

Migration cues and timing in leatherback sea turtles

Scott A. Sherrill-Mix, Michael C. James, and Ransom A. Myers*

Department of Biological Sciences, Dalhousie University, 1355 Oxford Street, Halifax, Nova Scotia, Canada B3H 4J1

Atlantic leatherback sea turtles migrate annually from foraging grounds off eastern Canada and the northeastern United States to southern foraging and breeding areas. Using Cox's proportional hazards model, we investigated the individual timing of the southward migrations of 27 turtles equipped with satellite-linked transmitters off Nova Scotia compared with turtle characteristics and satellite-measured ocean variables. Latitude, longitude, 1-week lagged average sea surface temperature, and 1-week lagged average chlorophyll-a concentration appear to influence the probability of departure. Higher temperature and, in the northern range of the study, higher chlorophyll concentration increased departure rates, perhaps due to the acceleration of the life cycle of the leatherback's gelatinous prey and/or increased feeding efficiency in these areas. This study highlights the opportunity to use satellite telemetry and environmental data to examine the cues for and timing of animal migrations and expands the study of migration timing to include a new species and environment. *Key words:* *Dermochelys coriacea*, migration cues, modeling, oceanographic variables, satellite telemetry. [*Behav Ecol* 19:231–236 (2008)]

The leatherback sea turtle, *Dermochelys coriacea*, is a large pelagic reptile found throughout the world's temperate and tropical oceans. Declared critically endangered in 2000 (Sarti Martinez 2000), leatherback populations may be reduced to only 34 500 mature females worldwide, with the majority of turtles found in the Atlantic Ocean (Spotila et al. 1996). Atlantic leatherbacks nest on beaches in South America, the Caribbean, Florida, and Africa. Each year adult leatherbacks migrate from their northern foraging grounds, including critical habitat off eastern Canada (James, Sherrill-Mix, et al. 2006), to breeding and foraging areas in tropical and subtropical waters (James, Ottensmeyer, and Myers 2005; Eckert et al. 2006).

Although we are beginning to understand aspects of leatherback turtle temperate foraging behavior (James, Davenport, and Hays 2006; James, Sherrill-Mix, et al. 2006; Jonsen et al. 2007) and migration (Hays et al. 2004; James, Myers, and Ottensmeyer 2005; Jonsen et al. 2006), we have little understanding of what variables influence the transition between these 2 states. Cues for the onset of migration have been studied extensively in birds (e.g., Both et al. 2005; Shamoun-Baranes et al. 2006) and fish (e.g., Quinn et al. 1997; White and Knights 1997); however, this has not been the case with large pelagic vertebrates such as whales and sea turtles. As many leatherbacks utilize high-latitude foraging areas in the summer and fall before migrating south thousands of kilometers (Ferraro et al. 2004; Hays et al. 2004; James, Ottensmeyer, and Myers 2005; Eckert et al. 2006), this species is well suited for investigations of potential migratory cues.

Feeding observations (James and Herman 2001) and stomach content analyses (Bleakney 1965; den Hartog and van Nierop 1984) suggest that leatherback turtles migrate to northern waters to consume jellyfish. Although little is known about the temporal or spatial distributions of the leatherback's gelatinous prey, jellyfish abundance has been linked to environ-

mental factors (reviewed in Purcell 2005). Regional ocean temperatures predict abundance in several species of jellyfish (Purcell and Decker 2005) and salps (Tew and Lo 2005). Moreover, indices of large-scale climate variability, such as the North Atlantic Oscillation (NAO) index, often correlate with jellyfish abundance (Lynam et al. 2004, 2005; Purcell and Decker 2005). As high chlorophyll concentrations indicate productive areas (Behrenfeld and Falkowski 1997) and jellyfish growth can be accelerated with higher prey concentrations (Lucas and Lawes 1998), chlorophyll-a concentrations may also correlate with jellyfish abundance. If the abundance of the leatherback's gelatinous prey is related to temperature, the NAO, or chlorophyll, these variables might predict leatherback behavior.

Environmental effects on migration have been observed in other migratory animals. For example, temperature has a significant effect on the arrival date of some migrating birds (Sparks and Braslavská 2001; Hüppop O and Hüppop K 2003; Gunnarsson et al. 2006). The NAO also appears to affect the migratory schedule of many birds (Forchhammer et al. 2002; Hüppop O and Hüppop K 2003; Rainio et al. 2006). In the marine environment, regional sea surface temperature (SST) affects the upstream migration of salmon and trout (Jonas et al. 2004) and spawning migrations of squid (Sims et al. 2001).

The effects of environmental conditions on leatherback abundance and behavior remain poorly understood. The frequency of volunteered leatherback sightings appears to be related to SST (James, Sherrill-Mix, et al. 2006; James et al. 2007), but whether this is due to increased numbers of turtles or increased sighting effort is unclear. McMahon and Hays (2006) suggest that the range of leatherbacks is limited to SSTs greater than 15 °C; however, turtles are routinely seen in Canadian waters below this temperature (James, Sherrill-Mix, et al. 2006). SST appears to influence the distribution (Davenport 1997), nesting date (Weishampel et al. 2004), remigration interval (Solow et al. 2002), and interesting interval (Hays et al. 2002) in some cheloniid sea turtles. However, as leatherbacks can maintain body temperature well above ambient (Frair et al. 1972; James and Mrosovsky 2004), generalizing these results to this species may not be warranted.

Although continuous long-term telemetry data from individual animals present an opportunity to look at the effects of fine-scale environmental correlates (otherwise impossible with

*Deceased.

Address correspondence to S.A. Sherrill-Mix. E-mail: sherrill@mathstat.dal.ca.

Received 30 June 2007; revised 25 September 2007; accepted 26 September 2007.

population abundance data), no studies have attempted to quantify the effects of environmental variation on the timing of migration using satellite-derived positions. Such studies will be limited to observational data as manipulation is impossible. Here we use telemetry data obtained from 27 leatherback turtles and satellite-derived environmental variables to investigate the role of environmental correlates, latitudinal and longitudinal position, and turtle body size and sex on the timing of southward migration.

METHODS

Leatherback turtles were captured and equipped with Argos satellite-linked transmitters off mainland Nova Scotia (approximately 44°N, 64°W) and Cape Breton Island (ca. 47°N, 60°W) (James, Myers, and Ottensmeyer 2005). State-space estimates of latitude and longitude for each 6-h period of the turtle's track were obtained (Jonsen et al. 2007). The state-space model also estimates the behavioral mode of the turtle as either foraging or transiting (e.g., migration and movement between foraging areas) based on differences in turn angle and travel rate distributions (for details see Jonsen et al. 2007). Based on these estimates, we can determine the first 6-h transiting period of the southerly migration (defined here as continuous movement uninterrupted by foraging to below 36°N). The last dates of foraging were consistent with migration dates estimated from speed and diving behavior (James, Ottensmeyer, et al. 2006). We inferred foraging prior to migration in tracking data (see supplementary movie) from 27 turtles. Five turtles were tracked through 2 northern foraging seasons and 6 records were censored before migration departure was observed, resulting in a data set of 32 foraging seasons and 26 migration departures.

Fourteen satellite tags provided direct measures of SST. Because the state-space estimates do not correspond directly to the time that the tag recorded SST, the median SST for observations within the 6-h period was used. For tags without SST recorders ($n = 13$) and for gaps in the track of tags equipped with SST sensors, satellite-derived SSTs were used. SSTs were interpolated from Geostationary Operational Environmental Satellite (GOES) within 1 day of the observation or, if GOES data were unavailable, the best quality estimates within 0.1° of the turtle's estimated position from Advanced Very High Resolution Radiometer (AVHRR) Oceans Pathfinder (version 5) data. Both the AVHRR and GOES data were obtained from the Physical Oceanography Distributed Active Archive Center at the National Aeronautics and Space Administration Jet Propulsion Laboratory (<http://podaac.jpl.nasa.gov>). Where both satellite-derived and tag-measured SSTs were available, the 2 measurements were highly correlated ($r = 0.83$, $n = 2979$).

Monthly NAO estimates were obtained from the National Weather Service NAO Web site (<http://www.cpc.ncep.noaa.gov/data/teledoc/nao.shtml>). Depths were interpolated from the S2004 bathymetry grid, a combination of Smith and Sandwell (1997) and General Bathymetric Charts of the Oceans data of Marks and Smith (2006). The average chlorophyll-a concentrations within 3 days and 0.2° of turtle locations were calculated from Sea-viewing Wide Field-of-view Sensor (SeaWiFS) (1999–2001) or SeaWiFS merged with Moderate-resolution Imaging Spectroradiometer (2002–2005) measurements using data obtained from the Ocean Color Web (<http://oceancolor.gsfc.nasa.gov/>).

Because oceanographic conditions may be transient, we also calculated a lagged average of the temperatures and chlorophyll concentrations experienced by the turtle for the previous week. Weeks with greater than 50% available values were included.

Tracks from satellite-tagged animals are often cut short unexpectedly (e.g., tag failure or animal mortality). Ignoring or making arbitrary assumptions about these censored individuals is inappropriate (Castro-Santos and Haro 2003). Cox's proportional hazards model, a technique for the study of mortality and mechanical failure, is effective for the analysis of censored data (Cox 1972). As this method also allows time-dependent covariates (e.g., SST and chlorophyll) (Andersen and Gill 1982) and does not require assumptions about how departure rate changes over the season (Cox 1972), we suggest that Cox's model is well suited to the study of migration using satellite-tracking data.

The concept of hazard, the probability of an event given that it has not yet happened, is useful in modeling events that can only happen once (e.g., migration departure). In this case, the hazard corresponds to the departure rate, which is the chance of a turtle leaving on its southward migration given that it has not already left.

Here we used Cox's model to analyze time-dependent latitude, latitude², longitude, longitude², day length, depth, SST, 1-week lagged average SST, chlorophyll-a concentration, 1-week lagged average chlorophyll, and monthly NAO index along with the static variables of tagging location, sex, carapace length, maturity (≥ 140 cm standard curved carapace length), and 2-way interactions between these variables in relation to the probability of a turtle leaving for the south. Variables were added and removed by stepwise selection using the Akaike's information criterion (AIC) as implemented in R (version 2.4). Standard errors were estimated based on jackknife estimates of the variance leaving out individual turtles. The sensitivity of the analysis was investigated by in turn lowering the foraging threshold of the behavioral estimates of the state-space model, weighting the Cox model by the inverse of the total of the estimated variances of the latitude and longitude estimates and decimating the data by a factor of 2, 4, and 8.

RESULTS

Location and behavior estimates were available for 8998 6-h periods prior to migration. One-week lagged temperature averages were obtained for 8082 observations, and lagged chlorophyll averages were obtained for 8077 observations. The average departure date was 23 October (95% confidence interval [CI]: 12 October to 3 November; range: 8 September to 13 January).

The final departure model selected by AIC included latitude, longitude, longitude², 1-week lagged SST, 1-week lagged average chlorophyll, and the interaction of 1-week lagged average chlorophyll with latitude (see Table 1). Other variables did not improve the model as measured by AIC and were excluded from the analysis. The estimated effects were not qualitatively different after varying the threshold for inferred foraging, weighting the data by the uncertainty in the estimated positions or decimating the data. Given these observations, Cox's model appears suitable for the study of migration cues.

The location of the turtle had a significant relationship with departure rate. Leatherback departure rate increased with latitude with the effect becoming stronger in waters with higher chlorophyll concentrations. For each 1° increase in latitude at the mean chlorophyll concentration of 0.72 mg/m³, the departure rate increased by a factor of 3.24 (95% CI: 1.87–5.61). Although departure rate increased consistently with latitude, the effects of longitude exhibited a minimum departure rate at 63.6°W longitude with departure rate increasing exponentially with distance from that meridian (see Figure 1).

Environmental conditions were also related to departure rate. Each 1 °C increase in 1-week lagged temperature increased the departure rate by 48.7% (95% CI: 0.71–120%). Departure

Table 1
Results from stepwise Cox’s proportional hazards modeling of the onset of migration in leatherback turtles tagged off Nova Scotia

Variable	Range	Mean	β	Standard error	<i>P</i> value
Latitude	36.1–50.0°N	42.6°N	0.619	0.233	0.008
Longitude	75.6–51.6°W	64.7°W	−5.98	1.22	0.000001
Longitude ²	2665–5718	4211	0.047	0.0098	0.000002
Temperature	10.6–26.2 °C	17.7 °C	0.397	0.199	0.046
Chlorophyll	0.12–3.22 mg/m ³	0.72 mg/m ³	−34.0	12.5	0.007
Chlorophyll:latitude	4.7–147	40.0	0.777	0.27	0.005

Temperature and chlorophyll are the average of the SSTs and chlorophyll-a concentrations experienced by the turtle the prior week. The mean and range of the variables for all 8998 observations 6-h periods of the study are shown for comparison.

rate was not significantly affected by 1-week lagged average chlorophyll concentration in the central latitudes (39.1°N–45.0°N) of the study area. At latitudes greater than 45.0°N, higher chlorophyll concentrations increased departure rate. The effect of chlorophyll strengthened with latitude up to a 128.3-fold increase in departure rate (95% CI: 10.9–1506) for a 1-mg/m³ change at the maximum latitude 50.0°N (Table 1).

In addition to estimating the proportional change in chance of departure, Cox’s proportional hazards model can also estimate the baseline departure rates (at the means of all variables). The probability of turtle departure is characterized by

a preliminary period with little chance of departure followed by a rapid increase of departure probability to almost certain departure (Figure 2).

If the turtles in this study are assumed to be random samples of the populations in these areas and their departure rates are not affected by tagging, population-level migration departure patterns can be inferred from these departure rates. These results translate to different 50% and 95% departure times for turtles in various areas of the northwest Atlantic (see Table 2 and Figure 1).

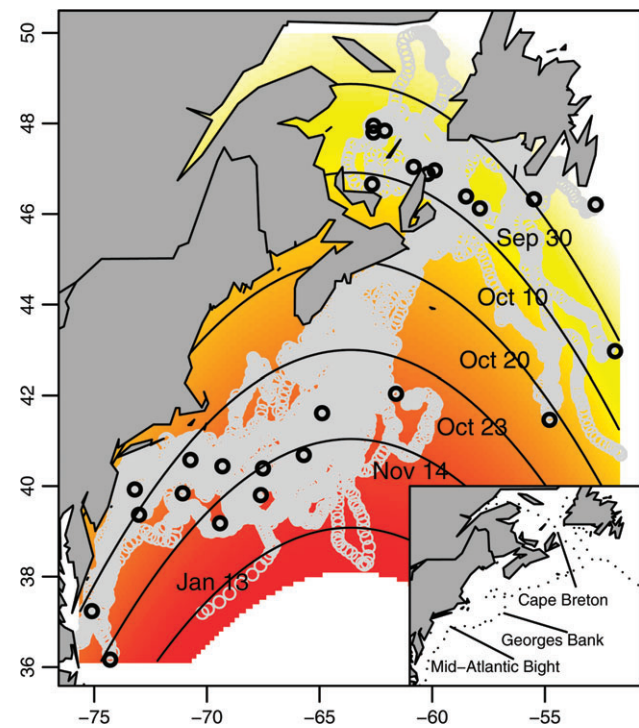


Figure 1
 Contour plot of the relative departure rates for turtles foraging in northern waters as predicted by Cox’s proportional hazards model. Red indicates the lowest departure rates and yellow the highest. Contour lines indicate a 10-fold increase in departure rate from the line below them. Dates indicate date of 50% departure for that contour line. Gray circles indicate turtle positions, and black circles indicate departures. Chlorophyll and SST were set at mean values (17.7 °C and 0.72 mg/m³). Inset shows locations discussed in the paper. Inset dotted gray lines follows the 200-m depth contour.

DISCUSSION

Leatherback departure rate was significantly related to the position of the turtle. Compensation for distance traveled could explain earlier departures from foraging areas further

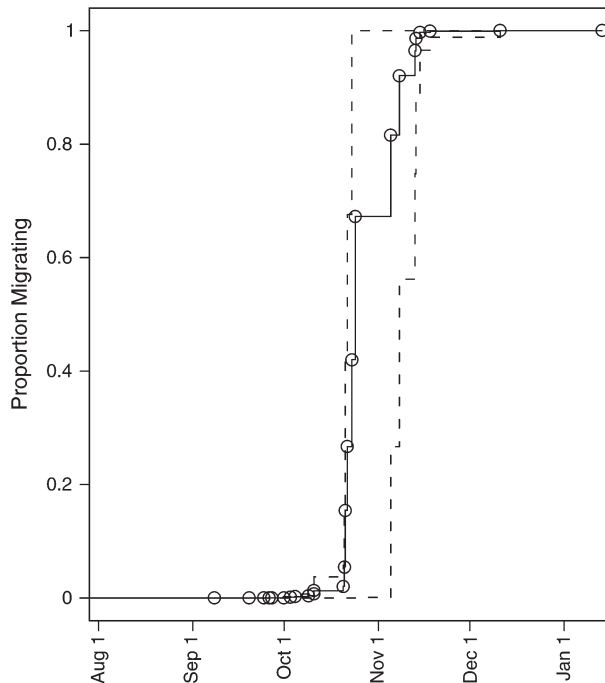


Figure 2
 Predicted proportion of leatherbacks that have initiated their southward migration at mean latitude, longitude, and 1-week lagged average temperature and chlorophyll for the study. Points indicate turtle departures, and dashed lines show the 95% confidence limits.

Table 2
Predicted departure times for 50% and 95% of the leatherback turtles at a few representative locations (see Figure 1)

Location	50% Departure	95% CI	95% Departure	95% CI
Cape Breton (47°N, 60°W)	4 October	−3.7 to 6.3	10 October	−6.3 to 9.6
Georges Bank (41°N, 66°W)	13 November	−8.3 to 27.7	11 December	−27.7 to 33.4
Mid-Atlantic Bight (40°N, 72°W)	24 October	−2.6 to 11.6	12 November	−19.6 to 0.3

The 95% CIs are in days. One-week lagged average chlorophyll and SST were held steady at their mean value for the data set (17.7 °C and 0.72 mg/m³).

from southern nesting and wintering grounds. Animals foraging in more distant areas would be expected to depart earlier. For example, in black-tailed godwit (*Limosa limosa*), the distance between foraging and breeding areas does not predict arrival date (Gunnarsson et al. 2006). However, the difference in distance between leatherback foraging areas near Cape Breton (47°N, 60°W) and the largest nesting colonies in French Guiana and Suriname (5°N, 54°W) (Spotila et al. 1996) and the distance between more southern foraging areas near Georges Bank (41°N, 66°W) and these colonies is only about 500 km. Based on a mean swim speed for internesting leatherbacks of 0.63 m/s (Eckert 2002), this difference could be traversed in as few as 10 days, whereas the predicted difference in 50% departure times is more than a month. Moreover, faster minimum speeds based on telemetry appear common in migrating turtles (James, Myers, and Ottensmeyer 2005).

Leatherback turtles might initiate migration when the abundance of their prey declines. Such a response to varying prey has been observed in other species. For example, barnacle geese (*Branta leucopsis*) appear to migrate when fat deposition rates decline (Prop et al. 2003). River herring (*Alosa pseudoharengus*, *Alosa aestivalis*) are also more likely to begin downstream migration when prey abundance is low (Yako et al. 2002). Leatherbacks may leave when feeding efficiency and rate of fat deposition declines past a certain threshold.

However, the decline of available prey alone does not explain differences in foraging patterns observed in these turtles. Leatherbacks tagged off Nova Scotia appear to focus foraging activity in 2 broad areas of the temperate northwest Atlantic: more northern waters (>44°N) near Cape Breton, southern Newfoundland and the southern portion of the Gulf of St Lawrence; and relatively southern waters (<44°N) along the Scotian Shelf, Georges Bank, and Mid-Atlantic Bight. Only 2 leatherbacks foraged both above and below 44°N, and in these cases, the majority of foraging corresponded to a single region (above 44°N: 11% and 88%). This behavior is unexpected, as the more northern turtles are departing for their migration while other turtles are still foraging in more southern waters. Although these turtles departing from higher latitudes could migrate south along the continental shelf and continue foraging later into the season, this behavior has not yet been observed.

So why might leatherbacks in the north migrate so much earlier? Perhaps, relative prey consumption rates differ between areas, with northern turtles benefiting from enhanced feeding efficiency and more rapid energy assimilation over shorter periods of prey availability than their southern counterparts. Differences in departure date due to habitat quality have been observed in migrating birds (Gill et al. 2001; Norris et al. 2004).

Our results demonstrate that leatherbacks stay longer in waters near 63.6°W. This longitude lies between Georges Bank and Cape Breton Island (Figure 1) and may indicate that

these 2 areas provide foraging opportunities later into the season than nearby longitudes. Georges Bank is one of the most productive shelf ecosystems in the world (Backus and Bourne 1987). Waters off the northeast tip of Cape Breton are a primary field site for our research on leatherbacks, and we directly observe many turtles foraging there. Moreover, volunteered sightings (James, Sherrill-Mix, et al. 2006) and telemetry data (James, Ottensmeyer, and Myers 2005) suggest that both areas are critical foraging habitat.

We found that leatherbacks are more likely to depart from warmer and, in the northern range of this study, more chlorophyll-rich waters. This is surprising as cheloniid turtles depart northern foraging areas as water temperatures cool (Morreale et al. 1992). Moreover, jellyfish are often more abundant in warmer waters (Purcell 2005), and higher temperature and chlorophyll concentration predict higher productivity (Behrenfeld et al. 2005), suggesting that leatherbacks would benefit from longer residency in these areas. One possible explanation for these earlier departures is that jellyfish medusa often deteriorate and die after spawning (Brewer 1989; Lucas 2001), and higher temperature and food availability can advance the scyphozoan life cycle (Lucas and Lawes 1998; Purcell et al. 1999). Therefore, higher temperature and chlorophyll concentrations may indicate environments where jellyfish reach sexual maturity faster and thus senesce earlier in the season. If this accelerated life cycle provides higher than normal foraging opportunities earlier in the season and lower foraging opportunities later, leatherbacks would be expected to depart earlier from areas with higher temperatures and chlorophyll concentrations. Such correlations between earlier migration and better forage have been observed in other species (Marra et al. 1998; Saino et al. 2004).

Leatherback departure rate did not increase with decreasing temperature, and 21% of the location data (444 turtle-days) were from waters with SSTs estimated to be colder than the 15 °C limit proposed by McMahon and Hays (2006). These findings corroborate identification of physiological and behavioral adaptations to cold-water foraging in this species (Frair et al. 1972; James and Mrosovsky 2004).

Fishery interactions with both long line and fixed gear are a threat to leatherback turtles (Lewison et al. 2004; James, Ottensmeyer, and Myers 2005). This analysis provides information that could be used to guide various management actions aimed at mitigating capture of turtles, such as time–area closures. By considering the temporal distribution of an endangered species in a particular area, conservation efforts can be more effectively targeted and the economic impact can be minimized (Myers et al. 2007).

Research on the fitness consequences of early arrival to nesting areas for both male and female turtles and the spatial and temporal distribution of gelatinous prey would provide a better context for future leatherback migration studies. With the rapid proliferation of wildlife telemetry and environmental data sets, we urge that studies of fine-scale migration cues be expanded to other species and environments.

FUNDING

Canadian Wildlife Federation, Census of Marine Life-Future of Marine Animal Populations, Environment Canada, Fisheries and Oceans Canada, George Cedric Metcalf Charitable Foundation, Mountain Equipment Co-op, National Fish and Wildlife Foundation (USA), National Marine Fisheries Service (USA), Natural Sciences and Engineering Research Council of Canada, Pew Charitable Trust, TD Canada Trust Friends of the Environment Foundation, and World Wildlife Fund Canada

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.behco.oxfordjournals.org/>.

We thank B. Fricker, H. Fricker, J. Fricker, K. Martin, and B. Mitchell for their instrumental contributions to all aspects of fieldwork. Thanks are also extended to I. Jonsen and W. Blanchard for statistical assistance. We are grateful to S. Eckert, C. Harvey-Clark, and C. Ryder for advice and encouragement.

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