Leatherbacks at high latitudes: when do they migrate south?

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Abstract

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Introduction

The leatherback sea turtle, *Dermochelys coriacea*, is a large pelagic medusivore found worldwide ranging from tropical to temperate oceans. Declared endangered in 1982 and critically endangered in 2000, Atlantic leatherbacks may be reduced to only 20-30,000 mature females (Spotila et al., 1996). These turtles nest on beaches in Florida, the Caribbean, South America and Africa. Waters off Nova Scotia (James et al., 2006c) and the northeastern US [ref?] provide a critical foraging habitat for these turtles. Each year adult leatherbacks migrate

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from their northern foraging grounds to nesting beaches in the south (James et al., 2005b).

While we are beginning to understand aspects of the migratory (James et al., 2005a; Jonsen et al., 2006) and foraging (James et al., 2006c,a; Jonsen et al., In Press) [probably should include some other lab here too] phase of the turtle's lifestyle, we have little understanding of what drives the change between these two states (James et al., 2006b) [kind of]. Although the cues for the onset migration of migration have been studied extensively in birds (e.g. [various]) and fish (e.g. [various]), few studies exist on large pelagic, and often endangered, organisms such as whales [need to verify this a bit more] and sea turtles. As one of the farthest migrating and largest reptiles, migratory cues for leatherback turtles may provide an excellent opportunity to further our understanding of migratory processes [needs work].

Breeding and foraging area temperature has a significant effect on the arrival date of many migrating birds (Gunnarsson et al., 2006; Hüppop and Hüppop, 2003; Sparks and Braslavská, 2001). In the marine environment, regional sea surface temperature affects the upstream migration of salmon and trout (Jonas et al., 2004) and and spawning migrations of squid (Sims et al., 2001). The North Atlantic Oscillation (NAO), an indicator of large scale temperature change, also appears to affect the migratory schedule of many birds (Gunnarsson et al., 2006; Hüppop and Hüppop, 2003; Rainio et al., 2006) and squid (Sims et al., 2001).

While satellite telemetry from tagged animals is becoming more and more common [ref?], few studies have attempted to use this data to investigate migration cues. Martell et al. (2001) found sexual and regional differences in

osprey migration timing and Craig et al. (2003) found sexual and maturity differences in humpback whales but neither investigated migration triggers. Although these data present an opportunity to look at the effects of fine scale environmental correlates otherwise impossible with population level data, few, if any, studies have attempted quantitative analysis of migration cues based on satellite derived positions.

Data from [XX] leatherback turtles tagged off Nova Scotia between 1999 and 2004 (James et al., 2005a) provide an excellent opportunity dataset for studying migratory cues. In this study, we will use these data and satellite derived environmental variables to investigate the role of environmental correlates, turtle characteristics and position on migration timing.

Methods

Using the methods of Jonsen et al. (In Press), we estimated latitude, longitude, and behavioral mode for every six hours of a turtle's track [is this the right way to say this? probably not since we didn't actually do it]. Based on these estimates, the last six hour foraging period before migration, defined here as continuous movement uninterrupted by foraging to below 36°N, can be determined. Turtles not estimated to have foraged in the north after tagging were excluded from this analysis.

Sea surface temperatures (SST) were obtained directly from tags for 15 Kiwisat [correct name MIKE?] tags. Since the state-space estimates do not correspond directly to tag observations, the median recorded SST for observations within three hours of the standardized times was used. For tags without SST

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recorders and for gaps in the track of SST equipped tags, satellite derived SST's were used. Sea surface temperature were interpolated from Geostationary Operational Environmental Satellite (GOES) within one day of the observation or, if GOES were unavailable, obtained from the mean of the best quality estimates within .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 NASA Jet Propulsion Laboratory (`http://podaac.jpl.nasa.gov`).

Since the sea surface temperatures may be transient, we also obtained a lagged average temperature for the previous week for each period to provide an index of the environment the turtle had been experiencing. To reduce the effect of small periods of missing values, weeks with less than 20% missing temperatures were included. Monthly North Atlantic Oscillation estimates were obtained from the National Weather Service NAO website (`http://www.cpc.ncep.noaa.gov/data/teledoc/` Depths were interpolated from [depth ref]. Daylength was calculated as [formula].

Since migration can only occur once per season per individual, normal models are not appropriate. Luckily, methods originally used for failure and mortality estimates have been developed that are appropriate for data like these (Castro-Santos and Haro, 2003). Cox proportional hazard survival regression provides a model for counted mortality. Unlike normal regression techniques, the proportional hazard method allows for individuals which are censored before an event is observed. By using Cox methods, we are able to use all the available data up until tag or harness failure and allow for time dependent covariates. We analyzed time dependent latitude, latitude^2, longitude, longitude^2, day

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length, sea surface temperature, 1-week lagged average sea surface temperature and monthly NAO index along with the static variables of sex, length of turtle, and maturity of turtle (>140 cm standard curved carapace length) in relation to the chance of a turtle leaving for the south. Variables were added and removed by bidirectional stepwise regression.

Results

Premigration foraging was observed in 27 turtles over 32 foraging seasons. The last date of foraging appeared to agree well with migration dates estimated from speed and diving behavior (James et al., 2006b). From these turtles, location and behavior estimates were available for 8998 six hour periods prior to migration. Temperatures were obtained for 8106 observations and 1-week lagged temperature for 6490 observations.

Monthly NAO, length of turtle, depth, sex, latitude^2, sea surface temperature, 1-week lagged temperature average and year were not significant and were removed from the model. Latitude, longitude, longitude^2, and maturity were significantly related to migration departure (see Table 1). There were no significant interactions between the variables.

For each degree north turtles are 88 (95% CI: 34-164) percent more likely to leave on a given day. Turtles are most likely to stay longer near 63.9°W with risk of leaving increasing exponentially as longitude moves away from this values (Figure 1.) Juvenile turtles are 3.8 (95% CI: 1.16-12.49) times more likely to leave on a given day than an adult turtle (Figure 2).

If these turtles are assumed to be random samples of the population and

Variable	β	p-value
Latitude	0.644	0.00020
Longitude	3.733	0.00024
Longitude^2	0.029	0.00032
Juvenile	1.384	0.02400

Table 1

Results from stepwise Cox proportional hazard modelling of the onset of migration in northern foraging leatherback turtles.

Location	Latitude	Longitude	Length	50% Departure	95% Departure
Cape Breton	47	-60	Adult	Oct 11	Oct 21
Cape Breton	47	-60	Juvenile	Sep 27	Oct 11
Georges Bank Slope	42	-65	Adult	Nov 13	Jan 13
Georges Bank Slope	42	-65	Juvenile	Oct 22	Nov 13
New York Shelf	40	-74	Adult	Oct 22	Nov 13
New York Shelf	40	-74	Juvenile	Oct 11	Oct 22

Table 2

Departure times for 50% and 95% of the leatherback turtle on different foraging grounds and size classes assuming the turtles migration dates were not affected by tagging and that tagged turtles are a random sample of the populations.

are not affected by tagging, these risks translate to different 50% and 95% departure times for turtles in different areas of the northwest Atlantic (see Table 2) and life stages (Figure 2).
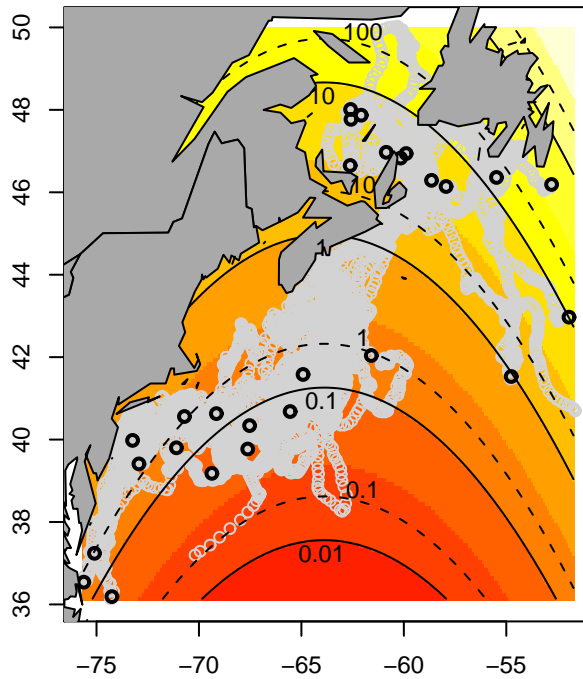
Fig. 1. Contour plot of relative chance of departure for turtles foraging in northern waters. Contour lines and coloring show risk relative to the median adult value for adults (solid line) and juveniles(dashed line).

Discussion

We found that leatherback turtles depart at different times in different parts of their range but that these differences did not appear to be directly related to sea surface temperature. Juvenile turtles leave significantly earlier than adults.

Unlike birds whose migratory schedule is altered by photoperiod (Gwinner, 1996) and temperature (Gunnarsson et al., 2006), turtle departure dates do not directly correlate with day length or temperature. This may indicate that abundance of the gelatinous prey of the turtles does not correlate well with either of the variables. Another possible reason is that there appears to be two different late season foraging behaviors for leatherbacks. Of the 32 foraging seasons, only two included foraging both above and below 44°N and in these
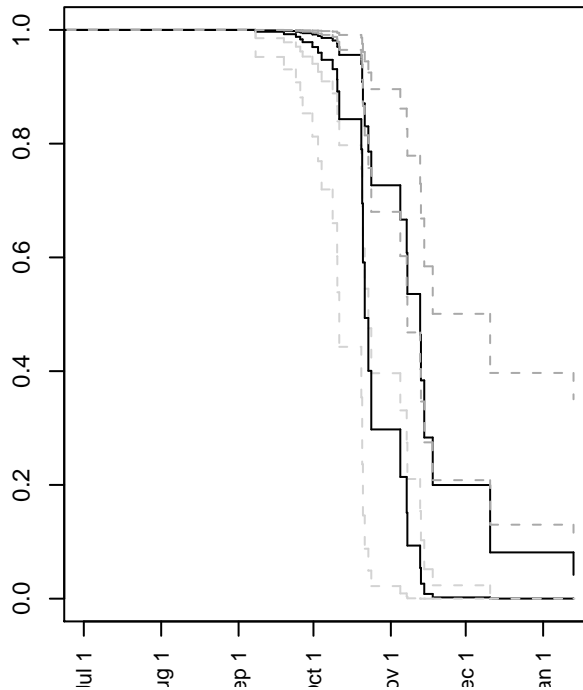
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Fig. 2. Survival plot for adult and juvenile leatherbacks. Grey lines show 95% confidence limits. [placeholder]

cases one region had an obvious large majority of the foraging (88% and 89%) [plot?]. This is especially strange since the more northern turtles are departing for their migration while southern turtles are still foraging. Although these northern turtles could migrate along the coast and continue foraging, this behavior has not yet been observed. This may indicate some difference in relative consumption rates between turtles in different areas.

Birds foraging in lower quality habitat arrive later to breeding grounds (Norris et al., 2004; Gill et al., 2001). When released on the edge of the Gulf of Mexico, lean red-eye vireos attempt to forage while fat birds initiate migration (Sandberg and Moore, 1996). Barnacle geese forage in patchy unpredictable habitat and appear to migrate when fat deposition rates decline (Prop et al., 2003). The gelatinous prey of leatherbacks also appears PATCHY [MIKE ref] and leatherback turtles may leave when fat deposition reaches a certain thresh-

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old. If the metabolic needs of juveniles are less than a mating adult or young turtles are less efficient at foraging, a fat deposition threshold would explain their earlier departure. Different migration times for juveniles have also been observed in humpback whales (Craig and Herman, 1997) and some but not all bird species (Woodrey and Chandler, 1997).

Migrating birds appear to compensate for greater distances between foraging and breeding areas (Gunnarsson et al., 2006). Compensation for distance traveled could explain earlier departures from the Cape Breton area but the distance between Cape Breton and Georges Bank is about 700 km. The mean swim speed for internesting leatherbacks is .63 m/sec. In a straight line, this translates to 54 km/day. While extrapolating from instantaneous swim speeds may not be entirely accurate, it does show the capabilities of these animals and faster minimum speeds based on telemetry appear common in migrating turtles (James et al., 2005a). Since distances that a turtle could cover in 13 days results in over a month difference in 50% departure times, the distance alone seems like an unlikely explanation for these data. Latitudinal correlation with departure dates unexplained by distance has also been observed in swallows (Sparks and Braslavská, 2001).

For birds, migration timing is a balance between optimal fuel loading and early arrival. Early arriving birds are often the most fecund [ref] and arrival date is heritable in barn swallow (Møller, 2001) and salmon (Bentzen et al., 2001). It is unclear whether leatherback turtles have the same evolutionary pressures as birds. Without the need to feed young, earlier arrival may not necessarily correlate with breeding success. But since female leatherbacks nest several times in a season [ref], early arrival may allow more time in the breeding area and more clutches. Male turtles migrate to nesting areas every year to

attempt to mate with females [ref]. Male turtles arriving earlier may optimize their fitness by having the most breeding opportunities. Future research on the fitness consequences of early arrival would be very helpful.

The methods of Jonsen et al. (In Press) appear well suited to determining migration dates from satellite telemetry and combine well with failure and mortality estimation techniques. By studying individual migrations, these methods will allow the verification of population level predictions and fine scale determination of the effects of environmental correlates. A better understanding of migration also helps target conservation and research efforts (Myers et al. [Current Bio]) [needs work].

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