The diving behaviour of green turtles undertaking oceanic migration to and from Ascension Island: dive durations, dive profiles and depth distribution

G. C. Hays[1],[*], S. Åkesson[2], A. C. Broderick[1], F. Glen[1], B. J. Godley[1], P. Luschi[3], C. Martin[1], J. D. Metcalfe[4] and F. Papi[3]

[1]*School of Biological Sciences, University of Wales Swansea, Singleton Park, Swansea SA2 8PP, UK*, [2]*Department of Animal Ecology, Lund University, Ecology Building, SE-223 62 Lund, Sweden*, [3]*Dipartimento di Etologia, Ecologia, Evoluzione, University of Pisa, Via A. Volta 6, I-56126 Pisa, Italy* and [4]*The Centre for Environment, Fisheries and Aquaculture Science, Lowestoft Laboratory, Lowestoft NR33 0HT, UK*

*e-mail: g.hays@swan.ac.uk

Summary

Satellite telemetry was used to record the submergence duration of green turtles (*Chelonia mydas*) as they migrated from Ascension Island to Brazil (*N*=12 individuals) while time/depth recorders (TDRs) were used to examine the depth distribution and dive profiles of individuals returning to Ascension Island to nest after experimental displacement (*N*=5 individuals). Satellite telemetry revealed that most submergences were short (<5 min) but that some submergences were longer (>20 min), particularly at night. TDRs revealed that much of the time was spent conducting short (2–4 min), shallow (approximately 0.9–1.5 m) dives, consistent with predictions for optimisation of near-surface travelling, while long (typically 20–30 min), deep (typically 10–20 m) dives had a distinctive profile found in other marine reptiles. These results suggest that green turtles crossing the Atlantic do not behave invariantly, but instead alternate between periods of travelling just beneath the surface and diving deeper. These deep dives may have evolved to reduce silhouetting against the surface, which would make turtles more susceptible to visual predators such as large sharks.

Key words: satellite telemetry, turtle, *Chelonia mydas*, diving, migration.

Introduction

Long-distance animal migration has provoked huge interest amongst biologists because it represents a central life-history trait for a variety of birds, insects, mammals and reptiles. Key lines of research have been to document the routes that animals follow, the navigational mechanisms used and the physiological and behavioural adjustments that allow journeys to be completed (Alerstam, 1996; Piersma and Lindström, 1997; Wehner, 1998). To tackle these questions, a variety of approaches have been used with, classically, mark/recapture studies being used to discover migration routes and destinations (Perdeck, 1958), laboratory experiments in controlled environments being used to test the biological compasses that may be employed (for reviews, see Emlen, 1975; Able, 1980; Wiltschko and Wiltschko, 1991) and organ analysis of dead specimens being used to look at changes in body condition (Åkesson et al., 1992; Piersma et al., 1999).

While all these approaches have produced major advances in our knowledge, they all provide only integrated measures of processes occurring during migration and do not reveal any intricacies of temporal patterns within migration. Establishing how the behaviour and physiology of animals change within a long-distance migration is logistically challenging but has now started to be addressed through the advent of reliable telemetry and logging equipment. First, for example, satellite tracking using the Argos system has allowed the routes of long-distance migrants to be reconstructed in hitherto unimagined detail and has revealed that animals may follow very straight-line courses for hundreds of kilometres, presumably through the use of reliable biological compasses (Cochran, 1987; Gudmundsson et al., 1995; Papi and Luschi, 1996; Kjellén et al., 1997). Second, some physical data (e.g. pressure, temperature, speed) can be relayed *via* satellite transmitters, allowing insights into the physiological ecology of animals in remote locations (Weimerskirsh et al., 1994; Hays et al., 1999; Hindell et al., 1999; Pennycuick et al., 1999). However, the limited available bandwidth of the Argos system severely constrains the amount of data that can be transmitted so that, for example, complete dive profiles cannot generally be obtained for marine animals. This constraint of the Argos system has led to the use of artificial displacements of animals carrying data loggers, rather than transmitters, so that their behaviour can be recorded in even more detail as they travel (Webb et al., 1998).

A paradigmatic group of long-distance migrants are marine turtles, with both conventional mark/recapture and satellite tracking showing that several populations and species may move thousands of kilometres between breeding grounds and feeding areas. For example, the green turtles (*Chelonia mydas*) that nest at Ascension Island in the middle of the Atlantic migrate at the end of the nesting season to feeding grounds along the South American coast, over 2200 km distant (Luschi et al., 1998). These turtles are thought not to feed either during their oceanic crossings or while at Ascension Island (Mortimer and Carr, 1987) and, hence, it might be hypothesised that during migration their behavioural repertoire would be very narrow, with individuals simply swimming continuously to attain their destination with the minimal energy consumption. However, limited dive information from five individuals has recently suggested that the behaviour during migration for this population is not invariant (Hays et al., 1999). Here we use (i) information obtained from satellite transmitters and (ii) results from the first displacement experiments in which turtles have been allowed to migrate back to a starting point while carrying time/depth recorders to reveal the details of their diving behaviour while they are travelling across the ocean.

Materials and methods

Satellite tracking studies

Satellite transmitters (platform terminal transmitters or PTTs) were attached to adult female green turtles (*Chelonia mydas*) at the end of the nesting season (May and June) on Ascension Island (7°57′S, 14°22′W) in both 1997 and 1998. Turtles consistently follow very straight-line courses to Brazil (for plots of tracks, see Luschi et al., 1998). We used two models of PTT to derive submergence information: Telonics ST-6 and ST-14 (Telonics Inc., Mesa, Arizona, USA). These PTTs contained a salt-water switch to suppress transmissions when submerged. This switch was also used to record submergence duration, with the mean submergence duration being integrated into 6 h periods. The start of these 6 h periods was determined from the time that the PTT was switched on, so that we could identify 6 h periods that were predominantly (>80 %) at night or predominantly during the day. The minimum duration of submergence that was required before a dive was logged was either 10 s or 1 min, depending on the PTT, but this difference had no discernible implications for the recorded mean submergence values. Submergence duration was recorded for 12 individuals.

Time/depth recorder (TDR) studies

Beach patrols located turtles nesting early in the season at Ascension Island between December 1999 and February 2000. Once they had laid their clutch, turtles were placed into large, padded wooden crates before being transported by truck to the nearby Georgetown pierhead (<1 km). Then, using a forklift truck, cranes and barges, they were loaded onto the merchant ship *MV Ascension* and displaced between 60 and 270 km away from the island prior to release. Animals were kept shaded and moist at all times. Prior to deployment, a TDR (LTD_100, LOTEK Marine Technologies, St John's, Newfoundland, Canada) was attached to the carapace using quick-setting epoxy resin. The TDR recorded the depth at 12 s intervals to a resolution of 4 cm.

To relocate the turtles, nesting beaches on Ascension Island were monitored. This was logistically challenging because of the very high numbers nesting on the island and involved over 20 island residents spending more than 200 man-nights patrolling beaches. When instrumented females were found, the TDR was removed and the dive data offloaded. In total, nine turtles were instrumented with TDRs, of which seven were re-sighted during subsequent nesting. Of these, the TDR was cracked and filled with sea water in two cases, while in five cases intact undamaged TDRs were recovered and all the depth data successfully offloaded. Dive data were analysed using bespoke software (MultiTrace, Jensen Software Systems, Laboe, Germany). To extract the dive variables for each long-duration dive (>5 min), dives were defined as starting when the rate of descent was greater than $0.3 \, \text{m s}^{-1}$ and ending when both the rate of ascent was more than $0.3 \, \text{m s}^{-1}$ and the depth was less than 10 % of the maximum for that dive. The time when turtles returned to Ascension Island was readily apparent in each dive record with the commencement of flat-bottomed U-shaped dives indicative of individuals remaining on the sea bed (Hays et al., 2000).

The height of nesting females was measured with a ruler (to the highest point on the carapace) when they were on compact level sand.

Results

Satellite tracking studies

For all individuals, there was a tendency for the mean submergence duration within 6 h periods to be short (<5 min), but for several individuals there were also instances of 6 h periods where the mean submergence duration was longer (Fig. 1). There were variable patterns to the occurrence of these longer-duration submergences during migration: sometimes they occurred throughout migration (Fig. 1A,F); in one case, they occurred predominantly in the middle of migration (Fig. 1C); while sometimes they occurred towards the end of migration (Fig. 1D,G). For 10 of the 12 individuals, the mean submergence duration was significantly longer at night than during the day (*t*-tests, *P*<0.001).

Time/depth recorder (TDR) studies

A bimodal distribution of depths was recorded for the animals travelling back to Ascension Island, with peaks between 0.9 and 1.5 m and between 10 and 20 m (Fig. 2). When turtles were near the surface (less than 5 m), it was often difficult to identify individual dives, presumably because turtles could sometimes surface and then submerge again within the 12 s sampling interval of the loggers. However, when individual dives could be identified, they were always short (2–4 min). Longer-duration dives (20–30 min) were
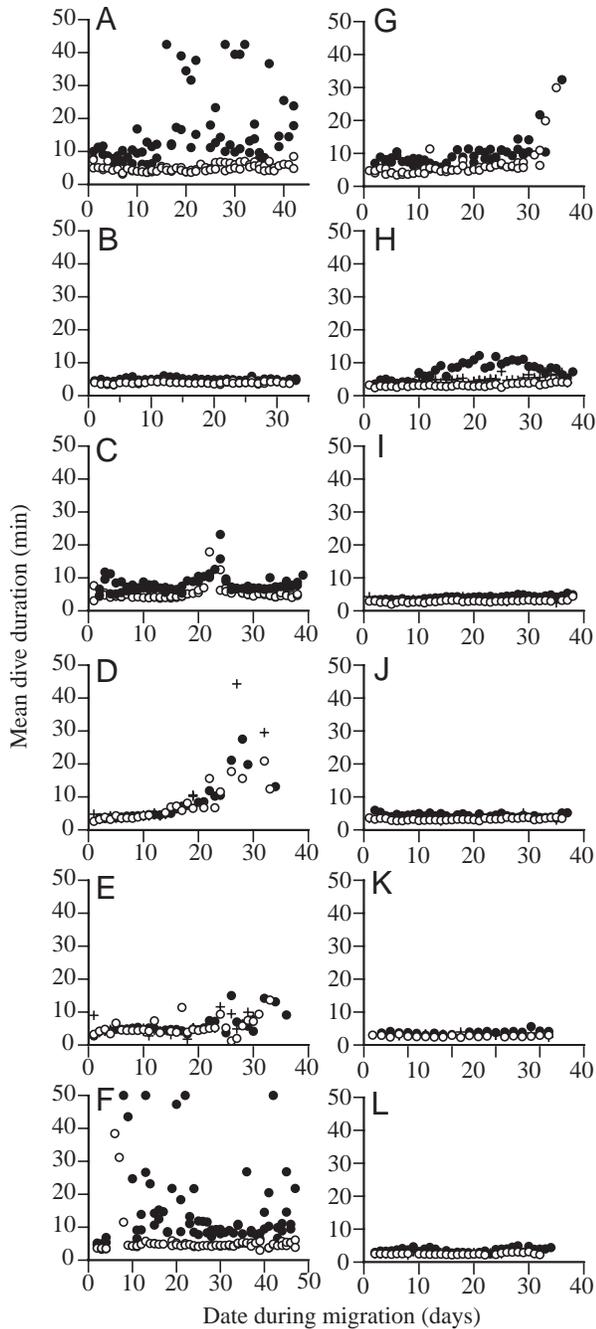
Fig. 1. The mean submergence duration recorded during 6 h intervals for 12 green sea turtles as they migrated from Ascension Island to Brazil. ●, night; ○, day; +, 6 h periods that straddle dusk and dawn. Four periods of long submergences (between 55 and 67 min) in F are plotted as 50 min to allow equal scaling of the *y*-axis in the different plots while maintaining easy visual comparison between the different parts of the figure.
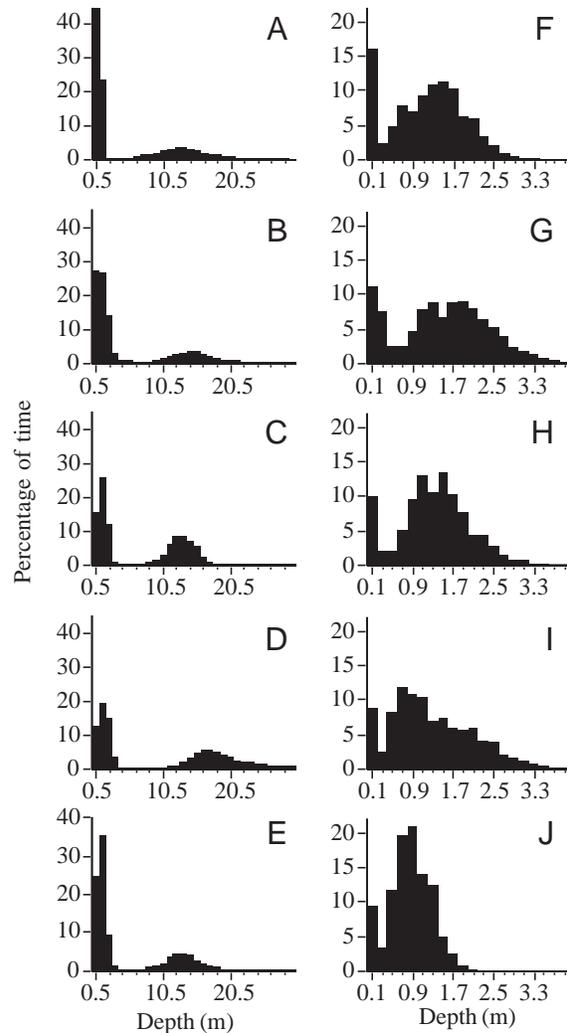

Fig. 2. For time/depth-recorder-equipped turtles, the depth distribution recorded as individuals travelled back to Ascension Island. (A–E) The percentage of time spent in each 1 m depth increment, revealing a bimodal pattern of depth utilisation, with peaks near the surface and between approximately 10 and 20 m. (F–J) The near-surface depth distribution in more detail, showing the percentage of time spent in 20 cm depth increments excluding dives deeper than 5 m.

always associated with the turtles diving deeper, with two distinct dive profiles being common (Fig. 3). In type 1 dives, turtles descended to a maximum depth, then gradually ascended during the course of the dive, before a final more rapid ascent; in type 2 dives, the gradual ascent phase was preceded by the turtles descending deeper than in a type 1 dive and then ascending rapidly to a depth similar to the maximum depth of type 1 dives. For all individuals, type 1 and 2 dives occurred mainly at night (Fig. 4). While the maximum depth of type 2 dives was deeper than for type 1, the respective mean depths were very similar (Table 1).

The height of nesting turtles ranged between 27 and 43 cm, with a mean of 36 cm (*N*=28).

Discussion

Over the last 20 years, there has been some deployment of TDRs onto turtles during the internesting period because the general fidelity of females to particular nesting beaches facilitates instrument recovery (Eckert et al., 1986, 1989;
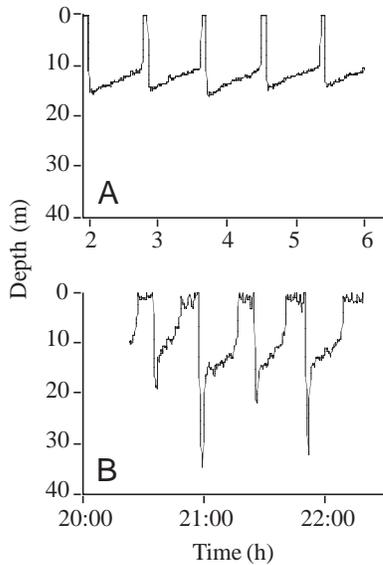
Fig. 3. Examples of (A) type 1 and (B) type 2 dives. In both dive types, most of the dive was spent in a period of gradual ascent, with this phase being preceded by a short period of more rapid ascent for type 2 dives. Time is shown as GMT, which equals local time at Ascension Island. For each of five turtles migrating back to Ascension Island, 99.4 %, 92.5 %, 100 %, 99.1 % and 96.7 % of dives more than 5 min in duration were either type 1 or type 2.
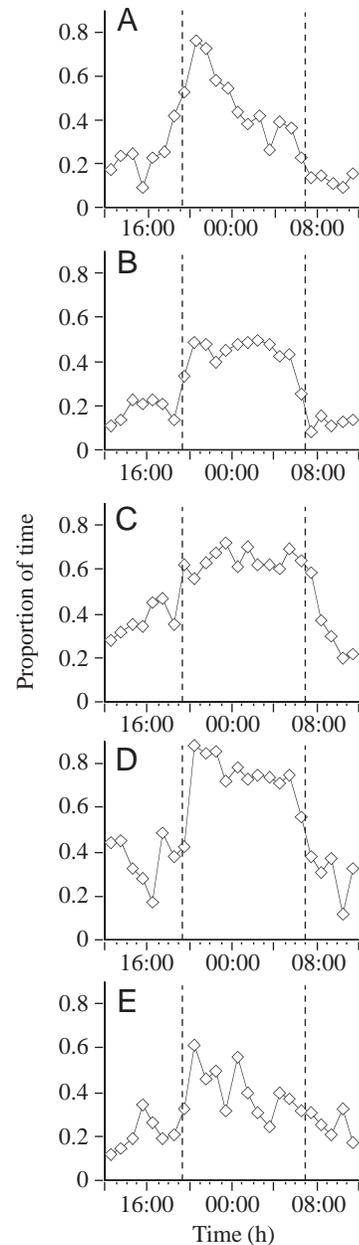

Fig. 4. For five turtles migrating back to Ascension Island, the proportion of time each hour spent conducting type 1 and 2 dives. For all individuals, there was a nocturnal peak in the occurrence of these midwater resting dives. Times are GMT, with sunrise and sunset (calculated at the midpoint between Ascension Island and the point of release) shown by the dashed vertical lines.

Minamikawa et al., 1997, 2000). However, information about the diving behaviour of turtles while they are undertaking long-distance migrations between nesting and foraging areas is far more scant. In the present study, we have demonstrated a dichotomy in dive types during oceanic swimming by green turtles. Satellite telemetry revealed that, while most of submergences are short, periods of longer submergences are often seen during migration. This dichotomy was confirmed through the deployment of TDRs on displaced turtles which revealed short, shallow dives and longer, deeper dives. In fact, since the satellite transmitters calculated the mean submergence duration over 6 h periods, it is likely that the true incidence of long submergences during migration from Ascension Island to Brazil was underestimated, since a small number of long dives will have little impact on the mean submergence duration calculated over such intervals when all other submergences are only a few minutes long.

Although the diving behaviour of a number of air-breathing vertebrates has been documented, many species also survey the water column (for example, for food) while they are travelling, so that their dives are to tens or hundreds of metres. However, there is little or no food available for herbivorous green turtles (*Chelonia mydas*) while they are swimming across the ocean to their nesting beaches, and we would therefore expect that minimisation of their cost of transport, rather than foraging, would be the key factor driving their swimming depth. In this regard, the optimum strategy is not to swim at the surface, where surface drag is high, but instead to swim below the surface where drag is reduced (Hertel, 1966). Specifically, drag

is minimised once the depth is approximately 2.5–3 times an animal's body thickness. Our finding that migrating turtles spent much of their time at a depth of approximately 0.9–1.5 m is consistent with this prediction that they are swimming at the shallowest depth that minimises their cost of transport.

The two typical deep dive profiles that were identified have been recorded both for marine turtles during their internesting period in coastal waters and for sea snakes (Graham et al., 1975, 1987; Minamikawa et al., 1997, 2000; Rubinoff et al.,

Table 1. *Mean values of the maximum and mean depths of type 1 and 2 dives and their duration for five green turtles*

| Individual | N | Type 1 dives | | | N | Type 2 dives | | |
		Maximum depth (m)	Mean depth (m)	Duration (min)		Maximum depth (m)	Mean depth (m)	Duration (min)
1	164	17.5±4.0	13.8±2.9	27.7±5.8	15	20.1±4.4	14.1±2.9	22.0±4.2
2	106	18.8±6.5	14.8±4.5	28.9±13.3	86	38.1±14.3	17.9±3.6	18.7±7.5
3	167	16.2±1.4	13.5±1.2	27.4±8.5	13	20.6±2.5	13.1±1.2	23.7±11.2
4	71	26.3±6.0	20.6±4.3	31.3±6.8	21	30.7±9.0	19.9±4.5	27.3±6.0
5	57	17.2±2.5	13.6±1.6	27.2±4.7	47	34.0±11.9	16.4±3.7	21.9±4.7

Values are means ± S.D.

1986). During the gradual ascent phase, it is known (from the use of activity sensors) that individuals may remain almost motionless 'hanging' in midwater, and these distinctive dive types are believed to minimise the energy expenditure of submerged animals, i.e. these may be midwater 'resting' dives of some aquatic reptiles. In other cases individuals may swim during the gradual ascent phase (Graham et al., 1987). The gradual ascent phase of these midwater dives has been attributed to a gradual loss of buoyancy as a result of removal of O_2 from the lungs without a corresponding replacement of CO_2 and, as such, individuals ascend very gradually to maintain neutral buoyancy.

The relatively deep excursions at the start of type 2 dives are enigmatic, although one suggestion is that these excursions represent the exploration of the water column (Graham et al., 1975, 1987). This conclusion that turtles undertaking oceanic migration may dive relatively deeply is as exciting as it is unexpected. Many years ago, Archie Carr, the pioneer of sea turtle research, speculated that migrating turtles might rest during migration but logically reasoned that, being air-breathers, they might rest at the surface, where they would have continuous access to air (Carr, 1967). Our results show that this is not the case and, in fact, that turtles spend very little time at the surface.

What are the ultimate and proximate reasons for turtles diving deeply during their trans-oceanic crossing? In some birds, there may be breaks during migration during which individuals feed and/or wait for favourable winds before continuing their journey (Weber et al., 1998; Åkesson and Hedenström, 2000). However, neither of these conditions is likely to apply to green turtles since (i) being herbivorous, they are thought not to feed during migration and (ii) there is unlikely to be a short-term temporal change in the currents that help carry the turtles back to Brazil (Luschi et al., 1998). The predominantly nocturnal pattern of deep diving that we observed has also been found during the inter-nesting period at Ascension Island (Hays et al., 2000) and for other species of marine turtle while individuals are at their feeding grounds (van Dam and Diez, 1996) and may be linked to why migrating turtles travel faster during the day than at night (Luschi et al., 1996, 1998). It might be that, as has been suggested for some migrating birds (Gudmundsson et al., 1995), there is a physiological reason limiting the ability of

turtles to maintain their optimum speed of travel throughout migration and so they must periodically rest, with these rest periods occurring at night because of an innate diurnal activity cycle in this group.

Deep diving clearly necessitates periods of ascent to the surface to breathe followed by descent, and so these vertical movements must come with some associated energetic cost. There is, therefore, presumably some counterbalancing advantage to deep diving. Although there are few predators of adult marine turtles, it is known that they may be attacked by large sharks (Stancyk, 1995; Fergusson et al., 2000), and adults at Ascension Island are seen missing parts of flippers, presumably as a result of predatory attacks. By diving below the surface, turtles will reduce the extent to which they are silhouetted against the surface and, hence, their risk of being observed by foraging sharks. Indeed, the dorso-ventral countershading of green turtles (darker above, light below) is also presumably an evolutionary response to predatory risk. An analogous use of a sub-surface refuge to reduce the risk of predation has also been proposed for elephant seals (*Mirounga angustirostris*) when digesting and assimilating food (Le Boeuf et al., 1982; Crocker et al., 1997), suggesting that the surface may, in general, be a risky place for air-breathing marine animals.

However, while seals may rest a few hundred metres below the surface, the typical deep dive for green turtles was between approximately 13 and 21 m. This range for the mean depth of type 1 and 2 dives corresponds approximately to the depths at which green turtles rest on the sea bed during the internesting period at Ascension Island (Hays et al., 2000), i.e. the depth of pelagic/midwater and neritic/benthic dives is similar. This depth selection may be driven by the ability of turtles to achieve neutral buoyancy. We have argued that approximately 20 m is the maximum depth at which Ascension Island green turtles can attain neutral buoyancy after diving with fully inflated lungs (Hays et al., 2000); i.e. if turtles were to dive any deeper, they would be negatively buoyant and would therefore (i) sink further during the dive if not resting on the sea bed and (ii) need to expend energy overcoming negative buoyancy to return to the surface. Therefore, green turtles presumably do not routinely dive any deeper as this would increase the energetic costs of descent and ascent.

In summary, we have shown, for the first time, the dive

profiles and depth distribution of turtles undertaking oceanic migration and have identified a dichotomy between short, near-surface dives, which probably reflect travelling, and deeper, longer-dives.

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