



THEME SECTION

Leatherback turtles satellite-tagged in European waters

Thomas K. Doyle^{1,*}, Jonathan D. R. Houghton², Pádraig Frank O'Súilleabháin³,
Victoria J. Hobson², Ferdia Marnell⁴, John Davenport⁵, Graeme C. Hays²

¹Coastal & Marine Resources Centre, University College Cork, Glucksman Marine Facility, Naval Base, Haulbowline, Cobh, Cork, Ireland

²Institute of Environmental Sustainability, Department of Biological Sciences, Swansea University, Singleton Park, Swansea SA2 8PP, UK

³Salmon Fisherman's Association, Baile Na nGall, Dingle (Daingean Uí Chúis), Ireland

⁴National Parks and Wildlife Service, of the Department of Environment, Heritage and Local Government, 7 Ely Place, Dublin 2, Ireland

⁵Department of Zoology, Ecology and Plant Sciences, University College Cork, Distillery Fields, North Mall Cork, Ireland

ABSTRACT: The North Atlantic is considered a stronghold for the critically endangered leatherback sea turtle. However, limited information exists regarding the movements of individuals to and from the seas off Europe's northwesterly fringe, an area where leatherbacks have been historically sighted for the past 200 yr. Here, we used satellite telemetry to record the movements and behaviour of 2 individuals bycaught in fisheries off the southwest coast of Ireland. The turtle T1 (tagged 1 September 2005; female; tracked 375 d) immediately travelled south via Madeira and the Canaries, before residing in West African waters for 3 mo. In spring, T1 migrated north towards Newfoundland where transmissions ceased. T2 (29 June 2006; male; 233 d) travelled south for a short period before spending 66 d west of the Bay of Biscay, an area previously asserted as a high-use area for leatherbacks. This prolonged high latitude summer residence corresponded with a mesoscale feature evident from satellite imagery, with the implication that this turtle had found a rich feeding site. A marked change in dive behaviour was apparent as the turtle exited this feature and provided useful insights on leatherback diving behaviour. T2 headed south in October 2006, and performed the deepest-ever dive recorded by a reptile (1280 m) southwest of Cape Verde. Unlike T1, T2 swam southwest towards Brazil before approaching the major nesting beaches of French Guiana and Surinam. Importantly, these tracks document the movement of leatherbacks from one of the remotest foraging grounds in the North Atlantic.

KEY WORDS: Dermochelys · Summer residence · Northeast Atlantic · Ireland · High-use area · Abundance · Male · Deepest dive

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

Understanding the movement of endangered species throughout their range is an important criterion for species conservation. This is particularly true for widely roaming marine species that may utilise entire oceans (Bonfil et al. 2005). The critically endangered leatherback sea turtle *Dermochelys coriacea* is a case in point.

For this species, the entire North Atlantic may be considered a stronghold (Ferraro et al. 2004, Hays et al. 2004b, James et al. 2005a, 2006, Eckert 2006), yet limited information exists regarding the movements of individuals to and from the seas off Europe's northwesterly fringe (Brongersma 1972, Duron 1978, Duguay et al. 1980, Houghton et al. 2006, Witt et al. 2007, Godley et al. 2008, this Theme Section [TS]). Yet establishing such

parameters is important, especially for endangered species where knowledge of their range and movements may be critical in helping to define important areas where conservation measures need to be implemented.

The leatherback sea turtle nests on tropical and subtropical beaches. Outside the nesting season individuals undertake extensive trans-oceanic migrations (Hughes et al. 1998, Ferraroli et al. 2004, Hays et al. 2004b, Eckert 2006) before returning to breed with a 2 to 4 yr cycle (McDonald & Dutton 1996). During the summer and autumn months leatherbacks are observed seasonally at locations very distant from their breeding grounds, such as the eastern Canadian seaboard (James & Herman 2001, James et al. 2005a) and in northern Europe (Brongersma 1972, Duguay et al. 1980, Houghton et al. 2006, Witt et al. 2007, King & Berrow in press). Such sightings reveal the seasonal occurrence of a population as a whole rather than the timing of seasonal high latitude occupation by specific individuals. A pattern of sightings over a protracted seasonal timescale might therefore represent either (1) different individuals passing through an area over a long period, (2) specific individuals remaining in an area for a long time, or (3) a combination of these 2 scenarios. Distinguishing between these different scenarios is possible, in theory, by tracking individuals, although such studies are difficult to perform. Pioneering studies in Nova Scotia, Canada, have involved the capture of leatherback turtles at sea, fitting satellite tags to individuals and then recording their subsequent movements (James et al. 2005a,b,c). This work is much more challenging than fitting satellite tags to females while ashore during nesting (indeed, over 75% of the published tracking studies have tracked females from nesting grounds, see Godley et al. 2008), and has the advantage of allowing detailed information to be gained about the movements of both males and females at the foraging grounds (James et al. 2005c). Such efforts have confirmed that the coastal waters off Nova Scotia are an important foraging site for leatherbacks, with individual turtles remaining in residence in this area sometimes for several months over the summer, feeding on jellyfish and improving their body condition (James & Herman 2001, James et al. 2005a).

Whether this same scenario applies to the seas off northern Europe has yet to be empirically established, yet leatherbacks have been historically sighted in this area for the past 200 yr (Brongersma 1972, Duguay et al. 1980, Houghton et al. 2006, Witt et al. 2007, King & Berrow in press). Here we describe the results of the first 2 leatherback turtles fitted with satellite tags in Europe; these come almost 30 yr after Duron (1978) attached radio tags to 2 leatherbacks in the La Rochelle area, France. We reveal whether individual turtles may

stay for long periods in northern European waters over the summer, and consider the implications of the remoteness of northern Europe from the species' breeding grounds in terms of species' abundance and migration schedule.

MATERIALS AND METHODS

Attachment of tags. Two turtles were fitted with satellite tags (Satellite Relay Data Loggers, SRDLs, manufactured by the Sea Mammal Research Unit, St Andrews) close to Dingle (Daingean Uí Chúis) (52.24° N, 10.30° W) on the west coast of Ireland; 1 turtle in 2005 (T1), and 1 in 2006 (T2). Both turtles became entangled in fishing gear prior to tag attachment. The tag was attached to T1 using a harness system, whereas for T2 the tag was attached directly to the carapace. Both tags were attached under license from the National Parks and Wildlife Service of the Department of the Environment, Heritage and Local Government, Ireland.

On 31 August 2005 T1 was found by a local fisherman entangled in a lobster pot rope approximately 0.2 km from the harbour of Cuas (52.24° N, 10.30° W). The turtle was brought into Cuas harbour and then transported to Dingle Oceanworld Aquarium (www.dingle-oceanworld.ie/) to check that it was in good health. In the aquarium the turtle was sexed (female) and a satellite tag was attached using a flexible harness that has variously been described in detail elsewhere (Eckert & Eckert 1986, Hays et al. 2004a, Myers & Hays 2006). The turtle was released from the same harbour on 1 September 2005.

T2 became entangled in a salmon drift net on 29 June 2006, approximately 0.5 km from Cuas harbour. The turtle was removed from the fishing gear and brought safely into nearby shallow waters, where an SRDL was fitted using a direct attachment method (see Fossette et al. 2008, this TS). Three holes (6.5 mm diameter) were drilled through the anterior end of central keel of the carapace (which is mainly cartilaginous tissue) and served as an attachment point for the SRDL/baseplate. The carapace was disinfected with Betadine® (Viatrix Pharma) before and after drilling. There was no visible sign of discomfort during drilling, i.e. the animal did not react or flinch in any way. The baseplate is shaped like a catamaran with the SRDL glued on top. A small amount of antifouling paint was applied over parts of the tag to prevent bio-fouling. For attachment to the turtle, cable ties were fitted through the drilled holes in the turtle's keel and then fed through pre-drilled holes in the baseplate. The turtle was sexed (male) and released immediately after attachment of the SRDL.

Track reconstruction, description of recorded behaviours, and remote sensing. SRDLs were located and tracks reconstructed using the Argos system (www.clsamerica.com/). Each Argos location is provided with a measure of its accuracy, called the location class (LC). Only the most accurate locations (LC 1, 2, and 3, see Hays et al. 2004b, James et al. 2005a) were used to reconstruct the track of T2. However, for T1 it was also necessary to use LC A locations (Fig. 1) after 10 November 2005, when normal functioning of its SRDL was impaired (Hays et al. 2001 have shown LC A locations to be comparable with LC 1 locations). Any LC A locations that had a maximum rate of travel $>5 \text{ km h}^{-1}$ were removed from analysis (James et al. 2005a).

As well as location, 5 different measures of diving behaviour were recorded and relayed by the SRDLs

(McMahon et al. 2007): (1) shallow-form dives ($<10 \text{ m}$) that provided information on dive duration, surface duration and maximum dive depth obtained; (2) deep-form dives ($\geq 10 \text{ m}$) that provided information on dive shape, duration, and maximum depth (henceforth referred to as 'individual deep-form dive profiles'); (3) summary statistics of all events that occurred during a 6 h period including the number of shallow-form and deep-form dives, the mean duration ($\pm \text{SD}$) of deep- and shallow-form dives, mean depth ($\pm \text{SD}$) of deep- and shallow-form dives, maximum depth of deep dives, and the proportion of time spent either diving or at the surface (Hochscheid et al. 2005) (these summary statistics are based on all the data recorded by the SRDL which is continuously logging all dives); (4) temperature-depth profiles of the deepest dive that occurred during a 4 h window; and (5) the maximum depth recorded. The precision of depth measurements was 30 m at 1000 m, and 0.5 m near the surface. Surface time is determined by a wet/dry saltwater switch and when the animal is above a minimum depth (2 m). Dives start when turtles are below 2 m for 30 s and end when they are above 2 m for 0 s or dry at any time. Deep dives begin at 10 m. For further details of dive behaviour and temperature data see McMahon et al. (2005) and Myers & Hays (2006), respectively.

The track of T2 (within the area west of the Bay of Biscay) was superimposed on contemporaneous maps of sea surface height anomalies (SSHA) available for download as images from the Colorado Centre for Astrodynamic Research website http://argo.colorado.edu/~realtime/gsfc_global-real-time_ssh/. Each SSHA map, which is objectively analyzed to a $\frac{1}{4}$ degree spatial resolution, is based on the latest 10 d of Jason, 17 d of Geosat Follow-On, and 35 d of Envisat and ERS-2 along-track data from the nadir pointing altimeters (Leben et al. 2002) (i.e. satellites sample along repeating ground tracks of 10, 17 and 35 d). The interpolation uses a time correlation of about 12 d, using different windows on the data, but never changing the time scale. These SSHA map averages can resolve meso-scale ocean eddies with diameters as small as 75 to 100 km at mid-latitudes. All SSHA data was fitted to track data in ArcGIS, and later inserted into Microsoft PowerPoint to create a short animation of track superimposed over SSHA data.

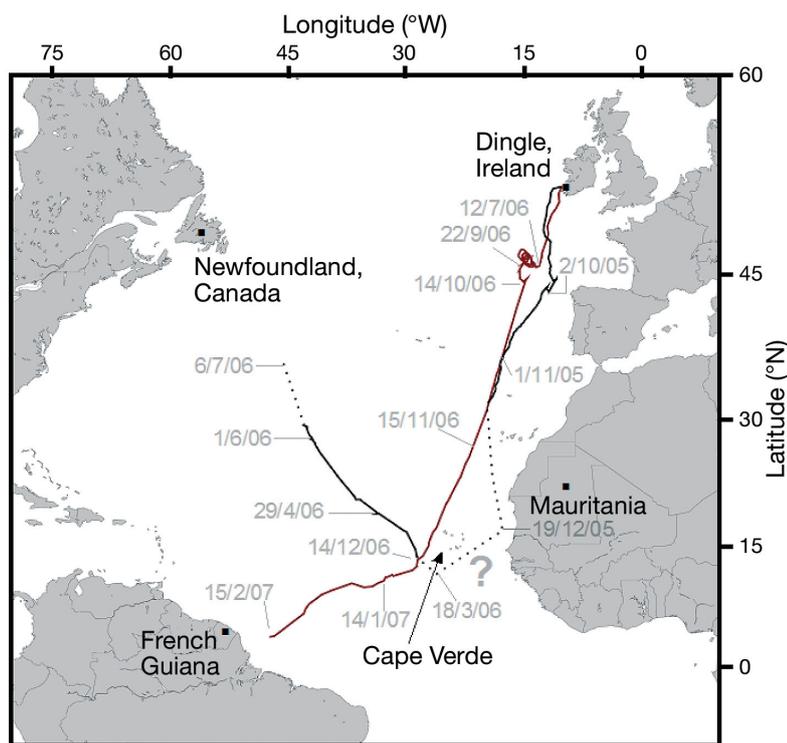


Fig. 1. *Dermochelys coriacea*. Complete track of female leatherback in a sub-bathal year away from the nesting grounds (straight curved carapace length, SCCL = 153 cm, tagged 1 September 2005) (black track with dotted sections) and male turtle foraging in the northeast Atlantic before returning to breeding grounds (SCCL = 166 cm, tagged 29 June 2006) (red track). Dotted section denotes section of female track where locations were intermittently received. The female spent 3 mo between Mauritania and Cape Verde. The southernmost (recorded) point of her journey was due south of Cape Verde (18 March 2006), and from this date onwards she travelled northwest until transmissions ceased on 6 July 2006. The male resided in an area west of the Bay of Biscay for 66 d in a mesoscale feature evident from satellite telemetry data and was located 700 km from the major rookeries of French Guiana and Surinam when transmissions ceased on 15 February 2006. Male turtle performed deepest dive ever recorded by a reptile (1280 m) just south west of Cape Verde. All dates are dd/mm/yy

RESULTS

Movements

T1 quickly left the west coast of Ireland (1 September 2005) and immediately headed southwards for approximately 20 d. Off the northwest coast of Spain, T1's movement changed from directed motion to an erratic motion for a period of approximately 3 wk before heading south again (Fig. 1). On 10 November 2005, 350 km northeast of Tenerife, regular transmissions of locations diminished, most probably as a result of bio-fouling of the saltwater switch that synchronises transmissions with surfacing events. Thereafter, analysis of the intermittent locations revealed that T1 passed 160 km west of Mauritania, and reached her furthest point south on 3 March 2006, 400 km south-southwest of the Cape Verde Islands (Fig. 1). Although a limited number of locations were received, T1 spent approximately 3 mo in West African waters. From her furthest point south, she swam in a very directed path towards Canada, at which point we received a final Argos location on 7 July 2006, 1300 km southeast of Newfoundland.

T2 quickly left the area where he was tagged, and travelled south (Fig. 1). By 10 July 2006, just over 11 d after release the turtle was west of the Bay of Biscay, 700 km from the release point. The turtle then remained in the same general area for the next 66 d, making large loops in a clockwise motion. When the track data was overlaid on SSHA data (see 'Materials and methods' for details), it can be seen that T2's tracks closely followed the outer edge of the mesoscale feature (see yellow area centred around the location $\sim 46^\circ$ to 46.5° N and $\sim 15^\circ$ W in animation in Appendix 1, available as Supplementary Material at: www.int-res.com/articles/suppl/n004p023_apps/, and Fig. 2) (see also Luschi et al. 2003, Gaspar et al. 2006, Hays et al. 2006 for similar findings). Further in-depth analysis of this mesoscale feature using a much finer resolution, in conjunction with analysis of the turtle's location, temperature and dive data are needed to fully resolve the exact overlap between the two, i.e. was the turtle always rotating around the edge of this feature or did it go in and out of it? The mesoscale feature itself is identifiable as an anticyclonic eddy (i.e. it rotates clockwise and has a warm core) (Isla et al. 2004). Anticyclonic eddies are a recurrent mesoscale structure in the Bay of Biscay circulation and are shed from the slope current that flows along the Iberian slope (Isla et al. 2004). The turtle completed 3 large loops in close association with this mesoscale feature during the period from 8 July 2006 to 11 September 2006, i.e. taking approximately 20 d to complete one loop. T2's travel around

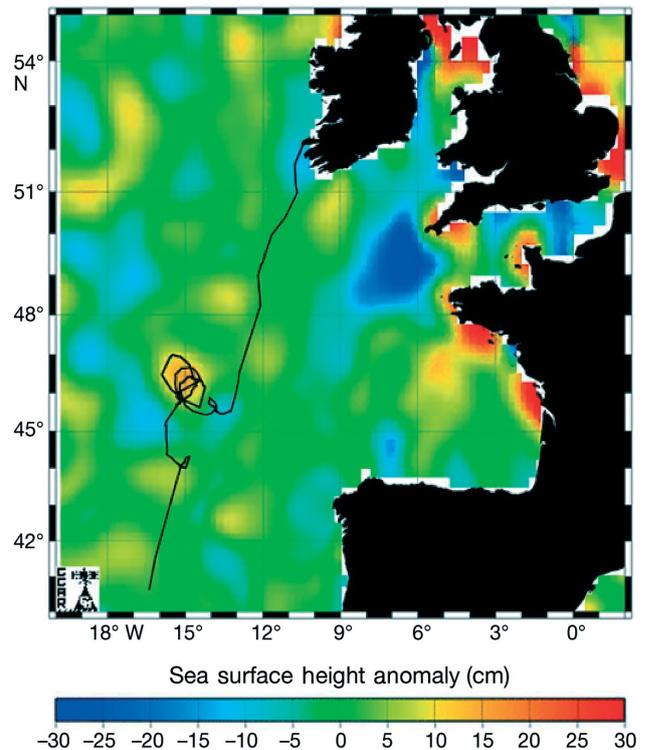


Fig. 2. *Dermochelys coriacea*. The track of turtle T2 overlaid on a sea surface height anomaly image from 4 September 2006. T2 resided for 66 d in an anticyclonic mesoscale feature (yellow area), with the turtle looping around in the same direction (clockwise). See Appendix 1, available as Supplementary Material at: www.int-res.com/articles/suppl/n004p023_apps/ for animation of this high latitude protracted residence

this feature is clearly indicated by a plot of distance from the release point versus the number of days since the animal was tagged (Fig. 3). After leaving this anomaly (11 September 2006), T2 headed south and then southeast before describing a much smaller loop. Then, on 14 October 2006, T2 swam south-southwest covering approximately 3200 km (in an almost perfect linear direction) before reaching Cape Verde on 4 December 2006. After Cape Verde, T2 travelled southwest towards the coast of South America and was only 700 km from Yalimapo Beach (a major nesting beach) in French Guiana when transmissions ceased.

Dive behaviour

For T1, 229 6 h summaries of dive statistics were received (representing 15% of the total time tracked) (Table 1). T1 spent 71% of her time diving (below 2 m for >30 s), 95% of the dives being deep-form dives. For individual 6 h dive periods the mean number of deep-

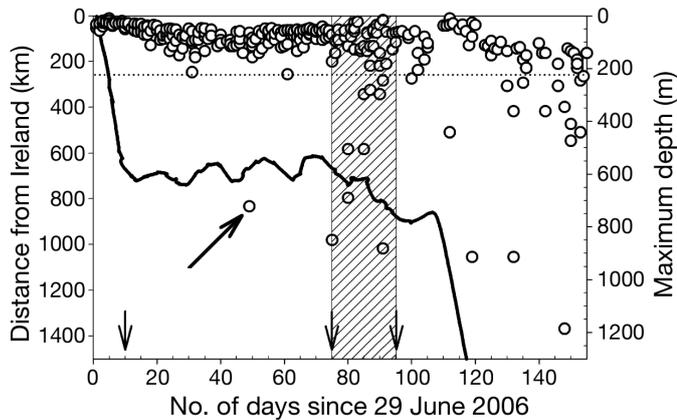


Fig. 3. *Dermochelys coriacea*. Distance of turtle T2 from the release site plotted against the number of days since it was satellite tagged (solid line). Each individual open circle (O) equals the maximum dive depth obtained during a 6 h period (e.g. 00:00 to 06:00 h) with its corresponding day number since deployment. The cyclical movement away from and towards Ireland from Day 10 to Day 74 (8 July 2006 to 10 September 2006) corresponds with the sea height anomaly (mesoscale feature) overlay in Fig. 2. Thick arrow points to the only 6 h period within mesoscale feature when the maximum dive depth obtained was >225 m. Hatched area highlights dive behaviour post mesoscale. Small inverted arrows point to Days 10 (8 July 2006), 75 (11 September 2006), and 95 (1 October 2006). Dotted line: 225 m depth contour. Note how T2 tended to dive deeper as it moved further south; a similar behaviour was reported in previous studies (Eckert 2006, Hays et al. 2006)

form dives was 15 (SD = 7), mean depth of deep-form dives was generally shallower than 100 m (97% of all dives), and the maximum dive depth was generally shallower than 150 m (94% of all dives). Analysis of the individual dive profiles received ($n = 1228$, 10 to 200 m range) showed a similar pattern (Fig. 4a). No dives received from the 6 h summaries or individual dive profiles were greater than 200 m; however, a maximum depth of 615 m was recorded (see description of recorded behaviours in 'Materials and methods') during mid-November 2005.

Analysis of T2's 6 h summary data received ($N = 382$, representing 41% of the total time tracked) (Table 1) revealed that for individual 6 h dive periods the mean

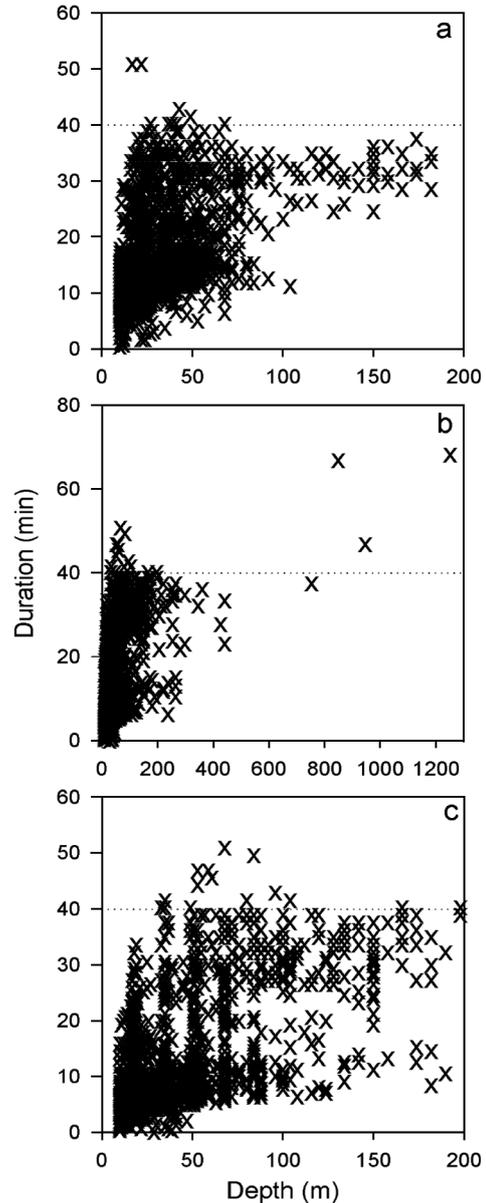


Fig. 4. *Dermochelys coriacea*. Dive duration as a function of maximum depth for all long-form dives. (a) All dives for T1 ($n = 1228$, range ≥ 10 m). (b) All dives for T2 ($n = 1815$). (c) All dives in the range 10 to 200 m for T2 ($n = 1783$). Dotted line equals point beyond (i.e. 40 min) which very few dives were recorded

Table 1. *Dermochelys coriacea*. Summary information from 2 satellite-relayed data logger (SRDL) deployments on leatherbacks tagged off Dingle (Daingean Uí Chúis), southwest Ireland. For explanation of location classes and dive forms, see 'Materials and methods'

Turtle ID	Dates (dd/mm/yy)	Days tracked	No. of links in each Argos location class					Deep-form dives	Shallow- form dives	No. of 6 h summaries	
			B	A	0	1	2				3
T1	01/09/05–10/09/06	375	342	183	98	71	33	13	1228	293	229
T2	29/06/06–16/02/07	233	321	178	152	108	55	18	1815	479	382

number of deep-form dives was 19 (SD = 11), mean depth of deep-form dives was generally shallower than 150 m (95% of all dives), and the maximum dive depth was generally shallower than 200 m (88% of all dives), with very deep dives recorded occasionally. The maximum dive depth obtained was 1280 m (date and location: 16 December 2006, southwest of Cape Verde), and represents the deepest dive ever recorded for a reptile (see Hays et al. 2004a for previous record). The deepest dive profile received was to 1250 m for a dive lasting 68.5 min. T2 spent 54% of its time diving, 98% of the dives being deep-form dives. Analysis of the individual deep-form dive profiles received (N = 1815, range 10 to 1280 m) showed a similar pattern (Fig. 4b,c).

T2's dive behaviour within mesoscale

The maximum dive depth obtained per 6 h period by T2 was less within the mesoscale feature (mean = 79.7 m, n = data obtained for 162 periods of 6 h over 66 d, SD = 60.4 m) than immediately after it left the feature (mean = 163.0 m, n = data obtained for 51 periods of 6 h over 20 d, SD = 194.0 m) (Student's $t_{53} = 3.02$, $p = 0.0039$). In addition 5 out of the nine 6 h periods within which the turtle was recorded to dive deeper than 500 m occurred in these 20 d after leaving the feature and only one within the feature.

DISCUSSION

The extensive oceanic migrations of leatherback turtles (Hughes et al. 1998, Ferraroli et al. 2004, Hays et al. 2004b, James et al. 2005a, Eckert 2006) raise interesting ecological questions given the patchy and seasonally abundant nature of their prey (Graham et al. 2001). To fully understand this behaviour, it is necessary to identify where and when individuals display periods of protracted residency indicative of some degree of foraging success. We appreciate that various quantitative movement analyses such as first passage time analysis (e.g. Bailey & Thompson 2006) and state space models (Jonsen et al. 2006) can be used to objectively assess changes in the behaviour of tracked animals. However, even the relatively simple analyses we performed in the present study were adequate to show clear changes in behaviour for the tracked turtles. In a recent study, Eckert (2006) suggested a 'high-use area' for the Iberian Peninsula and the Bay of Biscay based on a post-nesting female tracked from Trinidad that arrived in late autumn. Our tracking results for turtles tagged off Ireland complement this previous study, with T2 (and to a

lesser extent T1) spending a large amount of time within this region (post-tagging). However, an important difference is that the tracks of T2 demonstrate the first protracted 'summer' residence of a leatherback in the northeast Atlantic (NEA) previously asserted from turtle sightings and strandings data (Brongersma 1972, Duguy et al. 1980, Houghton et al. 2006, Witt et al. 2007, King & Berrow in press). These tracks also demonstrate the individual differences in space utilisation by leatherback turtles in the NEA; for example, previous studies have shown that distinct coastal 'jellyfish hotspots' in the Irish Sea may be important foraging areas (Houghton et al. 2006) with associated coastal foraging behaviour. Here we show that alternative strategies exist (i.e. foraging in mesoscale features in the Bay of Biscay region) that help form a conceptual model of leatherback habitat utilization in the NEA.

A limiting factor for many marine tracking studies is that the observed behaviour (foraging?) occurs in oceanic areas where accurately quantifying prey densities and foraging success is difficult. Several authors have implied good foraging conditions because mesoscale features (both warm and cold core eddies) are associated with higher prey abundance (Shoop & Kenney 1992, Lutcavage 1996, Luschi et al. 2003, Hays et al. 2006, Eckert 2006, Polovina et al. 2006). Here, too, we suggest that the residence of T2 in a mesoscale feature for several months implied that there were good foraging conditions. Our assumptions are based on 2 signatures: (1) a marked change in movement (i.e. from directed travel to looping around in a mesoscale feature) (Fig. 2) (see Gaspar et al. 2006, Hays et al. 2006), and (2) a marked change in dive behaviour. For example, during the 66 d within the mesoscale T2 rarely dived deeper than 225 m; however, T2's exit from this patch corresponded with a notable change in its diving behaviour (Fig. 3), i.e. the performance of many very deep dives (nine 6 h periods showed a maximum dive depth >225 m, including 5 that were >500 m). The adaptive significance of such deep dives is uncertain as they are performed only rarely (Eckert et al. 1986, Hays et al. 2004b), but the co-occurrence of many deep dives with the timing of T2's exit from the anomaly may suggest that these deep dives are speculative dives in search of prey when turtles have left a good prey field. However, in common with previous studies (e.g. Bradshaw et al. 2007) we showed that deep dives by leatherbacks were relatively rare. For example, of 3043 deep-form dive profiles we recorded for the 2 individuals only 32 were deeper than 200 m, and only 4 deeper than 500 m. Leatherbacks therefore seem to spend most of their time living at epi-pelagic (<200 m) depths (Hays et al. 2004b, Sale et al. 2006). Furthermore, in line with previous studies (e.g. Brad-

shaw et al. 2007) there appeared to be a clear ceiling in dive duration around 40 min (Fig. 4). We could not determine the exact causal factors for T2's resumption of a southward migration, but the contrast between the following southern leg of almost 3200 linear km and the previous protracted residency is remarkable, and is supportive of at least 2 behaviours: foraging (looping tracks) and then travelling (linear track). However, Luschi et al. (2003) found that complete looping is not always the behaviour associated with leatherback utilization of an eddy, i.e. curved or straight travel along the edge of an eddy (both warm and cold core eddies) may also be indicative of their use for foraging (Polovina et al. 2006).

Leatherback turtles seen at high latitude have clearly migrated large distances from their nesting beaches. Nova Scotia (44°N, 60°W) (representative of the northwest Atlantic, NWA) is approximately 4400 km from Awala Yalimapo, French Guiana (5.7°N, 53.9°W), and 3800 km from Galera Point, Trinidad and Tobago (11°N, 61°W), both of which hold some of the largest nesting populations of leatherbacks in the northern hemisphere (Rivalan et al. 2005, Eckert 2006). Parts of northern Europe where leatherbacks are sighted each summer lie considerably further away from these nesting sites. For example, the shortest distance from either of these beaches to the west coast of Ireland is around 6500 km, so 2100 km further than Nova Scotia. However, considering the track of T2 (Fig. 1) and a very similar track of a female tracked in the opposite direction (Eckert 2006), the actual distance between northern Europe and the nesting beaches is probably closer to 7700 km (or approximately twice the distance needed to swim to Nova Scotia). As the maximum sustained speed of travel for adult leatherback turtles is around 32.5 km d⁻¹ (Hays et al. 2006, but see Eckert 2006 for higher estimates), a post-nesting turtle would take a minimum period of around 126 or 220 d to travel from French Guiana to Nova Scotia and Ireland, respectively. Given that the females depart the nesting beaches around May to July (Eckert 2006, Hays et al. 2006), the earliest that most females might arrive off Nova Scotia and the west coast of Ireland would be late August and mid-November, respectively. Indeed, a turtle that left Trinidad in mid-June 1995 arrived in the Bay of Biscay area in November (Eckert 2006). However, the southerly migration from Nova Scotia commences during September to November (James et al. 2005a,b), and similarly this may also be inferred for Ireland, as the majority of leatherback sightings off Ireland and the UK occur in July to September (Houghton et al. 2006). In short, these calculations suggest that female leatherbacks might very rarely travel as far north as the coast of Ireland in the year

they nest, but may do so to Nova Scotia. However, in their 'sabbatical years' away from the nesting beaches, females probably initiate their northerly migration sooner and from a closer location (i.e. from Cape Verde), and hence can arrive in northern Europe earlier in the season. The timing of the northerly migration of T1 on 18 March 2006 lends support to this idea (Fig. 1). For male leatherbacks, however, it is far more likely that they might reach the NEA in the years that they have bred, as they may leave the breeding grounds much earlier in the year than females (James et al. 2005c).

Although very simple, these calculations highlight the remoteness of the NEA when compared with the NWA, and the subsequent effects this extra distance has on the seasonal timing of movements of both males and females to this area. However, distance may also have an important bearing on the density of leatherbacks that may seasonally occupy these 2 areas, and a comparison of abundance estimates of the number of leatherbacks observed from aerial surveys in the 2 areas suggests this may be the case. For example, Shoop & Kenney (1992) found 6.85 leatherbacks per 1000 km of track flown over continental shelf waters of Nova Scotia to Cape Hatteras (NWA); Murphy et al. (2006) found 40.00 leatherbacks per 1000 km of track in nearshore waters off South Carolina (NWA); Brown & Tobin (1999) found 5.11 leatherbacks per 1000 km of track off Nova Scotia (NWA). In contrast, aerial surveys carried out by the authors in the Irish and Celtic Seas during 2003 to 2006 only observed 0.25 leatherbacks per 1000 km of track flown (unpubl. data, but see Houghton et al. 2006 for methods). Therefore, we suggest that this marked difference in abundance estimates may be the result of the remoteness of the NEA from the tropical nesting beaches.

In summary, these first tracking results for leatherbacks in Europe lend support to the suggestion that the Bay of Biscay region within the NEA is a relatively high-use area that plays a central role in the feeding ecology and trajectory of body condition for some individuals. We have shown the first protracted summer residence for leatherbacks in the area and documented their subsequent movements for up to a year. Spatial analysis of the distance to the NEA has provided important insights on the dynamics and seasonal timing of movements of both sexes to this remote region. While we appreciate a sample size of $n = 2$ is small for leatherbacks tracked from Ireland, the logistical difficulties of this work mean that obtaining larger sample sizes will take many years and might be unrealistic. Yet the conservation implications of this work are immediate and pressing and hence we feel it is important to disseminate our results to conservation biologists, turtle researchers and policy makers alike.

Acknowledgements We thank the local salmon fishing community of Chorca Dhuibhne, Dingle Oceanworld Aquarium, and the Coastal and Marine Resources Centre for their assistance and support. Thanks are also due to M. Cronin, V. Hyland, K. Flannery, J. Flannery, M. Lynch, A. Murphy, H. Pearson, T. J. Scanlon, J. Smith, M. O'Conneide, S. O'Conchuir, G. O'Sullivan, and the O'Suilleabhain family. T.K.D. thanks J. Y. Georges for inviting him to partake in fieldwork in French Guiana to demonstrate the new direct attachment of electronic devices to leatherbacks, and R. Leben for providing advice on the SSHA data used in this study. All tagging was carried out under the strict guidance and approval of National Parks and Wildlife Service of the Department of Environment, Heritage and Local Government, Ireland. The authors acknowledge use of the Maptool program for analysis and graphics of Fig. 2 in this study (www.seaturtle.org). This work was partially supported by INTERREG IIIA, a component programme of the European Regional Development Fund. National Parks and Wildlife Service of the Department of Environment, Heritage and Local Government, Ireland and the Marine Institute Ireland provided additional funds in 2006.

LITERATURE CITED

- Bailey H, Thompson P (2006) Quantitative analysis of bottlenose dolphin movement patterns and their relationship with foraging. *J Anim Ecol* 75:456–465
- Bonfil R, Meyer M, Scholl MC, Johnson R and others (2005) Transoceanic migration, spatial dynamics, and population linkages of white sharks. *Science* 310:100–103
- Bradshaw CJA, McMahon CR, Hays GC (2007) Behavioral inference of diving metabolic rate in free-ranging leatherback turtles. *Physiol Biochem Zool* 80:209–219
- Brongersma LD (1972) European Atlantic turtles. *Zool Verh* 121:1–318
- Brown MW, Tobin D (1999) Vessel and aerial surveys for North Atlantic right whales in Canadian waters, 1998. Final report: Contract F5245-8-0064, Bedford Institute of Oceanography, Halifax
- Duguy R, Duron M, Alzieu C (1980) Observations de tortues luth (*Dermodochelys coriacea*) dans les Pertuis Charentais en 1979. *Ann Soc Sci Nat Charente-Marit* 6:681–691
- Duron M (1978) Contribution à l'étude de la biologie de *Dermodochelys coriacea* (Linné) dans les Pertuis Charentais. University of Bordeaux, Talence
- Eckert SA (2006) High-use oceanic areas for Atlantic leatherback sea turtles (*Dermodochelys coriacea*) as identified using satellite telemetered location and dive information. *Mar Biol* 149:1257–1267
- Eckert SA, Eckert KL (1986) Harnessing leatherbacks. *Mar Turtle News* 37:1–3
- Eckert SA, Nellis DW, Eckert KL, Kooyman GL (1986) Diving patterns of 2 leatherback sea turtles (*Dermodochelys coriacea*) during internesting intervals at Sandy Point, St-Croix, United States Virgin Islands. *Herpetologica* 42:381–388
- Ferraroli S, Georges JY, Gaspar P, Le Maho Y (2004) Endangered species — where leatherback turtles meet fisheries. *Nature* 429:521–522
- Fossette S, Corbel H, Gaspar P, Le Maho Y, Georges JY (2008) An alternative technique for the long-term satellite tracking of leatherback turtles. *Endang Species Res* 4:33–41
- Gaspar P, Georges JY, Fossette S, Lenoble A, Ferraroli S, Le Maho Y (2006) Marine animal behaviour: Neglecting ocean currents can lead us up the wrong track. *Proc R Soc Lond B Biol Sci* 273:2697–2702
- 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 Species Res* 4:3–22
- Graham WM, Pages F, Hamner WM (2001) A physical context for gelatinous zooplankton aggregations: a review. *Hydrobiologia* 451:199–212
- Hays GC, Akesson S, Godley BJ, Luschi P, Santidrian P (2001) The implications of location accuracy for the interpretation of satellite-tracking data. *Anim Behav* 61:1035–1040
- Hays GC, Houghton JDR, Isaacs C, King RS, Lloyd C, Lovell P (2004a) First records of oceanic dive profiles for leatherback turtles, *Dermodochelys coriacea*, indicate behavioural plasticity associated with long-distance migration. *Anim Behav* 67:733–743
- Hays GC, Houghton JDR, Myers AE (2004b) Endangered species — pan-Atlantic leatherback turtle movements. *Nature* 429:522
- Hays GC, Hobson VJ, Metcalfe JD, Righton D, Sims DW (2006) Flexible foraging movements of leatherback turtles across the North Atlantic Ocean. *Ecology* 87:2647–2656
- Hochscheid S, Bentivegna F, Hays GC (2005) First records of dive durations for a hibernating sea turtle. *Biol Lett* 1:82–86
- Houghton JDR, Doyle TK, Wilson MW, Davenport J, Hays GC (2006) Jellyfish aggregations and leatherback turtle foraging patterns in a temperate coastal environment. *Ecology* 87:1967–1972
- 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
- Isla JA, Ceballos S, Huskin I, Anadón R, Álvarez-Marqués F (2004) Mesozooplankton distribution, metabolism and grazing in an anticyclonic slope water oceanic eddy (SWODDY) in the Bay of Biscay. *Mar Biol* 145:1201–1212
- James MC, Herman TB (2001) Feeding of *Dermodochelys coriacea* on medusae in the northwest Atlantic. *Conserv Biol* 4:202–205
- James MC, Ottensmeyer CA, Myers RA (2005a) Identification of high-use habitat and threats to leatherback sea turtles in northern waters: new directions for conservation. *Ecol Lett* 8:195–201
- James MC, Myers RA, Ottensmeyer CA (2005b) Behaviour of leatherback sea turtles, *Dermodochelys coriacea*, during the migratory cycle. *Proc R Soc Lond B Biol Sci* 272:1547–1555
- James MC, Eckert SA, Myers RA (2005c) Migratory and reproductive movements of male leatherback turtles (*Dermodochelys coriacea*). *Mar Biol* 147:845–853
- James MC, Sherrill-Mix SA, Martin K, Myers RA (2006) Canadian waters provide critical foraging habitat for leatherback sea turtles. *Biol Conserv* 133:347–357
- Jonsen ID, Myers RA, James MC (2006) Robust hierarchical state-space models reveal diel variation in travel rates of migrating leatherback turtles. *J Anim Ecol* 75:1046–1057
- King GL, Berrow SD (in press) Marine turtles in Irish waters. *Ir Nat J*
- Leben R, Born G, Engebret BR (2002) Operational altimeter data processing for mesoscale monitoring. *Mar Geod* 25:3–18
- Luschi P, Sale A, Mencacci R, Hughes GR, Lutjeharms JRE, Papi F (2003) Current transport of leatherback sea turtles (*Dermodochelys coriacea*) in the ocean. *Proc R Soc Lond B Biol Sci* 270:S129–S132
- Lutcavage ME (1996) Planning your next meal: leatherback travel routes and ocean fronts. In: Keinath JA, Barnard DE, Musick JA, Bell BA (eds) *Proc 15th Annu Workshop on Sea Turtle Biology and Conservation*. NOAA Tech

- Mem NMFS-SEFSC-387, US Dept of Commerce, Washington, DC, p 355
- McDonald DL, Dutton PH (1996) Use of PIT tags and photo identification to revise remigration estimates of leatherback turtles (*Dermochelys coriacea*) nesting in St. Croix, U.S. Virgin Islands, 1979–1995. *Chelonian Conserv Biol* 2:148–152
- McMahon CR, Autret E, Houghton JDR, Lovell P, Myers AE, Hays GC (2005) Animal-borne sensors successfully capture the real-time thermal properties of ocean basins. *Limnol Oceanogr Methods* 3:392–398
- McMahon CR, Bradshaw CJA, Hays GC (2007) Satellite tracking reveals unusual diving characteristics for a marine reptile, the olive ridley turtle *Lepidochelys olivacea*. *Mar Ecol Prog Ser* 329:239–252
- Murphy TM, Murphy SR, Griffin DB, Hope CP (2006) Recent occurrence, spatial distribution, and temporal variability of leatherback turtles (*Dermochelys coriacea*) in near-shore waters of South Carolina, USA. *Chelonian Conserv Biol* 5:216–224
- Myers AE, Hays GC (2006) Do leatherback turtles *Dermochelys coriacea* forage during the breeding season? A combination of data-logging devices provide new insights. *Mar Ecol Prog Ser* 322:259–267
- Polovina JJ, Uchida I, Balazs G, Howell EA, Parker D, Dutton P (2006) The Kuroshio extension bifurcation region: a pelagic hotspot for juvenile loggerhead sea turtles. *Deep-Sea Res II* 53:326–339
- Rivalan P, Prevot-Julliard AC, Choquet R, Pradel R, Jacquemin B, Girondot M (2005) Trade-off between current reproductive effort and delay to next reproduction in the leatherback sea turtle. *Oecologia* 145:564–574
- Sale A, Luschi P, Mencacci R, Lambardi P and others (2006) Long-term monitoring of leatherback turtle diving behaviour during oceanic movements. *J Exp Mar Biol Ecol* 328:197–210
- Shoop CR, Kenney RD (1992) Seasonal distributions and abundances of loggerhead and leatherback sea turtles in waters of the Northeastern United States. *Herpetol Monogr* 6:43–67
- Witt MJ, Broderick AC, Johns DJ, Martin C, Penrose R, Hoogmoed MS, Godley BJ (2007) Prey landscapes help identify potential foraging habitats for leatherback turtles in the NE Atlantic. *Mar Ecol Prog Ser* 337:231–244

Editorial responsibility: Brendan Godley (Editor-in-Chief), University of Exeter, Cornwall Campus, UK

*Submitted: September 4, 2007; Accepted: November 23, 2007
Proofs received from author(s): December 18, 2007*