FLEXIBLE FORAGING MOVEMENTS OF LEATHERBACK TURTLES ACROSS THE NORTH ATLANTIC OCEAN

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Abstract. Some marine species have been shown to target foraging at particular hotspots of high prey abundance. However, we show here that in the year after a nesting season, female leatherback turtles (*Dermochelys coriacea*) in the Atlantic generally spend relatively little time in fixed hotspots, especially those with a surface signature revealed in satellite imagery, but rather tend to have a pattern of near continuous traveling. Associated with this traveling, distinct changes in dive behavior indicate that turtles constantly fine tune their foraging behavior and diel activity patterns in association with local conditions. Switches between nocturnal vs. diurnal activity are rare in the animal kingdom but may be essential for survival on a diet of gelatinous zooplankton where patches of high prey availability are rare. These results indicate that in their first year after nesting, leatherback turtles do not fit the general model of migration where responses to resources are suppressed during transit. However, their behavior may be different in their sabbatical years away from nesting beaches. Our results highlight the importance of whole-ocean fishing gear regulations to minimize turtle bycatch.

Key words: ARGOS; diel vertical migration; dive; jellyfish; leatherback turtle; Levy flight; migration; movement rules; penguin; satellite tracking; seal; whale.

INTRODUCTION

A general principle in behavioral ecology is that consumers tend to aggregate in the most profitable food patches where expected consumption rates are highest (Stephens and Krebs 1986). Predator density is often closely linked with high biodiversity "hotspots" of prey and other species (Worm et al. 2005) because productive habitat types containing prey aggregations are likely to be selected over less dense areas, as access to high consumption rates of high-quality prey increases net energy intake and growth rates. Some predators of common prey that are widely distributed also track closely spatial changes in prey concentrations through time (Sims et al. 2005), presumably maintaining consumption rates above a lower threshold. This "prey tracking" may represent a strategy to equalize environmental heterogeneity in food resources by moving to where prey are most likely to be found. However, where best to move in finding above-threshold prey concentrations presents a problem for predators that live in environments where the spatiotemporal patterns and dynamics of prey distribution are unpredictable across multiple scales. Extreme patchiness is problematic for predators because resource distributions change such that no stable prior expectation of when and where to

forage can be acquired without appropriate searching (Giraldeau 1997).

The abundance of marine zooplankton is highly heterogeneous over a very broad range of scales and is determined by numerous stochastic factors, thus making it difficult to predict in space and time with any certainty (Steele and Henderson 1992). As such, the open sea is arguably one of the most extreme environments in terms of the variance, or patchiness, in food supply to higher trophic levels. This generalized unpredictability means that large marine predators that specialize on zooplankton (e.g., baleen whales) must make decisions about the relative value of encountered prey types without a complete knowledge of overall resource availability (Lessells 1995). Because the prey field is highly changeable, behavioral strategies that adapt rapidly to change, by altering search patterns in response to food concentrations for example (Bartumeus et al. 2003), should be favored by natural selection. Therefore, the movement and behavioral strategies utilized by large planktivores should reflect a fine, but fast-adapting balance between searching for new, perhaps richer, prey patches, and remaining within a particular prey hotspot. Opting to remain in a patch may represent a suboptimal choice because the patch may decline in quality due to an increasing number of competitors arriving (Sutherland 1996). In contrast, moving longer distances searching for patches not yet visited by competitors could provide a solution with an overall net benefit (Viswanathan et al. 1996), while if prey is sparse the expectation is that animals might not
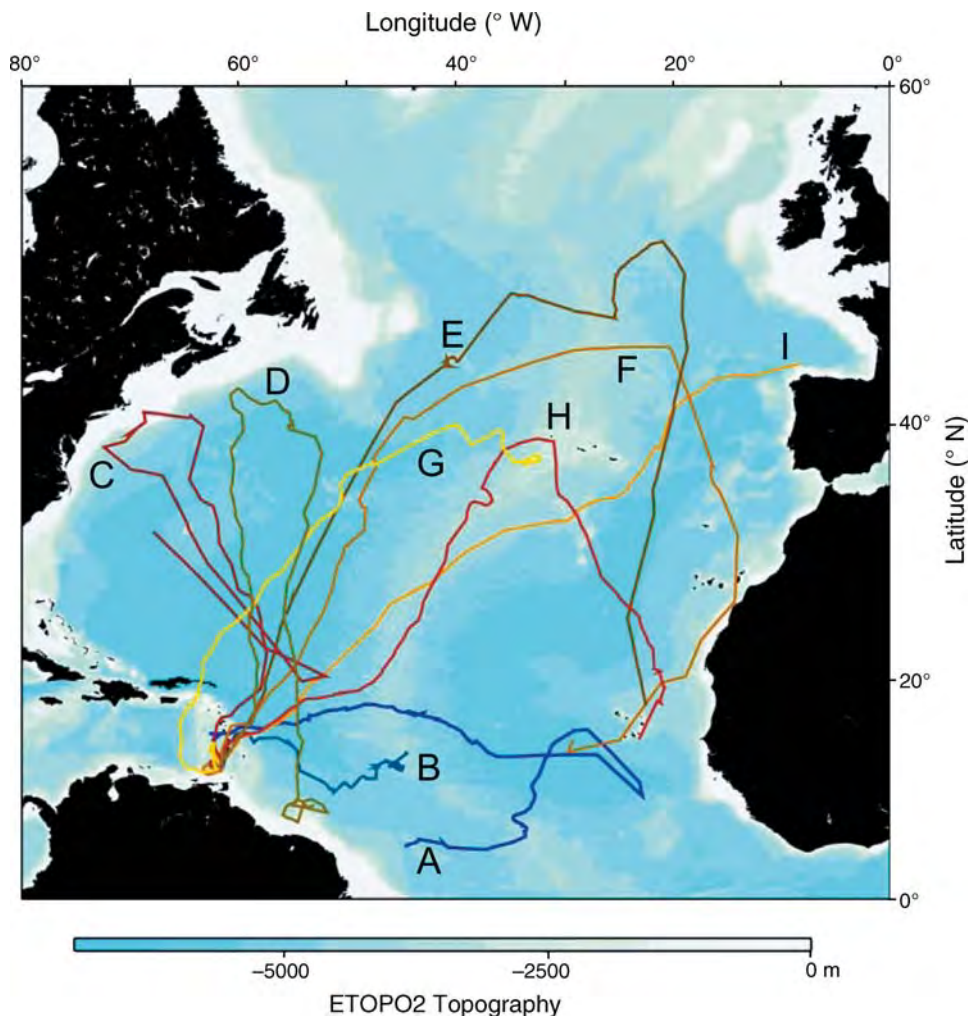
FIG. 1.   The complete tracks of nine leatherback turtles traveling in the North Atlantic. This plot updates the previously reported (up to January 2004) tracks of these turtles (Hays et al. 2004b). For turtle C the final straight-line course is a reflection of the very few locations that were obtained toward the end of tracking. The bathymetry shows that the turtles spent the majority of their time in oceanic waters (>1000 m). Turtles C and F briefly ventured into shallower water on the continental shelf (indicated in white). The length of tracking for individuals turtles was: turtle A, 332 days; turtle B, 373 days; turtle C, 368 days; turtle D, 251 days; turtle E, 297 days; turtle F, 375 days; turtle G, 181 days; turtle H, 255 days; turtle I, 431 days.

stop in specific areas if prey densities fail to attain a lower threshold value.

At present it is not well understood how extreme patchiness in food supply may structure the long-term movements and population distribution of large plank-tivores. The world's largest turtle, the leatherback turtle (*Dermochelys coriacea*) is a specialist feeder on gelati-nous zooplankton and undertakes ocean-wide post-nesting movements (Ferraroli et al. 2004, Hays et al. 2004b). It has been suggested that they migrate long distances to feeding hotspots that may then be occupied for long time periods (Ferraroli et al. 2004). This hypothesis fits the general concept of animal migration, that post-breeding movements associated with little or no feeding typifies migration to specific destinations

where feeding at higher intensity occurs (Dingle 1996). Nevertheless, it is equally plausible that leatherback turtles remain on the move almost continuously, only stopping to take advantage of rarely encountered prey such as large jellyfish. We therefore set out to test the general hypothesis that, as with other marine verte-brates, specific foraging hotspots may play a key role in the life history of this species, thereby circumventing the problems associated with dietary specialization. We further examine whether behavioral plasticity, fine-tuned to local conditions, occurs in response to varying environmental fields. We combine long-term tracking with satellite-relayed behavioral and remotely sensed environmental data as individuals ranged across the entire North Atlantic for periods of over one year.
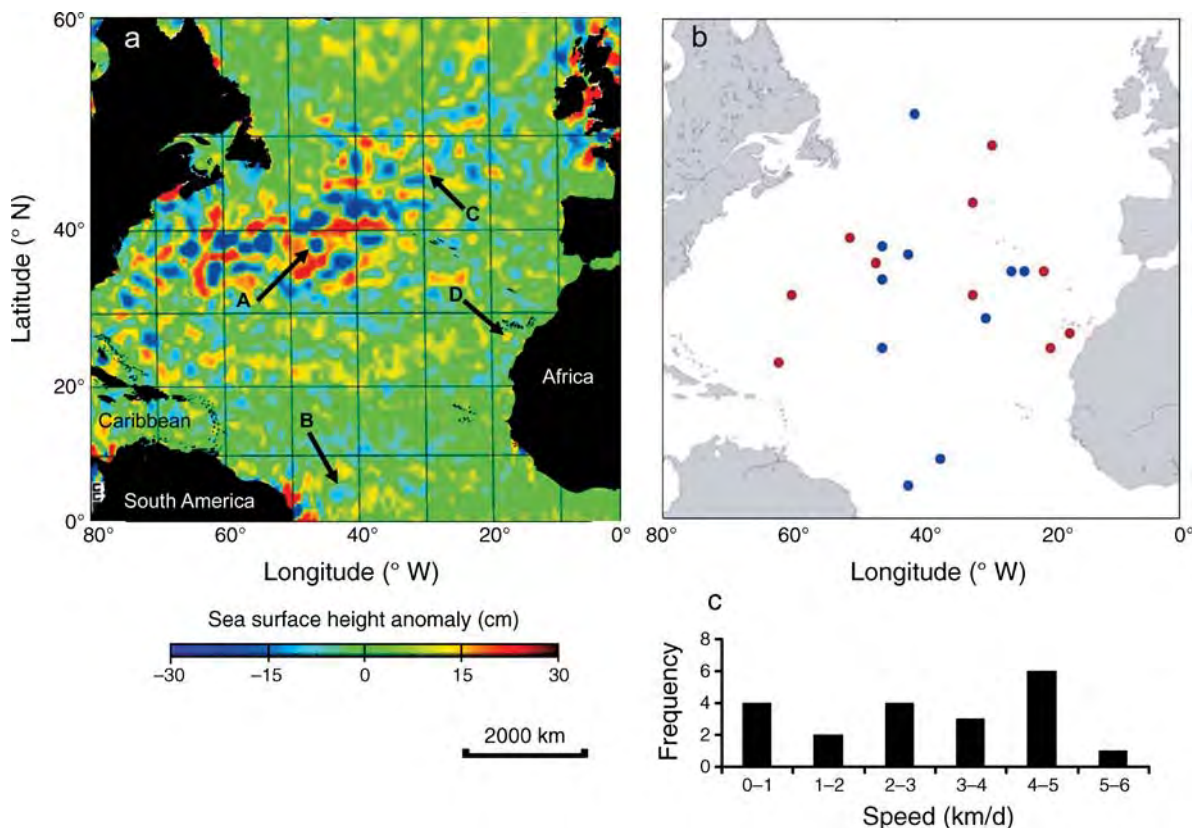
Fig. 2. (a) Image of sea surface height anomalies in the North Atlantic on 15 October 2003. Cyclonic features (cold water, anticlockwise rotation of water) are indicated in blue, and anticyclonic features (warm water, clockwise rotation) are in red. Arrows show the features at this date that were tracked to assess their rate of travel (features A and B are cyclonic; C and D are anticyclonic). (b) Start locations of the features tracked (cyclonic features in blue; anti-cyclonic features in red), showing the spatial range of mesoscale features analyzed. (c) The frequency distribution of the rate of travel for 20 mesoscale features tracked for several weeks.

METHODS

Turtle tracking and diving behavior

Nine adult female leatherback turtles that had nested on the north shore of Grenada, Caribbean (12°12′ N, 61°36′ W) were tracked using satellite relayed dataloggers (SRDLs) linked to the Argos system. As well as providing location data, SRDLs also transmitted comprehensive information about turtle diving behavior, including depth and duration of individual dives (see Appendix A).

Argos location inaccuracies mean that speed of travel estimates determined from successive locations may still be subject to large error (Hays et al. 2001). We therefore determined the speed of travel by using pairs of locations that were at least three days apart. Because many locations could be obtained each day, often there was some overlap in the dates covered by successive speed of travel calculations, i.e., the procedure provided repeated independent estimates of speed of travel. Following procedures outlined previously (Hays et al. 2001) we confirmed the robustness of these speed

calculations by identifying a strong autocorrelation between successive speed estimates. Finally, using all the independent estimates of speed, we determined the mean daily speed of travel for each individual.

Mapping tracks on remote-sensed imagery

Location and oceanographic data were incorporated into a geographic information system (GIS; ESRI 2004) allowing the overlay and analysis of biological and oceanographic spatial data. High resolution data sets covering the ocean surface include measurements taken from various types of sensors (including radiometers, scatterometers, and radars). Data on the sea surface temperature were acquired from the AVHRR (advanced very high resolution radiometer) on board the NOAA 14 satellite. The data used from June 2002 to September 2004 were received as a 4-km product as monthly composites. Pixel values were calibrated to temperature values in intervals of 0.1°C, areas with temperatures of less than −3°C were defined as cloud and were masked out, and a land mask of the North Atlantic coastline was applied to each image. Additional monthly composites
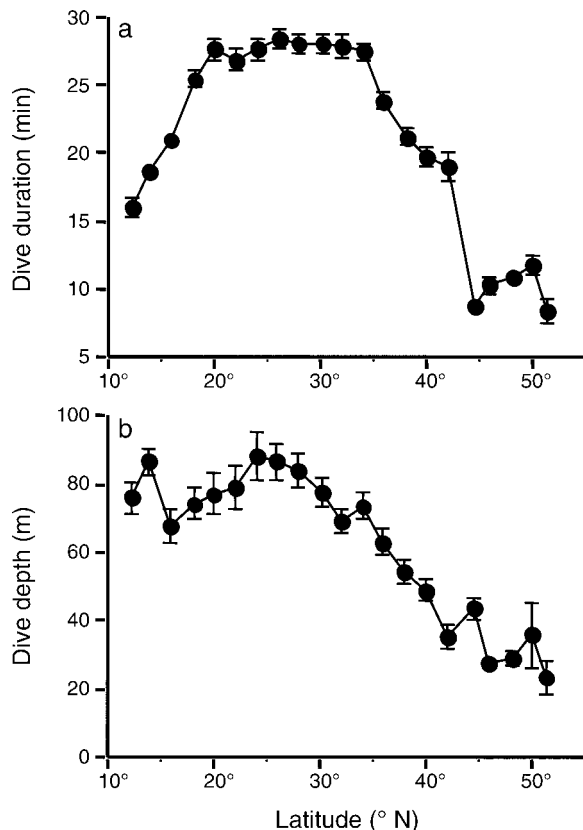
FIG. 3. For seven turtles (C–I) that headed northeast into the North Atlantic, the variation with latitude for (a) mean dive duration and (b) mean dive depth. Error bars indicate ±2 SE.

of sea surface temperature data from the NOAA Geostationary Operational Satellite (GOES satellite) provided data free from cloud contamination (*available online*).[5] The GOES images have a spatial resolution of 5.6 km and an accuracy of ±0.5°C.

The measurements of sea surface height anomalies (SSHA) were made from TOPEX/Poseidon satellite altimetry data, with a sea level measurement accuracy of 4.2 cm. The satellite images were incorporated into the GIS for spatial and temporal analysis. Fourteen-day maps of turtle tracks and remotely sensed images were combined for illustrative purposes.

Chlorophyll *a* concentration has been estimated from monthly composites (from June 2002 to September 2004) from the Sea-viewing Wide Field-of view Sensor (SeaWiFS satellite) LAC (Local Area Coverage), with a spatial resolution of 9 km[2]. Pixel values were calibrated to 0.1 mg/m^{3}; cloud and land masks were applied to the images. Data from the MODIS satellite-based sensor allowed analysis of higher resolution (4 km) monthly images (*available online*).[6]

Speed of movement of mesoscale features

To assess how mesoscale features moved within the North Atlantic we used TOPEX/Poseidon altimetry data to identify 10 cyclonic and 10 anticyclonic features that spanned a range of latitudes (0–60° N) and dates (July 2002–September 2004). TOPEX/Poseidon weekly composites were attained from the Colorado Center for Astrodynamics Research (*available online*).[7] We used a GIS to identify the middle of each feature and then measured the distance moved by each feature at seven-day intervals until the feature was no longer visible.

RESULTS

The nine female turtles were tracked as they left the Caribbean between May and July at the end of the nesting season and followed for between 181 and 431 days (Fig. 1). Turtles dispersed widely from the Caribbean with individuals initially traveling north, northeast, and east (Fig. 1). Turtles A and B spent all their time in the tropical Atlantic. Turtle C traveled close to Cape Cod (northeastern coast of USA) by September, overwintered close to Bermuda, and then the next year traveled back toward the northeastern coast of the USA. Turtle F traveled northeast from the Caribbean and then down the eastern Atlantic close to the shore of Africa. By the end of the track (July 2004) she was located southwest of the Cape Verde Islands. Turtle I traveled northeast from the Caribbean to just east of the Azores where she remained throughout the winter before moving onward into the Bay of Biscay, France, the next spring. For several of the turtles that traveled farthest north (turtles C, D, E, F, and H) the general pattern was for individuals to reach high latitudes in the autumn before heading south at the start of the winter.

Mesoscale oceanographic features within the geographic range covered by turtles were most intense in the northeastern Atlantic associated with the Gulf Stream and the North Atlantic Current (Fig. 2a). Features were relatively fixed in their position, moving <5 km/d (Fig. 2b). As such, turtles associating with a particular feature for a prolonged period would be expected to show a decrease in speed of travel.

There were systematic changes in diving behavior with turtle position. For example, for the seven turtles (C–I) that headed northeast into the North Atlantic dives initially became longer as turtles headed north (Fig. 3a, b). Dives were initially relatively deep, but then became progressively shallower as turtles headed north. At the northern range limit dives were very shallow and short. Systematic changes in dive behavior were not confined to the turtles that migrated north but were also seen in the two turtles that remained at low latitudes throughout tracking (turtles A and B). For turtle A dives became

progressively shallower and shorter, while for turtle B dives progressively lengthened and then shortened.

Accompanying these systematic changes in dive depth and duration were changes in the diel dive activity, nocturnal diving being more pronounced at high latitudes (Appendix B). South of 9° N there was a clear peak in diving around dusk and dawn and generally shallow diving throughout the 24-h cycle (Appendix C). Between 18° and 30° N there was a clear pattern of more diving at night and shallow diving at night vs. deeper diving during the day. North of 38° N there was no strong diel pattern in diving and diving was relatively shallow. While these analyses consider some general patterns, distinct changes in behavior were also seen within individuals. For example during the first part of the track for turtle A there was more nocturnal diving, but this switched to a pattern of more diving at dusk and dawn toward the end of the track (Appendix D).

Generally turtles traveled at speeds of ~30–35 km/d although speed was not invariant. We saw a few examples where speeds of travel became very slow (<10 km/d). In all cases these slow speeds were confirmed by visual analysis of the tracks, which showed individuals remaining in the same place for extended periods. Slow periods of travel occurred over much of the latitudinal range experienced by turtles and sometimes, but not always, were associated with strong mesoscale features and changes in dive behavior. Some case examples from different turtles highlighting periods of slow travel are detailed next.

For turtle E the speed of travel was generally between 25 and 70 km/d but around day 230 (18 August 2003) this dropped to below 10 km/d. Around this time dives became very short (mean 8 min) and shallow (<40 m), and the turtle situated itself between a positive and negative sea surface height anomaly (Fig. 4). However, short, shallow dives did not only occur in association with this weak feature, but were a general pattern of this turtle's behavior at high latitudes.

For turtle C the speed of travel was between 25 and 50 km/d as the turtle traveled northward toward Cape Cod (Appendix E). Around day 230 (5 August 2003) the speed of travel dropped to ~10 km/d and stayed slow for several weeks. This period corresponded to a shift toward short and shallow dives and occurred as the turtle crossed the Gulf Stream, first crossing it in a northerly direction before returning south. The oceanographic feature with which she interacted was easily detectable by satellite images of chl-a concentration (Appendix E) and sea surface temperature where the temperature decreased from 19°C to 13°C over a distance of 163 km. However there was no single feature visible in the sea height images that the turtle associated with. Rather the change in behavior seemed to be related to a general change in the oceanographic regime.

For turtle I the speed of travel progressively declined from ~50 km/d to 20 km/d as the turtle traveled to an area east of the Azores. There were then no locations from 8 January 2004 until the turtle was located in the same area on 7 June 2004 (Appendix F). This lack of locations was most probably due to failure of the transmitter's saltwater switch. The reappearance of the turtle close to where she "disappeared," implies the turtle remained more or less in the same place for many months. During this period, dives became short and shallow. This area was characterized by very low chlorophyll levels of <0.01 mg/m³. The SSHA images around these dates did not reveal any strong mesoscale features in this area.

Similarly turtle B spent a prolonged period of time (4 April to 3 June 2003) in approximately the same place. The sea surface temperature and chlorophyll concentration images (Appendix G) show turtle B's movements in the region, and no clear signal for a mesoscale feature is visible. Despite the prolonged residence in this region, the diving behavior of turtle B did not change, with dive durations remaining at ~30 minutes and to depths of 75 m.

The variability in rates of travel across individuals is illustrated in Appendix H, which shows frequency histograms for daily speed of travel for all tracked turtles. The prolonged residence of turtle I east of the Azores as well as turtle B in the western tropical Atlantic are clearly evident by an increase in the relative frequency of low speeds of travel. Overall across all nine turtles the modal speed of travel was 32.5 km/d (Fig. 5). Less than 10% of the total time was spent traveling at <5 km/h and <20% at <10 km/h.

DISCUSSION

Regional fidelity

Despite the fact that it is now widely reported that leatherback turtles may range across very large scales (many thousands of kilometers; Luschi et al. 2003, Ferraroli et al. 2004, Hays et al. 2004b, James et al. 2005b), there is increasing evidence that individuals may maintain at least some broad level of fidelity to different foraging ranges. For example, leatherbacks equipped with satellite tags on foraging grounds off Nova Scotia have been shown to move widely, traveling back to low latitudes in the winter before northerly summer movements back to broadly the same area occupied the previous year (James et al. 2005b). Similarly, two turtles that we tracked moving northward from the Caribbean to the northeastern coast of North America, confined their movements to the western Atlantic. The five individuals that we tracked heading northeast from the Caribbean in the direction of northern Europe, always stayed in the eastern Atlantic, and the two individuals tracked heading eastward from the Caribbean confined their movements to the tropical Atlantic. This evidence suggests that leatherbacks might leave their breeding sites heading toward some broad geographic region, e.g., western Atlantic, eastern Atlantic, or tropical Atlantic to which they maintain fidelity.
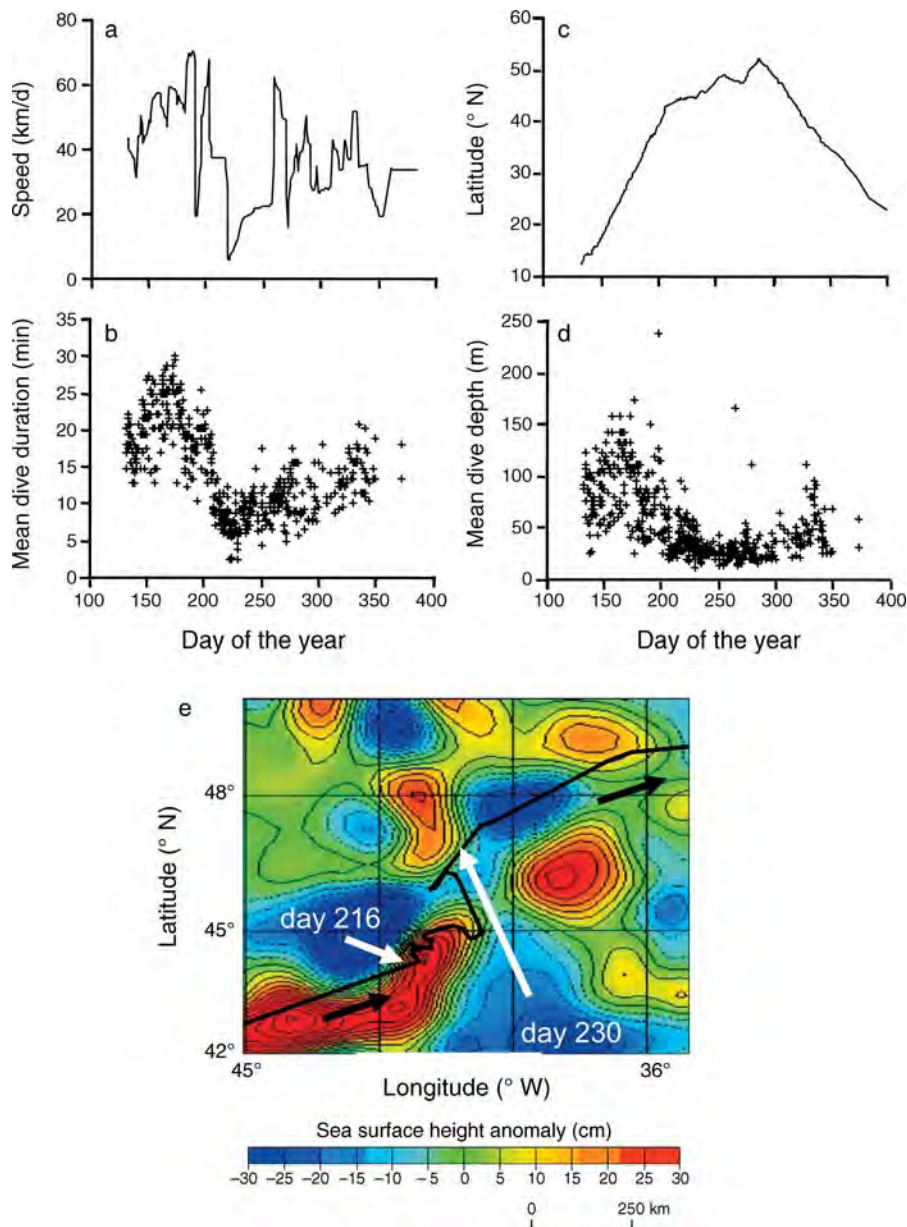
FIG. 4.   For turtle E (a) the daily speed of travel, (b) mean duration of dives recorded in individual 6-h intervals, (c) the latitude as a function of date to indicate overall pattern of movement, and (d) the mean depth of dives recorded in individual 6-h intervals. Panel (e) shows the track of turtle E in September 2003 (days 210–240 span the entry and exit of the turtle in this panel) in relation to sea surface height anomaly (SSHA). The SSHA image shows the turtle making convoluted movements along the productive edges of warm eddies, days 216–230 (indicated by white arrow and day numbers). Black arrows indicate direction of travel.

Behavioral plasticity

Within their broad fidelity to different regions of the North Atlantic, leatherbacks dive as they travel. This contrasts with some other marine vertebrates, such as penguins, which travel near the surface as they commute to prey patches close to their breeding sites (Radl and Culik 1999). The implication is that leatherback turtles continually forage as they travel. There have been a number of recent studies examining the variation in

leatherback turtle behavior as they move large distances (Hughes et al. 1998, Hays et al. 2004a, James et al. 2005a, b, Sale et al. 2006). The results we present here are consistent with a general pattern for behavioral plasticity in this species, presumably reflecting changing prey fields. In the Atlantic, the changes in turtle dive behavior appear to be regionally specific. Turtles entering the Atlantic following the end of the breeding season show consistent increases in dive duration presumably reflecting increasing prey encounter (Hays et al. 2004a)

as well as a diel component in diving that probably reflects feeding on vertical migrating plankton (Eckert et al. 1986, 1989, Hays et al. 2004a). A diel pattern of vertical migration, deep in the day and shallow at night, has been seen in many species of zooplankton, including jellyfish (for review see Hays 2003), and therefore in the daytime prey are probably too deep for leatherbacks to forage profitably, so less time is spent diving. The dive pattern exhibited once turtles entered the Atlantic was, however, not invariant. For example, one of the clearest patterns was for periods of very short shallow dives at high latitudes. This pattern has been seen recently for turtles equipped with satellite tags near Nova Scotia, Canada, and probably reflects the continuous near surface distribution of gelatinous prey at such latitudes (James et al. 2005a), with turtles bringing jellyfish to the surface for consumption. Indeed leatherback turtles at the surface have been directly observed in both the northwestern and northeastern Atlantic feeding on large jellyfish (Duron 1978, James and Herman 2001). In contrast to these two general patterns, at the southernmost latitudes (<9° N) that turtles reached after long periods of travel, we saw a pattern of diving mostly at dusk and dawn. Such a pattern is probably another manifestation of turtles feeding on vertically migrating prey. Yet in this case, prey come so close to the surface at night that deep dives are not required. Deep dives occur only at dawn and dusk as zooplankton migrate downward and upward, respectively, and are still shallow enough to make diving profitable.

It is known in general terms that gelatinous zooplankton may sometimes show patterns of normal diel vertical migration (DVM; Andersen et al. 1992, 1997, Youngbluth and Båmstedt 2001), but may sometimes also be found near the surface during the daytime (Brodeur et al. 2002, Graham et al. 2003). However, overall descriptions of basin-wide patterns of diel vertical migration in gelatinous zooplankton are not available. Our latitudinal changes in turtle dive behavior provide strong evidence that there is a systematic change in the depth distribution of gelatinous zooplankton in the North Atlantic with, for example, a preponderance of shallow living forms at high latitude vs. deeper living forms exhibiting strong DVM at midlatitudes. This conclusion is supported by other telemetry studies with leatherback turtles in the North Atlantic (James et al. 2005a).

There is increasing evidence that a wide variety of marine vertebrates show such behavioral plasticity in diving. For example, Galapagos fur seals have been shown to vary their dive depth in association with the lunar cycle, diving deeper on a full moon and vice versa, presumably because their prey within the deep-scattering layer are found deeper in the water column on brighter nights (Horning and Trillmich 1999). Similarly long-term tracking of basking sharks has shown a switch from deeper diving during the night to deeper diving during the day in different parts of this species range in
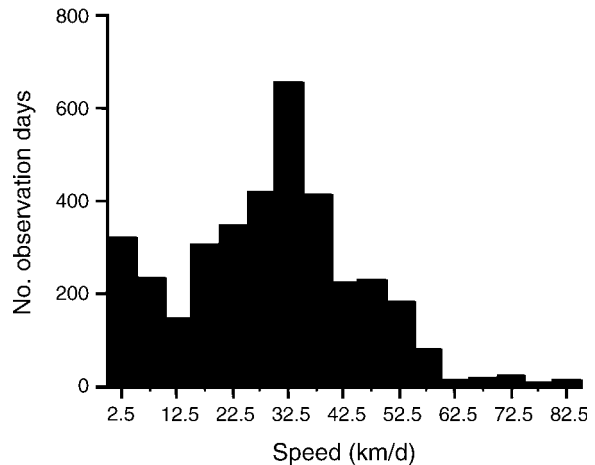

FIG. 5. For all nine turtles pooled, the frequency distribution for the daily speeds of travel.

association with differing behaviors (normal DVM vs. reverse DVM) of the prey (Sims et al. 2005). Taken together in combination with our findings, these results suggest that behavioral plasticity in diving behavior in response to local prey behavior is probably a common feature of marine vertebrates, being found in marine mammals, fish, reptiles, and most probably other groups such as marine birds as well.

Associations with mesoscale oceanographic features

Plankton are patchily distributed in the world's oceans, although certain factors may combine to lead to elevated levels of productivity at mesoscales (tens of kilometers), including the presence of oceanographic features such as rings, eddies, and fronts (Lévy et al. 1999, Lima et al. 2002). These features are essentially static relative to the normal swimming speeds of leatherback turtles in the North Atlantic. The speed and direction of travel for any marine animals will be a consequence of the swimming speed and direction of the individual as well as the currents, i.e., it is possible that in a strong current an animal might not be swimming but will still be advected horizontally (e.g., Luschi et al. 2003). Oceanographic conditions will vary in different ocean basins and sometimes mesoscale features may move fast or be ephemeral. However, the relatively static nature of mesoscale features in the North Atlantic suggests that any leatherbacks targeting these features for foraging would show a clear signal of reduced travel speed. It has previously been reported that marine vertebrates, including turtles, may slow down and forage in association with mesoscale features, presumably because of elevated abundance of food at such sites. However the intuitive appeal of these associations may mask a more complicated picture. First, plankton biomass and productivity are not universally elevated in association with oceanographic features (Graham et al. 2001). Second, marine vertebrates have specific diets,

and so it is presumably the abundance of key prey species that is most important to foraging success rather than simply elevated levels of overall plankton productivity.

Initial studies have suggested that leatherbacks target their foraging on the edges of warm eddies (Ferraroli et al. 2004). While this behavior certainly does occur on occasion, our overall results suggest a different picture of leatherback movements with the underlying pattern being that many individuals spend the majority of their time moving continuously around the Atlantic with only a proportion of individuals remaining in hotspots for extended periods. However, two of the nine turtles did show prolonged residence in one area, suggesting that sometimes turtles did not simply travel more or less continuously. Overall the movement pattern shown by an individual is probably driven by whether an abundant and long-term prey field is encountered or not. In the context of our results it should be noted that fundamental to the ecology of leatherback turtles (and indeed other species of marine turtle) is the fact females do not breed every year. Instead a nesting season is generally followed by an interval of several years before the next nesting season, with this "remigration interval" typically being 2–4 years (McDonald and Dutton 1996). In these "sabbatical" years away from the breeding grounds, leatherbacks might have a different pattern of movement and foraging success.

Hotspots where turtles remained for extended periods often had no discernable sea surface signature that would indicate a mesoscale feature. This pattern contrasts, for example, with selective foraging of albatrosses, loggerhead turtles, bluefin tuna, and basking sharks at frontal features (Sims and Quayle 1998, Polovina et al. 2000, Nel et al. 2001, Royer et al. 2004). Clearly the importance of mesoscale features varies across species, presumably because of some combination of their search abilities (e.g., speed of travel and sensory perception) as well as the spatial distribution of their prey. Further, while general associations between zooplankton and certain mesoscale oceanographic features have been noted, little is known about the factors driving the abundance and distribution of specific gelatinous zooplankton, primarily because of the problems of sampling these delicate organisms (Graham et al. 2001).

Conclusions

In summary we suggest that simple rules might be driving the movement of leatherbacks. Within a northerly and southerly range limit, individuals appear to have broad regional fidelity. They travel in fairly straight lines, continuously foraging as they travel, but taking advantage of patches of high prey abundance that they opportunistically encounter. Sometimes, but not always, these prey hotspots are reflected by mesoscale oceanographic features detected in remote sensed imagery. Dive depth is shaped by the prey distribution, and so diving

behavior changes (e.g., depth and diel periodicity) as turtles travel. Prey patches are exploited, presumably until the benefit from staying in the patch drops below some threshold level. However, our results suggest that encounters with patches of high prey abundance, sufficient to make the turtle slow down and exploit the patch, are relatively rare, at least in their first year after nesting. Given the pressing concerns for the conservation status of the leatherback turtles, there is an urgent need for measures to be introduced to mitigate mortality in fisheries. Our results reiterate the wide-ranging movements of leatherbacks and their generally epipelagic diving, which corresponds with the wide-ranging deployment of epipelagic long-lines hooks throughout the Atlantic (Lewison et al. 2004). Importantly we show that while turtles occasionally slow down and show residence in specific areas, simply protecting turtles at these times from fishing induced mortality will be insufficient, because turtles spend long periods traveling between hotspots. Rather we suggest that the key to reducing bycatch is the modification of fishing gear across ocean basins (e.g., by changing hook types; Watson et al. 2005), so that turtles are not caught so often.

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APPENDIX A

A description of turtle tracking and diving behavior (*Ecological Archives* E087-160-A1).

APPENDIX B

A figure showing the variation in diel dive index at different latitudes for nine turtles (*Ecological Archives* E087-160-A2).

APPENDIX C

A figure showing the total proportion of time spent diving to >10 m in each hour and the mean dive depth for three latitudinal bands (*Ecological Archives* E087-160-A3).

APPENDIX D

A figure showing the difference in diel diving behavior by turtle A during different sections of the track (*Ecological Archives* E087-160-A4).

APPENDIX E

A figure showing the daily speed of travel, mean duration of dives, the latitude, and the mean depth of dives for turtle C (*Ecological Archives* E087-160-A5).

APPENDIX F

A figure showing the daily speed of travel, mean duration of dives, the latitude, and the mean depth of dives for turtle I (*Ecological Archives* E087-160-A6).

APPENDIX G

A figure showing the track of turtle B, situated off the northeast coast of Brazil, overlaid onto images of sea surface temperature and chlorophyll concentration (*Ecological Archives* E087-160-A7).

APPENDIX H

A figure showing frequency distributions of the daily speed of travel for each turtle (*Ecological Archives* E087-160-A8).