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THEME SECTION

Utility of geolocating light loggers for indicating at-sea movements in sea turtles

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ABSTRACT: As marine turtles traverse entire ocean basins, a number of techniques have been developed to gather information on their movements at sea. These range from basic methods, such as mark and recapture using flipper tags, to more technically advanced, expensive approaches, such as satellite tracking. Here we report the first published use of geolocation by light, using global location sensing (GLS) units, to estimate the locations of marine turtles in the Mediterranean. We attached units to 9 green *Chelonia mydas* and 3 loggerhead *Caretta caretta* turtles which had nested in Cyprus in previous years. One individual of each species was also fitted with a satellite transmitter for comparison. GLS units were retrieved on subsequent visits made by instrumented turtles during the same nesting season. In total, 28 GLS units were recovered from 12 individuals. The mean great-circle distance between the mean daily position calculated from satellite tracking and the corresponding mean light-based geolocation over the same time period was 50.3 km for green turtles and 57.6 km for loggerhead turtles. We suggest that GLS technology offers potential utility for identifying large-scale movements, migratory pathways, and over-wintering or foraging sites of adult female marine turtles.

KEY WORDS: Geolocation · Accuracy · Marine turtles · Migration · Inter-nesting · Cyprus · Mediterranean

INTRODUCTION

Studying the movements of large marine vertebrates at sea is logistically challenging. Many species range across entire ocean basins and, moreover, show markedly differing distributions during different life stages or seasons (Schmidt 1923, Scheffer 1952, Block et al. 2001, Akesson 2002, Phillips et al. 2005). As a result, there are significant gaps in our knowledge of their at-sea distribution, ecology and behaviour, in comparison to most similarly sized terrestrial vertebrates. Seminal studies concentrated on the analysis of large spatial movements using comparatively low-tech methodologies such as mark and recapture (Hardy 1940, Wolfson 1948, Woodbury et al. 1956, Meylan 1982). However, the reliance on serendipitous tag returns provides limited insight into individual movements. Major inadequacies include pronounced spatial and temporal biases in recording and reporting rates, the lack of any indication as to the route taken or activity pattern during the intervening period; also, definition of the endpoint of migration is difficult.

Radio/sonic tracking has provided data on localised small-scale movements (Thompson & Miller 1990, Williams & Rothery 1990, Nagelkerken et al. 2003). However, it is logistically challenging to stay within range of the study animals, and this approach is therefore inappropriate for monitoring wide-ranging or fast-moving species (Ray et al. 1978, Montgomery et al. 1981, Collazo & Epperley 1995, Fedak et al. 2002). These inad-

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equacies catalysed the development of satellite tracking, which has global coverage and allows the detailed tracking of individual movements over large spatial scales (Gillespie 2001). The use of satellite tracking in marine vertebrates has increased exponentially over the last decade (Godley et al. 2008, this Theme Section [TS]).

Initially units were very large, and although progressive miniaturisation has occurred, satellite tracking equipment is still relatively expensive to purchase and operate. This typically limits the number of study animals. Additionally, limited battery life, biofouling, failure to secure long-term attachment in most species, and antenna fragility can lead to reduced transmission duration.

Geolocation (Global Location Sensing, GLS, logging) offers the possibility of a long-term, less expensive alternative to satellite tracking. GLS logging by light uses the timings of sunrise, sunset and the resultant day length and timing of local noon to derive an estimation of global position (i.e. longitude and latitude) (Wilson et al. 1992, Hill 1994). This technique has been used to reveal large-scale patterns in the movements of terrestrial vertebrates, pinnipeds, fish, and marine birds (DeLong et al. 1992, LeBoeuf et al. 1993, Hunter et al. 2003, Croxall et al. 2005, Phillips et al. 2005). The main limitation with GLS logging is that of location accuracy. It does not share the same fine-scale resolution as satellite telemetry (Beck et al. 2002, Phillips et al. 2004), and many of the more affordable devices require recovery, meaning that they can only realistically be used on animals that have a high likelihood of recapture i.e. those with high site fidelity such as marine turtles, seals and seabirds. Accuracy is low around the vernal and autumnal equinoxes, when latitudinal estimation is difficult or impossible (Wilson et al. 1992, Welch & Eveson 1999). Errors also result from cloud cover, shading and a change in location of the device between dawn and dusk (Wilson et al. 1992). To improve overall accuracy, previous studies have applied filters and smoothing functions (Worton 1989, 1995, Sibert et al. 2003, Phillips et al. 2004, 2005, Wilson et al. in press) and incorporated concurrent temperature or depth information (LeBoeuf et al. 2000, Beck et al. 2002, Teo et al. 2004, Domeier et al. 2005, Nielsen et al. 2006).

The life history of marine turtles has until recently been poorly described, with most studies concentrating on their behaviour at nesting beaches during egg laying, with details of the greatest proportion of their life spent at sea remaining relatively unknown. Tag recoveries have provided limited information regarding post nesting movements (Carr 1982, Meylan 1982, Godley et al. 2003b, Seminoff et al. 2003, Lazar et al. 2004,) or ontogenetic changes in distribution of individuals (Musick & Limpus 1997). Radio tracking has been used to estimate foraging ranges (Seminoff et al. 2002), directions of movements when leaving a rookery (Addison et al. 2002) and inter-nesting movements (Starbird et al. 1999). However, to date, the greatest insights into the at-sea behaviour of marine turtles have been gleaned using satellite telemetry (Morreale et al. 1996, Papi et al. 1997, Hughes et al. 1998, Hays et al. 2001a, Hatase et al. 2002, Ferraroli et al. 2004; reviewed by Godley et al. 2008). Cost restriction has limited the sample size and therefore the generality of such results. A less expensive alternative utilising information from a larger sample of tracked animals would allow for better elaboration of dispersal patterns, although cost-effectiveness will be dictated by efficacy of device recovery.

Within the Mediterranean, most of the main nesting beaches for the loggerhead turtle *Caretta caretta* and green turtle *Chelonia mydas* are now well documented (Broderick et al. 2002). The next challenge is to discover the important migratory corridors, feeding grounds and over-wintering sites for these species, as these are as yet largely unknown. Limited work to date using satellite telemetry has provided some insights into these locations, but given the small sample sizes (Godley et al. 2002, 2003b, Broderick et al. 2007), the relative importance of these regions is equivocal. Identifying important habitats may aid us in reducing interactions with fisheries, a significant global source of marine turtle mortality (Godley et al. 1998, Bugoni et al. 2001, Lewison et al. 2003, 2004). The loggerhead turtle in the Mediterranean is particularly vulnerable to demersal and pelagic long-line fishing and trawling (Laurent et al. 1996, Casale 2003, Pinedo & Polacheck 2004).

In the present paper, we assess the error in using GLS units to estimate location of marine turtles between repeated nesting visits to the same rookery in north Cyprus over a period of 3 mo. To date, we are unaware of any published studies testing the efficacy of GLS technology in turtles, although data logging devices measuring a range of parameters, including light, have been deployed in the past (Sato et al. 1995, R. Wilson pers. comm. to B. J. Godley). This is somewhat surprising as this approach lends itself extremely well to the study of marine turtles as they (1) disperse widely over 100s or sometimes 1000s of kilometres; (2) possess a hard shell, which allows device attachment and retention for several years; (3) move relatively slowly, which may reduce the error involved in this technique compared with that found in other faster-moving animals; and (4) adult females deposit multiple clutches per season and exhibit strong levels of nest site fidelity, which facilitates the recovery of devices within and between breeding seasons.

MATERIALS AND METHODS

Between June and August of 2004, fieldwork was carried out at Alagadi beach, northern Cyprus (35° 33′ N, 33° 47′ E). Alagadi is situated on the north coast of Cyprus and has been the site of intensive monitoring of green and loggerhead turtles since 1992 (Broderick et al. 2003). The beach is divided into 2 bays by a rocky outcrop and totals 2 km in length. Turtles that had nested at Alagadi in a previous nesting season were selected for this study as within-season fidelity and clutch frequency was likely to be higher than in other individuals. These factors would increase the likelihood of GLS unit recovery within the season.

Two individuals were fitted with both a GLS unit and satellite transmitter (1 green turtle: Kiwisat 101, Sirtrack, Havelock North, New Zealand; 13.5 × 4.5 × 1.8 cm, total mass 162 g; and 1 loggerhead turtle: ST-18 Telonics, Mesa, AZ, USA; 14.0 × 4.8 × 3.3 cm, total mass 275 g). GLS units (2 × 1.7 × 1.1 cm with a total mass of 9 g, British Antarctic Survey, Cambridge, UK) were placed into a specially designed housing (5.9 × 5.9 × 3.0 cm, mass 48 g) to enable easy exchange/removal. Satellite transmitters were attached to the second central carapace scute, with the GLS housings attached directly behind the transmitter on the third central scute. Both device housings and satellite transmitters were attached using a 2-part epoxy resin after suitable preparation of the carapace (Godley et al. 2003a) during the egg-laying and nest-covering stage of nesting. Resin was smoothed and fared around devices in order to reduce hydrodynamic drag and bio-fouling (Watson & Granger 1998). On each subsequent nesting event for that individual, the GLS unit was retrieved and replaced by another device. Only loggerhead turtles required restraint, owing to the relatively short nesting duration (approx. 30 to 60 min); this restraint took the form of a 4-sided plywood corral with inter-linking sides. Sand piled around the sides gave the structure extra rigidity. Once the resin had set, the box was dismantled, and the turtle allowed to return to the sea (maximum duration of restraint 1 h).

In total, GLS units were deployed 4 times on the loggerhead turtle and twice on the green turtle fitted with satellite transmitters, with total deployment periods spanning 64 and 27 d respectively. There were an additional 36 logger deployments, resulting in 22 datasets from 10 different individuals (2 loggerhead and 8 green turtles; Table 1). The GLS units measured light intensity every 60 s, recording the maximum light levels during each 10 min interval (Afanasyev 2004). Light data were analysed using MultiTrace software (Jensen Software Systems). The most appropriate dawn/dusk threshold and angle of elevation (–4.9°) were determined from initial analysis of a subsample of 8 files, on the assumption that on the first day after deployment and the last day preceding recapture the turtles were close to the nesting beach. Fixed threshold values (the mean from this subsample) were then used in the processing of all files.

To further contextualize the likely inter-nesting movements of this population we used past satellite tracking data from 4 turtles (3 green and 1 loggerhead turtle) tracked in 1998–2002, in addition to the 1 individual of each species tracked in the study season (Godley et al. 2002, 2003a and unpubl. data). Data were processed and maps generated using Arc View v.8.3 (ESRI GIS and mapping software) and Satellite Tracking and Analysis Tool (STAT) (Coyne & Godley 2005).

Accuracy of light-based geolocation was calculated by comparing either the mean daily satellite-derived and mean daily GLS unit positions or by comparing the satellite-derived positions and derived light-based geolocation that were closest in real time. Only satellite transmitter location classes 3, 2 and 1 (typical accuracy of 150 to 1000 m; Keating et al. 1991, Argos 1996, Hays et al. 2001b) were used in these calculations. Great circle distances were used in the calculation of errors.

Table 1. Summary of global location sensing (GLS) unit deployments at Alagadi beach, north Cyprus during 2004. Number of days with data recorded for each logger are in chronological order in terms of attachment date. A–M: green turtles; N–P: loggerhead turtles

Individual	Deployments	Recovered units	Days for each unit
A[a]	3	2	14, 13
B	5	4	15, 12, 13, 13
C	2	1	16
D	5	4	14, 12, 13, 13
E	2	1	28
F	2	1	14
G	2	2	14, 12
H	2	2	12, 11
I	2	1	35
J	1	0	0
K	1	0	0
L	1	0	0
M	1	0	0
N[a]	5	4	17, 13, 11, 23
O	3	2	13, 21
P	5	4	19, 14, 12, 12
Total	42	28	

[a]Also tracked by satellite telemetry

RESULTS

Most turtles tracked by satellite remained in the proximity of Alagadi beach throughout the inter-nesting period. The mean maximum distance travelled during the inter-nesting period for green and loggerhead turtles was 15.6 km (SD 17.2, range 2.5 to 40.0 km, n = 4 green turtles; n = 9 inter-nesting periods) and 20.1 km (SD 21.6, range 4.8 to 35.4 km, n = 2 loggerhead turtles; n = 5 inter-nesting periods), respectively, with no significant difference between the 2 species (Mann-Whitney $U_5 = 3.0$, $p > 0.05$). The mean GLS locations taken from the 28 inter-nesting periods of the 12 tracked turtles demonstrated a centre significantly closer to Alagadi for green turtles than loggerhead turtles (green turtles: mean 68.9 km, SD 20.9, range 48.6 to 121.5 km, n = 18; Fig. 1a; loggerhead turtles: mean 107.5 km, SD 48.2, range 53.2 to 212.2 km, n = 10; Fig 1b; Mann-Whitney $U_{27} = 34.0$, $p < 0.01$).

The mean great-circle distance between the mean daily satellite positions and mean light-based geolocation for the same day were similar in green and loggerhead turtles (green turtles: mean 50.4 km, SD 19.4, range 15.5 to 86.1 km, n = 13; loggerhead turtles: mean 57.6 km, SD 30.2, range 23.3 to 103.3 km, n = 5: Fig 2a). Similar results were obtained when comparing the mean light-based geolocation with the satellite position closest in time (green turtles: mean 62.1 km, SD 31.0, range 5.6 to 108.3 km, n = 13; loggerhead turtles: 55.3 km, SD 24.0, range 27.8 to 85.5 km, n = 5: Fig. 2b). There were no significant inter-specific or inter-methodological differences in error (Kruskal-Wallis [KW] = 1.437, p = 0.6970)

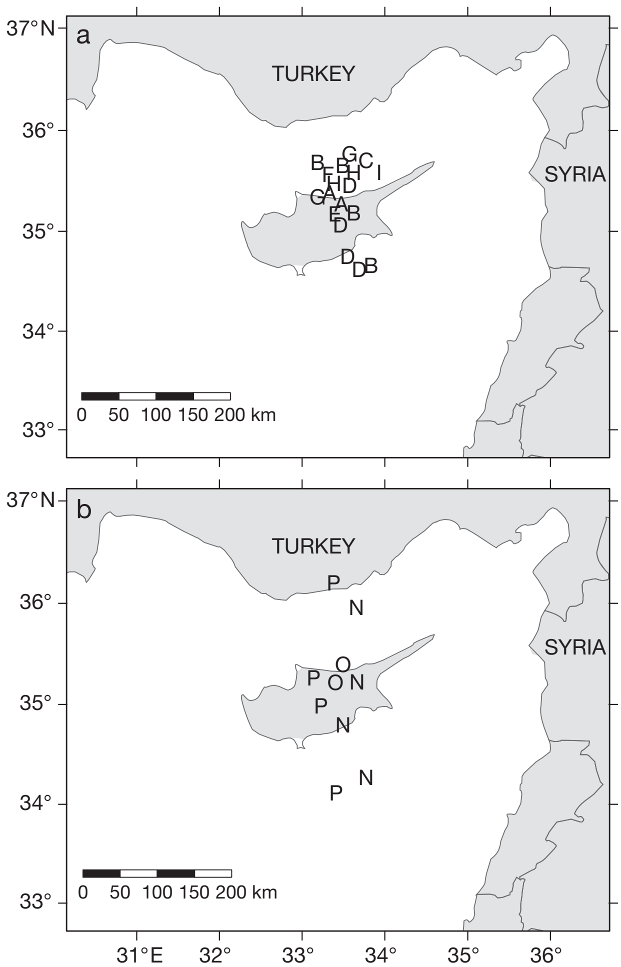

Fig. 1. *Chelonia mydas* and *Caretta caretta*. Mean inter-nesting location of (a) 9 green turtles and (b) 3 loggerhead turtles tracked using global location sensing (GLS) loggers in 2004. Each letter signifies an individual turtle to allow comparisons of multiple deployments (see Table 1 for details)

DISCUSSION

Based on the satellite tracking, the inter-nesting movements of both species were similar, with most females appearing to stay close to Alagadi. Geolocation results also indicated that both species remained close to the nesting site, and also suggested a greater range in the dispersal distance of loggerhead com-

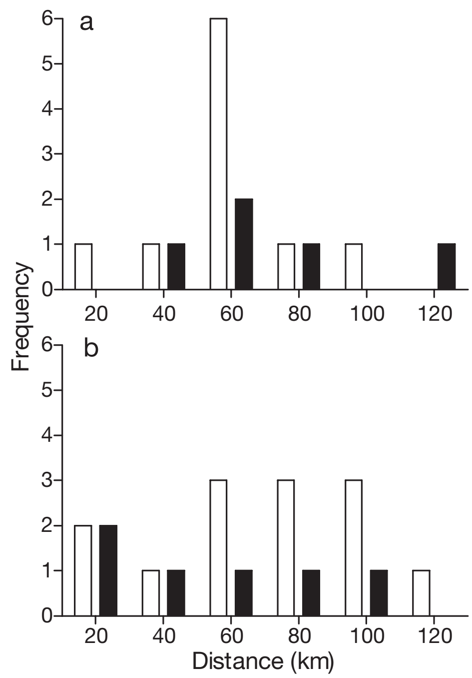

Fig. 2. Accuracy of geolocation estimates in kilometres when assessed by comparing mean global location sensing (GLS) position with (a) mean satellite-transmitter location, and (b) closest satellite-transmitter location in time. Green turtles *Chelonia mydas* shown by white bars, and loggerhead turtles *Caretta caretta* by black bars

pared to green turtles. That this is a genuine difference in the distance travelled is not borne out by the limited satellite tracking data. An alternative explanation is a behavioural difference affecting the accuracy of the GLS unit. This may take the form of differences in dive depths, and/or time spent at depth, as light intensity is rapidly attenuated with depth or water quality. The 2 species differ in feeding strategy; green turtles in the inter-nesting period are thought to graze on sea grasses (Hochscheid et al. 1999, Hays et al. 2002b), whereas loggerhead turtles, should they remain within the neritic zone, feed by infaunal mining (Preen 1996) and would therefore be expected to forage among the benthos (Hatase et al. 2002, Houghton et al. 2002). As sea grass beds are most productive in shallower waters, it might be expected that green turtles would generally feed at shallower depths. Furthermore, if loggerhead turtles were foraging in soft substrata, there may be considerable disturbance of the sediments, leading to an increase in water turbidity and therefore greater light attenuation.

The average errors in our geolocation estimates were 50 to 60 km, based on mean positions calculated from the concurrent satellite transmitter and GLS data from 2 turtles. As expected, latitudinal error was greater than longitudinal error. Mean geolocation errors calculated in previous studies of other taxa vary considerably, from 34 to >1000 km (for a review, see Phillips et al. 2004). Marine turtles swim slowly and during the nesting season remain relatively faithful to the vicinity of the nesting beach. Therefore, they probably move little between dawn and dusk each day, which improves timing information. However, the accuracy of devices deployed for long periods on migrant turtles is unlikely to be as high as in this short-term study, when we may have been fortunate with regard to atmospheric conditions and cloud cover. There are also a number of other issues which need to be taken into consideration, as described below.

Shading or changes in sensor orientation also reduce the accuracy of geolocation estimates. During this study one of the housings was irreparably damaged, and although the likelihood of this recurring could be reduced by more posterior placement, this would need to be traded off against possible reduction in light-gathering capabilities. Following the final clutch of the season, GLS units were deployed upon nesting females to test their robustness and durability during the remigration interval.

Accuracy levels may fluctuate during different stages of turtle migration and at over-wintering/foraging grounds where water turbidity might vary, or the animals might forage at different depths, shelter in caves or under overhangs. When turtles are migrating across open-water, they spend the majority of the time at shallow depths, which should enable good light-gathering opportunities. However, this is when sea turtles travel the greatest distances in a 24 h period (Godley et al. 2002, Luschi et al. 2003), which might affect the estimates of day length and timing of local noon, and therefore both latitude and longitude. One factor which should ease data interpretation, at least in the Mediterranean basin, is that adults migrate to coastal regions: our studies to date have shown that females over-winter in Cyprus, Egypt, Libya, Syria and Turkey (Fig. 3; Broderick et al. 2007). Hence, likely locations should be constrained latitudinally (in most cases), or longitudinally. Given the large spatial scales of these movements and despite the relatively low accuracy of geolocation methods, extremely useful information should therefore be obtained on timing of movement and location of wintering/foraging grounds (Broderick et al. 2007). In addition, turtles tracked from north Cyprus exhibit a high degree of site fidelity, remaining in the same areas for 12 to 48 mo (Godley et al. 2002, Broderick et al. 2007). Such areas should be readily identifiable using smoothing or kernelling techniques (Phillips et al. 2004, Wilson et al. in press). Complementary data logging devices such as temperature loggers used in conjunction with GLS technology can improve geolocation accuracy (LeBoeuf et al. 2000, Beck et al. 2002). The logged temperature can be compared with known sea surface temperatures (SST) to improve latitudinal estimates (Sims et al. 2003, Teo et al. 2004). A possible cause for concern in deployments of many months duration in the marine environment is bio-fouling, which would seriously reduce the light-gathering capabilities of GLS loggers. However, within the Mediterranean basin, epibiont loading on marine turtles appears to be lower than in many other oceanic

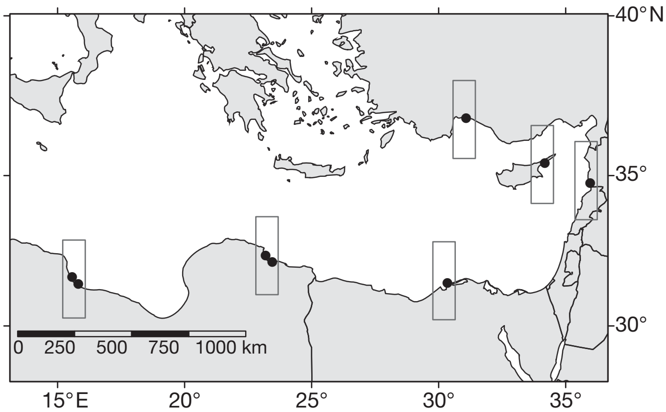

Fig 3. *Chelonia mydas* and *Caretta caretta*. Over-wintering or feeding grounds of satellite-tracked turtles from north Cyprus (●) (Godley et al. 2002, 2003; n = 6 green turtles, n = 2 loggerhead turtles). Boxes represent the observed range of global location sensing (GLS) location errors found during the inter-nesting period in 2004 (longitude: 95 km; latitude: 335 km)

regions (B. J. Godley pers. obs.) and hopefully useable data will be gathered from over-wintering sites before bio-fouling becomes an issue.

It is clear from the promising level of accuracy found in this pilot study and the spatial scales over which these species move within the Mediterranean (Godley et al. 2002, 2003a, Broderick et al. 2007) that long-term GLS deployments hold great potential for unlocking information on important migratory corridors and over-wintering/foraging grounds of female turtles. Provided that a sufficient quantity of GLS units can be attached and recovered successfully, this technique has the potential to offer fundamental insights into sea turtle biology and conservation. However, a location error of over 50 km for GLS tracking suggests single application of GLS units may not be suitable to examine the small-scale movements of animals (e.g. inter-nesting period of marine turtles). Given that all species of marine turtles are of conservation concern, data gleaned from this type of study will help inform the international research community, enabling effective targeting of mitigation, designation of marine protected areas (MPAs) etc. Given the profound conservation significance of this work, we hope that the publication of our data will galvanise further utilisation of this tracking technology.

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LITERATURE CITED

Addison DS, Gore JA, Ryder J, Worley K (2002) Tracking post-nesting movements of loggerhead turtles (*Caretta caretta*) with sonic and radio telemetry on the southwest coast of Florida, USA. Mar Biol 141:201–205

Afanasyev V (2004) A miniature daylight level and activity data recorder for tracking animals over long periods. Mem Natl Inst Polar Res Spec Issue 58:227–233

Akesson S (2002) Tracking fish movements in the ocean. Trend Ecol 17:56–57

Argos (1996) User's manual. Argos/CLS, Toulouse

Beck CM, McMillan JI, Bowen WD (2002) An algorithm to improve geolocation positions using sea surface temperature and dive depth. Mar Mamm Sci 18:940–951

Block B, Dewar H, Blackwell S, Williams T and 7 others (2001) Migratory movements, depth preferences, and thermal biology of Atlantic bluefin tuna. Science 293:1310–1314

Broderick AC, Glen F, Godley B, Hays G (2002) Estimating the number of green and loggerhead turtles nesting annually in the Mediterranean. Oryx 36:227–235

Broderick AC, Glen F, Godley BJ, Hays GC (2003) Variation in reproductive output of marine turtles. J Exp Mar Biol Ecol 288:95–109

Broderick AC, Coyne MS, Fuller WJ, Glen F, Godley BJ (2007) Fidelity and over-wintering of sea turtles. Proc R Soc Lond Ser B Biol Sci 274(1617):1533–1538

Bugoni L, Krouse L, Petry MV (2001) Marine debris and human impacts on sea turtles in southern Brazil. Mar Pollut Bull 42:1330–1334

Carr A, Meylan AB, Mortimer JA, Bjorndal KA, Carr T (1982) Surveys of sea turtle populations and habitats in the western Atlantic. National Oceanic and Atmospheric Administration, Panama City

Casale P, Nicolosi P, Freggi D, Turchetto M, Argano R (2003) Leatherback turtles (*Dermochelys coriacea*) in Italy and in the Mediterranean basin. Herpetol J 13:135–139

Collazo J, Epperly S (1995) Accuracy tests for sonic telemetry studies in an estuarine environment. J Wildl Manag 59: 181–188

Coyne MS, Godley BJ (2005) Satellite Tracking and Analysis Tool (STAT): an integrated system for archiving, analysing and mapping animal tracking data. Mar Ecol Prog Ser 301:1–7

Croxall JP, Silk JRD, Phillips RA, Afanasyev V, Briggs DR (2005) Global circumnavigations: tracking year-round ranges of non breeding albatrosses. Science 307:249–250

DeLong R, Stewart B, Hill R (1992) Documenting migrations of northern elephant seals using day length. Mar Mamm Sci 8:155–159

Domeier ML, Kiefer D, Nasby-Lucas N, Wagschal A, O'Brien F (2005) Tracking Pacific bluefin tuna (*Thunnus thynnus orientalis*) in the northeastern Pacific with an automated algorithm that estimates latitude by matching sea-surface-temperature data from satellites with temperature data from tags on fish. Fish Bull 103(2):292–306

Fedak M, Lovell P, McConnell B, Hunter C (2002) Overcoming the constraints of long range radio telemetry from animals: getting more useful data from smaller packages. Integr Comp Biol 42:3–10

Ferraroli S, Georges JY, Gaspar P, Le Maho Y (2004) Where leatherback turtles meet fisheries. Nature 429:521

Gillespie T (2001) Remote sensing of animals. Prog Phys Geog 25:355–362

Godley BJ, Gucu A, Broderick A, Furness R, Solomon S (1998) Interaction between marine turtles and artisanal fisheries in the eastern Mediterranean: a probable cause for concern? Zool Middle East 16:49–64

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

Godley BJ, Broderick AC, Glen F, Hays GC (2003a) Post-nesting movements and submergence patterns of loggerhead marine turtles in the Mediterranean assessed by satellite tracking. J Exp Mar Biol Ecol 287:119–134

Godley BJ, Lima EHSM, Åkesson S, Broderick AC, Glen F, Godfrey MH, Luschi P, Hays GC (2003b) Movement patterns of green turtles in Brazilian coastal waters described by satellite tracking and flipper tagging. Mar Ecol Prog Ser 253:279–288

Godley BJ, Blumenthal JM, Broderick AC, Coyne MS, Godfrey MH, Hawkes LA, Witt MJ (2008) Satellite tracking of sea turtles: Where have we been and where do we go next? Endang Spec Res 4:3–22

Hardy A (1940) Whale-marking in the Southern Ocean. Geogr J 96:345–350
Hatase H, Takai N, Matsuzawa Y, Sakamoto W, Omuta K, Goto K, Arai N, Fujiwara T (2002) Size-related differences in feeding habitat use of adult female loggerhead turtles *Caretta caretta* around Japan determined by stable isotope analyses and satellite telemetry. Mar Ecol Prog Ser 233:273–281
Hays GC, Akesson S, Broderick AC, Glen F and 5 others (2001a) 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 GC, Akesson S, Godley BJ, Luschi P, Santidrian P (2001b) The implications of location accuracy for the interpretation of satellite-tracking data. Anim Behav 61:1035–1040
Hays G, Broderick A, Godley B, Lovell P, Martin C, McConnell B, Richardson S (2002a) Bi-phasal long-distance migration in green turtles. Anim Behav 64:895–898
Hays GC, Glen F, Broderick AC, Godley BJ, Metcalfe JD (2002b) Behavioural plasticity in a large marine herbivore: contrasting patterns of depth utilisation between two green turtle (*Chelonia mydas*) populations. Mar Biol 141: 985–990
Hill R (1994) Theory of geolocation by light levels. In: LeBoeuf BJ (ed) Elephant seals: population ecology, behaviour and physiology. University of California Press, Berkeley, CA, p 227–236
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
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
Hughes GR, Luschi P, Mencacci R, Papi F (1998) The 7000-km oceanic journey of a leatherback turtle tracked by satellite. J Exp Mar Biol Ecol 229:209–217
Hunter E, Aldridge J, Metcalfe J, Arnold G (2003) Geolocation of free-ranging fish on the European continental shelf as determined from environmental variables. Mar Biol 142:601–609
Keating K, Brewster W, Key C (1991) Satellite telemetry: performance of animal-tracking ystems. J Wildl Manag 55:160–171
Laurent L, El-Mawla A, Bradai MN, Demirayak F, Oruc A (1996) Reducing sea turtle mortality induced by Mediterranean fisheries: trawling activity in Egypt, Tunisia and Turkey. Report for WWF International Mediterranean Programme. WWF Project 9E0103, Rome
Lazar B, Margaritoulis D, Tvrtkovic N (2004) Tag recoveries of the loggerhead sea turtle *Caretta caretta* in the eastern Adriatic Sea: implications for conservation. J Mar Biol Assoc UK 84:475–480
LeBoeuf BJ, Crocker DE, Blackwell S, Morris P, Thorson P (1993) Sex differences in diving and foraging behaviour of northern elephant seals. Symp Zool Soc Lond 66:149–178
LeBoeuf BJ, Crocker DE, Grayson J, Gedamke J, Webb PM, Blackwell SB, Costa DP (2000) Respiration and heart rate at the surface between dives in northern elephant seals. J Exp Biol 203:3265–3274
Lewison RL, Crowder LB, Shaver DJ (2003) The impact of turtle excluder devices and fisheries closures on loggerhead and Kemp's ridley strandings in the western Gulf of Mexico. Conserv Biol 17:1089–1097
Lewison RL, Freeman SA, Crowder LB (2004) Quantifying the effects of fisheries on threatened species: the impact of pelagic longlines on loggerhead and leatherback sea turtles. Ecol Lett 7:221–231
Luschi P, Hays GC, Papi F (2003) A review of long-distance movements by marine turtles, and the possible role of ocean currents. Oikos 103:293–302
Meylan AB (1982) Sea turtle migration — evidence from tag returns. In: Bjorndal KA (ed) Biology and conservation of sea turtles. Smithsonian Institution Press, Washington, DC, p 91–100
Montgomery GG, Best RC, Yamakoshi M (1981) A radiotracking study of the Amazonian manatee *Trichechus inuguis* (Mammalia: Sirenia). Biotropica 13(2):81–85
Morreale S, Standora EA, Spotila JR, Paladino FV (1996) Migration corridor for sea turtles. Nature 384:319–320
Musick JA, Limpus CJ (1997) Habitat utilisation and migration in juvenile sea turtles. In: Lutz P, Musick JA (eds) The biology of sea turtles. CRC Press, Boca Raton, FL, p 137–163
Nagelkerken I, Pors LPJJ, Hoetjes P (2003) Swimming behaviour and dispersal patterns of headstarted loggerhead turtles *Caretta caretta*. Aquat Ecol 37:183–190
Nielsen, A, Bigelow KA, Musyl MK, Sibert JR (2006) Improving light-based geolocation by including sea surface temperature. Fish Oceanogr 15(4):314–325
Papi F, Luschi P, Crosio E, Hughes GR (1997) Satellite tracking experiments on the navigational ability and migratory behaviour of the loggerhead turtle. Mar Biol 129:215–220
Phillips RA, Silk JRD, Croxall JP, Afanasyev V, Briggs DR (2004) Accuracy of geolocation estimates for flying seabirds. Mar Ecol Prog Ser 266:265–272
Phillips RA, Silk JRD, Croxall JP, Afanasyev V, Bennett VJ (2005) Summer distribution and migration of nonbreeding albatrosses: individual consistencies and implications for conservation. Ecology 81:2386–2396
Pinedo MC, Polacheck T (2004) Sea turtle by-catch in pelagic longline sets off southern Brazil. Biol Conserv 19(3): 335–339
Preen AR (1996) Infaunal mining: a novel foraging method of loggerhead turtles. J Herpetol 30(1):94–96
Ray GC, Mitchell ED, Wartzok D, Kozicki VM, Maiefski R (1978) Radio tracking of a fin whale (*Balaenoptera physalus*). Science 202:521–524
Sato K, Sakamoto W, Matsuzawa Y, Tanaka H, Minamikawa S, Naito Y (1995) Body temperature independence of solar radiation in free-ranging loggerhead turtles, *Caretta caretta*, during internesting periods. Mar Biol 123:197–205
Scheffer VB (1952) Outline for the ecological life history studies of marine mammals. Ecology 33:287–296
Schmidt J (1923) The breeding places of the eel. Phil Trans R Soc Lond Ser B 211:179–208
Seminoff JA, Resendiz A, Nichols WJ (2002) Home range of green turtles *Chelonia mydas* at a coastal foraging area in the Gulf of California, Mexico. Mar Ecol Prog Ser 242: 253–265
Seminoff JA, Jones TT, Resendiz A, Nichols WJ, Chaloupka MY (2003) Monitoring green turtles (*Chelonia mydas*) at a coastal foraging area in Baja California, Mexico: multiple indices describe population status. J Mar Biol Assoc UK 83:1355–1362
Sibert JR, Musyl MK, Brill RW (2003) Horizontal movements of bigeye tuna (*Thunnus obesus*) near Hawaii determined by Kalman filter analysis of archival tagging data. Fish Oceanogr 12(3):141–151
Sims DW, Southall EJ, Richardson AJ, Reid PC, Metcalfe JD (2003) Seasonal movements and behaviour of basking sharks from archival tagging: no evidence of winter hibernation. Mar Ecol Prog Ser 248:187–196

Starbird CH, Hillis-Starr Z, Harvey JT, Eckert SA (1999) Internesting movements and behaviour of hawksbill turtles (*Eretmochelys imbricata*) around Buck Island National Monument, St. Croix, U.S. Virgin Islands. Chelonian Conserv Biol 3(2):237–243

Teo SLH, Boustany A, Blackwell S, Walli A, Weng KC, Block BA (2004) Validation of geolocation estimates based on light level and sea surface temperature from electronic tags. Mar Ecol Prog Ser 283:81–98

Thompson PM, Miller D (1990) Summer foraging activity and movements of radio-tagged common seals (*Phoca vitulina* L) in the Moray Firth, Scotland. J Appl Ecol 27: 492–501

Watson K, Granger R (1998) Hydrodynamic effect of a satellite transmitter on a juvenile green turtle. J Exp Biol 201:2497–2505

Welch D, Eveson JP (1999) An assessment of light-based geoposition estimates from archival tags. Can J Fish Aquat Sci 56:1317–1327

Williams TD, Rothery P (1990) Factors affecting variation in foraging and activity patterns of gentoo penguins (*Pygoscelis papua*) during the breeding season at Bird Island, South Georgia. J Appl Ecol 27:1042–1054

Wilson RP, Ducamp JJ, Rees G, Culik BM, Niekamp K (1992) Estimation of location: global coverage using light intensity. In: Priede IG, Swift SM (eds) Wildlife telemetry: remote monitoring and tracking of animals. Ellis Horward, Chichester, p 131–134

Wilson RP, Rees G, Lage J, Pütz K and 5 others (in press) Determination of animal position at sea using changes in diel light intensity. Proc 5th Eur Conf Wildlife Telemetry. CNRS, Strasbourg

Wolfson A (1948) Bird migration and the concepts of continental drift. Science 108:23–30

Woodbury AM, Ricker WE, Cottam C, Taber RD, Pendleton RC (1956) Symposium: uses of marking animals in ecological studies. Ecology 37:665–689

Worton BJ (1989) Kernal methods for estimating the utilisation distribution in home range studies. Ecology 70:164–168

Worton BJ (1995) Using Monte Carlo simulations to evaluate kernel-based home range estimators. J Wildl Manag 59(4):794–800

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