 9. *Caretta caretta*. Time allocation to dives of increasing duration in 7 overwintering loggerhead turtles identified by the following codes: (a) 15383, (b) 9541, (c) 9543, (d) A, (e) B, (f) E and (g) G

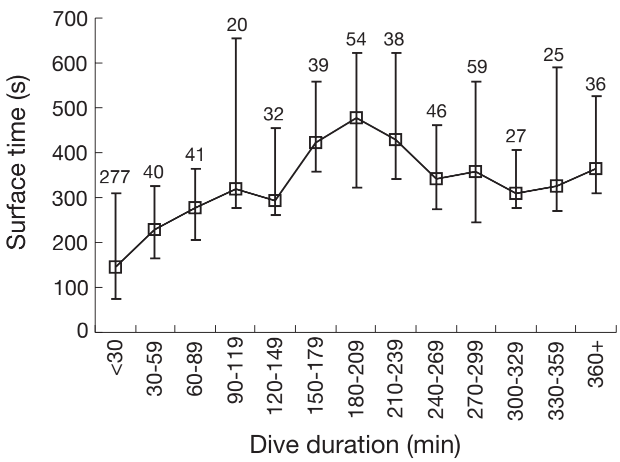

Fig. 10. *Caretta caretta*. Surface duration as a function of dive duration during winter dives of 8 loggerhead turtles. Median and 25 and 75 percentiles of surface time are shown for categories of dive duration. Numbers indicate sample size in each duration category

DISCUSSION

Marine turtles are rarely seen at the surface during winter and the location of the wintering habitat is often unidentified. For this reason, data on free-ranging turtles are limited and are mostly retrieved with the aid of electronic devices, such as archival tags or satellite transmitters. Telemetry provides a powerful tool to investigate behavioural traits during poorly known life phases. Despite the loss of some individuals and the technical failures encountered with some of the SRDLs, this study encompasses the most extensive data set on the overwintering ecology of sea turtles.

Nine loggerhead turtles tracked during the winter in the Mediterranean showed similar diving patterns, although individual turtles chose different geographical sites in which to overwinter. Most of the places visited by the turtles in this study were already known nesting areas or foraging grounds for this species. While turtles are also seen during the winter in the Adriatic Sea, in Greece and in Tunisia, it was formerly proposed that the turtles feeding in the Tyrrhennian Sea migrate to the eastern Mediterranean basin when water temperatures fall below 20°C (Bentivegna 2002). However, temperature differences between winter sites in this study were relatively small, and it is questionable whether the turtles would travel long distances simply to experience water 2°C warmer, particularly considering that all turtles adopted similar diving behaviours during the winter. Moreover, turtles moved to distant sites soon after their release, independent of the time of year, indicating that temperature probably played a minor role in the timing of journeys. Instead, movements appeared to be size related, since the bigger turtles tended to overwinter farther away from the release site. The fact that some of the smaller turtles stayed close to the release site (and, thus, the original capture site) indicates that these were probably local neritic juveniles, which do not engage in extensive migrations as adult turtles do (Bentivegna 2002, Bolten 2003).

If these turtles prefer warmer temperatures in which to overwinter, they would have to travel to the south-eastern sector of the Mediterranean. Unfortunately, no data exist on the diving behaviour of loggerhead turtles overwintering in the eastern Mediterranean with which we could compare our results. In Libya, green turtles were reported to adopt quiescent behaviour during the winter period (Godley et al. 2002), but these turtles also continued to surface and did not hibernate. Loggerhead turtles, which tolerate lower temperatures better than green turtles, are even less likely to be found hibernating in this warmer part of the Mediterranean.

The choice of microclimates at the winter site was also limited. Vertical temperature profiles of the overwintering habitats clearly showed that turtles were not in a position to select a preferred temperature over the depth range they used. It is, however, possible that the turtles buried themselves in the mud on the bottom of the sea, as observed in other regions, where they might have encountered slightly warmer temperatures (Felger et al. 1976, Carr et al. 1980, Ogren & McVea 1995). The large proportion of U-dives indicated that the turtles were spending most of their time at a specific depth, most likely resting on the sea floor, although some benthic foraging cannot be excluded. We are confident that the vast majority of U-dives were resting dives for several reasons: (1) resting occurs in bouts of long dives (Hays et al. 2000a); (2) foraging dives can be expected to be shorter because of their increased activity levels (Hays et al. 2000b); and (3) feeding rates are greatly reduced at cold temperatures (Moon et al. 1997, Hochscheid et al. 2004). Turtles that want to make use of essential resources such as oxygen or food have to retain their capability of locomotion, so that they can ascend to the surface for gas exchange or move in search for food (Ultsch 1989). Irrespective of the winter site, all turtles (except Turtle B) stayed close to the coast and in shallow waters, and no offshore movements during the winter period were noted, as reported previously for other regions (Epperly et al. 1995, Godley et al. 2002). The depth range used by the turtles allowed benthic foraging, while the water surface was within reach at any time in less than 2 min (travelling at an average vertical descent/ascent rate of 0.28 m s^{-1} (Houghton et al. 2002)). Two turtles (B and E) retained sufficient mobility to cover great horizontal distances during the winter, though they travelled much slower than migrating loggerhead turtles normally do (Bentivegna 2002). The cold water temperatures may have slowed down their movements, or rather, since these 2 turtles also allocated much time to long resting dives, periods for travelling were limited.

As expected, the diving behaviour, particularly the duration of dives, was affected by low temperatures, which lead to reduced activity and to a lower metabolic rate (Jackson 2000, Southwood et al. 2003, Hochscheid et al. 2004). Thus, during the cold winter months all turtles spent many hours at a time resting in apnoea. While seasonally varying dive durations have already been observed in captive loggerhead turtles (Bentivegna et al. 2003), the increase in dive duration with decreasing water temperature in wild individuals was much more pronounced (Fig. 6). This discrepancy is probably attributable to the confined depth available to captive turtles. In essence, to rest at the bottom of a 1 m deep tank, turtles have to dive with only partially inflated lungs because otherwise they would be too buoyant to remain stationary at the shallow depth (Hochscheid et al. 2003). However, in nature, we would expect turtles to optimise the time spent resting at the bottom by maximising their oxygen reserves after full inspiration (Hays et al. 2000a, Hays et al. 2004). This is only possible when they subsequently dive to a depth where they gain neutral or slightly negative buoyancy, which was not possible for the captive turtles. In the present study, resting turtles spent most of their time at depths between 20 and 30 m, which may be the optimal depth range for diving with full oxygen stores.

Although the turtles did not go into prolonged underwater hibernation, their behaviour suggests a state of dormancy during the many hours spent on the sea floor. Arousal occurred infrequently and was probably initiated before oxygen reserves were exhausted. This is supported by the fact that surface time was constant for all dives lasting 3 h and longer. There was practically no time to wash out lactate accumulated during anaerobic metabolism, because turtles spent less than 8 min at the surface and the long dives occurred in sequences providing no opportunity for post-dive lactate clearance for long periods (>24 h) (Hochachka & Somero 2002).

Turtles were subject to temperatures between 12 and 15°C, yet it cannot be excluded that underwater hibernation would occur if water temperatures fell below 12°C. In any case, it is not likely to be a regular overwintering strategy, and it may even be hazardous for turtles to reduce their ability to move because if temperatures fall below 10°C, they may become cold-stunned. Cold-stunning occurs at temperatures between 8 and 10°C whereby smaller turtles are affected first (Spotila et al. 1997). They lose their ability to dive and control buoyancy, and float passively at the surface, becoming moribund if the temperature stays low or decreases further. Sea turtles die at temperatures between 5 and 6.5°C (Schwartz 1978), whereas freshwater turtles hibernate at still lower temperatures (Ultsch 1989, Reese et al. 2001). In fact, such low temperatures are unlikely to be encountered in the regions where sea turtles occur and spend the winter. Therefore, although loggerhead turtles function over a temperature range of at least 20°C between the seasonal maxima, they are poorly adapted to extremely low temperatures, compared to their freshwater relatives.

CONCLUSIONS

Loggerhead turtles dived for longer and became more quiescent at lower temperatures, but as long as temperatures were above 10°C they retained their ability to move to another place or even to forage when they had the opportunity. Free-ranging loggerhead turtles overwintering in the Gulf of Gabès were found with full stomachs and intestines, confirming that they continue to feed during the cold period (Laurent & Lescure 1994). Loggerhead turtles showed a great capacity for long aerobic dives at low temperatures, which allowed them to rest in a dormant state for most of the time and keep energetic costs at a minimum, without truly hibernating. The regulating physiological mechanisms that are at work during this winter dormancy certainly need further investigation; however, we conclude that sea turtles, at least those overwintering in the Mediterranean, are by no means obligatory hibernators. Moreover, it can be expected that overwintering strategies vary within the Mediterranean basin since temperatures in the eastern part are higher, which potentially allow turtles to retain their activity and continue foraging, while having reduced quiescent periods. Higher temperatures and food intake rates result in faster growth rates in juveniles (Balazs & Chaloupka 2004) and possibly shorter remigration intervals in reproductive turtles. Elucidating how the mode of overwintering affects the reproductive cycle of loggerhead turtles on a long-term basis would be worth exploring, considering that postnesting turtles from one area move to various distant foraging and overwintering habitats (Margaritoulis et al. 2003).

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LITERATURE CITED

Balazs GH, Chaloupka M (2004) Spatial and temporal variability in somatic growth of green sea turtles (*Chelonia mydas*) resident in the Hawaiian archipelago. Mar Biol 145: 1043–1059

Bentivegna F (2002) Intra-Mediterranean migrations of loggerhead sea turtles (*Caretta caretta*) monitored by satellite telemetry. Mar Biol 141:795–800

Bentivegna F, Hochscheid S, Minucci C (2003) Seasonal variability in voluntary dive duration of the Mediterranean loggerhead turtle, *Caretta caretta*. Sci Mar 67:371–375

Bolten AB (2003) Variation in sea turtle life history patterns: neritic vs. oceanic developmental stages. In: Lutz PL, Musick JA, Wyneken J (eds) The biology of sea turtles, Volume II. CRC Press, Boca Raton, FL, p 243–257

Carr A, Ogren L, McVea CJ (1980) Apparent hibernation by the Atlantic loggerhead turtle off Cape Canaveral, Florida. Biol Conserv 19:7–14

Epperly SP, Braun JC, Chester AJ, Cross FA, Merriner JV, Tester PA (1995) Winter distribution of sea turtles in the vicinity of Cape Hatteras and their interactions with the summer flounder trawl fishery. Bull Mar Sci 56:547–568

Felger RS, Cliffton K, Regal PJ (1976) Winter dormancy in sea turtles: independent discovery and exploitation in the Gulf of California by two local cultures. Science 191:283–285

Godley BJ, Richardson S, Broderick AC, Coyne MS, Glen F, Hays GC (2002) Long-term satellite telemetry of the movements and habitat utilisation by green turtles in the Mediterranean. Ecography 25:352–362

Hays GC, Adams CR, Broderick AC, Godley BJ, Lucas DJ, Metcalfe JD, Prior AA (2000a) The diving behaviour of green turtles at Ascension Island. Anim Behav 59:577–586

Hays GC, Hochscheid S, Broderick AC, Godley BJ, Metcalfe JD (2000b) Diving behaviour of green turtles: dive depth, dive duration and activity levels. Mar Ecol Prog Ser 208: 297–298

Hays GC, Metcalfe JD, Walne AW (2004) The implications of lung regulated buoyancy control for dive depth and duration. Ecol 85:1137–1145

Hochachka PW, Somero GN (eds) (2002) Biochemical adaptation: mechanism and process in physiological evolution. Oxford University Press, New York

Hochscheid S, Godley BJ, Broderick AC, Wilson RP (1999) Reptilian diving: highly variable dive patterns in the green turtle *Chelonia mydas*. Mar Ecol Prog Ser 185:101–112

Hochscheid S, Bentivegna F, Speakman JR (2003) The dual function of the lung in Chelonian sea turtles: buoyancy control and oxygen storage. J Exp Mar Biol Ecol 297:123–140

Hochscheid S, Bentivegna F, Speakman JR (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, Hays GC (2005) First records of dive durations for a hibernating sea turtle. Biol Lett 1:82–86

Houghton JDR, Broderick AC, Godley BJ, Metcalfe JD, Hays GC (2002) Diving behaviour during the internesting interval for loggerhead turtles *Caretta caretta* nesting in Cyprus. Mar Ecol Prog Ser 227:63–70

Jackson DC (2000) Living without oxygen: lessons from the freshwater turtle. Comp Biochem Physiol A 125:299–315

Laurent L, Lescure J (1994) L'Hivernage des tortues caouannes *Caretta caretta* (L.) dans le sud Tunisien. Rev Ecol (Terre Vie) 49:63–86

Margaritoulis D, Argano R, Baran I, Bentivegna F and 11 others (2003) Loggerhead turtles in the Mediterranean sea: present knowledge and conservation perspectives. In: Bolten AB, Witherington BE (eds) Loggerhead sea turtles. Smithsonian Books, Washington, DC, p 175–198

McMahon CR, Autret E, Houghton JDR, Lovell P, Meyers AE, Hays GC (2005) Animal-borne sensors successfully capture the real-time thermal properties of ocean basins. Limnol Oceanogr: Methods 3:392–398

Moon DY, MacKenzie DS, Owens DW (1997) Simulated hibernation of sea turtles in the laboratory: I. Feeding, breathing frequency, blood pH, and blood gases. J Exp Zool 278: 372–380

Myers AE, Lovell P, Hays GC (2006) Tools for studying animal behaviour: validation of dive profiles relayed via the ARGOS satellite system. Anim Behav 71:989–993
Ogren L, McVea CJ (1995) Apparent hibernation by sea turtles in North American waters. In: Bjorndal KA (ed) Biology and conservation of sea turtles. Smithsonian Institution Press, Washington, DC, p 127–132
RAC/SPA (2004). Guidelines to improve the involvement of marine rescue centres for marine turtles. RAC/SPA, Tunis
Reese SA, Crocker CE, Carwile ME, Jackson DC, Ultsch GR (2001) The physiology of hibernation in common map turtles (*Graptemys geographica*). Comp Biochem Physiol A 130:331–340
Schwartz FJ (1978) Behavioral and tolerance responses to cold water temperatures by 3 species of sea turtles (Reptilia, Chelonidae) in North Carolina. In: Henderson GE (ed) Proc Florida and Interregional Conf Sea Turtles (33), 1978, St. Petersburg. Florida Marine Research Publications, St. Petersburg, FL, p 16–18
Southwood AL, Reina RD, Jones VS, Jones DR (2003) Seasonal diving patterns and body temperatures of juvenile green turtles at Heron Island, Australia. Can J Zool 81: 1014–1024
Spotila JR, O'Connor MP, Paladino FV (1997) Thermal biology. In: Lutz PL, Musick J (eds) The biology of sea turtles. CRC Press, Boca Raton, FL, p 297–314
Ultsch GR (1989) Ecology and physiology of hibernation and overwintering among freshwater fishes, turtles, and snakes. Biol Rev 64:435–516
Ultsch GR (2006) The ecology of overwintering among turtles: where turtles overwinter and its consequences. Biol Rev 81: 339–367

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