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Behaviour of leatherback sea turtles, *Dermochelys coriacea*, during the migratory cycle

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Leatherback sea turtles, *Dermochelys coriacea*, undertake broad oceanic movements. While satellite telemetry has been used to investigate the post-nesting behaviour of female turtles tagged on tropical nesting beaches, long-term behavioural patterns of turtles of different sexes and sizes have not been described. Here we investigate behaviour for 25 subadult and adult male and female turtles satellite-tagged in temperate waters off Nova Scotia, Canada. Although sex and reproductive condition contributed to variation in migratory patterns, the migratory cycle of all turtles included movement between temperate and tropical waters. Marked changes in rates of travel, and diving and surfacing behaviour, accompanied southward movement away from northern foraging areas. As turtles approached higher latitudes the following spring and summer, they assumed behaviours consistent with regular foraging activity and eventually settled in coastal areas off Canada and the northeastern USA. Behavioural patterns corresponding to various phases of the migratory cycle were consistent across multiple animals and were repeated within individuals that completed return movements to northern waters. We consider the potential biological significance of these patterns, including how turtle behaviour relates to predator avoidance, thermoregulation and prey distribution.

Keywords: *Dermochelys coriacea*; diving; migration; foraging; thermoregulation; satellite telemetry

1. INTRODUCTION

Satellite telemetry is now widely used to study the migrations of many marine vertebrates (Le Boeuf *et al.* 2000; Block *et al.* 2001; Boustany *et al.* 2002); however, persistent challenges surrounding long-term instrument attachment and performance normally prevent collection of behavioural data throughout complete migratory cycles. Marine turtles have become popular candidates for satellite tracking studies (Papi *et al.* 1997; Hays *et al.*1999; Polovina *et al.* 2000). Yet, as many species are difficult to find and humanely capture in their oceanic habitat, much of what is known about the large-scale movements of these animals is limited to post-nesting behaviour of mature females tagged on nesting beaches. This is true of the leatherback turtle (*Dermochelys coriacea*), the largest of all sea turtle species, now globally endangered and facing possible extinction in the Pacific (Spotila *et al.* 2000). Shelf and slope waters in temperate and boreal regions of the Atlantic support enhanced zooplankton productivity in the summer and fall (Myers *et al.* 1994; McLaren *et al.* 2001), including large cnidarian species (e.g. *Cyanea capillata* and *Aurelia aurita*) that are prey for leatherbacks (Bleakney 1965; den Hartog & van Nierop 1984; Holland *et al.* 1990; James & Herman 2001). Seasonal aggregations of leatherbacks in these areas have been verified by aerial surveys (Shoop & Kenny 1992) and fisheries observer data (Witzell 1999). Satellite telemetry suggests that waters off eastern Canada and the northeastern USA constitute high-use habitat for these animals (James *et al.* 2005).

Recent tracking studies of nesting female leatherbacks tagged in the Caribbean and South America show that many turtles travel northward after nesting (Eckert 1998; Ferraroli *et al.* 2004; Hays *et al.* 2004*a*), presumably to take advantage of high seasonal concentrations of prey. While the diving behaviour of leatherbacks has been described as they displace from equatorial nesting areas (Hughes *et al.* 1998; Hays *et al.* 2004*b*), longer-term movement data have not been available, particularly for those turtles that use northern waters, to enable comparison of behaviour at northern latitudes with return travel to tropical waters. Here we consider the movement, diving and surface behaviour of 25 leatherbacks equipped with satellite transmitters off Nova Scotia, Canada, including 10 that were tracked during round-trip migrations between temperate and tropical waters.

2. METHODS

Turtles were captured at the surface in waters off Nova Scotia, Canada, using a breakaway hoop net operated from a 10.5 m commercial fishing boat. Each turtle was guided up a stern ramp on to a raised platform, where curved carapace length (CCL) and curved carapace width were measured, a microchip (AVID brand) was implanted in the right shoulder muscle, and monel tags (style no. 49; National Band and Tag Company, Newport, Kentucky) were applied to the rear flippers. Satellite-linked transmitters integrating time–depth recorders (SLTDRs: models SSC3 and SDR-T16, Wildlife Computers, Redmond, WA, USA) and surface time sensors (KiwiSat 101, Sirtrack Ltd., Havelock North, NZ) were attached to the carapace using a custom-fitted harness made of nylon webbing and polyvinyl tubing, integrating corrodable links to ensure release (Eckert 2002). Turtles were repeatedly doused with buckets of sea water while aboard, and were normally released within 30 min of capture. All procedures were approved by the Dalhousie University

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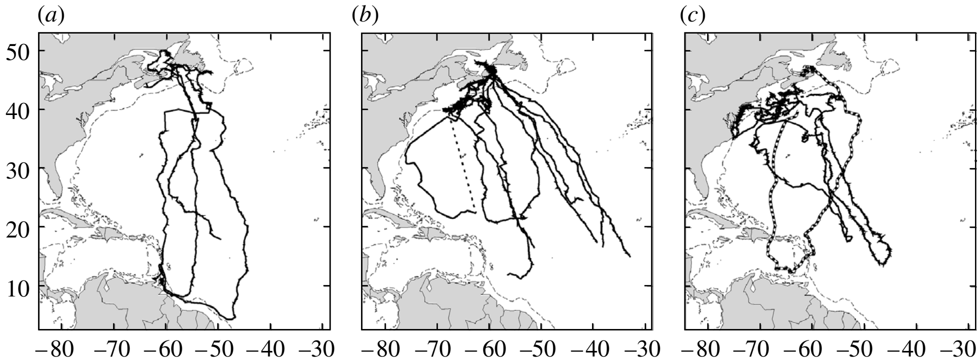

Figure 1. Tracks of 15 leatherback turtles equipped with satellite-linked time–depth recorders off Nova Scotia, Canada. (*a*) Mature males, $n=3$, (*b*) mature females, $n=9$ and *(c)* subadults, $n=3$. Thin dashed line: 1000 m depth contour; bold dashed line: portion of track when location data not received; bordered dashed line: subadult that entered the Caribbean Sea; *x*-axis, degrees longitude; *y*-axis, degrees latitude.

Committee on Animal Care and licensed by Fisheries and Oceans Canada.

SLTDRs collected and relayed data on time at depth, time at temperature, maximum dive depth and dive duration (each binned within 14 user-defined data ranges) over 6 h collection periods. Time at depth reflected all time when SLTDRs were submerged, whereas dives were registered only when turtles descended below 4 m ($n=12$ tags) or 6 m ($n=3$ tags). While SLTDRs simultaneously record data from different channels (e.g. depth, duration and temperature), data are transmitted in histogram format to increase ease of transfer via the limited bandwidth of the Argos satellite system (Fedak *et al.* 2002). This decreases the resolution of the data and restricts the types of analyses which can be performed, as the relationship between dive depth, duration and temperature of individual dives is lost. However, patterns of depth use and dive duration can be readily identified and related to the spatial and temporal characteristics of horizontal movements. As our purpose was to identify broad behavioural patterns during the migratory cycle, SLTDR data were considered at the resolution of 24 h rather than 6 h periods.

Satellite transmitters were located with the Argos system (http://www.argosinc.com). Argos assigns location class, an index of positional accuracy, to all derived locations. The analyses presented here used all positions with location classes 3, 2 and 1 (categorized to lie within 150 m, 150–350 m or 350–1000 m, respectively, of the tag's true position). Except where otherwise noted, location classes A, B and 0 (categorized to lie 1000 m or more from the tag's true position) were also used if they yielded rates of travel less than or equal to 5 $\mathrm{km\ h^{-1}}$, consistent with 99% of rates of travel calculated for this species (James *et al.* 2005). Positions of location class Z were omitted. From these filtered locations, median daily locations for each turtle were calculated, interpolating positions, assuming constant speed and direction, for days in which no positions were obtained for a given turtle. Rates of travel were calculated between positions of location class 3, 2 and 1 at least 2 h apart.

To evaluate surface behaviour, we considered data from KiwiSat satellite transmitters, which transmit the fraction of each 24 h period that the saltwater switch is dry. These values were matched to median daily locations for each turtle and the median surface time was found for each hexagonal area bin. Medians were chosen so that non-normality of the data would not unduly influence the estimate of the centre of each distribution.

3. RESULTS

Fifteen turtles were equipped with SLTDRs and 10 with KiwiSat satellite tags during summer, 2001–2003; 13 off mainland Nova Scotia (44°N, 64°W) and 12 off Cape Breton Island (47°N, 60°W). Of the 15 equipped with SLTDRs, there were three mature males, nine mature females and three subadults (CCL $<$ 140 cm; figure 1). In total, we received 33 171 positions (location class 3: 4.4%, 2: 12.2%, 1: 17.7%, 0: 14.9%, A: 21.7% and B: 29.1%) and kept 77% of the total after filtering. SLTDRs on six turtles transmitted long enough to show round-trip migrations to northern foraging areas. During the migratory cycle, turtles were seasonally resident in northern waters and swam a loop of 6000–12 000 km before returning to forage in continental shelf waters off Canada and/or the northeastern USA.

We found consistent patterns of behaviour among all turtles in our sample, which can be used to delineate distinct 'phases' of the migratory cycle. Often, changes in multiple measures delineated a shift between phases. To illustrate these phases, we present representative dive data and tracks from two leatherback turtles: turtle A, a mature female (CCL $=$ 155.5 cm) tagged in an inter-nesting year, and turtle B, a subadult (CCL $=$ 125.5 cm; figures 2 and 3). We present dive data for an additional subadult (turtle C: CCL $=$ 134.0 cm) and a mature male (turtle D: CCL $=$ 168.5 cm) in the Electronic Appendix (figures S1 and S2).

Phase A encompassed movements of turtles in northern shelf and slope waters (principally north of 38°N; figure 2). This phase was characterized by relatively low rates of travel, shallow diving (typically less than 50 m) and short dive durations (typically less than 12 min; figure 3*a–h*). Shelf waters in this region are generally less than 200 m deep. The slope waters grade from the shelf down to the abyssal plain at 4000 m and deeper.

The onset of phase B was delineated by increased rates of travel, the start of more consistent southward movements and large changes in diving behaviour. After an initial peak associated with departure from northern foraging areas, rates of travel decreased, but were typically higher and, in many turtles, less variable, than they had been during phase A (figure 3*a*,*b*). As turtles moved southward, dive depth and dive duration increased and the depths sampled by turtles became bimodally distributed (figure 3*c–h*). The maximum depths of the majority of dives were less than 6 m or fell within a range that shifted

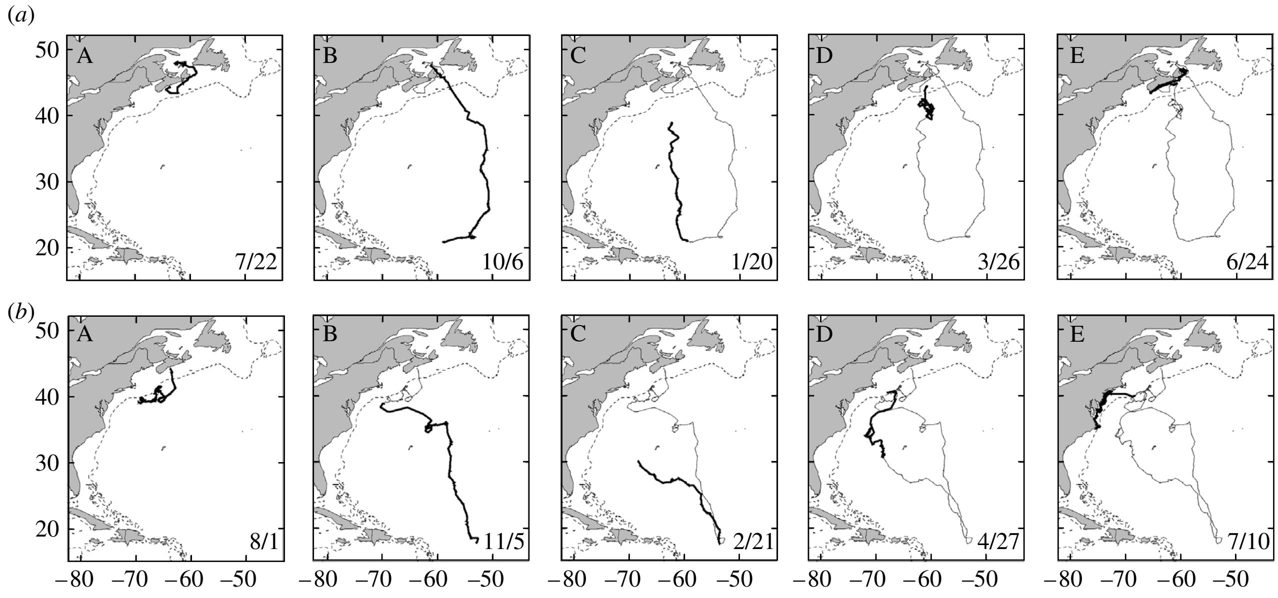

Figure 2. Tracks throughout the migratory cycle for two leatherback turtles tagged in coastal waters off Nova Scotia, Canada. Phase of the migratory cycle is indicated in top left corner of each panel. Bold line: movements during each phase; thin line: movements from previous phases; dashed line: 1000 m depth contour. Start month and day of each phase are indicated in bottom right corner of each panel. (*a*) Turtle A: mature female in inter-nesting year. Data to 18 September 2004. (*b*) Turtle B: subadult. Data to 22 October 2004. *x*-axis, degrees longitude; *y*-axis, degrees latitude.

from 4–78 m to 78–252 m (figure 3*e*,*f*), which revealed specific intermediate depth ranges that were not targeted by turtles. Occasional very deep dives, exceeding the user-defined depth ranges of the tags (greater than 400 m, $n=12$ tags; greater than 450 m, $n=3$ tags), were also recorded during this phase. This increasing bimodality in maximum dive depth with decreasing latitude was also readily apparent in dive duration (figure 3*g*,*h*).

Consistent northward movement marked the onset of phase C (figure 2). Rates of travel were similar to those during phase B (figure 3*a*,*b*), while the bimodality in maximum dive depth and dive duration decreased with northward movements (figure 3*e*–*h*). Therefore, the relationship between diving behaviour and latitude was similar to that in the previous phase.

In phase D, turtle movements generally continued northward towards shelf waters off Canada or the north-eastern USA (figure 2); however, there was a drop in average rate of travel and a dramatic change in diving behaviour (figure 3). During this phase, turtles arrived in waters corresponding to the continental slope (figure 2). Maximum dive depth no longer showed a bimodal distribution and was instead relatively uniform between 4 and 154 m (figure 3*e*,*f*). Dive duration showed an abrupt decrease and was generally less than 24 min (figure 3*g*,*h*).

Phase E encompassed movements primarily on the continental shelf and was marked by even shallower and shorter diving than turtles showed in phase D (less than 50 m, less than 12 min; figure 3*c*–*h*). Patterns of movement and diving behaviour for turtles in this northern phase were very similar to those recorded when animals were in phase A, indicating the completion of one migratory cycle and the initiation of a second.

These phases of the migratory cycle were typical both for female leatherbacks in their inter-nesting years and subadults, all of which spent phases B and C in pelagic waters (figure 1*b*,*c*) except for one subadult turtle, which entered and exited the Caribbean Sea but did not stop in near shore areas (figure 1*c*), and one mature female, which was resident in waters off southeastern USA during the first winter post-tagging (KiwiSat transmitter, track not shown). An additional behavioural phase, occurring between B and C, was observed in four mature males in waters adjacent to nesting beaches (see Electronic Appendix; figure S2, turtle D). The dates of transition between phases and the durations of the phases were variable between turtles (figure 4); however, the behavioural patterns within phases (e.g. figures 3, S1 and S2) were similar across turtles.

For the 10 turtles equipped with transmitters integrating surface time counters (KiwiSat: one subadult, seven mature females and two mature males), a maximum of 10% of the day was spent at the surface in most of the areas they used (figure 5), with the exception of waters north of 38°N, principally corresponding to phases A, D and E of the migratory cycle, where surface times were highest (maximum 41%). Surface times declined as turtles travelled to lower latitudes (phase B), which is consistent with the increasing dive durations recorded during this part of the migratory cycle.

4. DISCUSSION

Leatherback turtles tagged on tropical beaches have been recovered thousands of kilometres away (Pritchard 1976; James 2004; Troëng *et al.* 2004), attesting to their ability to range across vast areas of ocean. By gathering information on the movements and diving behaviour of many individuals of varyied sex and reproductive status, we can begin to understand the biological relevance of these remarkable movements. Turtles in this study have shown movements from the shelf and slope waters of the northwestern Atlantic southward through pelagic waters to tropical waters and back to the north all within one year. Movement and diving behaviour show clear differences between legs of this round-trip journey. However, the biological motivations for these changes in behaviour are

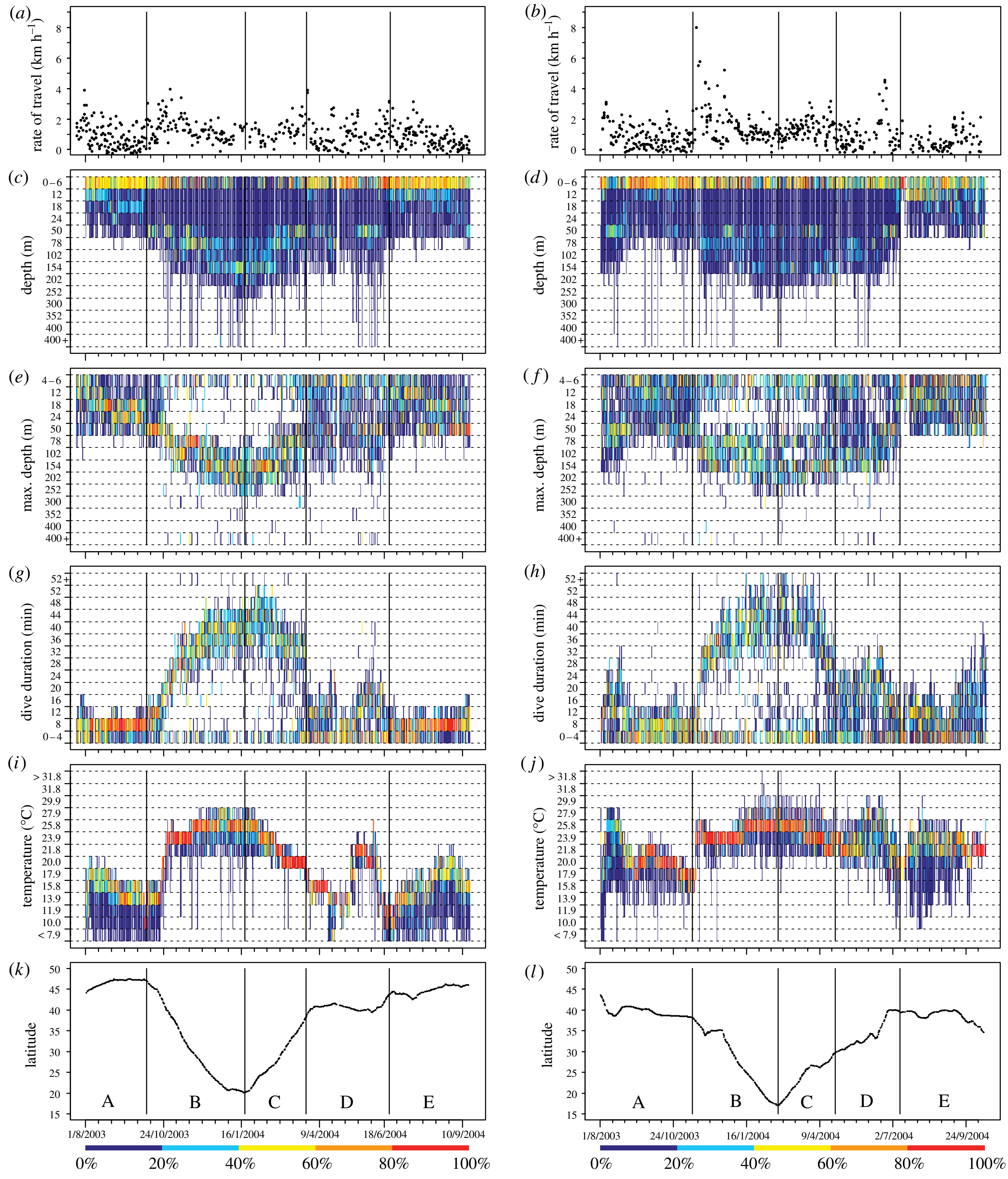

Figure 3. Ambient water temperature and the diving behaviour and latitudinal movements of two leatherback turtles tagged in coastal waters off Nova Scotia, Canada, spanning time from tagging until the day before second migration southward. Left column: turtle A; right column: turtle B. Ticks on time axis represent 14 day intervals. (*a*), (*b*) Rate of travel (km h^{-1}). (*c*), (*d*) Proportion of time (per 6 h sample) spent in different depth ranges. (*e*), (*f*) Proportion of maximum dive depths (per 6 h sample) in different depth ranges. (*g*), (*h*) Proportion of dives (per 6 h sample) of varying durations. (*i*), (*j*) Proportion of time (per 6 h sample) spent in different temperature ranges. (*k*), (*l*) Latitudinal movement. Capital letters indicate phases of the migratory cycle. Vertical lines indicate transitions between phases.

not always clear, particularly since many of the animals we tracked were not in their breeding or nesting years.

(**a**) ***Northern foraging***

We expect that one of the primary determinants of the movements and behaviour of leatherback turtles is the spatial and temporal distribution of their primary prey, the gelatinous plankton, largely of phylum Cnidaria (Bleakney 1965; den Hartog & van Nierop 1984). Unfortunately, only limited information exists on these planktonic species in the areas frequented by the turtles in this study. Instead, most research on the biology of these organisms comes from studies in coastal bays and fjords, while data from pelagic areas are scarce.

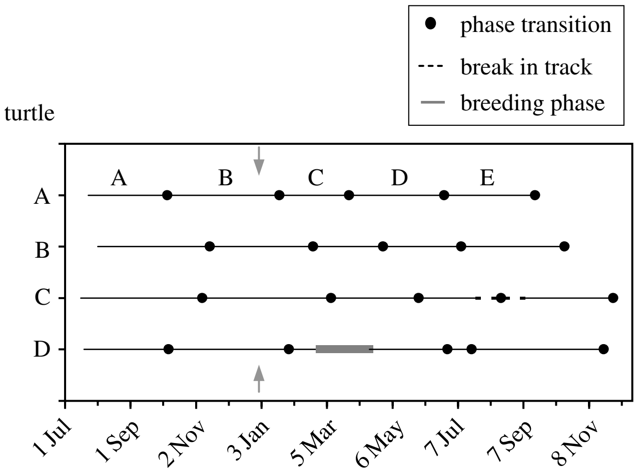

Figure 4. Timelines of migratory phases for four leatherback turtles equipped with satellite-linked time–depth recorders that completed round-trip migrations to northern foraging areas. Arrows indicate 1 January 2004. Capital letters indicate phase designations for turtle A; sequence is identical for turtles B–D. Turtle A: mature female; turtles B, C: subadults and turtle D: mature male. Turtle D showed additional breeding phase within phase C. Ticks on *x*-axis, 31 days.

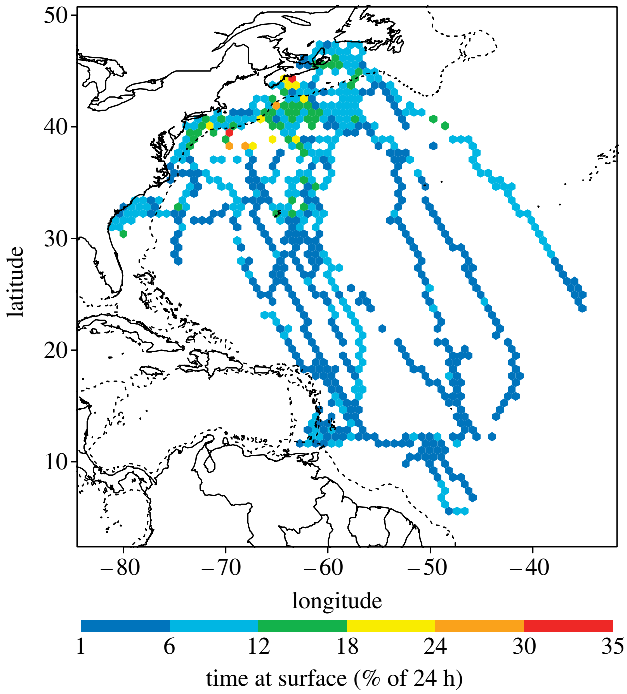

Figure 5. Time (% of 24 h period) spent at the surface by leatherback turtles equipped with KiwiSat transmitters ($n=10$). See §2 for calculation details.

The determinants of the timing and size of aggregations of medusae, the familiar free-swimming life stage of jellyfish, are poorly understood but there is general consensus that aggregations can be the result of two main factors: reproduction and physical oceanographic processes (Graham *et al.* 2001). For scyphomedusae like *C. capillata* and *A. aurita*, two common prey species of the leatherback turtle (den Hartog & van Nierop 1984), medusae develop after budding from the benthic sessile life stage over the winter or in the early spring. Through spring and summer, the medusae grow, feeding on zooplankton, and persist for four to eight months before spawning and dying (reviewed by Lucas 2001). *Cyanea capillata* medusae have been recorded annually in the Niantic River Estuary, Connecticut (USA), from March to late June or early July (Brewer 1989; Brewer & Feingold 1991). However, we have consistently observed leatherbacks feeding on large *C. capillata* off Cape Breton Island, Nova Scotia, until at least late September. This persistence of *C. capillata* into the fall is consistent with observations of this species and *A. aurita* through August and September in fjords in Denmark, Sweden and Japan (Gröndahl 1988; Olesen *et al.* 1994; Omori *et al.* 1995).

In general, medusa abundance is lower in pelagic versus coastal areas (Möller 1980; Mills 1995; Lucas 2001), which may reflect lower nutrient availability and greater distances from the coastal benthic life stages, although data in oceanic systems are sparse. However, physical transport of medusae can create local aggregations in pelagic waters, particularly at physical discontinuities such as shelf-breaks and upwelling zones (Graham *et al.* 2001).

Despite the lack of direct distributional data on gelatinous plankton in areas frequented by turtles in this study, many lines of evidence lead us to suggest that the leatherbacks we tracked use northern shelf and slope waters primarily for foraging. Low rates of travel, previously linked to foraging in other areas (Ferraroli *et al.* 2004), were observed in phases A, D and E. Moreover, leatherbacks sighted off Atlantic Canada (corresponding to areas frequented in phases A and E) are regularly observed handling jellyfish (*Cyanea* sp.) in their mouths at the surface (James & Herman 2001). Such prey handling normally involves repeated elevation of the head, which appears to facilitate swallowing (Eisenberg & Frazier 1983; James & Herman 2001). We frequently observed this behaviour, preceded by turtles biting large jellyfish into more manageable pieces (M. C. James, personal observation). While the occurrence of leatherbacks in potential foraging areas may be positively correlated with abundance of jellyfish at the surface (Grant *et al.* 1996), fieldwork off Nova Scotia has revealed that jellyfish are often not visible at the surface in the vicinity of turtles when prey handling is observed (James & Mrosovsky 2004). Therefore, leatherbacks foraging in shelf waters off Canada and the northeastern USA appear to search for and capture much of their prey at depth (figure 3), before returning to the surface to consume it (James & Mrosovsky 2004).

This pattern of foraging behaviour is consistent with the high proportion of time spent at the surface in northern waters (figure 5). Increased surface time at northern latitudes may also reflect basking, as we have routinely observed turtles resting at the surface during the middle part of the day and evening with both front and rear flippers extended and their heads lowered in the water. This posture, combined with the leatherback's dark dorsal colouring, may maximize absorption of solar radiation, facilitating both digestion and maintenance of body temperature in northern foraging areas where both cold ambient temperatures and consumption of large volumes of cold prey (Davenport 1998) may present thermal challenges. The surface time analysis presented here suggests that northern foraging areas may offer the best opportunities for estimating leatherback abundance from aerial surveys, due to the relatively large proportion of time spent at the surface in these areas.

Leatherback movements during phase D also appear to indicate foraging. Rate of travel dropped markedly from that shown in phases B and C, becoming consistent with rates of travel shown in phases A and E (figure 3*a*,*b*). Dive durations decreased and maximum dive depths lost the bimodality so distinctive of phases B and C (figure 3*e*–*h*). If indeed these behaviours represent foraging, we suggest that gelatinous prey in these pelagic and slope waters may be distributed at greater mean depth, and perhaps in a greater range of depths, than in the shelf areas further north.

(b) *Southern movements*

As leatherbacks left northern waters, they showed consistent changes in patterns of depth use, dive duration, rate of travel and time spent at the surface. What cues the onset of southward movements (phase B) is unclear; the departure date is variable among turtles (figure 4). However, in most turtles, it was marked by a rapid increase in rate of travel over the first few days to weeks. As average rates of travel during phases B and C are well above those associated with time spent in northern foraging areas, we expect that turtles are primarily transiting during these phases. While other sea turtles mainly conduct short and shallow dives during open ocean movements (Papi *et al.* 1997; Hays *et al.* 1999; Godley *et al.* 2003), the leatherbacks we tracked spent extended periods both in the uppermost depth bin (0–6 m) and at depths greater than 24 m, undertaking dives among the longest recorded during the migratory cycle (greater than 52 min). The gradual changes in dive duration and dive depth did not appear to be related to water depth, as both continued to increase even after turtles had moved far south of the continental slope and were travelling through areas characterized by relatively uniform bathymetry. Below, we consider alternative hypotheses to explain these changes in diving behaviour.

(i) *Predator avoidance*

Regular, long, deep diving in migrating green turtles may decrease susceptibility to visual predators such as large sharks by reducing silhouetting against the surface (Hays *et al.* 2001). Adult leatherbacks are believed to have few natural marine predators and the turtles we studied were all relatively large (125.5–168.5 cm CCL). Rare documentation of predation of leatherbacks by killer whales (*Orcinus orca*) (Caldwell & Caldwell 1969; Pitman & Dutton 2004) may suggest that this threat influences diving behaviour. We expect that such predation is normally directed at younger, smaller turtles. While the extent of natural predation on adults and subadults is unknown, if predation on these size classes is low, there must be alternative advantages to spending extended periods at depth during migration.

(ii) *Foraging*

Given the lack of distributional data on leatherbacks' primary prey in open ocean areas, it is difficult to predict how prey distribution might be influencing turtle diving behaviour through phases B and C. Post-nesting female leatherbacks in tropical pelagic waters show diurnal changes in diving behaviour consistent with a response to the distribution of gelatinous prey, which suggests foraging behaviour (Hays *et al.* 2004*b*). While moving between temperate and tropical waters, the turtles in this study showed a bimodal distribution of dive depths and durations somewhat similar to that reported by Hays *et al.* (2004*b*) and diel dive patterns that may correspond to the diel vertical migrations of their prey (M. C. James, C. A. Ottensmeyer, S. A. Eckert and R. A. Myers, unpublished data). However, our study and that of Hays *et al.* (2004*b*) are not strictly comparable due to differences in temporal resolution of the data and geographical zone considered. We also expect that there are large differences in body condition between female turtles that may not have eaten during a two-month nesting period (e.g. Hays *et al.* 2004*b*) and turtles that have foraged in northern areas for several months (this study). Indeed, leatherbacks utilizing foraging areas off eastern Canada are 33% heavier than nesting turtles of the same carapace length (James *et al.* 2005). Therefore, while some opportunistic foraging may occur among turtles departing northern foraging areas, feeding may not be their primary focus at that time. Average rates of travel much higher than those on the foraging grounds suggest that the focus of movements during phase B are primarily related to migration. However, in the southernmost portion of the migratory cycle, reduced rates of travel suggest that some foraging may occur, which is consistent with the interpretation of tropical foraging by Hays *et al.* (2004*b*). Moreover, some of the turtles we tracked travelled longitudinally for up to several hundred kilometres before turning north (e.g. figure 1*b*), which may also indicate foraging in tropical waters. After this brief period, northward travel during phase C revealed similar patterns to behaviour in phase B.

(iii) *Seasonal buoyancy changes*

Leatherbacks experience dramatic seasonal increases in adipose stores akin to those recorded in many marine mammals. In northern waters, we observe that increases in body fat are most apparent externally at the neck and around the rear flippers and tail, although thickening of the fibrous adipose layer underlying the shell (Goff & Stenson 1988) must certainly also occur. Adipose tissue contributes to buoyancy (Webb *et al.* 1998; Beck *et al.* 2000; Biuw *et al.* 2003); therefore, leatherbacks inhabiting foraging areas in temperate waters will be more buoyant than they are at other times of year and as adipose reserves are depleted during migration (Prange 1976), buoyancy will probably also be reduced.

Other sea turtles can modify their inspired lung volume, an important oxygen store, to adjust their buoyancy during dives (Milsom 1975; Minamikawa *et al.* 1997; Hays *et al.* 2000; Hays *et al.* 2004*c*) or select specific depths to maintain neutral buoyancy (Minamikawa *et al.* 2000). In these cases, changes in body condition may influence patterns of dive duration and depth, as has been reported in marine mammals (Webb *et al.* 1998; Beck *et al.* 2000; Biuw *et al.* 2003). In contrast to the hard-shelled turtles, the primary oxygen stores in leatherbacks are in the blood and tissues rather than the lungs (Lutcavage *et al.* 1992) and little information is available on their buoyancy control. Buoyancy control has been studied in other species of sea turtle (e.g. Minamikawa *et al.* 2000; Hochscheid *et al.* 2003; Hays *et al.* 2004*c*) and marine mammals (e.g. Webb *et al.* 1998). Novel approaches will be required before the relationships between body fat, buoyancy, lung volume and diving behaviour can be clarified for leatherbacks.

(iv) *Thermoregulation*

Increases in dive depth and length during migratory phases may assist with thermoregulation. Among sea turtles, the leatherback has extraordinary lower thermal tolerance limits, conferred by various anatomical and physiological adaptations which function to maintain body temperature while in cold water (Paladino *et al.* 1990; James & Mrosovsky 2004). In contrast, leatherbacks may face a different thermal challenge in tropical seas: overheating (James & Mrosovsky 2004). While warm core temperatures may increase the capacity for leatherbacks to undertake rapid migrations by enhancing the power output of their muscles, as shown in tuna (Altringham & Block 1997), intense muscle activity combined with relatively high ambient temperatures may require the use of not only physiological mechanisms, including changes in metabolism and blood flow (Paladino *et al.* 1990), but also behavioural mechanisms to dissipate heat during migration. Therefore, just as ascent to warmer waters following deep dives below the thermocline may serve to warm the core temperatures of some large pelagic fishes (Holland *et al.* 1992; Cartamil & Lowe 2004), behavioural thermoregulation in leatherbacks may include diving to deeper waters to cool body temperature during periods of elevated activity, such as during migration. The targeted depth would be expected to increase as the water temperature increased with decreasing latitude, as seen in this study. Simultaneous recording of dive depth, ambient temperature and body temperature during both foraging and migration would greatly increase our understanding of potential behavioural thermoregulatory mechanisms used by this species.

(c) ***Migratory cycle***

Satellite telemetry has recently revealed high-use habitat for leatherbacks in waters off eastern Canada and the northeastern USA (James *et al.* 2005). This investigation into leatherback turtle movements and diving behaviour provides additional evidence that temperate shelf and slope waters of the northwest Atlantic support extensive foraging by adult male and female turtles, as well as subadults.

Leatherback turtles in this study showed round-trip migrations between temperate feeding areas and tropical waters. While leatherbacks have not previously been tracked through round-trip migrations to feeding areas, findings from other studies are consistent with the pattern shown here. Specifically, most leatherbacks tracked from tropical nesting beaches in the western Atlantic swim to temperate latitudes (Eckert 1998; Ferraroli *et al.* 2004; Hays *et al.* 2004*a*), with longer track-lines revealing subsequent movements southward. Other telemetry studies reveal that not all leatherbacks are destined for the northern areas used by the turtles in our study. Post-nesting, some turtles travel eastward, northeast or southward (Eckert 1998; Ferraroli *et al.* 2004; Hays *et al.* 2004*a*,*b*) to other foraging zones. Regardless of their location, individual fidelity to general foraging areas may be a common phenomenon among Atlantic leatherbacks.

Mature male leatherbacks tagged off Nova Scotia complete round-trip migrations from northern foraging areas to southern, often coastal, breeding destinations, where they can remain resident for up to several months (James *et al.* in press). A similar pattern is presumably true for females in their nesting years, as animals tagged in Canadian waters have been observed nesting the following spring (M. C. James, unpublished data) and turtles have been captured in Canadian waters within six months of nesting (Goff *et al.* 1994). Therefore, the movements of mature male leatherbacks and females in their nesting years is consistent with a migratory cycle involving travel between disparate feeding and nesting sites observed in other species of sea turtle (Luschi *et al.* 1998; Godley *et al.* 2002).

Our results also illustrate that, with few exceptions, mature females in their inter-nesting years and subadults remain largely in pelagic waters far from shore during the southern portion of their migration. This pattern is particularly intriguing since there is not an obvious reproductive benefit for extensive southward movements for these individuals, in contrast to mature males and females in their nesting years.

One possibility is that this strategy maximizes foraging efficiency. Tropical waters appear to offer some foraging opportunities, consistent with Hays *et al.* (2004*b*). An additional profitable zone for northern-foraging leatherbacks may be the pelagic and slope waters traversed by turtles in phase D. In this phase, behaviour consistent with more regular foraging was observed in all tracked turtles. We speculate that in waters off the shelf, blooms of gelatinous plankton may be more ephemeral and more patchily distributed than in shelf waters, but may appear earlier. There is some indication in Europe that *A. aurita* blooms may appear earlier in more southerly latitudes due to higher ambient temperatures (Lucas 2001). If this is the case in the northwestern Atlantic for this and other jellyfish species, subadults and inter-nesting female leatherbacks may swim southward post-foraging in part to position themselves to exploit emerging prey resources on the way north. Swimming northwards in the spring may allow turtles to opportunistically forage on temperate spring blooms of jellyfish en route to more predictable and abundant prey resources in slope waters and, later, in shelf waters off Canada and the northeastern USA.

For leatherbacks that use northern foraging areas, following this long-distance migratory pattern every year may be a simpler behavioural strategy than modifying the pattern greatly in years when reaching a southern destination is not necessary for reproduction. While the energetic costs associated with northward migration are probably large, our data suggest that these are compensated for by a lengthy, productive foraging period in northern waters. We urge further research into the spatial and temporal distribution of the gelatinous plankton and the diet of leatherbacks so that we may more clearly identify the determinants and constraints of leatherback turtle movements and diving behaviour.

5. CONCLUSION

Many adult and subadult leatherbacks migrate long distances to temperate waters, where foraging efficiency is enhanced by exploiting prey at readily locatable oceanographic features such as the continental shelf and slope off eastern Canada and the northeastern USA. While mature females return every 2–3 years to tropical nesting beaches and mature males may return annually to breed in the vicinity of these areas, for subadult turtles and females in their inter-nesting years, a return to pelagic habitats in southern waters offers some foraging opportunities and may also serve to position turtles for opportunistic seasonal feeding en route to northern foraging areas. By integrating diving behaviour, horizontal movements and field observations it is possible to identify how turtles use pelagic and coastal areas. The long period of time spent by turtles in foraging areas may make them especially vulnerable to incidental capture in fisheries.

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REFERENCES

Altringham, J. D. & Block, B. A. 1997 Why do tuna maintain elevated slow muscle temperatures? Power output of muscle isolated from endothermic and ectothermic fish. *J. Exp. Biol.* **200**, 2617–2627.

Beck, C. A., Bowen, W. D. & Iverson, S. J. 2000 Seasonal changes in buoyancy and diving behaviour of adult grey seals. *J. Exp. Biol.* **203**, 2323–2330.

Biuw, M., McConnell, B. J., Bradshaw, C. J. A., Burton, H. & Fedak, M. 2003 Blubber and buoyancy: monitoring the body condition of free-ranging seals using simple dive characteristics. *J. Exp. Biol.* **206**, 3405–3423.

Bleakney, J. S. 1965 Reports of marine turtles from New England and eastern Canada. *Can. Field Nat.* **79**, 120–128.

Block, B. A., *et al.* 2001 Migratory movements, depth preferences, and thermal biology of Atlantic bluefin tuna. *Science* **293**, 1310–1314.

Boustany, A. M., Davis, S. F., Pyle, P., Anderson, S. D., Le Boeuf, B. J. & Block, B. A. 2002 Satellite tagging: expanded niche for white sharks. *Nature* **415**, 35–36.

Brewer, H. R. 1989 The annual pattern of feeding, growth, and sexual reproduction in *Cyanea* in the Niantic River Estuary, Connecticut. *Biol. Bull.* **1776**, 272–281.

Brewer, R. H. & Feingold, J. S. 1991 The effect of temperature on the benthic stages of *Cyanea* (Cnidaria: Scyphozoa), and their seasonal distribution in the Niantic River estuary, Connecticut. *J. Exp. Mar. Biol. Ecol.* **152**, 49–60.

Caldwell, D. K. & Caldwell, M. C. 1969 Addition of the leatherback sea turtle to the known prey of the killer whale, *Orcinus orca*. *J. Mammal.* **50**, 636.

Cartamil, D. P. & Lowe, C. G. 2004 Diel movement patterns of ocean sunfish *Mola mola* off southern California. *Mar. Ecol. Prog. Ser.* **266**, 245–253.

Davenport, J. 1998 Sustaining endothermy on a diet of cold jelly: energetics of the leatherback turtle *Dermochelys coriacea*. *Br. Herpetol. Soc. Bull.* **62**, 4–8.

den Hartog, J. C. & van Nierop, M. M. 1984 A study on the gut contents of six leathery turtles *Dermochelys coriacea* (Linnaeus) (Reptilia: Testudines: Dermochelyidae) from British waters and from the Netherlands. *Zool. Verh. Leiden* **209**, 1–36.

Eckert, S. A. 1998 Perspectives on the use of satellite telemetry and other electronic technologies for the study of marine turtles, with reference to the first year-long tracking of leatherback sea turtles. In *Proceedings of the 17th Annual Sea Turtle Symposium* (ed. S. P. Epperly & J. Braun), p. 294. Miami: NOAA Technical Memorandum NMFS-SEFC-415.

Eckert, S. A. 2002 Swim speed and movement patterns of gravid leatherback sea turtles (*Dermochelys coriacea*) at St. Croix, US Virgin Islands. *J. Exp. Biol.* **205**, 3689–3697.

Eisenberg, J. F. & Frazier, J. 1983 A leatherback turtle (*Dermochelys coriacea*) feeding in the wild. *J. Herpetol.* **17**, 81–82.

Fedak, M., Lovell, P., McConnell, B. J. & 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, J.-Y. & Le Maho, Y. 2004 Where leatherback turtles meet fisheries. *Nature* **429**, 521–522.

Godley, B. J., Richardson, S., Broderick, A. C., Coyne, M. S., Glen, F. & Hays, G. C. 2002 Long-term satellite telemetry of the movements and habitat utilisation by green turtles in the Mediterranean. *Ecography* **25**, 352–362.

Godley, B. J., Broderick, A. C., Glen, F. & Hays, G. C. 2003 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.

Goff, G. P. & Stenson, G. B. 1988 Brown adipose tissue in leatherback sea turtles: a thermogenic organ in an endothermic reptile? *Copeia* **1988**, 1071–1075.

Goff, G. P., Lien, J., Stenson, G. B. & Fretey, J. 1994 The migration of a tagged leatherback turtle, *Dermochelys coriacea*, from French Guiana, South America, to Newfoundland, Canada, in 128 days. *Can. Field Nat.* **108**, 72–73.

Graham, W. M., Pagès, F. & Hamner, W. M. 2001 A physical context for gelatinous zooplankton aggregations: a review. *Hydrobiologia* **451**, 199–212.

Grant, G. S., Malpass, H. & Beasley, J. 1996 Correlation of leatherback turtle and jellyfish occurrence. *Herpetol. Rev.* **27**, 123–125.

Gröndahl, F. 1988 A comparative ecological study on the scyphozoans *Aurelia aurita*, *Cyanea capillata* and *C. lamarckii* in the Gullmar Fjord. *Mar. Biol.* **97**, 541–550.

Hays, G. C., Luschi, P., Papi, F., del Seppia, C. & Marsh, R. 1999 Changes in behaviour during the internesting period and postnesting migration for Ascension Island green turtles. *Mar. Ecol. Prog. Ser.* **189**, 263–273.

Hays, G. C., Adams, C. R., Broderick, A. C., Godley, B. J., Lucas, D. J., Metcalfe, J. D. & Prior, A. A. 2000 The diving behaviour of green turtles at Ascension Island. *Anim. Behav.* **59**, 577–586.

Hays, G. C., Akesson, S., Broderick, A. C., Glen, F., Godley, B. J., Luschi, P., Martin, C., Metcalfe, J. D. & Papi, F. 2001 The diving behaviour of green turtles undertaking oceanic migration to and from Ascension Island: dive durations, dive profiles and depth distribution. *J. Exp. Biol.* **204**, 4093–4098.

Hays, G. C., Houghton, J. D. & Myers, A. E. 2004*a* Pan-Atlantic leatherback turtle movements. *Nature* **429**, 522.

Hays, G. C., Houghton, J. D. R., Isaacs, C., King, R. S., Lloyd, C. & Lovell, P. 2004*b* First records of oceanic dive profiles for leatherback turtles, *Dermochelys coriacea*, indicate behavioural plasticity associated with long-distance migration. *Anim. Behav.* **67**, 733–743.

Hays, G. C., Metcalfe, J. D. & Walne, A. W. 2004*c* The implications of lung-related buoyancy control for dive depth and duration. *Ecology* **85**, 1137–1145.

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

Holland, D. L., Davenport, J. & East, J. 1990 The fatty acid composition of the leatherback turtle *Dermochelys coriacea* and its jellyfish prey. *J. Mar. Biol. Assoc. UK* **70**, 761–770.

Holland, K. N., Brill, R. W., Sibert, J. R. & Fournier, D. A. 1992 Physiological and behavioral thermoregulation in bigeye tuna *Thunnus obesus*. *Nature* **358**, 410–412.

Hughes, G. R., 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.

James, M. C. 2004 *Dermochelys coriacea* (leatherback sea turtle) migration and dispersal. *Herpetol. Rev.* **35**, 264.

James, M. C. & Herman, T. B. 2001 Feeding of *Dermochelys coriacea* on medusae in the northwest Atlantic. *Chelonian Conserv. Biol.* **4**, 202–205.

James, M. C. & Mrosovsky, N. 2004 Body temperatures of leatherback turtles (*Dermochelys coriacea*) in temperate waters off Nova Scotia, Canada. *Can. J. Zool.* **82**, 1302–1306.

James, M. C., Ottensmeyer, C. A. & Myers, R. A. 2005 Identification of high-use habitat and threats to leatherback sea turtles in northern waters: new directions for conservation. *Ecol. Lett.* **8**, 195–201. (doi:10.1111/j.1461-0248.2004.00710.x.)

James, M. C., Eckert, S. A. & Myers, R. A. In press. Migratory and reproductive movements of male leatherback turtles (*Dermochelys coriacea*). *Mar. Biol.* (doi:10.1007/s00227-005-1581-1.)

Le Boeuf, B. J., Crocker, D. E., Costa, D. P., Blackwell, S. B., Webb, P. M. & Houser, D. S. 2000 Foraging ecology of northern elephant seals. *Ecol. Monogr.* **70**, 353–382.

Lucas, C. H. 2001 Reproduction and life history strategies of the common jellyfish, *Aurelia aurita*, in relation to its ambient environment. *Hydrobiologia* **451**, 229–246.

Luschi, P., Hays, G. C., Del Seppia, C., Marsh, R. & Papi, F. 1998 The navigational feats of green sea turtles migrating from Ascension Island investigated by satellite telemetry. *Proc. R. Soc. B* **265**, 2279–2284. (doi:10.1098/rspb.1998.0571.)

Lutcavage, M. E., Bushnell, P. G. & Jones, D. R. 1992 Oxygen stores and aerobic metabolism in the leatherback sea turtle. *Can. J. Zool.* **70**, 348–351.

McLaren, I. A., Head, E. & Sameoto, D. D. 2001 Life cycles and seasonal distributions of *Calanus finmarchicus* on the central Scotian Shelf. *Can. J. Fish. Aquat. Sci.* **58**, 659–670.

Mills, C. E. 1995 Medusae, siphonophores, and ctenophores as planktivorous predators in changing global ecosystems. *ICES J. Mar. Sci.* **52**, 575–581.

Milsom, W. K. 1975 Development of buoyancy control in juvenile Atlantic loggerhead turtles, *Caretta c. caretta*. *Copeia* **1975**, 758–762.

Minamikawa, S., Naito, Y. & Uchida, I. 1997 Buoyancy control in diving behavior of the loggerhead turtle, *Caretta caretta*. *J. Ethol.* **15**, 109–118.

Minamikawa, S., Naito, Y., Sato, K., Matsuzawa, Y., Bando, T. & Sakamoto, W. 2000 Maintenance of neutral buoyancy by depth selection in the loggerhead turtle *Caretta caretta*. *J. Exp. Biol.* **203**, 2967–2975.

Möller, H. 1980 A summer survey of large zooplankton, particularly scyphomedusae, in North Sea and Baltic. *Meeresforschung* **28**, 61–68.

Myers, R. A., Barrowman, N. J., Mertz, G., Gamble, J. & Hunt, H. G. 1994 *Analysis of continuous plankton recorder data in the Northwest Atlantic 1959–1992. Canadian Technical Report of Fisheries and Aquatic Sciences*, vol. 1966.

Olesen, N. J., Frandsen, K. & Riisgard, H. U. 1994 Population dynamics, growth and energetics of jellyfish *Aurelia aurita* in a shallow fjord. *Mar. Ecol. Prog. Ser.* **105**, 9–18.

Omori, M., Ishii, H. & Fujinaga, A. 1995 Life history strategy of *Aurelia aurita* (Cnidaria, Scyphomedusae) and its impact on the zooplankton community of Tokyo Bay. *ICES J. Mar. Sci.* **52**, 597–603.

Paladino, F. V., O'Connor, M. P. & Spotila, J. R. 1990 Metabolism of leatherback turtles, gigantothermy, and thermoregulation of dinosaurs. *Nature* **344**, 858–860.

Papi, F., Luschi, P., Crosio, E. & Hughes, G. R. 1997 Satellite tracking experiments on the navigational ability and migratory behaviour of the loggerhead turtle *Caretta caretta*. *Mar. Biol.* **129**, 215–220.

Pitman, R. L. & Dutton, P. H. 2004 Killer whale predation on a leatherback turtle in the northwest Pacific. *Pacific Sci.* **58**, 497–498.

Polovina, J. J., Kobayashi, R. D., Parker, M. D., Seki, P. M. & Balazs, H. G. 2000 Turtles on the edge: movement of loggerhead turtles (*Caretta caretta*) along oceanic fronts, spanning longline fishing grounds in the central North Pacific, 1997–1998. *Fish. Oceanogr.* **9**, 71–82.

Prange, H. D. 1976 Energetics of swimming of a sea turtle. *J. Exp. Biol* **64**, 1–12.

Pritchard, P. C. H. 1976 Post-nesting movements of marine turtles (Cheloniidae and Dermochelyidae) tagged in the Guianas. *Copeia* **1976**, 749–754.

Shoop, C. R. & Kenny, R. D. 1992 Seasonal distributions and abundances of loggerhead and leatherback sea turtles in waters of the northeastern United States. *Herpetol. Monogr.* **6**, 43–67.

Spotila, J. R., Reina, R. D., Steyermark, A. C., Plotkin, P. T. & Paladino, F. V. 2000 Pacific leatherback turtles face extinction. *Nature* **405**, 529–530.

Troëng, S., Chacón, D. & Dick, B. 2004 Possible decline in leatherback turtle *Dermochelys coriacea* nesting along the coast of Caribbean Costa Rica. *Oryx* **38**, 395–403.

Webb, P. M., Crocker, D. E., Blackwell, S. B., Costa, D. P. & Le Boeuf, B. J. 1998 Effects of buoyancy on the diving behaviour of northern elephant seals. *J. Exp. Biol.* **201**, 2349–2358.

Witzell, W. N. 1999 Distribution and relative abundance of sea turtles caught incidentally by the US pelagic longline fleet in the western North Atlantic Ocean, 1992–1995. *Fish. Bull.* **97**, 200–211.

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