

AN ANALYSIS OF MIGRATORY CUES AND POTENTIAL  
TAGGING EFFECTS IN THE LEATHERBACK SEA TURTLE

by

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DEPARTMENT OF BIOLOGY

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*To my supervisor, Ram Myers  
and my mother, Michele Sherrill-Mix*

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## **Abstract**

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, I investigated the individual timing of the southward migrations of 27 turtles equipped with satellite-linked transmitters off Nova Scotia compared to 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 lifecycle of the leatherback's gelatinous prey and/or increased feeding efficiency in these areas. I also investigated the effects of handling and tagging on leatherbacks. Turtles are much more likely to begin migration and swim speeds are significantly higher in the first week after capture. I inferred 17 of 42 turtles departed Canadian waters immediately after tagging without foraging. Turtles were more likely to immediately begin their migration if they were tagged later in the year or if they were tagged following entanglement in fishing gear. Although it remains uncertain whether these effects are due to capture and/or tagging and whether they are detrimental to the turtle, this study does emphasize the necessity of considering tag effects on these animals. This thesis expands the study of migration timing to include a new species and environment and highlights potential tagging effects on leatherbacks captured at sea.



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# Chapter 1

## Introduction

The leatherback turtle (*Dermochelys coriacea* Vandelli, 1761) is the largest and most widely distributed turtle in the world. In the Atlantic, waters off Nova Scotia provide critical foraging habitat (James et al., 2006). Each year, adult leatherbacks migrate thousands of kilometers from these northern foraging grounds to wintering and nesting areas in the south (James et al., 2005,?, 2007).

The sole extant member of the family Dermochelyidae, the leatherback is one of the largest reptiles, with leatherbacks in Canadian waters measured at greater than 170 cm curved carapace length and over 600 kilograms (James et al., 2007). With its large size, subdermal fat and possibly thermogenic adipose tissue (Greer et al., 1973; Goff and Stenson, 1988; Paladino et al., 1990), this turtle can inhabit cold waters while maintaining body temperatures up to 18°C above ambient (Frair et al., 1972; James and Mrosovsky, 2004). This capacity allows leatherbacks to have the widest range of any reptile (Ferraro et al., 2004; Hays et al., 2004; James et al., 2005).

Leatherbacks are highly adapted to their pelagic lifestyle. With the leatherback's reduced internalized shell and long flippers, speeds up to 10 km/hr have been observed from tag-mounted swim speed sensors (Eckert, 2002) and satellite tracking data (James et al., 2005). Like other sea turtles, the leatherback's esophagus is lined with spike-like papillae and isolated from the stomach by a sphincter which likely allows them to retain their gelatinous prey while expelling ocean water to reduce salt intake (Lutz, 1997). Lachrymal salt excretion glands further maintain balance (Lutz and Hudson, 1986).

Leatherbacks spend a large amount of time deep below the surface. In northern waters, they spend about one-third of their time below 6 m. During migration, leatherbacks display large diel differences in diving behavior with 80% of their time spent below 6 m during the night and 18% during the day (James et al., 2006). The deepest dives recorded for a leatherback have been >1000 m (Eckert et al., 1989;

Hays et al., 2004; Sale et al., 2006) and turtles can stay submerged for more than an hour (Southwood et al., 1999; Hays et al., 2004; Sale et al., 2006). Leatherbacks exhibit mild bradycardia during short dives and more dramatic slowing, down to 3.6 beat/min, in longer deeper dives (Southwood et al., 1999). Similar to marine mammals and unlike other sea turtles, the leatherback has relatively small lungs and has large stores of oxygen in their blood and muscle tissue (Lutcavage et al., 1990, 1992).

Leatherbacks subsist on jellyfish, salps and other gelatinous prey (Bleakney, 1965; den Hartog and van Nierop, 1984; James and Herman, 2001). Occasional reports of gut contents other than jellyfish appear to be species commensal with jellyfish (Bleakney, 1965; Frazier et al., 1985). Fatty acid analyses also confirm a medusan specialization (Holland et al., 1990). On this diet, they appear to grow faster than any other turtle, possibly reaching maturity and a corresponding 6000-fold increase in mass in an average of 13–14 years (Zug and Parham, 1996).

With an estimated cost for a round-trip migration of 1.2 million Calories (Wallace et al., 2006) and whole jellyfish providing at best 41 Calories/kg (Lutcavage and Lutz, 1986; Doyle et al., 2007), turtles would be expected to consume at least 29 tons of jellyfish to fuel their migration. This energetic burden is on top of the daily energy cost of about 90 kg of jellyfish (Wallace et al., 2006). As leatherbacks appear to forage little, if at all, near nesting grounds (Myers and Hays, 2006) and may have limited opportunities for foraging during migration (James et al., 2006), it would seem that leatherbacks are able to obtain massive amounts of prey over a relatively short amount of time while in northern waters.

Unfortunately, in many areas, leatherback populations have dropped precipitously. Declared endangered in 1982 and critically endangered worldwide in 2000 (Sarti Martinez, 2000), Atlantic leatherbacks may be reduced to only 20–30,000 mature females (Spotila et al., 1996) and Pacific leatherbacks are nearly extirpated (Spotila et al., 2000; Kaplan, 2005) due to fishery bycatch and nesting beach poaching mortality and egg collection (Southeast Fisheries Science Center, 2001; Turtle Expert Working Group, 2007). Incidental capture in fisheries is a major cause of mortality in most leatherback populations (Frazier and Montero, 1990; Eckert, 1997; Spotila et al., 2000; Lum, 2006). In the northern Atlantic, attention has been focused on longline fishery

interactions but mortality from hooking is rare in leatherbacks (Garrison, 2003) while entanglement in lines of fixed fishing gear is a growing concern (Godley et al., 1998; James et al., 2005). Ingestion of plastics, perhaps mistaken for prey, may also be a problem (Mrosovsky, 1981; Duguy et al., 2002).

## 1.1 Data

Although Bleakney in 1965 suggested that leatherbacks were residents of Canadian waters, little scientific study of their distribution was conducted until Martin and James (2005) established the Nova Scotia Leatherback Turtle Working Group, a network of fishers and volunteers who report sighting of leatherback turtles. This group has been successful in collecting opportunistic observations of leatherback turtles in Nova Scotian waters (James et al., 2006).

Using some of these volunteer fishers and their fishing boats, the Canadian Sea Turtle Research Project (CSTRP) began to capture leatherback turtles in Nova Scotian waters in 1999. To study these wide ranging animals, CSTRP deployed Argos satellite-linked platform transmitting terminal (PTT) tags made by Telonics (Mesa, AZ, USA), Sirtrack (Havelock North, New Zealand), and Wildlife Computers (Redmond, WA, USA) which recorded position and other environmental variables (James et al., 2005) using specially designed harnesses (Eckert and Eckert, 1986; Eckert, 2002). Data from 42 turtles is now available.

Unfortunately, Argos's doppler-based position estimates from diving organisms are of variable quality with many observations having non-normal and non-symmetric error distributions (Vincent et al., 2002). Jonsen et al. (2003) proposed using state-space models of animal behavior (Anderson-Sprecher and Ledolter, 1991) in a Bayesian form to deal with these complicated error distributions and animals' generally nonlinear behavior. The state-space approach has proved useful for modeling leatherback movements and is better able to discern underlying behavior than traditional techniques (Jonsen et al., 2006). This method has been improved by including different movement parameters into the model based on estimates of the animal's behavioral states like foraging and migration (Morales et al., 2004; Jonsen et al., 2005). Jonsen et al. (2007) has applied these switching state space models to the leatherback turtle tracks.

Remotely-sensed information from satellite observatories has revolutionized oceanography (Dickey and Bidigare, 2005). Satellite instrumentation can now sense such variables as sea surface temperature, chlorophyll concentration, geostrophic currents and wind speed (Dickey and Bidigare, 2005). Much of this oceanographic information is freely available on the internet (Robinson, 2004). Combining these environmental data with marine animal satellite telemetry offers the potential for novel ecological analyses (e.g. Polovina et al., 2004; Baumgartner and Mate, 2005; Ream et al., 2005).

## 1.2 Goals

With their long annual voyages between southern wintering and nesting grounds and northern foraging grounds, leatherback turtles provide a unique opportunity to study migration. Most studies on migration cues have focused on birds (e.g. Both et al., 2005; Shamoun-Baranes et al., 2006) and fish (e.g. Quinn et al., 1997; White and Knights, 1997). Migration cues in reptiles or the pelagic ocean have never been detailed. In Chapter 2, I investigate the individual timing of the southward migrations of turtles equipped with satellite-linked transmitters off Nova Scotia compared to turtle characteristics and satellite-measured ocean variables.

With more than 137 turtles and 15,363 days of tracking in the north Atlantic alone (Turtle Expert Working Group, 2007), it is important to measure any effect of tagging both for the sake of the animals and the conclusions drawn from these data. There have been suggestions that leatherbacks may exhibit tagging effects (James et al., 2006) and intensive handling on nesting beaches appears to cause significantly longer interesting periods and altered diving behavior (Wallace et al., 2005). Determining tagging effects in these animals is difficult, as it is impossible to observe a control group. In Chapter 3, I explore the effects of tagging and handling evident in migration and swimming behavior of tagged leatherbacks.

## 1.3 Publications during thesis research

Canadian waters provide critical foraging habitat for leatherback turtles. M.C. James, S.A. Sherrill-Mix, K.E. Martin & R.A. Myers. 2006. *Biological Conservation*. 133:347-357

- Population characteristics and seasonal migrations of leatherback sea turtles at high latitudes. M.C. James, S.A. Sherrill-Mix & R.A. Myers. 2007. *Marine Ecology Progress Series*. 337:245-254
- Saving endangered whales at no cost. R.A. Myers, S.A. Boudreau, R.D. Kenney, M.J. Moore, A.A. Rosenberg, S.A. Sherrill-Mix & B. Worm. 2007. *Current Biology*. 17:R10-R11
- Migration cues and timing in leatherback sea turtles. S.A. Sherrill-Mix, M. C. James & R.A. Myers. *In press*. *Behavioral Ecology*.
- Tagging effects on leatherback sea turtles. S.A. Sherrill-Mix & M. C. James. *In review*. *Endangered Species Research*.

## Chapter 2

### Migration Cues

#### 2.1 Introduction

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 et al., 2006), to breeding and foraging areas in tropical and subtropical waters (James et al., 2005; Eckert et al., 2006).

While we are beginning to understand aspects of leatherback turtle temperate foraging behavior (James et al., 2006,?; Jonsen et al., 2007) and migration (Hays et al., 2004; James et al., 2005; Jonsen et al., 2006), we have little understanding of what variables influence the transition between these two 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 (Ferraroli et al., 2004; Hays et al., 2004; James et al., 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 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 environmental 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 leatherback 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 and Hüppop, 2003; Gunnarsson et al., 2006). The NAO also appears to affect the migratory schedule of many birds (Forchhammer et al., 2002; Hüppop and Hüppop, 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 et al., 2006, 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 et al., 2006). SST appears to influence the distribution (Davenport, 1997), nesting date (Weishampel et al., 2004), remigration interval (Solow et al., 2002) and internesting 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 population abundance data), no studies have attempted to quantify the effects of environmental variation on the timing of migration using satellite-derived positions. 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.

## 2.2 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 (approximately 47°N, 60°W) (James et al., 2005). State-space estimates of latitude and longitude for each six-hour 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 six-hour transiting period of the southerly migration (defined here as continuous movement uninterrupted by foraging to below 36°N). The last dates of foraging were largely consistent with migration dates estimated from speed and diving behavior (James et al., 2006). We inferred foraging prior to migration in tracking data from 27 turtles. Five turtles were tracked through two northern foraging seasons and six records were censored before migration departure was observed, resulting in a dataset of 32 foraging seasons and 26 migration departures.

Fourteen satellite tags provided direct measures of sea surface temperature. Since the state-space estimates do not correspond directly to the time that the tag recorded SST, the median recorded SST for observations within the six-hour 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 one day of the observation or, if GOES data were unavailable, 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>). Where both satellite-derived and tag-measured SST were available, the two measurements were highly correlated ( $r=.89$ ).

Monthly North Atlantic Oscillation (NAO) estimates were obtained from the National Weather Service NAO website (<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 (GEBCO) data (Marks and Smith, 2006). The average chlorophyll-a concentrations within three days and  $0.2^\circ$  of turtle locations were calculated from Sea-viewing Wide Field-of-view Sensor (SeaWiFS) (1999–2001) or SeaWiFS merged with Moderate-resolution Imaging Spectroradiometer (MODIS) (2002–2005) measurements using data obtained from the Ocean Color Web (<http://oceancolor.gsfc.nasa.gov/>).

Since 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, 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, latitude<sup>2</sup>, longitude, longitude<sup>2</sup>, 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 ( $\geq 140$  cm standard curved carapace length) and two-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 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 two, four and eight.

### 2.3 Results

Location and behavior estimates were available for 8998 six-hour 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 October 23 (95% Confidence Interval (CI): Oct 12–Nov 3, range: September 8–January 13).

The final departure model selected by AIC included latitude, longitude, longitude<sup>2</sup>, 1-week lagged SST, 1-week lagged average chlorophyll and the interaction of 1-week lagged average chlorophyll with latitude (see Table 2.1). 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.

The location of the turtle had a significant effect on 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/m<sup>3</sup>, departure rate increased by a factor of 3.24 (95% CI 1.87-5.61). While 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

Variable	Range	Mean	$\beta$	SE	p-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	<0.00001
Longitude <sup>2</sup>	2665–5718	4211	0.047	0.0098	<0.00001
Temperature	10.6–26.2°C	17.7°C	0.397	0.199	0.046
Chlorophyll	0.12–3.22 mg/m <sup>3</sup>	0.72 mg/m <sup>3</sup>	-34.0	12.5	0.007
Chlorophyll:Latitude	4.7–147	40.0	0.777	0.27	0.005

Table 2.1: Results from stepwise Cox’s proportional hazards modeling of the onset of migration in leatherback turtles tagged off Nova Scotia. Temperature and chlorophyll are the average of the sea surface temperatures and chlorophyll-a concentrations experienced by the turtle the prior week. The mean and range of the variables for all 8998 six-hour periods of the study are shown for comparison. SE stands for standard error.

2.1).

Environmental conditions also affected departure rate. Each 1°C increase in 1-week lagged temperature increased the departure rate by 48.7% (95% CI: .71–120%). Departure 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/m<sup>3</sup> change at the maximum latitude 50.0°N (Table 2.1).

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 2.2).

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 2.2 and Figure 2.1).

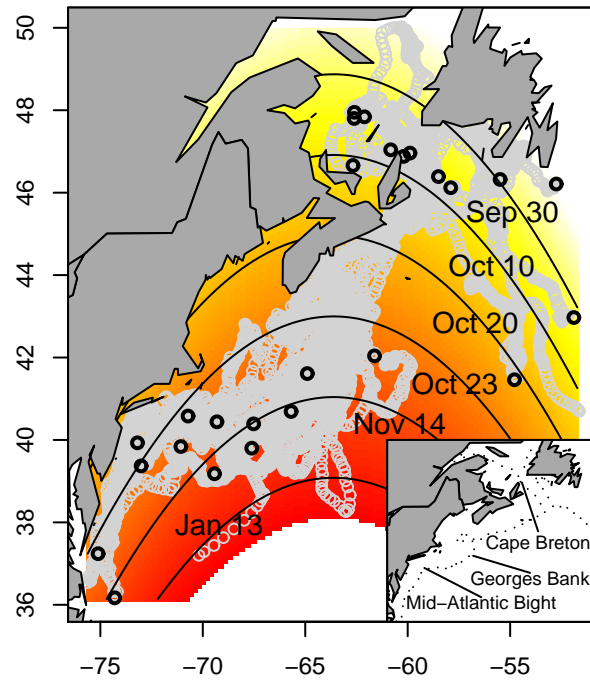


Figure 2.1: Contour plot of the relative departure rates for leatherbacks foraging in northern waters. Red indicates the lowest departure rates and yellow the highest. Contour lines indicate a ten-fold increase in departure rate from the line below them. Dates indicate date of 50% departure for that contour line. Gray circles indicate turtle positions and black circles indicate departures. Chlorophyll and sea surface temperature was set at mean values ( $17.7^{\circ}\text{C}$  and  $0.72\text{ mg/m}^3$ ). Inset shows locations discussed in the paper. Inset dotted grey lines follows the 200 meter depth contour.

Location	50% Depart	95% CI	95% Depart	95% CI
Cape Breton ( $47^{\circ}\text{N}$ , $60^{\circ}\text{W}$ )	Oct 4	-3.7–6.3	Oct 10	-6.3–9.6
Georges Bank ( $41^{\circ}\text{N}$ , $66^{\circ}\text{W}$ )	Nov 13	-8.3–27.7	Dec 11	-27.7–33.4
Mid-Atlantic Bight ( $40^{\circ}\text{N}$ , $72^{\circ}\text{W}$ )	Oct 24	-2.6–11.6	Nov 12	-19.6–0.3

Table 2.2: Departure times for 50% and 95% of the leatherback turtles at a few representative locations (See Figure 2.1). The 95% confidence intervals (CI) are in days. One-week lagged average chlorophyll and sea surface temperature were held steady at their mean value for the data set ( $17.7^{\circ}\text{C}$  and  $0.72\text{ mg/m}^3$ ).

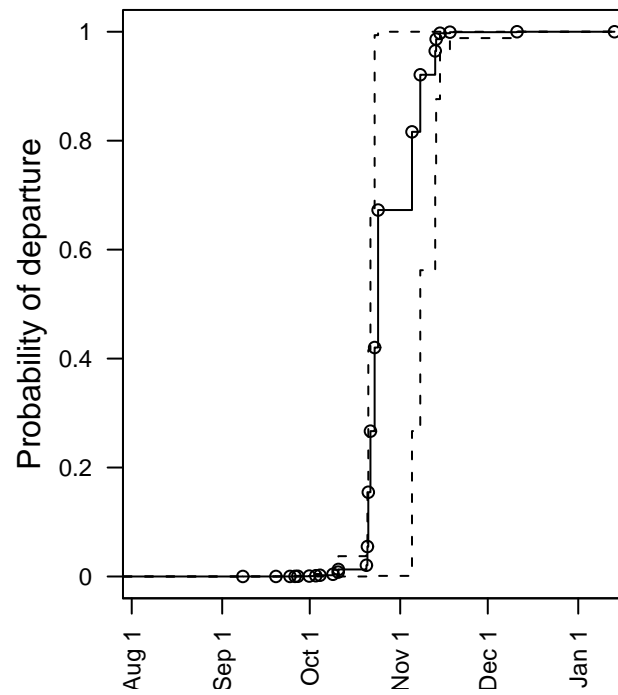


Figure 2.2: Proportion of leatherbacks that have initiated their southward migration at mean latitude, longitude, and 1-week lagged average temperature and chlorophyll for the study. Points indicate turtle departures and dashed lines show the 95% confidence limits.

## 2.4 Discussion

Leatherback departure rate was significantly affected by the position of the turtle. Compensation for distance traveled could explain earlier departures from foraging areas further from southern nesting and wintering grounds. Animals foraging in more distant areas would be expected to depart earlier. For example, in black-tailed godwit the distance between foraging and breeding areas does not predict arrival date (Gunnarsson et al., 2006). However, the difference in distance between 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 .63 m/sec (Eckert, 2002), this difference could be traversed in as few as 10 days, while 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 et al., 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 appear to migrate when fat deposition rates decline (Prop et al., 2003). Herring are also more likely to begin downstream migration when prey abundance is low (Yako et al., 2002). The abundance of the gelatinous prey of leatherbacks fluctuates (Graham et al., 2001), thus these turtles 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 two 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 two 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 differs 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  $63.6^{\circ}\text{W}$ . This longitude lies between Georges Bank and Cape Breton Island (Figure 2.1) and may indicate that these two 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 et al., 2006) and telemetry data (James et al., 2005) suggest that both areas are critical foraging habitat.

We found that leatherbacks are more likely 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 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 foraging 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 longline and fixed gear are a threat to leatherback turtles (Lewison et al., 2004; James et al., 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 datasets, we urge that studies of fine-scale migration cues be expanded to other species and environments.

## Chapter 3

### Handling Effects

#### 3.1 Introduction

To study a far-ranging deep-diving animal like the leatherback turtle over time, it is necessary to attach some sort of transmitter. Unfortunately, attaching tags to animals is not without risks (Godfrey and Bryant, 2003) and animals can be harmed both by distress from capture and the physiological impacts of tagging (Hawkins, 2004).

Negative effects of capture and tagging have been observed in many marine animals. In Adélie penguins, harnesses severely impaired foraging with 87% of animals tagged late in the season abandoning their young (Watanuki et al., 1992). Detrimental effects were observed in other penguins but were decreased by using glue instead of harnesses, using smaller tags, implanting the tag surgically, and tagging earlier in the season (Wilson et al., 1986; Watanuki et al., 1992; Hull, 1997; Ballard et al., 2001; Green et al., 2004). Yet a recent study found that even applying a band to a king penguin halves young bird's survival chances (Gauthier-Clerc et al., 2004).

Effects on larger animals are often less severe. No long term effects of tagging were observed in Hawaiian monk seals (Baker and Johanos, 2002) or northern fur seal (Trites, 1991) while foraging and resting periods were longer for tagged Antarctic fur seals (Walker and Boveng, 1995). Long-term handling effects on polar bears were small but short-term displacement was common (Ramsay and Stirling, 1986).

Due to their oil secretions and flexible skin-covered carapace, leatherbacks pose a significant challenge when tagging. Unlike other turtles, tags can not be glued to the carapace. Eckert and Eckert (1986) designed special padded backpack-like harnesses for these turtles. Even with these custom harnesses, carapace damage can occur from an improperly attached harness (Eckert and Eckert, 1986; Troëng et al., 2006). Hydrodynamic analysis estimates that a glued on transmitter will decrease a green turtle's swim speed by 11% (Watson and Granger, 1998) though the effect of a harness and tag assembly on this much larger turtle remains uncertain.

Previous studies have hinted at some tag effects in leatherbacks. James et al. (2006) suspected some short term tag effects and excluded data from the first week of tagging from their analysis. Immediately after capture, many leatherback turtles dive deeper than any other time in short-term tracking and then move at high speeds (James, Sherrill-Mix and Myers, Unpublished data). In nesting turtles, Wallace et al. (2005) report significantly longer interesting periods and altered diving behavior in more intensively handled turtles.

Though easy to overlook and tempting to ignore, there is a moral imperative to thoroughly study any deleterious effects of research when working with endangered species. The cost to the individual, and therefore potentially the population when numbers are few, must be weighted especially heavily against the benefits for science and conservation. Here we investigate the effects of tagging through differences in movement and migration rate using positions estimated by state-space models from 42 leatherback turtles.

### 3.2 Methods

The speed at which turtles move may be an indicator of short-term tagging effect. The state-space modeled estimates of Jonsen et al. (2007) provide a useful dataset for studying this displacement. At small time scales, minor amounts of noise, common in Argos data, can greatly skew estimates of speed. The coordinates output from the state-space model are best estimates of the turtle's position and should be more robust than traditional filters which can obscure underlying patterns (Jonsen et al., 2006). In addition, the switching state-space model provides estimates of behavioral mode (Jonsen et al., 2007) that can discriminate between turtles' foraging and transiting behavioral states. Transiting behavior can be further split into movement between foraging grounds and migration, defined here as continuous movement uninterrupted by foraging to below 36°N. Here we use all available positions above 36° N from the first season tracks of 42 turtles.

In order to separate displacement due to geostrophic water mass movement from directed locomotion (Gaspar et al., 2006), geostrophic current velocities were obtained from weekly Maps of Absolute Dynamic Topography (MADT) from Segment Sol multissions d'ALTimétrie, d'Orbitographie et de localisation précise)(SSALTO)/Data

Unification and Altimeter Combination System (DUACS) data distributed by Aviso (<http://www.jason.oceanobs.com/>). Current velocities at turtle positions were interpolated from these current maps. Turtle swim speeds were then adjusted by current velocity.

Increased swim speeds may be an indication of tagging effect. To investigate any changes in swim speed during the tracking, the effects of week after capture and whether the turtle was migrating or still foraging on individual swim speeds were modeled using a generalized linear mixed-effects model. As variance appears to increase with higher predicted speeds, I used a Gamma distribution with an identity link. To account for repeated measurements on the same turtles, a variable indicating individual turtles was included as a random effect and a one-step autocorrelation structure was included.

Many turtles appear to directly depart northern waters immediately after tagging without inferred foraging. To investigate this phenomenon, the probability of immediate departure was modeled using a generalized linear model with a binomial distribution. Julian day, carapace length, maturity, sea surface temperature at release, day length, tagging location (Halifax area or Cape Breton), sex and whether the turtle had been entangled in fishing gear prior to tagging were selected using stepwise regression based on the Akaike information criterion (AIC).

When discussing the results of binomial regression analysis it is useful to think of probability in terms of odds ( $\frac{p}{1-p}$ ) where  $p$  is the probability of an event, e.g. a turtle departing without feeding. For example if the probability of immediate departure is .25 the odds of immediate departure will be 0.333 (1:3).

Reports of harnessed turtles later observed on nesting beaches were collected (James et al., 2007).

### 3.3 Results

Positions from 11,996 six-hour periods were available and geostrophic currents were obtained for 11,590 positions. Time after capture and whether the turtle was migrating south were significantly related to leatherback speed in the generalized linear mixed-effect model. The mean speed of migrating turtles determined by the model was 2.69 km/hr (95% CI: 2.23–2.84) and the estimated speed of turtles remaining in

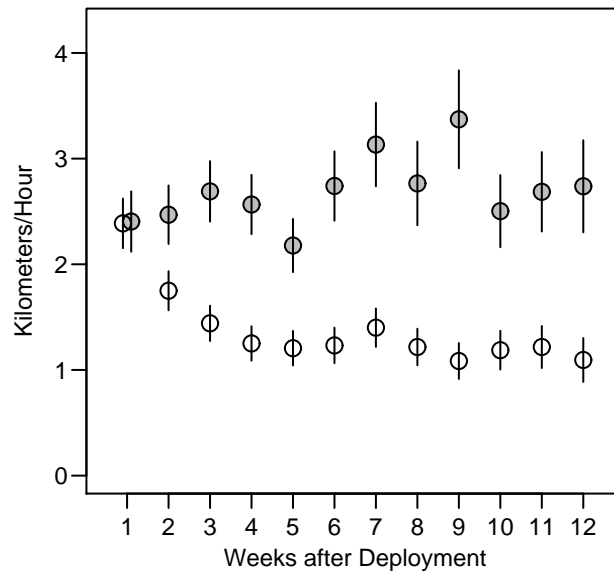


Figure 3.1: Comparison between the mean speed of migrating leatherbacks (grey circles) and leatherbacks remaining in northern waters (white circles) in relation to week after capture as predicted by a generalized linear mixed-effect model based on migration status and week. Vertical lines indicate 95% confidence intervals.

the north was 1.37 km/hr (95% CI: 1.23–1.51).

Migrating turtles moved on average 1.31 km/hr (95% CI: 1.16–1.47) faster than their counterparts remaining in northern waters. The first week after capture was the only week in which the speed of turtles remaining in the north was not significantly slower than that of migrating turtles (Figure 3.1) with the mean speed of turtles remaining in the north 1.11 km/hr (95% CI: 0.90–1.31) faster than in the remaining weeks. The second week after capture also showed a smaller but still significant increase of 0.52 km/hr (95% CI: 0.37–0.66) over the remaining weeks (Figure 3.1).

Immediate departure without foraging was inferred in 17 of the 42 turtles. A precipitous peak in migration departure can be seen immediately after capture in Figure 3.2. This large pulse of departures sharply contrasts the gradual migration rate in the remaining days.

Date of tagging and whether the turtle had been entangled in fishing gear were related to the probability of foraging before southward migration based on the AIC (Table 3.1). Each day later in the year increased the odds of immediate southward migration by 19.7% (95% CI: 7.11–33.8%) (Figure 3.3). The odds of immediate

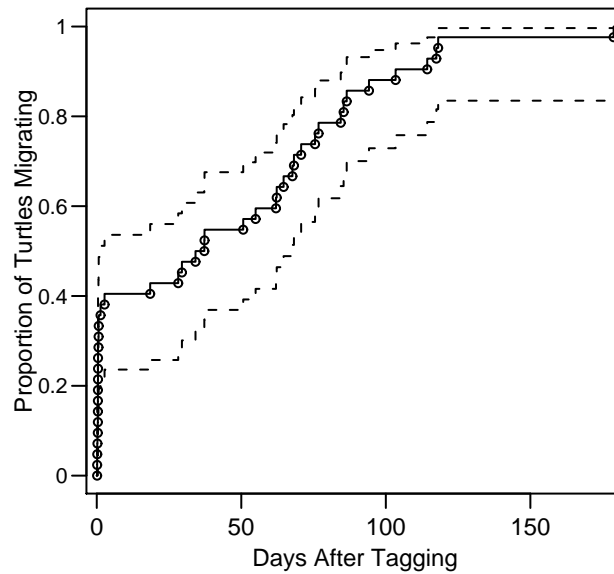


Figure 3.2: Proportion of leatherbacks migrating in relation to days after tagging (solid line). Circles indicate migration departures ( $n=39$ ) and x's indicate tag or harness failures before migration was observed ( $n=3$ ). Dashed lines indicate 95% confidence intervals.

Variable	$\beta$	Standard Error	p-value
Julian Day	-0.18	0.057	0.0015
Fishing Interaction	-6.22	2.79	0.026

Table 3.1: Results from stepwise generalized linear modeling of the probability of foraging before southward migration.

migration for turtles captured in fishing gear before tagging were 503 (95% CI: 2.11–120,200) times higher than in unentangled turtles (Figure 3.3). For turtles that did not migrate immediately, the median time until foraging was 12.7 (Range: 0.175–48.9) days after release and the median length of stay after release was 67.7 (Range: 18.2–178.5) days.

Ten of the 27 PTT-tagged female turtles have been reobserved on nesting beaches in Colombia (1), Costa Rica (2), French Guiana (1), Panama (2), Suriname (2), and Trinidad (2) from 0.6 to 3.8 years later. Six of these turtles were observed on nesting beaches in the nesting season immediately after their capture in Canadian waters. Five of the six turtles had departed northern waters without foraging.

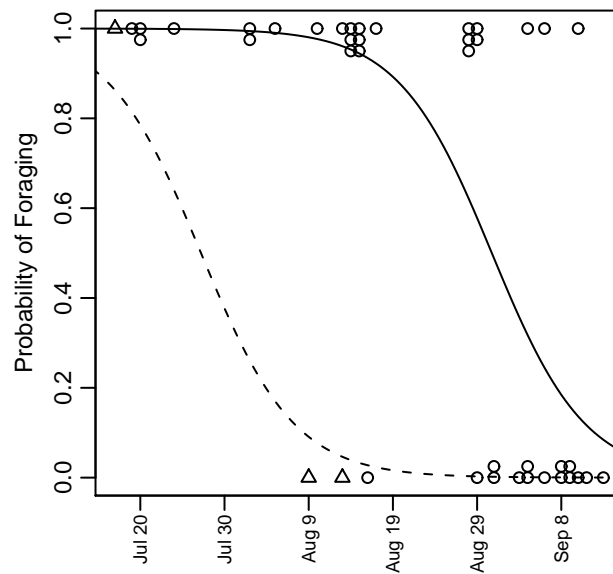


Figure 3.3: Probability of foraging before southward migration for leatherbacks tagged on a given date after incidental capture in fishing gear (triangles,  $n=3$ ) and directly captured by the field research team (circles,  $n=39$ ). The lines indicate predicted probability of foraging for direct captured (solid) and fishing gear entangled (dashed) turtles.

### 3.4 Discussion

Short-term effects of handling on leatherbacks can be seen in the increased median speed of non-migrating turtles in the first and second weeks after capture. This short-term displacement may disrupt foraging as turtles that did not migrate immediately took a median of 12.7 days to begin foraging.

With 40% of tagged turtles departing immediately after capture, it appears that capture or tagging in northern waters can also trigger southward migration. Turtles captured later in the year are more likely to depart without inferred foraging. Whether this is due to the turtle already having obtained an acceptable amount of food stores or seasonal increases in zugunruhe is unknown. Although tagging has been known to cause the delay or abortion of migration (Bernard et al., 1999; Olney et al., 2006), this is the first report of handling potentially triggering migration.

If immediate departure from northern foraging grounds is detrimental then tag effects could be reduced by tagging earlier in the year and not tagging turtles obtained from fishing gear. This would have the added benefit of acquiring more data from northern waters. These results suggest that to achieve a 50% chance of northern

foraging, turtles in the northwest Atlantic should be tagged prior to August 30 or if obtained from fishing, gear prior to July 26. If a 95% probability of northern foraging is desired, turtles would have to be tagged before August 13 or for highly-stressed turtles July 9.

It seems unlikely that harnesses are highly detrimental as reproduction does not appear to be inhibited. Most males migrate to breeding areas in the months after tagging (James et al., 2005). Of 27 satellite-tagged females, 10 have been resighted on nesting beaches, a proportion higher than many nesting beaches (Girondot and Fretey, 1996; Hughes, 1996; Steyermark et al., 1996). Six of the resighted turtles nested within one year of tagging and appeared on the nesting beach without harnesses and five of these had departed northern waters without inferred foraging. Although this suggests that tagging is not a major detriment, effects on turtle health should not be ruled out as the reptile reproductive cycle is robust to moderate stressors (Moore and Jessop, 2003).

Proper harnessing techniques may reduce tagging effects. With an estimated energetic cost of migration of 1.2 million Calories (Wallace et al., 2006) and lipids providing approximately 8.6 Calories/g (Henen, 1997), turtles would be expected to lose at least 139 kg of body fat over the course of their migration. James et al. (2005) found turtles measured midway through the foraging season were indeed 33% heavier than turtles measured on nesting beaches. When harnessing turtles this dramatic change in mass must be accounted for by including elastic materials, especially on nesting beach deployments from which turtles will increase in weight by at least a third. Corrodible links to allow the harness to fall off after the duration of the study are also essential (Troëng et al., 2006).

Although harnesses built with corrodible links and sized correctly appear unlikely to cause severe harm to turtles, it may be time to consider alternatives to the harness. Tag technology has progressed greatly since studies began and current tags are only a fraction of the size of the originals. Although the only reported use did not succeed (Lutcavage et al., 2001), direct attachment is becoming more enticing with decreasing tag size. How the potential injuries and impacts incurred from direct attachment compare to those associated with harnessing remains to be seen.



Without a control group, assessing the effects of tagging on leatherbacks is difficult and several questions remain. Whether there are behavioral differences between tagged turtles and the natural population remains uncertain. In this study, the effects of harnessing and the effects of capture could not be differentiated. This leaves the large question of whether the migration and speed effects observed in this study occur in all handled turtles or only among those equipped with harnesses.

If handling alone increases the chance of migration departure and immediate departure is detrimental to the turtle then any capture of turtles during the foraging season could be deleterious. In addition, although leatherbacks are often released alive from fishing gear and assumed to be unharmed, this study highlights potential post-capture effects for these animals. Unfortunately, we will be unable to differentiate capture effects from tagging effects until comparative data from turtles tagged by other methods are available.

With tagging appearing to cause short-term displacement and foraging disruption and the potential long-term effects of premature migration, researchers must take care that their research does not harm the very animals they are trying to conserve. Further work is necessary to determine and minimize the fitness costs of these tagging effects.

## Chapter 4

### Conclusions

In Chapter 2, I detail the effects of position, sea surface temperature and chlorophyll concentration on migration departure rates in leatherback turtles. To fully understand these migratory behaviors, a better understanding of the evolutionary context is necessary both in the northern foraging areas and the southern destination of their migration. In the north, the temporal and spatial distribution of jellyfish prey remains the largest question. Recent studies have shown several potential methods for elucidating jellyfish distributions (Witt et al., 2007; Houghton et al., 2006; Doyle et al., 2007). In the south, studies on the fitness effects of the timing of adult male and female arrival to waters off nesting beaches are needed. For example, one feasible study would be to examine whether females that arrive earlier lay more clutches perhaps using methods similar to Rivalan et al. (2006). Investigating whether earlier nests experience different conditions (e.g. different temperature (Hawkes et al., 2007) or hurricane risk (Pike and Stiner, 2007)) would also be beneficial.

In Chapter 3, I show that tagging and/or handling appears to influence leatherback turtle behavior. Turtles are much more likely to begin migration and swim speeds are higher in the first week after capture. Turtles tagged later in the foraging season or following entanglement in fishing gear are more likely to begin their southward migration immediately. Further research is necessary to determine if these effects are detrimental to turtles and whether the effects are due to capture or tagging. One possible method of testing what effect handling alone has on turtles would be to use short-term tags mounted on suction cups to compare the behavior of turtles tagged without capture, turtles captured and released and turtles captured and released with harnesses or other attachment devices. Direct attachment has been proposed as an alternative to harnessing leatherbacks (Lutcavage et al., 2001). The effects of these two methods could be compared using methods similar to those presented here.

Godley (2007) suggests that although the alleged goal of most sea turtle tagging is

conservation, few studies translate into improved conservation. This work highlights the opportunity to use satellite telemetry and environmental data to examine the cues for and timing of animal migrations and the effects of handling and tagging. By understanding the migratory schedule of and tagging effects on leatherbacks and potentially other satellite-tracked species, we can more efficiently and effectively target conservation and research efforts.

## Bibliography

- Andersen, P. K. and R. D. Gill (1982). Cox's regression model for counting processes: a large sample study. *Ann Stat* 10, 1100–1120.
- Anderson-Sprecher, R. and J. Ledolter (1991). State-space analysis of wildlife telemetry data. *Journal of the American Statistical Association* 86, 596–602.
- Backus, R. H. and D. W. Bourne (Eds.) (1987). *Georges Bank*. Cambridge, MA: MIT Press.
- Baker, J. D. and T. C. Johanos (2002). Effects of research handling on the endangered Hawaiian monk seal. *Mar Mamm Sci* 18, 500–512.
- Ballard, G., D. G. Ainley, C. A. Ribic, and K. R. Barton (2001). Effect of instrument attachment and other factors on foraging trip duration and nesting success of Adélie penguins. *Condor* 103, 481–490.
- Baumgartner, M. F. and B. R. Mate (2005). Summer and fall habitat of North Atlantic right whales (*Eubalaena glacialis*) inferred from satellite telemetry. *Can J Fish Aquat Sci* 62, 527–543.
- Behrenfeld, M. J., E. Boss, D. A. Siegel, and D. M. Shea (2005). Carbon-based ocean productivity and phytoplankton physiology. *Global Biogeochem Cycles* 19, GB1006.
- Behrenfeld, M. J. and P. G. Falkowski (1997). Photosynthetic rates derived from satellite-based chlorophyll concentration. *Limnol Oceanogr* 42, 1–20.
- Bernard, D. R., J. J. Hasbrouck, and S. J. Fleischman (1999). Handling-induced delay and downstream movement of adult chinook salmon in rivers. *Fish Res* 44, 37–46.
- Bleakney, J. S. (1965). Reports of marine turtles from New England and eastern Canada. *Can Field-Nat* 79, 120–128.
- Both, C., R. G. Bijlsma, and M. E. Visser (2005). Climatic effects on timing of spring migration and breeding in a long-distance migrant, the pied flycatcher *Ficedula hypoleuca*. *J Avian Biol* 36, 368–373.
- Brewer, R. H. (1989). The annual pattern of feeding, growth, and sexual reproduction in *Cyanea* (Cnidaria: Scyphozoa) in the Niantic River Estuary, Connecticut. *Biol Bull* 176, 272–281.
- Castro-Santos, T. and A. Haro (2003). Quantifying migratory delay: a new application of survival analysis methods. *Can J Fish Aquat Sci* 60, 986–996.

- Cox, D. R. (1972). Regression models and life-tables. *J Roy Stat Soc Ser B (Stat Method)* 34, 187–220.
- Davenport, J. (1997). Temperature and the life history strategies of sea turtles. *J Therm Biol* 22, 479–488.
- den Hartog, J. C. and M. M. van Nierop (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.
- Dickey, T. D. and R. R. Bidigare (2005). Interdisciplinary oceanographic observations: the wave of the future. *Scientia Marina* 69 (Suppl. 1), 23–42.
- Doyle, T. K., J. D. R. Houghton, S. M. Buckley, G. C. Hays, and J. Davenport (2007). The broad-scale distribution of five jellyfish species across a temperate coastal environment. *Hydrobiologia* 579, 29–39.
- Doyle, T. K., J. D. R. Houghton, R. McDevitt, J. Davenport, and G. C. Hays (2007). The energy density of jellyfish: estimates from bomb-calorimetry and proximate composition. *J Exp Mar Biol Ecol* 343, 239–252.
- Duguay, R., P. Moriniere, and C. Le Milinaire (2002). Facteurs de mortalité observés chez les tortues marines dans le golfe de Gascogne. *Oceanol Acta* 1998, 383–388.
- Eckert, S. A. (1997). Distant fisheries implicated in the loss of the world’s largest leatherback nesting population. *Mar Turtle Newsl* 78, 2–7.
- 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.
- Eckert, S. A., D. Bagley, S. Kubis, L. Ehrhart, C. Johnson, K. Stewart, and D. DeFreese (2006). Internesting and postnesting movements and foraging habitats of leatherback sea turtles (*Dermochelys coriacea*) nesting in Florida. *Chelonian Conserv Biol* 5, 239–248.
- Eckert, S. A. and K. L. Eckert (1986). Harnessing leatherbacks. *Mar Turtle Newsl* 37, 1–3.
- Eckert, S. A., K. L. Eckert, P. Ponganis, and G. L. Kooyman (1989). Diving behavior of leatherback sea turtles (*Dermochelys coriacea*). *Can J Zool* 67, 2834–2840.
- Ferraroli, S., J.-Y. Georges, P. Gaspar, and Y. Le Maho (2004). Where leatherback turtles meet fisheries. *Nature* 429, 521–522.
- Forchhammer, M. C., E. Post, and N. C. Stenseth (2002). North Atlantic Oscillation timing of long- and short-distance migration. *J Anim Ecol* 71, 1002–1014.

- Frair, W., R. G. Ackman, and N. Mrosovsky (1972). Body temperature of *Dermochelys coriacea*: warm turtle from cold water. *Science* 177, 791–793.
- Frazier, J., M. D. Meneghel, and F. Achaval (1985). A clarification on the feeding habits of *Dermochelys coriacea*. *Journal of Herpetology* 19, 159–160.
- Frazier, J. and J. L. B. Montero (1990). Incidental capture of marine turtles by the swordfish fishery at San Antonio, Chile. *Mar Turtle Newsl* 49, 8–13.
- Garrison, L. P. (2003). Estimated bycatch of marine mammals and turtles in the U.S. Atlantic pelagic longline fleet during 2001-2002. NOAA Technical Memorandum NMFS-SEFSC-515, National Oceanic and Atmospheric Administration.
- Gaspar, P., J.-Y. Georges, S. Fossette, A. Lenoble, S. Ferrarol, and Y. Le Maho (2006). Marine animal behaviour: neglecting ocean currents can lead us up the wrong track. *Proc R Soc Lond , Ser B: Biol Sci* 273, 2697–2702.
- Gauthier-Clerc, M., J.-P. Gendner, C. A. Ribic, W. R. Fraser, E. J. Woehler, S. Descamps, C. Gilly, C. Le Bohec, and Y. Le Maho (2004). Long-term effects of flipper bands on penguins. *Proc R Soc Lond , Ser B: Biol Sci* 271, S423–S426.
- Gill, J. A., K. Norris, P. M. Potts, T. G. Gunnarsson, P. W. Atkinson, and W. J. Sutherland (2001). The buffer effect and large-scale population regulation in migratory birds. *Nature* 412, 436–438.
- Girondot, M. and J. Fretey (1996). Leatherback turtles, *Dermochelys coriacea*, nesting in French Guiana, 1978-1995. *Chelonian Conserv Biol* 2, 204–208.
- Godfrey, J. D. and D. M. Bryant (2003). Effects of radio transmitters: review of recent radio-tracking studies. In M. Williams (Ed.), *Conservation applications of measuring energy expenditure of New Zealand birds: Assessing habitat quality and costs of carrying radio transmitters*, Volume 214 of *Science for Conservation*, pp. 83–95.
- Godley, B. J. (2007). Satellite tracking in sea turtles: where, when, how much, and, above all, why? In *27th Annual Symposium on Sea Turtle Biology and Conservation*.
- Godley, B. J., M. Gaywood, R. Law, C. McCarthy, C. McKenzie, I. Patterson, R. Penrose, R. Reid, and H. Ross (1998). Patterns of marine turtle mortality in British waters (1992 - 1996) with reference to tissue contaminant levels. *J Mar Biol Assoc UK* 78, 973–984.
- Goff, G. P. and G. B. Stenson (1988). Brown adipose tissue in leatherback sea turtles: a thermogenic organ in an endothermic reptile? *Copeia* 1988, 1071–1075.
- Graham, W. M., F. Pagès, and W. M. Hamner (2001). A physical context for gelatinous zooplankton aggregations: a review. *Hydrobiologia* 451, 199–212.

- Green, J. A., J. L. Tanton, A. J. Woakes, I. L. Boyd, and P. J. Butler (2004). Effects of long-term implanted data loggers on macaroni penguins *Eudyptes chrysolophus*. *J Avian Biol* 35, 370–376.
- Greer, A. E., J. D. Lazell, and R. M. Wright (1973). Anatomical evidence for a counter-current heat exchanger in the leatherback turtle (*Dermochelys coriacea*). *Nature* 244, 181.
- Gunnarsson, T. G., J. A. Gill, P. W. Atkinson, G. Gélinaud, P. M. Potts, R. E. Croger, G. A. Gudmundsson, G. F. Appleton, and W. J. Sutherland (2006). Population-scale drivers of individual arrival times in migratory birds. *J Anim Ecol* 75, 1119–1127.
- Hawkes, L. A., A. C. Broderick, M. H. Godfrey, and B. J. Godley (2007). Investigating the potential impacts of climate change on a marine turtle population. *Global Change Biol* 13, 923–932.
- Hawkins, P. (2004). Bio-logging and animal welfare: practical refinements. *Mem Natl Inst Polar Res* 58, 58–68.
- Hays, G. C., A. C. Broderick, F. Glen, B. J. Godley, J. D. R. Houghton, and J. D. Metcalfe (2002). Water temperature and interesting intervals for loggerhead (*Caretta caretta*) and green (*Chelonia mydas*) sea turtles. *J Therm Biol* 27, 429–432.
- Hays, G. C., J. D. R. Houghton, C. Isaacs, R. S. King, C. Lloyd, and P. Lovell (2004). 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., J. D. R. Houghton, and A. E. Myers (2004). Pan-Atlantic leatherback turtle movements. *Nature* 429, 522.
- Henen, B. T. (1997). Seasonal and annual energy budgets of female desert tortoises (*Gopherus agassizii*). *Ecology* 78, 283–296.
- Holland, D. L., J. Davenport, and J. East (1990). The fatty acid composition of the leatherback turtle *Dermochelys coriacea* and its jellyfish prey. *J Mar Biol Assoc UK* 70, 761–770.
- Houghton, J. D. R., T. Doyle, J. Davenport, and G. C. Hays (2006). Developing a simple, rapid method for identifying and monitoring jellyfish aggregations from the air. *Mar Ecol Prog Ser* 314, 159–170.
- Hughes, G. R. (1996). Nesting of the leatherback turtle (*Dermochelys coriacea*) in Tongaland, KwaZulu-Natal, South Africa, 1963-1995. *Chelonian Conserv Biol* 2, 153–158.
- Hull, C. L. (1997). The effect of carrying devices on breeding royal penguins. *Condor* 99(2), 530–534.

- Hüppop, O. and K. Hüppop (2003). North Atlantic Oscillation and timing of spring migration in birds. *Proc R Soc Lond , Ser B: Biol Sci* 270, 233–240.
- James, M. C., J. Davenport, and G. C. Hays (2006). Expanded thermal niche for a diving vertebrate: a leatherback turtle diving into near-freezing water. *J Exp Mar Biol Ecol* 335, 221–226.
- James, M. C., S. A. Eckert, and R. A. Myers (2005). Migratory and reproductive movements of male leatherback turtles (*Dermochelys coriacea*). *Mar Biol* 147, 845–853.
- James, M. C. and T. B. Herman (2001). Feeding of *Dermochelys coriacea* on medusae in the northwest Atlantic. *Chelonian Conserv Biol* 4, 202–205.
- James, M. C. and N. Mrosovsky (2004). Body temperatures of leatherback turtles (*Dermochelys coriacea*) in temperate waters off Nova Scotia, Canada. *Can J Zool* 82, 1302–1306.
- James, M. C., R. A. Myers, and C. A. Ottensmeyer (2005). Behaviour of leatherback sea turtles, *Dermochelys coriacea*, during the migratory cycle. *Proc R Soc Lond , Ser B: Biol Sci* 272, 1547–1555.
- James, M. C., C. A. Ottensmeyer, S. A. Eckert, and R. A. Myers (2006). Changes in diel diving patterns accompany shifts between northern foraging and southward migration in leatherback turtles. *Can J Zool* 84, 754–765.
- James, M. C., C. A. Ottensmeyer, and R. A. Myers (2005). Identification of high-use habitat and threats to leatherback sea turtles in northern waters: new directions for conservation. *Ecol Lett* 8, 195–201.
- James, M. C., S. A. Sherrill-Mix, K. E. Martin, and R. A. Myers (2006). Canadian waters provide critical foraging habitat for leatherback turtles. *Biol Conserv* 133, 347–357.
- James, M. C., S. A. Sherrill-Mix, and R. A. Myers (2007). Population characteristics and seasonal migrations of leatherback sea turtles at high latitudes. *Mar Ecol Prog Ser* 337, 245–254.
- Jonas, D., D. Johan, K. Lars, P. Erik, L. Anna, and R. Bjarne (2004). The timing of spawning migration: implications of environmental variation, life history, and sex. *Can J Zool* 82, 1864–1870.
- Jonsen, I. D., J. Mills Flemming, and R. A. Myers (2005). Robust state-space modeling of animal movement data. *Ecology* 86, 2874–2880.
- Jonsen, I. D., R. Myers, and M. C. James (2006). Robust hierarchical state-space models reveal diel variation in movement rates of migrating leatherback turtles. *J Anim Ecol* 75, 1046–1057.



- Jonsen, I. D., R. A. Myers, and M. C. James (2007). Identifying leatherback turtle foraging behaviour from satellite telemetry using a switching state-space model. *Mar Ecol Prog Ser* 337, 255–264.
- Jonsen, I. D., R. A. Myers, and J. Mills Flemming (2003). Meta-analysis of animal movement using state-space models. *Ecology* 84, 3055–3063.
- Kaplan, I. C. (2005). A risk assessment for Pacific leatherback turtles (*Dermochelys coriacea*). *Can J Fish Aquat Sci* 62, 1710–1719.
- Lewis, R. L., S. A. Freeman, and L. B. Crowder (2004). Quantifying the effects of fisheries on threatened species: the impact of pelagic longlines on loggerhead and leatherback sea turtles. *Ecol Lett* 7, 221–231.
- 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.
- Lucas, C. H. and S. Lawes (1998). Sexual reproduction of the scyphomedusa *Aurelia aurita* in relation to temperature and variable food supply. *Mar Biol* 131, 629–638.
- Lum, L. L. (2006). Assessment of incidental sea turtle catch in the artisanal gillnet fishery in Trinidad and Tobago, West Indies. *Applied Herpetology* 3, 357–268.
- Lutcavage, M. and P. L. Lutz (1986). Metabolic rate and food energy requirements of the leatherback sea turtle, *Dermochelys coriacea*. *Copeia* 1986, 796–798.
- Lutcavage, M., A. G. J. Rhodin, S. S. Sadove, and C. R. Conroy (2001). Direct carapacial attachment of satellite tags using orthopedic bioabsorbable mini-anchor screws on leatherback turtles in Culebra, Puerto Rico. *Mar Turtle Newsl* 95, 9–12.
- Lutcavage, M. E., P. G. Bushnell, and D. R. Jones (1990). Oxygen transport in the leatherback sea turtle *Dermochelys coriacea*. *Physiol Zool* 63, 1012–1024.
- Lutcavage, M. E., P. G. Bushnell, and D. R. Jones (1992). Oxygen stores and aerobic metabolism in the leatherback sea turtle. *Can J Zool* 70, 348–351.
- Lutz, P. L. (1997). *The Biology of Sea Turtles*, Chapter Salt, Water, and pH Balance in the Sea Turtle, pp. 343–361. CRC Press.
- Lutz, P. L. and D. M. Hudson (1986). Salt gland function in the leatherback sea turtle *Dermochelys coriacea*. *Copeia* 1986, 247–249.
- Lynam, C. P., S. J. Hay, and A. S. Brierley (2004). Interannual variability in abundance of North Sea jellyfish and links to the North Atlantic Oscillation. *Limnol Oceanogr* 49, 637–643.
- Lynam, C. P., S. J. Hay, and A. S. Brierley (2005). Jellyfish abundance and climatic variation: contrasting responses in oceanographically distinct regions of the North Sea, and possible implications for fisheries. *J Mar Biol Assoc UK* 85, 435–450.

- Marks, K. M. and W. H. F. Smith (2006). An evaluation of publicly available global bathymetry grids. *Mar Geophys Res* 27, 19–34.
- Marra, P. P., K. A. Hobson, and R. T. Holmes (1998). Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science* 282, 1884–1886.
- Martin, K. and M. C. James (2005). Conserving sea turtles in Canada: successful community-based collaboration between fishers and scientists. *Chelonian Conserv Biol* 4, 899–907.
- McMahon, C. R. and G. C. Hays (2006). Thermal niche, large-scale movements and implications of climate change for a critically endangered marine vertebrate. *Global Change Biol* 12, 1330–1338.
- Moore, I. T. and T. S. Jessop (2003). Stress, reproduction and adrenocortical modulation in amphibians and reptiles. *Horm Behav* 43, 39–47.
- Morales, J., D. T. Haydon, J. Friar, K. E. Holsinger, and J. M. Fryxel (2004). Extracting more out of relocation data: building movement models as mixtures of random walks. *Ecology* 85, 2436–2445.
- Morreale, S. J., A. B. Meylan, S. S. Sadove, and S. S. Standora (1992). Annual occurrence and winter mortality of marine turtles in New York waters. *Journal of Herpetology* 26, 301–308.
- Mrosovsky, N. (1981). Plastic jellyfish. *Mar Turtle Newsl* 17, 5–7.
- Myers, A. E. and G. C. Hays (2006). Do leatherback turtles *Dermochelys coriacea* forage during the breeding season? a combination of data-logging devices provide new insights. *Mar Ecol Prog Ser* 322, 259–267.
- Myers, R. A., S. A. Boudreau, R. D. Kenney, M. J. Moore, A. A. Rosenberg, S. A. Sherrill-Mix, and B. Worm (2007). Saving endangered whales at no cost. *Curr Biol* 17, R10–R11.
- Norris, D. R., P. P. Marra, T. K. Kyser, T. W. Sherry, and L. M. Ratcliffe (2004). Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proc R Soc Lond, Ser B: Biol Sci* 271, 59–64.
- Olney, J. E., R. J. Latour, B. E. Watkins, and D. G. Clarke (2006). Migratory behavior of American shad in the York River, Virginia, with implications for estimating in-river exploitation from tag recovery data. *Trans Am Fish Soc* 135, 889–896.
- Paladino, F. V., M. P. O'Connor, and J. R. Spotila (1990). Metabolism of leatherback turtles, gigantothermy, and thermoregulation of dinosaurs. *Nature* 344, 858–860.
- Pike, D. A. and J. C. Stiner (2007). Sea turtle species vary in their susceptibility to tropical cyclones. *Oecologia Online First*.

- Polovina, J. J., G. H. Balazs, E. A. Howell, D. M. Parker, M. P. Seki, and P. H. Dutton (2004). Forage and migration habitat of loggerhead (*Caretta caretta*) and olive ridley (*Lepidochelys olivacea*) sea turtles in the central North Pacific Ocean. *Fish Oceanogr* 13, 36–51.
- Prop, J., J. M. Black, and P. Shimmings (2003). Travel schedules to the high arctic: barnacle geese trade-off the timing of migration with accumulation of fat deposits. *Oikos* 103, 403–414.
- Purcell, J. E. (2005). Climate effects on formation of jellyfish and ctenophore blooms: a review. *J Mar Biol Assoc UK* 85, 461–476.
- Purcell, J. E. and M. B. Decker (2005). Effects of climate on relative predation by ctenophores and scyphomedusae on copepods in Chesapeake Bay during 1987–2000. *Limnol Oceanogr* 50, 376–387.
- Purcell, J. E., J. R. White, D. A. Nemazie, and D. A. Wright (1999). Temperature, salinity and food effects on asexual reproduction and abundance of the scyphozoan *Chrysaora quinquecirrha*. *Mar Ecol Prog Ser* 180, 187–196.
- Quinn, T. P., S. Hodgson, and C. Peven (1997). Temperature, flow, and the migration of adult sockeye salmon (*Oncorhynchus nerka*) in the Columbia River. *Can J Fish Aquat Sci* 54, 1349–1360.
- Rainio, K., T. Laaksonen, M. Ahola, A. V. Vahatalo, and E. Lehikoinen (2006). Climatic responses in spring migration of boreal and arctic birds in relation to wintering area and taxonomy. *J Avian Biol* 37, 507–515.
- Ramsay, M. A. and I. Stirling (1986). Long-term effects of drugging and handling free-ranging polar bears. *J Wildl Manage* 50, 619–626.
- Ream, R. R., J. T. Sterling, and T. R. Loughlin (2005). Oceanographic features related to northern fur seal migratory movements. *Deep-Sea Research II* 52, 823–843.
- Rivalan, P., R. Pradel, R. Choquet, M. Girondot, and A.-C. Prévot-Julliard (2006). Estimating clutch frequency in the sea turtle *Dermochelys coriacea* using stopover duration. *Mar Ecol Prog Ser* 317, 285–295.
- Robinson, I. S. (2004). *Measuring the Oceans from Space: The Principles and Methods of Satellite Oceanography*. Springer-Praxis Books.
- Saino, N., T. Szép, M. Romano, D. Rubolini, F. Spina, and A. P. Møller (2004). Ecological conditions during winter predict arrival date at the breeding quarters in a trans-Saharan migratory bird. *Ecol Lett* 7, 21–25.
- Sale, A., P. Luschia, R. Mencacci, P. Lambardi, G. R. Hughes, G. C. Hays, S. Benvenuti, and F. Papi (2006). Long-term monitoring of leatherback turtle diving behaviour during oceanic movements. *J Exp Mar Biol Ecol* 328, 197210.

- Sarti Martinez, A. (2000). *Dermochelys coriacea*. In *2006 IUCN Red List of Threatened Species*. <http://www.iucnredlist.org>.
- Shamoun-Baranes, J., E. van Loon, D. Alon, P. Alpert, Y. Yom-Tov, and Y. Leshem (2006). Is there a connection between weather at departure sites, onset of migration and timing of soaring-bird autumn migration in Israel? *Global Ecol Biogeogr* 15, 541–552.
- Sims, D. W., M. J. Genner, A. J. Southward, and S. J. Hawkins (2001). Timing of squid migration reflects north Atlantic climate variability. *Proc R Soc Lond , Ser B: Biol Sci* 268, 2607–2611.
- Smith, W. H. F. and D. T. Sandwell (1997). Global sea floor topography from satellite altimetry and ship depth soundings. *Science* 277, 1956–1962.
- Solow, A. R., K. A. Bjorndal, and A. B. Bolten (2002). Annual variation in nesting numbers of marine turtles: the effect of sea surface temperature on re-migration intervals. *Ecol Lett* 5, 742–746.
- Southeast Fisheries Science Center (2001). Stock assessments of loggerhead and leatherback sea turtles and an assessment of the impact of the pelagic longline fishery on the loggerhead and leatherback sea turtles of the western north atlantic. Technical Report U.S. Department of Commerce NOAA Technical Memorandum NMFS-SEFSC-455, National Marine Fisheries Service.
- Southwood, A., R. Andrews, M. Lutcavage, F. Paladino, N. West, R. George, and D. Jones (1999). Heart rates and diving behavior of leatherback sea turtles in the eastern Pacific Ocean. *J Exp Biol* 202, 1115–25.
- Sparks, T. H. and O. Braslavská (2001). The effects of temperature, altitude and latitude on the arrival and departure dates of the swallow *Hirundo rustica* in the Slovak Republic. *Int J Biometeorol* 45, 212–216.
- Spotila, J. R., A. E. Dunham, A. J. Leslie, A. C. Steyermark, P. T. Plotkin, and F. V. Paladino (1996). Worldwide population decline of *Dermochelys coriacea*: Are leatherback turtles going extinct? *Chelonian Conserv Biol* 2, 209–222.
- Spotila, J. R., R. D. Reina, A. C. Steyermark, P. T. Plotkin, and F. V. Paladino (2000). Pacific leatherback turtles face extinction. *Nature* 405, 529–530.
- Steyermark, A. C., K. Williams, J. R. Spotila, F. V. Paladino, D. C. Rostal, S. J. Morreale, M. T. Koberg, and R. Arauz (1996). Nesting leatherback turtles at Las Baulas National Park, Costa Rica. *Chelonian Conserv Biol* 2, 173–183.
- Tew, K. S. and W.-T. Lo (2005). Distribution of Thaliacea in SW Taiwan coastal waters in 1997, with special reference to *Doliolum denticulatum*, *Thalia democratica* and *T. orientalis*. *Mar Ecol Prog Ser* 292, 181–193.

- Trites, A. W. (1991). Does tagging and handling affect the growth of northern fur seal pups (*Callorhinus ursinus*)? *Can J Fish Aquat Sci* 48, 2436–2442.
- Troëng, S., R. Solano, A. Díaz-Merry, J. Ordoñez, J. Taylor, D. R. Evans, D. Godfrey, D. Bagley, L. Ehrhart, and S. Eckert (2006). Report on long-term transmitter harness retention by a leatherback turtle. *Mar Turtle Newsl* 111, 6–7.
- Turtle Expert Working Group (2007). An assessment of the leatherback turtle population in the Atlantic Ocean: a report of the Turtle Expert Working Group. Technical Report NMFS-SEFSC-555, National Oceanic and Atmospheric Administration.
- Vincent, C., B. J. McConnell, M. A. Fedak, and V. Ridoux (2002). Assessment of Argos location accuracy from satellite tags deployed on captive grey seals. *Mar Mamm Sci* 18, 156–166.
- Walker, B. G. and P. L. Boveng (1995). Effects of time-depth recorders on maternal foraging and attendance behavior of Antarctic fur seals (*Arctocephalus gazella*). *Can J Zool* 73, 1538–1544.
- Wallace, B. P., S. S. Kilham, F. V. Paladino, and J. R. Spotila (2006). Energy budget calculations indicate resource limitation in Eastern Pacific leatherback turtles. *Mar Ecol Prog Ser* 318, 263–270.
- Wallace, B. P., C. L. Williams, F. V. Paladino, S. J. Morreale, R. T. Lindstrom, and J. R. Spotila (2005). Bioenergetics and diving activity of internesting leatherback turtles *Dermochelys coriacea* at Parque Nacional Marino Las Baulas, Costa Rica. *J Exp Biol* 208, 3873–3884.
- Watanuki, Y., Y. Mori, and Y. Naito (1992). Adélie penguin parental activities and reproduction: effects of device size and timing of its attachment during chick rearing period. *Polar Biol* 12(5), 539–544.
- Watson, K. P. and R. A. Granger (1998). Hydrodynamic effect of a satellite transmitter on a juvenile green turtle (*Chelonia mydas*). *J Exp Biol* 201, 2497–2505.
- Weishampel, J. F., D. A. Bagley, and L. M. Ehrhart (2004). Earlier nesting by loggerhead sea turtles following sea surface warming. *Global Change Biol* 10, 1424–1427.
- White, E. M. and B. Knights (1997). Environmental factors affecting migration of the European eel in the Rivers Severn and Avon, England. *J Fish Biol* 50, 1104–1116.
- Wilson, R., W. Grant, and D. Duffy (1986). Recording devices on free-ranging marine animals: does measurement affect foraging performance? *Ecology* 67(4), 1091–1093.
- Witt, M. J., A. C. Broderick, D. J. Johns, C. S. Martin, R. Penrose, M. S. Hoogmoed, and B. J. Godley (2007). Prey landscapes help identify potential foraging habitats for leatherback turtles in the northeast Atlantic. *Mar Ecol Prog Ser* 337, 231–244.

- Yako, L. A., M. E. Mather, and F. Juanes (2002). Mechanisms for migration of anadromous herring: an ecological basis for effective conservation. *Ecol Appl* 12, 521–534.
- Zug, G. R. and J. F. Parham (1996). Age and growth in leatherback turtles, *Dermochelys coriacea* (Testudines: Dermochelyidae): a skeletochronological analysis. *Chelonian Conserv Biol* 2, 244–249.