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At-Sea Biology and Movements of Leatherback Turtles,

*Dermochelys coriacea*, in the Northwest Atlantic

by

Michael C. James

Submitted in partial fulfillment of the requirements
for the degree of Doctor of Philosophy

at

Dalhousie University
Halifax, Nova Scotia
July, 2005

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To my wife, Kathleen Elizabeth Martin,

and son, Aidan Michael Martin James
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Abstract

The endangered leatherback turtle, *Dermochelys coriacea*, has the broadest distribution of any sea turtle; however, research on this species has principally been limited to studies of the biology of nesting females, their interesting behaviour, and more recently, their post-nesting movements. To hasten this species’ recovery, research on the biology of leatherbacks and the threats they face in other areas of their range is needed. In collaboration with the fishing industry, I developed a field research program to study leatherbacks in waters off eastern Canada, where turtles aggregate seasonally to forage on gelatinous plankton.

In this thesis, I report on the degree to which leatherbacks maintain body temperature above ambient in northern waters, and discuss the implications of endothermy for leatherbacks in temperate and tropical areas. To study the local and long-distance movements of leatherbacks, I equipped 42 subadult and adult turtles with satellite tags in Canadian waters, the largest satellite telemetry study of this species in the Atlantic. I use movement data from this sample and morphometrics from foraging animals to identify previously unrecognized high-use habitat for leatherbacks in temperate shelf and slope waters of the northwest Atlantic, where entanglement data demonstrates turtles are at risk of interacting with both mobile and fixed-gear fisheries. I present tracklines that confirm annual return migrations to feeding areas, and describe patterns in turtle movement during these migratory cycles. I identify diel patterns in diving and surfacing behaviour both in northern foraging areas and during southward migration, and explore the potential biological significance of these patterns. Finally, I report on the first deployments of satellite tags on male leatherbacks, which provide new information on the location and timing of mating activity and suggest male fidelity for breeding areas.

Collectively, this work presents new information on the life history of the leatherback and demonstrates the importance of northern latitudes, and especially waters off Canada and the northeastern United States, to this species.
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Chapter 1. Introduction

1.1. Species Description

The leatherback sea turtle (*Dermochelys coriacea*) is the largest of all turtles, weighing as much as 900 kg. The sole member of the family Dermochelyidae, the leatherback is morphologically divergent from other sea turtles in several ways: seven longitudinal keels are present on the carapace, which is spade-shaped and terminates in a blunt point above the tail; the front flippers are exceptionally long and may exceed half the length of the carapace; the entire body is covered in skin; and there is a white or pink spot of varying size and shape on top of the head, which contrasts with the otherwise bluish-black dorsum.

The leatherback is more widely distributed than any other sea turtle, inhabiting all of the world’s oceans, and ranging from tropical to temperate—and even to boreal—waters. Earlier research has suggested that northern waters may be dominated by adult and large sub-adult animals (Bleakney 1965; Goff and Lien 1988; Duguy et al. 1997). Records of juveniles are exceedingly rare, but appear to be principally restricted to regions where surface water temperatures exceed 26 °C (Eckert 2002a). The more restricted geographic distribution of leatherbacks of smaller size classes may reflect exploitation of a diet different from that of adults and/or a narrower range of thermal tolerance (Eckert 2002a).

The capacity of subadult and adult animals to maintain body temperature far above ambient stems from a relatively large volume-to-surface-area ratio (Paladino et al. 1990), a thick insulating layer of fat (Goff and Stenson 1988), and several physiological adaptations, including counter-current heat exchange (Greer et al. 1973). Cold hardiness
has allowed the leatherback to exploit prey in regions where water temperatures fall well below the lower thermal tolerance limits of the other marine turtle species. Consequently, the leatherback is the only sea turtle known to regularly occur at high latitudes, including waters off Canada’s east coast.

Published accounts of leatherbacks from northern waters of the Atlantic have represented turtles caught in coastal fishing gear (e.g., Bleakney 1965; Brongersma 1972; Goff and Lien 1988; Duguy et al. 1998; Godley et al. 1998), and entanglement records from pelagic longline fishery observer programs (Witzell 1996, 1999; Lewison et al. 2004). However, sightings of leatherbacks voluntarily reported by fishermen and others have also been summarized (e.g. Duguy 1997; James 2000). Data on leatherback distribution and seasonal abundance in northern waters has been collected in a more standardized way through aerial surveys conducted along the coast of the United States (Shoop and Kenney 1992). Collectively, these records are consistent with the regular use of temperate northwest Atlantic waters by this species, as originally proposed by Bleakney (1965) and later reiterated by Lazell (1980). By the end of the twentieth century, leatherbacks were widely recognized to occur annually off the northeastern United States and eastern Canada, and both examination of stomach contents (Bleakney 1965) and behavioural observations (James and Herman 2001) suggested that turtles aggregated in northern waters to forage on seasonally abundant species of gelatinous macroplankton.
1.2. Context for Thesis Research

While it has become increasingly apparent that Atlantic leatherbacks regularly occur at high latitudes, there remains a fundamental lack of information regarding the biology of turtles in these areas. For example, where these animals come from, and when they arrive and depart northern waters is not known. Similarly, the question Bleakney (1965) posed regarding the destinations of leatherbacks encountered in northern waters has not been answered: “Do some individuals then turn southward to nesting sites in the Caribbean while others follow the Gulf Stream towards Europe?”

Given the leatherback’s status as endangered in Canada (COSEWIC 2001) and the recent tabling of federal endangered species legislation (Statutes of Canada 2002), both spatial and temporal information regarding leatherback movements in Canadian waters and an evaluation of the threat posed by various human activities there are required. Traditionally those areas of leatherback aggregation where turtles may be particularly vulnerable to human activities have been identified through fishery observer data collected from only a handful of commercial fleets. This has introduced considerable bias in our understanding of where turtles occur and the extent to which they interact with different fisheries. As leatherbacks have a propensity for becoming entangled in lines (Chan et al. 1988; Godley et al. 1998), it is critical that we broaden our approach to evaluating habitat use and the potential impact of threats in different areas by integrating information on the movements of the animals themselves.

Despite several decades of study, basic information about the leatherback’s life history and biology has not been collected. Only nesting female turtles, their eggs, and hatchlings have traditionally been readily available for research purposes. Therefore,
although the reproductive biology of females has been well described, information regarding other sex and size classes is lacking. For example, male leatherbacks and sub-adults have remained unstudied; nothing is known about their movements. Behaviour has not been described throughout migratory cycles. Finally, maintenance of elevated body temperatures in cold waters has been demonstrated experimentally in this species (Frair et al.); however, the degree to which free-swimming turtles maintain body temperature in northern waters has not been studied.

To answer these and other questions regarding the biology of leatherbacks from northern waters, research was conducted on a foraging population that occurs seasonally in waters off eastern Canada. Critical to this effort was expanding an existing collaboration with the fishing community (Martin and James 2005) to develop the capacity for both locating and humanely capturing leatherbacks at sea. During five seasons of fieldwork (2000-2004), 42 sub-adult and adult leatherbacks of both sexes were equipped with satellite-linked instruments off the coast of Nova Scotia. Other turtles were captured to support collaborative research on thermal biology and stock identification, and reports of leatherbacks entangled in fishing gear were collected from across Atlantic Canada.

1.3 Thesis Overview

Chapter 2

This chapter reports on the results of a study of the thermal biology of leatherbacks from temperate waters. The body temperatures of foraging turtles were recorded and compared to corresponding ocean surface temperature. Data from a turtle
equipped with a satellite-linked time-depth recorder were used to clarify the range of
ocean temperature experienced during foraging and to explore the implications of
foraging behaviour on thermoregulation. Findings are discussed with reference to
previous experimental testing of the capacity of leatherbacks to maintain body
temperature above ambient and the various physiological bases of endothermy that have
been proposed for this species.

Chapter 3

This chapter considers spatial use of 38 leatherbacks equipped with satellite-
linked transmitters off Nova Scotia and morphometrics of turtles in northern foraging
areas to clarify the importance of temperate waters of the northwest Atlantic to this
species. These data were combined with entanglement records to identify where turtles
are at risk of interacting with fisheries.

Chapter 4

This chapter is an investigation of movements, surface activity and diving
behaviour of leatherbacks satellite tracked during return migrations to northern foraging
areas, and an exploration of the potential ecological significance of the patterns observed.

Chapter 5

This chapter focuses on the diel diving patterns of leatherbacks during their
foraging period in northern waters and during southward migration, and considers how
such patterns may reflect behaviours associated with foraging and navigation.
Chapter 6

This chapter presents results from the first deployments of satellite tags on male leatherbacks and uses long-term movement data to test hypotheses concerning when and where mating in this species occurs. Findings are compared with those from studies of male behaviour in other species of sea turtle.

Chapter 7

This chapter is a summary of the principal results of this thesis research and a discussion of the implications of this work for the recovery of this endangered species.

1.4 Publications Resulting from Thesis Research


James, M. C., Martin, K. E., and Dutton, P. H. In press. Hybridization between a Green Turtle (*Chelonia mydas*) and Loggerhead Turtle (*Caretta caretta*) and the first record of a Green Turtle in Atlantic Canada. Canadian Field-Naturalist.


Chapter 2. Body Temperatures of Leatherback Turtles (*Dermochelys coriacea*) in Temperate Waters off Nova Scotia, Canada

2.1 Introduction

The leatherback turtle, *Dermochelys coriacea*, is a giant marine reptile that specializes on a diet of coelenterates. This prey is seasonally abundant in temperate and boreal waters. In 1965, Bleakney collated observations of active leatherbacks that appeared to be in good health in waters off New England and eastern Canada and suggested that these animals make regular migrations to temperate waters of the northwest Atlantic. How do leatherbacks manage to keep active and feed in temperatures that would induce lethargy, and even death, in most reptiles? Body temperatures of leatherbacks nesting in the tropics have been found to be about 3 °C above the water from which they emerged (Mrosovsky and Pritchard 1971), and dataloggers attached to implanted thermistors recorded subcarapacial temperatures as high as 3 °C above that of the sea surface during the internesting interval off the Pacific coast of Costa Rica (Southwood et al. 1999a). Such findings suggest that leatherbacks might be able to maintain their temperature above ambient levels even in cool waters. Mechanisms consistent with an ability to keep warm in cold water are countercurrent heat exchangers in the flippers, thermal inertia, a high volume to surface area ratio, different compositions of peripheral and central lipids, a thick fibrous lipid-saturated layer, and proposed regulation of blood flow (Frair et al. 1972; Greer et al. 1973; Goff and Stenson 1988; Davenport et al. 1990; Paladino et al. 1990).

However, some cautions are in order about the interpretation of the few data on leatherbacks from cold water. The logistics associated with locating and handling these
massive animals have hindered field studies of the thermal biology of this species at high latitudes. Deep body temperature data have previously been collected from two live leatherbacks from temperate waters. The first turtle, a male, was housed for 24 h in a tank with circulating 7.5 °C sea water following its capture off Nova Scotia, Canada (Frair et al. 1972). Fifteen minutes after it was removed from the water, the animal’s deep body core temperature was 18 °C above that of the tank (Frair et al. 1972). The second turtle, caught off Rhode Island, USA, registered deep body temperatures between 3.4 and 8.3 °C above ambient air temperature (Standora et al. 1984). The differential between deep body temperature and sea temperature was not measured. Although both records attest to the capacity for endothermy, these measurements followed lengthy periods of handling and confinement, and therefore, may be less reliable than those collected immediately after free-swimming leatherbacks are captured at sea.

Northern foraging habitat for the leatherback in the Atlantic includes waters off Eastern Canada (Bleakney 1965; Lazell 1980; Goff and Lien 1988), where the species has been observed in water as cold as 0 °C (Goff and Lien 1988). Leatherbacks are notoriously difficult to locate and capture at sea; however, collaboration with commercial fishers in Eastern Canada has yielded rare opportunities for fieldwork on this species. Here we report on body core temperature data collected from four adult females in waters off Nova Scotia. We relate our findings to ocean temperatures collected by a satellite-linked datalogger attached to a fifth leatherback foraging in the vicinity of three of these animals.
2.2 Materials and Methods

All turtles were handled in accordance with the principles and guidelines of the Canadian Council on Animal Care. A breakaway hoop-net, operated from a bowsprit attached to a 34-foot (1 foot = 0.3048 m) commercial fishing boat equipped with a stern ramp, was used to capture free-swimming leatherbacks in continental shelf waters off Nova Scotia, Canada. This type of net has been used to capture cheloniid sea turtles (Beavers and Cassano 1996), and pinnipeds and small cetacea (Asper 1975). The net was pursed over each turtle when it surfaced. The turtle was quickly brought alongside the boat, where a cargo net constructed of soft 2.5 cm mesh cotton netting was placed under it and secured around it. The turtle was then guided to the stern and moved up the ramp onto a raised platform built flush with the sides of the vessel.

Next, a 46 cm long, 0.6 cm diameter, type “T” thermocouple, stainless steel probe (model TJ36-CPSS; Omega Engineering, Inc., Stamford, Connecticut) was inserted into the cloacal opening. The probe was connected to a microprocessor-based handheld thermometer (model HH-21; Omega Engineering, Inc.). Temperature could be read to the nearest 0.1 °C. Calibration was checked by placing the probe in melting ice and readings were always within 0.1 °C of zero. Previous work (Mrosovsky 1980) suggested that it may be necessary to insert cloacal probes a minimum of 24 cm to measure core temperature of nesting leatherbacks. Therefore, the probe was slowly guided beyond this depth until any resistance was encountered. The probe was inserted beyond the tail and into the main body of the animal, and in all cases, probe depth exceeded the point at which temperature readings did not increase further. The immersion depth of the probe was recorded along with the temperature. To minimize potential error related to the use
of cloacal probes in the much longer tails of male leatherbacks (Frair et al. 1972), only females were studied (turtles A–D).

A bucket attached to a rope was then tossed over the side of the boat to retrieve a sample of sea water. The same probe was then promptly used to measure sea surface temperature. A second sample of water was then collected to confirm sea surface temperature.

Measurements occurred <10 min after capture, and all turtles were repeatedly doused with buckets of sea water while aboard. Following the collection of temperature measurements, curved carapace length (CCL) and curved carapace width (CCW) were recorded. Monel tags (style #49; National Band and Tag Company, Newport, Kentucky) were applied to the rear flippers and a passive integrated transponder (Avid™ brand) was implanted in the right shoulder muscle. Two turtles were also weighed with a digital hanging scale by raising them off the platform in the cargo net using a lever puller suspended from a tubular aluminum structure.

To better understand the range of temperature experienced by leatherbacks foraging in the vicinity, we considered ocean temperature data collected by a satellite-linked time–depth recorder (SLTDR) (model SSC3; Wildlife Computers, Inc., Redmond, Washington) incorporating a thermistor accurate to 0.15 °C. with a resolution of 0.13 °C. that was attached to an additional female turtle (turtle E). The instrument was deployed earlier in the summer off mainland Nova Scotia (44.273°N, -63.677°W); however, turtle E later moved ~400 km northeast to forage off Cape Breton Island. This leatherback actively foraged in shelf waters (<200 m deep) within a 30-km radius of the capture location of one of three leatherbacks studied in 2003 and captured within this radius.
(Figure 2.1). Temperature data were recorded as the proportion of each of four 6-h periods in a day spent in 2 °C bins from 8–10 °C to 30–32 °C. The instrument collected data for all four periods every day. To evaluate the range of temperature associated with leatherback foraging behavior in this particular area, we only considered temperature data collected during those days when ARGOS positions with assigned location qualities of 3, 2, and 1 (calculated to lie within 150, 150–350, and 350–1000 m, respectively, of the animal's true position) placed turtle E within the 30-km radius. Recognizing that the temperature of the water column changes with time, we limited our analysis to 3 days (i.e., 2, 3, and 6 September), including the day before the first two turtles were captured and the day the last turtle was captured. Corresponding temperature data from the SLTDR on turtle E were combined over this period to show the percentage of time that the animal spent at different temperatures.
Figure 2.1. Locations of four female leatherback turtles (*Dermochelys coriacea*) captured off Cape Breton Island, Nova Scotia. The solid square indicates the turtle that was caught in 2002 (turtle A). Solid triangles indicate turtles that were captured in 2003 (turtles B-D). Solid circles indicate ARGOS positions from an additional female turtle (turtle E) equipped with a satellite-linked sea temperature data recorder. Numbers besides the solid circles represent dates in September, 2003.
2.3. Results

One leatherback was captured in September 2002, and three leatherbacks were captured in September 2003 (Table 2.1). Curved carapace length ranged from 143 to 163 cm, indicating that all turtles were of breeding size, and one (turtle D) was confirmed to have previously nested on Matura Beach, Trinidad, after a microchip was detected in the right shoulder and a metal flipper tag was found on the left rear flipper (Table 2.1). The smallest turtle (turtle C) had a CCL of 143 cm and weighed 315 kg, and a second turtle (turtle A) had a CCL that was 9.5 cm longer and weighed 380 kg; therefore, each of the other two animals likely weighed a minimum of 315 kg. Body core temperatures ranged from 5.1 to 10.8 °C above ambient temperature (Table 2.2).

Turtle E foraged within a 30-km radius of turtle A for 3 of the 5 days considered (i.e., 2, 3, and 6 September; Figure 2.1) and experienced a wide range of temperature during this time (Figure 2.2). Although turtle E spent 60% of the 72-h sampling period in waters 16–18 °C, which corresponded to the point sea surface temperatures associated with three of the captured turtles, she spent 40% of her time at temperatures below 16 °C, including 32% at 12–16 °C and 6% at 10–12 °C.
<table>
<thead>
<tr>
<th>Turtle ID</th>
<th>Passive integrated transponder ID#</th>
<th>Date dd/mm/yyyy</th>
<th>Curved carapace length (cm)</th>
<th>Curved carapace width (cm)</th>
<th>Mass (kg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>017618055</td>
<td>16/09/2002</td>
<td>152.5</td>
<td>106.5</td>
<td>380</td>
</tr>
<tr>
<td>B</td>
<td>017069036</td>
<td>03/09/2003</td>
<td>151.3</td>
<td>105.1</td>
<td></td>
</tr>
<tr>
<td>C</td>
<td>132337156</td>
<td>03/09/2003</td>
<td>143.0</td>
<td>105.0</td>
<td>315</td>
</tr>
<tr>
<td>D</td>
<td>032010096</td>
<td>06/09/2003</td>
<td>162.8</td>
<td>113.6</td>
<td></td>
</tr>
</tbody>
</table>

Table 2.1. Morphometrics and capture locations of four female leatherback turtles off Nova Scotia, Canada.

<table>
<thead>
<tr>
<th>Turtle ID</th>
<th>Probe depth (cm)</th>
<th>Core temperature (°C)</th>
<th>Sea surface temperature (°C)</th>
<th>Differential temperature (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>38.5</td>
<td>25.8</td>
<td>15.0</td>
<td>10.8</td>
</tr>
<tr>
<td>B</td>
<td>42.0</td>
<td>21.6</td>
<td>16.5</td>
<td>5.1</td>
</tr>
<tr>
<td>C</td>
<td>41.0</td>
<td>24.7</td>
<td>16.7</td>
<td>8.0</td>
</tr>
<tr>
<td>D</td>
<td>45.0</td>
<td>25.2</td>
<td>16.4</td>
<td>8.8</td>
</tr>
<tr>
<td>Mean ± SD</td>
<td>41.63 ± 2.69</td>
<td>24.33 ± 1.87</td>
<td>16.15 ± 0.78</td>
<td>8.18 ± 2.36</td>
</tr>
</tbody>
</table>

Table 2.2. Core temperature and sea surface temperature measurements for four female leatherback turtles in waters off Nova Scotia, Canada.
Figure 2.2. Percent time at temperature for turtle E in waters off Cape Breton Island, Nova Scotia, during 3 days (2, 3 and 6 September 2003).
2.4 Discussion

The data reported here were derived from more natural conditions than those published previously, because measurements were taken from wild animals captured for this purpose and handled briefly rather than from leatherbacks that were found entangled in fishing gear for unknown periods and were transported to shore for study where they experienced confinement and additional handling. Despite the differences in procedures, the results support the conclusion of Frair et al. (1972) that leatherbacks can maintain temperature well above ambient levels.

However, our new data do not completely resolve the question of whether leatherbacks in cold water regulate their temperature at a more or less constant value. The temperature of the leatherback studied by Frair et al. (1972) was 25.5 °C; this was 18 °C above the temperature of the water in which it had been kept. The mean temperature of the four leatherbacks studied here was 24.3 °C; this was about 8 °C above the sea surface temperatures of 15–17 °C. In both cases the actual body temperatures were similar, but the cooler the water, the greater the excess of body temperature above ambient levels. This is consistent with regulation, but the point cannot be made with great precision because leatherbacks often dive below the surface to cooler waters (Figure 2.2).

If we assume the warmest water temperatures are at or near the surface, then the data from the leatherback instrumented to record temperature external to the body suggest that foraging leatherbacks spend considerable amounts of time below the surface, where temperatures are generally a few degrees cooler. This is consistent with our observations of leatherbacks off the coast of Nova Scotia. Although animals are regularly found in areas where jellyfish are abundant at the surface (James and Herman 2001), we have also
observed leatherbacks consuming jellyfish at the surface when such prey are not visible there. Therefore, in these instances, leatherbacks are likely capturing jellyfish at depth and returning to the surface to ingest their prey.

More information is needed to establish the existence of a regulated temperature level in leatherbacks. However, the more time the four animals studied here spent diving to water cooler than that recorded at the surface, the stronger the demonstration that, by whatever means, these turtles can maintain body temperature in cool water. As the turtle with the temperature recorder revealed, leatherbacks foraging in this area off Cape Breton Island may spend 40% of their time diving to cooler water. In addition, ingestion of cold prey could contribute to thermal challenges in foraging areas (Davenport 1998).

All of the leatherbacks considered here were similar in size and were adults. There are potentially large differences in the thermal biology of large and small leatherbacks, with larger animals being better able than small ones to keep warm in cold water. Paladino et al. (1990) considered the thermoregulatory capabilities of leatherbacks of different sizes by modelling heat exchange within a leatherback and between the leatherback and the environment, and concluded that bigger leatherbacks can maintain larger core–skin temperature differences. Moreover, the cloacal temperature (20-cm depth) of a captive immature leatherback weighing 23–26 kg was not appreciably warmer than that of a Kemp’s ridley sea turtle, *Lepidochelys kempii* (Garman, 1880), and a green turtle, *Chelonia mydas* (L., 1758), of similar mass, and in 20 °C water the leatherback was only about 1 °C warmer than ambient temperature (Mrosovsky 1980). Eckert (2002a) has suggested that differences in the thermoregulatory abilities of large
versus small leatherbacks may help explain the apparent absence of small leatherbacks (<100 cm CCL) in high-latitude foraging populations.

Once leatherbacks are large, they may use multiple mechanisms to help them keep warm in cold water. These include an insulating oily layer, high physical activity generating heat, and countercurrent heat exchange. Such adaptations raise the possibility that the greatest thermal challenges faced by this species might arise when it is in warm waters. The leatherback has the greatest distribution of any reptile, ranging from tropical to arctic waters. Body temperatures of leatherbacks that have emerged for nesting (Mrosovsky 1980) and those swimming offshore during their internesting interval (Southwood et al. 1999a) have revealed that temperatures as high as 30 °C or even greater can be reached. In these studies a variety of methods were used, including recording the temperature of eggs immediately after they were extruded, cloacal temperature, and subcarapacial implants of thermistors. It seems unlikely that the differences of 5 °C or more between leatherbacks in the tropics and those in cold waters stem only from methodological differences in these studies.

For further understanding of the thermal biology of leatherbacks, it would be instructive to have simultaneous recording of body temperature and surrounding ocean temperature for the same individual over periods long enough to include sojourns off tropical nesting beaches and in temperate foraging areas. With recent technological advances in wildlife satellite-telemetry instrumentation, this goal may not be out of reach much longer. Leatherbacks captured off Nova Scotia may prove ideal candidates for future studies of this nature, as these animals have a predictable migration to tropical waters following their high-latitude foraging period.
Chapter 3. Identification of High-Use Habitat and Threats to Leatherback Sea Turtles in Northern Waters: New Directions for Conservation

3.1. Introduction

A poor understanding of the distribution and movements of many marine vertebrates has impeded conservation of these species (Block et al. 2001). Such basic biological information is critical to identifying and evaluating potential sources of anthropogenic mortality and designing effective conservation plans. Movement data have had important implications for predicting how threats may impact upon populations and meta-populations of bluefin tuna (Block et al. 2001), wandering albatross (Inchausti and Weimerskirch 2002), South American fur seals (Thompson et al. 2003) and Florida panthers (Maehr et al. 2002). Incidental capture in fisheries has been implicated in the decline of many species (Tuck et al. 2001; Baum et al. 2003; Lewison et al. 2004), but because most analyses focus on observer data from only a fraction of fisheries with potential impacts, the importance of interactions occurring in other parts of a species’ range often remains virtually unknown. This is the case with the leatherback turtle (Dermochelys coriacea Vandelli 1761).

The leatherback is the largest of the turtles and is found in all of the world’s oceans, specializing on a diet of gelatinous plankton (Bleakney 1965). Following a sharp global population decline over the past two decades (Spotila et al. 1996, 2000), the species is now critically endangered (IUCN 2004) and may be facing imminent extinction in the Pacific (Spotila et al. 2000). While nesting female turtles and their eggs have received increasing levels of protection in some locations, conservation of this cosmopolitan reptile has been hampered by insufficient knowledge of its biology at sea.
Most available information comes from instrument deployments on nesting females (Eckert et al. 1989; Ferraroli et al. 2004; Hays et al. 2004a) and records of turtles incidentally captured in pelagic longline fisheries (Witzell 1999; Lewison et al. 2004). Recent studies have highlighted the broad oceanic movements of leatherbacks in the Atlantic (Ferraroli et al. 2004; Hays et al. 2004a), but relatively small sample sizes have, until now, precluded the identification of high-use areas (hotspots) where conservation efforts may be most effective. While it is known that this species is highly migratory (Ferraroli et al. 2004; Hays et al. 2004a), virtually nothing is known about its behaviour and biology in northern areas.

Here we investigate the biology of leatherbacks at northern latitudes and identify potential threats to turtles in these areas by considering information from three distinct data sets: satellite telemetry data from turtles tagged in Canadian waters, detailed morphometrics from northern foraging animals and entanglement records from shelf waters of Atlantic Canada. Insights from this synthesis highlight the importance of gathering long-term data from a large sample and thoroughly identifying key habitat when developing and implementing effective measures to ensure species survival.

3.2 Materials and Methods

*Satellite tag deployments*

We deployed five different models of platform transmitting terminals from three manufacturers: Telonics (Mesa, AZ, USA) ST-10 (n=1), Sirtrack (Havelock North, New Zealand) Kiwisat (n=17), Wildlife Computers (Redmond, WA, USA) SPOT3 (n=5); SSC3 (n=13); and SDRT-16 (n=2) in two different areas: waters off mainland Nova
Scotia (44° N 64° W, n=20 tags) and waters off Cape Breton Island (47° N 60° W, n=18 tags).

We captured foraging turtles at the surface using a breakaway hoop net operated from a bowsprit attached to a 10.5 m commercial fishing boat equipped with a stern ramp. Each captured animal was guided up the ramp onto a raised platform, where metal tags were applied to the rear flippers, an AVID™ (Calgary, Canada) microchip was injected into the shoulder muscle and morphometrics were recorded. We attached the satellite transmitters to the carapace using a custom-fitted harness made of nylon webbing and polyvinyl tubing, which incorporated corrodbile links to ensure release (modified after Eckert 2002b).

**Spatial use analysis**

We included all Argos-derived positions classified as 1, 2 or 3 (categorized by Argos to lie within 350–1000 m, 150–350 m, or 150 m, respectively, of the tag’s true position) in the spatial use analysis. Of 5459 rates of travel calculated between Argos positions classed 1–3 (n=22 turtles), only 57 (1.0%) were >5 km h⁻¹, all corresponding to movements shortly after tagging or the onset of southward migration. Therefore, we filtered all other Argos positions (location classes A, B and O) based on a maximum rate of travel of 5 km h⁻¹. Positions of location quality Z and those that clearly fell outside each turtle’s track were omitted. We calculated median daily locations for each turtle based on the filtered locations and then tallied the median locations for all turtles in hexagonal area bins.
Morphometric analysis

We obtained weight and corresponding curved carapace length (CCL) from live turtles and those recovered dead from fishing gear in Canadian waters (n=13). These included nine turtles measured by one of us (MCJ), two previously published records (Bleakney 1965; Threlfall 1978), corroborated by original field notes, and two of Bleakney's unpublished records. We compared these measurements with data for 102 nesting turtles from St Croix, US Virgin Islands (Boulon et al. 1996). Differences in weight between southern nesting and northern foraging turtles (CCL > 140 cm: individuals presumed to be adults) were analysed using constant slope ANCOVA after log transformation.

Entanglement records

From 1997 to 2003, we collected voluntarily reported georeferenced records of leatherbacks entangled in fixed gear in Atlantic Canada.

3.3. Results

We equipped 38 leatherback turtles with satellite tags at sea off Nova Scotia, Canada, during the summers of 1999–2003, and collected observations for 8288 tracking days, with a mean tag transmission life of 218 days. Eleven turtles were tracked for longer than 1 year. While all previous tracking studies have been limited to post-nesting movements of mature females tagged in specific nesting colonies, our sample of the first animals tagged in northern waters encompassed individuals from multiple disparate nesting sites both in their post-nesting and internesting years and included the first mature males (n=11) and juveniles (CCL < 140 cm, n=6) to be tracked via satellite.
Turtles concentrated their movements in waters off eastern Canada and the northeastern United States before assuming southward migrations, spending up to 4 months post-tagging in northern waters (Figure 3.1). While migration start date varied from 12 August to 15 December, most turtles left during October. Twenty-five of the tags transmitted long enough to show southern destinations (eight males, 12 females, five juveniles). While 11 turtles (44%) migrated to waters adjacent nesting beaches, including those along the northeast coast of South America and the Antilles (n=10) and off Panama and Costa Rica (n=1), other turtles migrated to pelagic waters between 5° and 23° N (n=12), or to shelf waters off the southeastern United States (n=2).

All turtles that departed southern waters assumed northward migrations (n=19, six males, seven females, six juveniles), most leaving in February and March (n=11). Twelve tags (32%) transmitted long enough to show a return to the northwest Atlantic, north of 38° N, with turtles typically arriving during June of the year after tagging (range: March 25 to August 16). Moreover, turtles usually returned to within several hundred kilometres of where they occurred the previous year (Figure 3.2). Four tags transmitted long enough to show a second southward trek the following autumn, a phenomenon which has not been previously demonstrated.

In eastern Canada, leatherbacks (measured alive or recovered dead from fishing gear) weighed 33% more (95% confidence interval= 26–40%, n=13, six males, seven females) than turtles of the same carapace length nesting at St. Croix, US Virgin Islands (Boulon et al. 1996) (Figure 3.3). The effect of sex was not statistically significant. Turtles nesting at St. Croix were of comparable size (range= 259–506 kg, n=102; Boulon et al. 1996) to other western Atlantic nesting populations, including Tortuguero, Costa
Rica (mean = 346.8 kg, SD = 55.4, range = 250–435 kg, n=22; Leslie et al. 1996), and French Guiana (mean = 339.3 kg, SD = 41.3, range = 250–415 kg, n=15; Girondot and Fretéy 1996).

From 1997 to 2003, we collected 83 records of leatherbacks interacting with fixed gear in shelf waters off eastern Canada. Of these records, 95% were of turtles entangled in buoy lines by one or both front flippers; 18% of all turtles were reported dead. Five free-swimming turtles were observed trailing attached ropes. As most interactions were voluntarily reported (n=78), these records surely represent only a small fraction of the total number of leatherback-fixed gear interactions occurring in Atlantic Canada.
Figure 3.1. Spatial use by 38 leatherback turtles equipped with Argos satellite tags in waters off Nova Scotia, Canada. Colour denotes the number of days turtle(s) were observed in each hexagon (width: 0.719° longitude, largest height: 0.709° latitude). US pelagic longline reporting areas: (a) Mid-Atlantic Bight, (b) Northeast Coastal and (c) Northeast Distant. Area (c) extends eastward to -20° longitude and northward to 55° latitude, and was closed to US pelagic longline vessels to protect marine turtles. Area (d), Grand Banks. Dashed line: 1000 m depth contour.
Figure 3.2. Return movements of eight satellite-tagged leatherbacks to northern latitudes of the northwest Atlantic. (a, e) Mature females; (f, g) mature males; (b, c, d, h) juveniles. Arrows show direction of movement. All turtles completed return migrations to temperate waters within 1 year of tagging. Dashed line: 1000 m depth contour.
Figure 3.3. Mass vs. curved carapace length for leatherback turtles weighed on nesting beaches at St. Croix, US Virgin Islands (n=102, open symbols, dashed line) (Boulon et al. 1996), and those weighed during their foraging period in Canadian waters (n=13, closed symbols, solid line). Circles: females, triangles: males. Lines fit by constant slope analysis of covariance after log transformation. The effect of sex was not statistically significant.
3.4 Discussion

The extensive tracks of leatherbacks presented here identify previously unrecognized high-use areas in continental shelf and slope waters (Figure 3.1), where, in contrast to pelagic zones, threats to leatherbacks have received little attention. The extended time periods during which leatherbacks use these northern areas place special emphasis on the need to protect turtles there.

Our sample shows that, upon departing northern habitats, leatherbacks do not migrate southward along common paths, but utilize broad expanses of ocean (Figure 3.1). A similar pattern has been shown for leatherback turtles migrating northward after nesting (Ferraroli et al. 2004; Hays et al. 2004a). Moreover, individual turtles in our study did not utilize consistent routes to and from northern areas (Figure 3.2), but exhibited foraging site fidelity to shelf and slope waters off Canada and the northeastern United States.

These are the first tracks to confirm annual round-trip migration in leatherbacks, a phenomenon we observed in juveniles, males and females in their internesting years. A flipper tag recovery has shown that a one-way post-nesting migration to northern waters may take as few as 4 months (Girondot and Fretey 1996). Therefore, return migrations may also be possible for females during their nesting years. While most males appeared to seek coastal areas in tropical waters, females in their internesting years and juveniles more commonly completed the southern part of the migratory loop in pelagic waters. Transatlantic movements have been documented for turtles departing Caribbean and South American nesting beaches (Ferraroli et al. 2004; Hays et al. 2004a), however, all turtles tagged in Canadian waters remained in the western Atlantic while tags were
transmitting. This pattern suggests that turtles occurring in Canadian waters may
principally originate from western, rather than eastern Atlantic nesting beaches.

Considerable energetic costs must accompany the roundtrip migrations of c.
10,000 km undertaken by the leatherbacks in this study. While weights of the same
individuals over the migration cycle are not available, we have presented the first
comparison of weights in northern and southern areas. Nesting female leatherbacks at St.
Croix lose an average of 2.0 kg per nesting (Eckert et al. 1989). Given the average
number of nests for females of this population (Boulon et al. 1996), this amounts to 10.5
kg over the nesting season, an amount far less than the typical weight difference between
the nesting females and the northern animals presented here. This comparison
underscores the significance of temperate feeding areas for this species.

Pelagic longline fishing has led to serious declines in many large pelagic species,
including sharks (Baum and Myers 2004) and loggerhead turtles (Caretta caretta
Linnaeus 1758) (Lewison et al. 2004). The global decline of leatherbacks has also been
largely attributed to incidental capture in fisheries (Spotila et al. 1996, 2000; Eckert and
Sarti 1997; Lewison et al. 2004), with pelagic longlines proposed as a key threat (Spotila
et al. 2000; Lewison et al. 2004). Recent leatherback conservation efforts in the North
Atlantic have focused on reducing interactions with pelagic longlines (Witzell 1999;
Lewison et al. 2004), including a closure affecting US vessels in the Northeast Distant
(NED) reporting area (U.S. Federal Register 2001; Figure 3.1). Surprisingly, none of the
turtles we tagged moved into the small region within the NED (south and east of the
Grand Banks) where pelagic longline effort is focused (Baum et al. 2003; Figure 3.1).
The leatherbacks found interacting with those fisheries may constitute a different set of
individuals. While area closures can be effective, they may not advance species conservation if fishing effort is simply displaced (Baum et al. 2003). In this case, closing the NED would likely increase interactions in other areas where pelagic longlining occurs, if effort were redirected there. Of particular concern are the northeast coastal and mid-Atlantic Bight US reporting areas where many turtles in our sample spend substantial amounts of time (Figure 3.1), and where longlining effort is already high (Baum et al. 2003). However, in pelagic waters, modifying fishing practices rather than implementing area closures may be ultimately more effective in conserving leatherbacks.

While turtle–fishery interactions in pelagic waters have been a major focus of recent conservation measures and controversy, threats to leatherbacks in shelf waters have been largely ignored. This persistent focus on pelagic fisheries is, in part, likely because of the inherent bias and geographical limitations of the source of the majority of data available on leatherbacks: observer data from the pelagic longline fleets, which clearly indicate a high level of turtle–fishery interactions. However, leatherbacks caught in pelagic longlines are normally entangled or hooked externally on this mobile gear (Garrison 2003) and are usually capable of swimming to the surface to breathe (Witzell and Cramer 1995). Therefore, for leatherback turtles, entanglement in pelagic longlines does not necessarily lead to mortality. In fact, observer data reveals that very few turtles are discovered dead on pelagic longlines, although post-release mortality remains unknown. Of 323 leatherbacks observed interacting with US pelagic longline gear in 2001 and 2002, only one (0.3%) was found dead (Garrison 2003). In contrast, as our data suggest, fishing gear anchored to the bottom (fixed gear) in shelf waters may lead to higher mortality per interaction because turtles entangled at depth or at the surface at low
tide will almost certainly drown. As fixed gear fisheries receive relatively little observer coverage, the magnitude of the threat they pose to leatherbacks has not been adequately recognized nor addressed.

As in Canadian waters, leatherbacks are regularly entangled in fixed gear in US waters off New York through Maine (Dwyer et al. 2003). Given that individual turtles in this study spend extended periods in both Canadian and US waters (Figure 3.1), leatherbacks are at risk of entanglement in both areas. Emerging data from coastal waters in the Caribbean and South America show that leatherbacks are also at risk of entanglement there, with large numbers of turtles regularly interacting with artisanal drift gillnet fisheries off the nesting beaches (Chevalier 2001; Lee Lum 2003). In fact, an estimated 3000 leatherback interactions with artisanal gillnet fishing gear occurred off Trinidad in 2000, with reported mortality rates of 28–34% (Lee Lum 2003). Turtles that forage in northern waters of the western Atlantic are among those at risk in these southern coastal areas (Figure 3.1), emphasizing that recovery of these animals will require multinational collaboration.

We are, as yet, unable to evaluate the relative severity of threats posed to leatherbacks by different fisheries and other sources of anthropogenic mortality. An analysis of this magnitude will first require detailed information on rates of capture and post-capture mortality resulting from interactions with fishing gear across the species entire range. Further data on turtle behaviour and movements, independent from fisheries, is also required. Only by synthesizing data from multiple sources will we be able to account for the biases in each and develop effective recovery strategies.
The combination of multiple independent data sets presented here offers new insight into the biology of leatherback turtles and demands that if we are to succeed in conserving these unique reptiles, we must look more broadly to identify where, when and how they are at risk. Protecting turtles in high-use areas may offer the best potential for their recovery, particularly if activities in those areas result in high mortality. In addition, closure of only some areas to pelagic longline fisheries will be of limited conservation value if fishing effort is redirected. By studying the biology and movements of a large sample of turtles of varying sex and size, we have identified key foraging areas in northern waters which fall outside those zones which have traditionally received the most management attention, yet which hold a substantial and largely undocumented threat.

We propose that an important component in the drastic declines of leatherbacks in the Atlantic and the Pacific may have been the underreported yet potentially widespread interactions of turtles with fishing gear in coastal and shelf waters. The impact of leatherback interactions with coastal and shelf fisheries in both temperate and tropical waters may be particularly important, as it is the mature and large subadult turtles, which may offer the greatest potential for population recovery, that aggregate to feed and breed in these areas. As leatherback numbers have reached critically low levels in the Pacific (Spotila et al. 2000), new hope for their recovery may come from studies in the Atlantic, where populations are still large enough to analyse trends. We urge rapid reduction of incidental capture in coastal and shelf fisheries to assist in the recovery of the leatherback worldwide.
Chapter 4. Behaviour of Leatherback Sea Turtles, *Dermochelys coriacea*,

During the Migratory Cycle

4.1. Introduction

Satellite telemetry is now widely used to study the migrations of many marine vertebrates (Le Boeuf et al. 2000; Block et al. 2001; Boustany et al. 2002); however, persistent challenges surrounding instrument attachment and performance over the long-term normally prevent collection of behavioural data throughout complete migratory cycles. Marine turtles have become popular candidates for satellite tracking studies (Papi et al. 1997; Hays et al. 1999; Polovina et al. 2000). Yet, as many species are difficult to find and humanely capture in their oceanic habitat, much of what is known about the large scale movements of these animals is limited to post-nesting behaviour of mature females tagged on nesting beaches. This is true of the leatherback turtle (*Dermochelys coriacea*), the largest of all sea turtle species, now globally endangered and facing possible extinction in the Pacific (Spotila et al. 2000). Shelf and slope waters in temperate and boreal regions of the Atlantic support enhanced zooplankton productivity in the summer and fall (e.g. Myers et al. 1994; McLaren et al. 2001), including large cnidarian species (e.g. *Cyanea capillata*, *Aurelia aurita*) that are prey for leatherbacks (Bleakney 1965; den Hartog and van Nierop 1984; Holland et al. 1990; James and Herman 2001). Seasonal aggregations of leatherbacks in these areas have been verified by aerial surveys (Shoop and Kenny 1992) and fisheries observer data (Witzell 1999). Satellite telemetry suggests that waters off Eastern Canada and the northeastern U.S.A. constitute high use habitat for these animals (James et al. 2005a).
Recent tracking studies of nesting female leatherbacks tagged in the Caribbean and South America show that many turtles travel northward after nesting (Eckert 1998; Ferraroli et al. 2004; Hays et al. 2004a), presumably to take advantage of high seasonal concentrations of prey. While the diving behaviour of leatherbacks has been described as they displace from equatorial nesting areas (Hughes et al. 1998; Hays et al. 2004b), longer term movement data has not been available, particularly for those turtles who use northern waters, to enable comparison of behaviour at northern latitudes with return travel to tropical waters. Here we consider movement, diving and surface behaviour from 25 leatherbacks equipped with satellite transmitters off Nova Scotia, Canada, including ten tracked during round trip migrations between temperate and tropical waters.

4.2 Materials and Methods

Turtles were captured at the surface in waters off Nova Scotia, Canada using a breakaway hoop net operated from a 10.5 m commercial fishing boat. Each turtle was guided up a stern ramp onto a raised platform, where curved carapace length (CCL) and curved carapace width (CCW) were measured, a microchip (AVID™ brand) was implanted in the right shoulder muscle and monel tags (style #49; National Band and Tag Company, Newport, Kentucky) were applied to the rear flippers. Satellite-linked transmitters integrating time-depth recorders (SLTDRs: models SSC3 and SDR-T16, Wildlife Computers, Redmond, WA, USA) and surface time sensors (KiwiSat 101, Sirtrack Ltd., Havelock North, NZ) were attached to the carapace using a custom-fitted harness made of nylon webbing and polyvinyl tubing, integrating corrodbile links to ensure release (Eckert 2002b). Turtles were repeatedly doused with buckets of sea water
while aboard, and were normally released within 30 min of capture. All procedures were approved by the Dalhousie University Committee on Animal Care and licensed by Fisheries and Oceans Canada.

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

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

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

4.3. Results

Fifteen turtles were equipped with SLTDRs and 10 with KiwiSat satellite tags during summer, 2001-2003; 13 off mainland Nova Scotia (44°N 64°W) and 12 off Cape Breton Island (47°N, 60°W). Of the 15 equipped with SLTDRs, there were three mature males, nine mature females, and three subadults (CCL <140 cm) (Figure 4.1). In total, we received 33171 positions (location class 3: 4.4%, 2: 12.2%, 1: 17.7%, 0: 14.9%, A: 21.7%, B: 29.1%) and kept 77% of the total after filtering. SLTDRs on six turtles transmitted long enough to show round-trip migrations to northern foraging areas. During the migratory cycle, turtles were seasonally resident in northern waters; and swam a loop of 6-12,000 km before returning to forage in continental shelf waters off Canada and/or the northeastern U.S.A.
We found consistent patterns of behaviour among all turtles in our sample, which can be used to delineate distinct "phases" of the migratory cycle. Often, changes in multiple measures delineated a shift between phases. To illustrate these phases, we present representative dive data and tracks from two leatherback turtles, turtle A, a mature female (CCL=155.5 cm) tagged in an interesting year, and turtle B, a subadult (CCL=125.5 cm) (Figures 4.2, 4.3). We present dive data for an additional subadult (turtle C: CCL=134.0 cm) and a mature male (turtle D: CCL=168.5 cm) in the supplementary material (section 4.6, Figures S1 and S2).

Phase A encompassed movements of turtles in northern shelf and slope waters (principally north of 38 °N) (Figure 4.2). This phase was characterized by relatively low rates of travel, shallow diving (typically <50 m) and short dive durations (typically <12 min) (Figure 4.3a-h). Shelf waters in this region are generally <200 m deep. The slope waters grade from the shelf down to the abyssal plain at 4000 m and deeper.

The onset of phase B was delineated by increased rates of travel, the start of more consistent movements southward and large changes in diving behaviour. After an initial peak associated with departure from northern foraging areas, rates of travel decreased, but typically were higher, and in many turtles, less variable, than they had been during phase A (Figure 4.3a,b). As turtles moved southward, dive depth and dive duration increased, and the depths sampled by turtles became bimodally distributed (Figure 4.3c-h). The maximum depths of the majority of dives were <6 m, or fell within a range that shifted from 4-78 m to 78-252 m (Figure 4.3e,f), which revealed specific intermediary depth ranges that were not targeted by turtles. Occasional very deep dives, exceeding the user-defined depth ranges of the tags (>400 m, n=12 tags; >450 m, n=3 tags) were also
recorded during this phase. This increasing bimodality in maximum dive depth with decreasing latitude was also readily apparent in dive duration (Figure 4.3g,h).

Consistent northward movement marked the onset of phase C (Figure 4.2). Rates of travel were similar to those during phase B (Figure 4.3a,b), while the bimodality in maximum dive depth and dive duration decreased with movements northward (Figure 4.3e-h). Therefore, the relationship between diving behaviour and latitude was similar to that in the previous phase.

In phase D, turtle movements generally continued northward towards shelf waters off Canada or the northeastern U.S.A. (Figure 4.2); however, there was a drop in average rate of travel and a dramatic change in diving behaviour (Figure 4.3). During this phase, turtles arrived in waters corresponding to the continental slope (Figure 4.2). Maximum dive depth no longer showed a bimodal distribution, and instead was relatively uniform between 4 and 154 m (Figure 4.3e,f). Dive duration showed an abrupt decrease and was generally <24 min (Figure 4.3g,h).

Phase E encompassed movements primarily on the continental shelf and was marked by even shallower and shorter diving than turtles showed in phase D (<50 m, <12 min; Figure 4.3c-h). Patterns of movement and diving behaviour for turtles in this northern phase were very similar to those recorded when animals were in phase A, indicating the completion of one migratory cycle and the initiation of a second.

These phases of the migratory cycle were typical both for female leatherbacks in their internesting years and subadults, all of which spent phases B and C in pelagic waters (Figure 4.1b,c), except for one subadult turtle which entered and exited the Caribbean Sea, but did not stop in nearshore areas (Figure 4.1c) and one mature female which was
resident in waters off southeastern U.S.A. during the first winter post-tagging (KiwiSat transmitter, track not shown). An additional behavioural phase, occurring between B and C, was observed in four mature males in waters adjacent nesting beaches (see supplementary material; section 4.6, Figure S2, turtle D). The dates of transition between phases and the durations of the phases were variable between turtles (Figure 4.4); however, the behavioural patterns within phases (e.g. Figure 4.3; section 4.6, Figure S1 and S2) were similar across turtles.

For the 10 turtles equipped with transmitters integrating surface time counters (KiwiSat: one subadult, seven mature females, two mature males), a maximum of 10% of the day was spent at the surface in most of the areas they utilized (Figure 4.5), with the exception of waters north of 38° N, principally corresponding to phases A, D and E of the migratory cycle, where surface times were highest (max. 41%). Surface times declined as turtles traveled to lower latitudes (phase B), which is consistent with the increasing dive durations recorded during this part of the migratory cycle.
Figure 4.1. Tracks of 15 leatherback turtles equipped with satellite-linked time-depth recorders off Nova Scotia, Canada. (a): mature males, n=3; (b): mature females, n=9; (c): subadults, n=3. Thin dashed line: 1000 m depth contour; bold dashed line: portion of track when location data not received; bordered dashed line: subadult that entered the Caribbean Sea.
Figure 4.2. Tracks throughout the migratory cycle for two leatherback turtles tagged in coastal waters off Nova Scotia, Canada. Phase of the migratory cycle indicated in top left corner of each panel. Bold line: movements during each phase; thin line: movements from previous phases; dashed line: 1000 m depth contour. Start month and day of each phase indicated in bottom right corner of each panel. (a) Turtle A: mature female in internesting year. Data to 18 September 2004. (b) Turtle B: subadult. Data to 22 October 2004.
Figure 4.3. Diving behaviour, ambient water temperature and latitudinal movements of two leatherback turtles tagged in coastal waters off Nova Scotia, Canada, spanning time from tagging until the day before second migration southward. Left column: turtle A; right column: turtle B. Ticks on time axis represent 14-day intervals. (a), (b): Rate of travel (km/h). (c), (d): Proportion of time (per 6-hour sample) spent in different depth ranges. (e), (f): Proportion of maximum dive depths (per 6-hour sample) in different depth ranges. (g), (h): Proportion of dives (per 6-hour sample) of varying durations. (i), (j): Proportion of time (per 6-hour sample) spent in different temperature ranges. (k), (l): Latitudinal movement. Capital letters indicate phases of the migratory cycle. Vertical lines indicate transitions between phases.
Figure 4.4. Timelines of migratory phases for four leatherback turtles equipped with satellite-linked time-depth recorders that completed round-trip migrations to northern foraging areas. Arrows indicate January 1, 2004. Bold letters indicate phase designations for turtle A; sequence identical for turtles B-D. Turtle A: mature female; turtles B, C: subadults; turtle D: mature male. Turtle D showed additional breeding phase within phase C. Ticks on x axis: 31 days.
Figure 4.5. Time (% of 24-hr period) spent at the surface by leatherback turtles equipped with KiwiSat transmitters (n=10). See methods for calculation details.
4.4 Discussion

Leatherback turtles tagged on tropical beaches have been recovered thousands of kilometers away (Pritchard 1976; James 2004; Troëng et al. 2004), attesting to their ability to range across vast areas of ocean. By gathering information on the movements and diving behaviour of many individuals of varied sex and reproductive status, we can begin to understand the biological relevance of these remarkable movements. Turtles in this study have shown movements from shelf and slope waters of the northwestern Atlantic southward through pelagic waters to tropical waters and back to the north all within one year. Movement and diving behaviour show clear differences between legs of this round-trip journey. However, the biological motivations for these changes in behaviour are not always clear, particularly since many of the animals we tracked were not in their breeding or nesting years.

(a) Northern Foraging

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

The determinants of the timing and size of aggregations of medusae, the familiar free-swimming life stage of jellyfish, are poorly understood, but there is general
consensus that aggregations can be the result of two main factors: reproduction and physical oceanographic processes (Graham et al. 2001). For scyphomedusae like *Cyanea capillata* and *Aurelia aurita*, two common prey species of the leatherback turtle (den Hartog and van Nierop 1984), medusae develop after budding from the benthic sessile life stage over the winter or in the early spring. Through spring and summer, the medusae grow, feeding on zooplankton, and persist for 4-8 months before spawning and dying (reviewed by Lucas 2001). *C. capillata* medusae have been recorded annually in the Niantic River Estuary, Connecticut (U.S.A.) from March to late June or early July (Brewer 1989; Brewer and Feingold 1991). However, we have observed leatherbacks feeding on large *C. capillata* off Cape Breton Island, Nova Scotia, consistently until at least late September. This persistence of *C. capillata* into the fall is consistent with observations of this species and *A. aurita* through August and September in fjords in Denmark, Sweden and Japan (Gröndahl 1988; Olesen et al. 1994; Omori et al. 1995).

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

Despite the lack of direct distributional data on gelatinous plankton in areas frequented by turtles in this study, many lines of evidence lead us to suggest that the leatherbacks we tracked use northern shelf and slope waters primarily for foraging. Low rates of travel, previously linked to foraging in other areas (Ferraroli et al. 2004), were
observed in phases A, D and E. Moreover, leatherbacks sighted off Atlantic Canada (corresponding to areas frequented in phases A and E) are regularly observed handling jellyfish (*Cyanea* sp.) in their mouths at the surface (James and Herman 2001). Such prey handling normally involves repeated elevation of the head, which appears to facilitate swallowing (Eisenberg and Frazier 1983; James and Herman 2001). We frequently observed this behaviour, preceded by turtles biting large jellyfish into more manageable pieces (M.C.J., personal observation). While the occurrence of leatherbacks in potential foraging areas may be positively correlated with abundance of jellyfish at the surface (Grant et al. 1996), fieldwork off Nova Scotia has revealed that jellyfish are often not visible at the surface in the vicinity of turtles when prey handling is observed (James and Mrosovsky 2004). Therefore, leatherbacks foraging in shelf waters off Canada and the northeastern U.S.A. appear to search for and capture much of their prey at depth (Figure 4.3), before returning to the surface to consume it (James and Mrosovsky 2004).

This pattern of foraging behaviour is consistent with the high proportion of time spent at the surface in northern waters (Figure 4.5). Increased surface time at northern latitudes may also reflect basking, as we have routinely observed turtles resting at the surface during the middle part of the day and evening with both front and rear flippers extended and their heads lowered in the water. This posture, combined with the leatherback’s dark dorsal colouring, may maximize absorption of solar radiation, facilitating both digestion and maintenance of body temperature in northern foraging areas, where both cold ambient temperatures and consumption of large volumes of cold prey (Davenport 1998) may present thermal challenges. The surface time analysis presented here suggests that northern foraging areas may offer the best opportunities for
estimating leatherback abundance from aerial surveys, due to the relatively large proportion of time spent at the surface in these areas.

Leatherback movements during phase D also appear to indicate foraging. Rate of travel dropped markedly from that shown in phases B and C, becoming consistent with rates of travel shown in phases A and E (Figure 4.3a,b). Dive durations decreased and maximum dive depths lost the bimodality so distinctive of phases B and C (Figure 4.3e-h). If indeed these behaviours represent foraging, we suggest that gelatinous prey in these pelagic and slope waters may be distributed at greater mean depth, and perhaps in a greater range of depths, than in the shelf areas further north.

(b) *Southern Movements*

As leatherbacks left northern waters, they showed consistent changes in patterns of depth utilization, dive duration, rate of travel and time spent at the surface. What cues the onset of southward movements (phase B) is unclear; the departure date is variable among turtles (Figure 4.4). However, in most turtles, it was marked by a rapid increase in rate of travel over the first few days to weeks. As average rates of travel during phases B and C are well above those associated with time spent in northern foraging areas, we expect that turtles are primarily transiting during these phases. While other sea turtles mainly conduct short and shallow dives during open ocean movements (Papi et al. 1997; Hays et al. 1999; Godley et al. 2003), the leatherbacks we tracked spent extended periods both in the upper-most depth bin (0-6 m) and at depths ≥24 m, undertaking dives among the longest recorded during the migratory cycle (>52 min). The gradual changes in dive duration and dive depth did not appear to be related to water depth, as both continued to
increase even after turtles had moved far south of the continental slope and were travelling through areas characterized by relatively uniform bathymetry. Below, we consider alternative hypotheses to explain these changes in diving behaviour.

(i) *Predator avoidance*

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

(ii) *Foraging*

Given the lack of distributional data on leatherbacks’ primary prey in open ocean areas, it is difficult to predict how prey distribution might be influencing turtle diving behaviour through phases B and C. Post-nesting female leatherbacks in tropical pelagic waters show diurnal changes in diving behaviour consistent with a response to the distribution of gelatinous prey, which suggests foraging behaviour (Hays et al. 2004b). While moving between temperate and tropical waters, the turtles in this study showed a bimodal distribution of dive depths and durations somewhat similar to that reported by
Hays et al. (2004b), and diel dive patterns that may correspond to the diel vertical migrations of their prey (M.C. James, C.A. Ottensmeyer, S.A. Eckert and R.A. Myers, unpublished data). However, our study and that of Hays et al. (2004b) are not strictly comparable due to differences in temporal resolution of the data and geographic zone considered. We also expect that there are large differences in body condition between female turtles that may not have eaten during a two-month nesting period (e.g. Hays et al. 2004b) and turtles that have foraged in northern areas for several months (this study). Indeed, leatherbacks that use foraging areas off eastern Canada are 33% heavier than nesting turtles of the same carapace length (James et al. 2005c). Therefore, while some opportunistic foraging may occur among turtles departing northern foraging areas, feeding may not be their primary focus at that time. Average rates of travel much higher than those on the foraging grounds suggest that the focus of movements during phase B are primarily related to migration. However, in the southernmost portion of the migratory cycle, reduced rates of travel suggest that some foraging may occur, which is consistent with the interpretation of tropical foraging by Hays et al. (2004b). Moreover, some of the turtles we tracked traveled longitudinally for up to several hundred kilometers before turning north (e.g. Figure 4.1b), which may also indicate foraging in tropical waters. After this brief period, northward travel during phase C revealed similar patterns to behaviour in phase B.

(iii) *Seasonal buoyancy changes*

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

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

(iv) Thermo regulation

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

(c) **Migratory cycle**

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

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

Mature male leatherbacks tagged off Nova Scotia complete round-trip migrations from northern foraging areas to southern, often coastal, breeding destinations, where they can remain resident for up to several months (James et al. 2005a). A similar pattern is presumably true for females in their nesting years, as animals tagged in Canadian waters have been observed nesting the following spring (M.C.J., unpublished data), and turtles have been captured in Canadian waters within six months of nesting (Goff et al. 1994). Therefore, the movements of mature male leatherbacks and females in their nesting years is consistent with a migratory cycle involving travel between disparate feeding and nesting sites observed in other species of sea turtle (Luschi et al. 1998; Godley et al. 2002a).
Our results also illustrate that, with few exceptions, mature females in their internesting years and subadults remain largely in pelagic waters far from shore during the southern portion of their migration. This pattern is particularly intriguing, since for these individuals, in contrast to mature males and females in their nesting years, there is not an obvious reproductive benefit for extensive southward movements.

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

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

4.5 Conclusion

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

(Figures S1 and S2)

Figure S1. Diving behaviour, ambient water temperature, longitudinal and latitudinal movements of sub-adult leatherback turtle (turtle C: curved carapace length: 134.0 cm) tagged in coastal waters off Nova Scotia, Canada, spanning time from tagging until day before second migration southward. Left column: turtle A; right column: turtle B. Ticks on time axis represent 14-day intervals. a: Proportion of time (per 6-hour sample) spent in different depth ranges. b: Proportion of time (per 6-hour sample) spent in different temperature ranges. c: Proportion of dives (per 6-hour sample) of varying durations. d: Proportion of maximum dive depths (per 6-hour sample) in different depth ranges. e: Longitudinal movement. f: Latitudinal movement.
Figure S2. Diving behaviour, ambient water temperature, longitudinal and latitudinal movements of a mature male leatherback turtle (turtle D: curved carapace length: 168.5 cm) tagged in coastal waters off Nova Scotia, Canada, spanning time from tagging until day before second migration southward. Left column: turtle A; right column: turtle B. Ticks on time axis represent 14-day intervals. a: Proportion of time (per 6-hour sample) spent in different depth ranges. b: Proportion of time (per 6-hour sample) spent in different temperature ranges. c: Proportion of dives (per 6-hour sample) of varying durations. d: Proportion of maximum dive depths (per 6-hour sample) in different depth ranges. e: Longitudinal movement. f: Latitudinal movement.
Chapter 5. Diel Diving Patterns of Leatherback Sea Turtles in Northern Foraging Areas and During Southward Migration

5.1. Introduction

The study of many organisms has revealed diel cycles (patterns which repeat daily), in behaviour. A common pattern among marine organisms, diel vertical migration (DVM), normally involves descent to deeper waters at dawn, followed by an ascent towards the surface at dusk (Hays 2003). DVM has been documented across a diverse range of taxa that includes small benthic herbivores (Rogers et al. 1998), and large pelagic vertebrates (Musyl et al. 2003; Weng and Block 2004). However, such diel movements, which are often mediated by light levels, have been most widely reported in zooplankton (e.g., Forward 1988). Interpretation of movement data collected from several planktivores has therefore been enhanced by understanding DVM in their prey. For example, diel changes in the depth preferences of basking sharks, *Cetorhinus maximus*, have recently been shown to be consistent with a response to DVM in zooplankton (Sims et al. 2003). Similarly, DVM in ocean sunfish, *Mola mola*, may represent tracking of gelatinous zooplankton (Cartamil and Lowe 2004).

Like the ocean sunfish, the leatherback turtle, *Dermochelys coriacea*, is a large marine vertebrate that exploits gelatinous zooplankton (Bleakney 1965; den Hartog and van Nierop 1984). The leatherback is the only marine turtle to specialize on gelatinous prey. It is also unique amongst sea turtles in its ability to inhabit cold northern waters (James and Mrosovsky 2004), with some adult and subadult turtles completing annual round-trip migrations from tropical waters to temperate waters (James et al. 2005c) to
forage on large jellyfish (James and Herman 2001). Diel dive patterns have been described for female leatherbacks during internesting intervals in tropical waters (Eckert et al. 1989; Eckert et al. 1996; Eckert 2002b) and during departure from nesting areas (Hays et al. 2004b). However, analyses of diel patterns of diving behaviour have not been reported for turtles in northern foraging areas nor during southward migration from these habitats.

Both field and experimental studies of gelatinous plankton suggest that diel vertical migration is normally light-dependent in these organisms and usually involves upward movement in the water column at dusk, and a downward movement at dawn (e.g. Mills 1983; Arkett 1984; 1989; Schuyer and Sullivan 1997; Bamstedt et al. 2001; Benovic et al. 2005), although reverse vertical migrations, and even an absence of vertical migration have been reported for some species (e.g. Mills 1983; Benovic et al. 2005). To determine if diving behaviour in leatherbacks parallels the normal pattern of diel vertical migration in gelatinous planktonic prey, we present diel patterns of diving and surfacing behaviour in foraging and migratory periods for leatherbacks equipped with satellite-linked dive recorders off Nova Scotia, Canada.

5.1. Materials and Methods

During the summers of 2001-2003, we captured leatherback turtles at the surface in waters off Nova Scotia, Canada using a breakaway hoop net operated from a 10.5 m commercial fishing boat (for methods, see James et al. 2005c). We attached satellite-linked time-depth recorders (SLTDR; models SSC3 (n=13) and SDR-T16 (n=2), Wildlife Computers, Redmond, WA, USA) to the carapace using a custom-fitted harness made of nylon webbing and polyvinyl tubing (Eckert 2002b). Harnesses incorporated corrodible
links to ensure their eventual release. Turtles were repeatedly doused with buckets of sea water while aboard, and were normally released within 30 min of capture. All procedures were approved by the Dalhousie University Committee on Animal Care and licensed by Fisheries and Oceans Canada.

SLTDRs collected and relayed data on time at depth, time at temperature, maximum dive depth and dive duration, binned within 14 user-defined data ranges over 6-hr collection periods. Periods were set such that one consistently encompassed night and one encompassed day: (Night: 2100-0300; Morning: 0300-0900; Day: 0900-1500; Evening: 1500-2100; Atlantic Daylight Time). Time at depth and time at temperature reflected all time when SLTDRs were submerged, whereas dives were registered only when turtles descended below 4 m (n=12 tags) or 6 m (n=3 tags). While SLTDRs simultaneously record data from different channels (e.g., depth, temperature), data are transmitted in histogram format to increase ease of transfer via the limited bandwidth of the Argos satellite system (Fedak et al. 2002). This decreases the resolution of the data; however, patterns of depth utilization and dive duration can be readily identified and related to the spatial and temporal characteristics of horizontal movements. SLTDRs also transmitted the combined proportion of each 6-hr period that the turtle was very close to the surface (<2 m: n=12; <3 m: n=3) or at the surface. These surface values for each period were matched to median daily locations for each turtle (see below) and the median surface time was found for each hexagonal area bin.

SLTDRs were located with the Argos system (http://www.argosinc.com). Argos assigns location class, an index of positional accuracy, to all derived locations. The analyses presented here used all positions with location classes 3, 2, or 1 (categorized to
lie within 150 m, 150-350 m, or 350-1000 m, respectively, of the tag's true position). We also used location classes A, B, and 0 (categorized to lie 1000m+ from the tag’s true position) if they yielded rates of travel $\leq 5$ km/h, consistent with 99% of travel rates calculated for a sample of 38 turtles tracked for an average of 218 days (James et al. 2005c). We omitted positions of location quality Z. From these filtered locations, we calculated median daily locations for each turtle, interpolating positions assuming constant speed and direction for days in which no positions were obtained for a given turtle.

Statistical Methods

To identify potential diel differences in turtle diving behaviour and ambient temperature among 6-hr periods, we fit linear mixed effects models in SAS (Littell et al. 1996). We assumed the variability among turtles was a normal random variable, to account for dependence among observations within a turtle. The variables of interest are listed in Tables 5.1 and 5.2; the values for model parameters were found using restricted maximum likelihood. Since the SLTDR tags present data binned into depth, time or temperature ranges, we used midpoints of each range for relevant calculations on variables such as means, ranges, maximums and minimums.

Our mixed effects models followed a similar general form. For example, the mean depth $y_{pid}$ in period $p$, turtle $i$ and day $d$, was modeled as:

$$y_{pid} = \mu_p + \alpha_i + e_{pid},$$
where $\mu_p$ is the mean depth for period $p$, the variability among turtles is described as a normal random variable $\alpha_i$ (i.e. $\alpha_i \sim \text{iid } N(0, \sigma_\alpha^2)$), as were the errors ($e_{pdi} \sim \text{iid } N(0, \sigma_e^2)$).

Of interest is $\mu_p$ and whether it differs between periods. To test for differences between periods, we used a Wald test (Littell et al. 1996). For percentages, we used a logit transformation and report logit back-transformed results. For other response variables, log transformations were made when it was found that this improved the normality of the residuals; we report model results back-transformed to the original units in these cases. In all cases, the transformations did not change the conclusions of the modeling. Confidence intervals (C.I.) for each estimated parameter are presented as 95%.

Mixed models were fit separately to data corresponding to two phases of the migratory cycle: when turtles were in northern foraging areas (7 days post-tagging to 7 days before start of sustained southward movements) and when they were traveling southward (between 36° and 21°N latitude) in the first season post-tagging (Figure 5.1). Eight turtles transmitted in the north long enough (> 14 days) to be included in the models. Some analyses include only seven northern turtles, to exclude, where appropriate, one SLTDR programmed with different data range bins. Thirteen turtles transmitted during southward migration, ten with identical tag settings. We focus on the differences between the night and day periods since the morning and evening periods each encompass dramatically different light levels.
5.3. Results

Fifteen turtles were equipped with SLTDRs: seven off mainland Nova Scotia (44°N, 64°W), and eight off Cape Breton Island (47°N, 60°W). These included three subadults (curved carapace length: CCL <140 cm), nine mature females, and three mature males. All turtles showed consistent dive patterns.

Northern Foraging

Ten turtles remained in shelf and slope waters off Eastern Canada and the northeastern United States for between 5 and 121 days after tagging before migrating south. While in these northern waters, turtles exhibited similar depth use and dive durations through all of the 6-hour periods (see Figure 5.2 for representative turtle). Most of each period was spent in the top 6 m of the water column during all four periods (e.g., mixed model estimates: night period: 67%, day period: 62%; see Table 5.1 and Figure 5.3 for day-night comparison). Mean turtle depth (by time) during this northern phase was very shallow (night: 7.1 m; day: 8.6 m), and maximum depth per period averaged close to 30 m (night: 28 m; day: 34 m). Statistically, mean depth, maximum depth and the proportion of time spent within 0-6 m of the surface differed significantly between the night and day periods (Table 5.1).

Turtles made dives of similar average duration (night: 4.9 min; day: 4.7 min), and showed a similar range of dive durations (Table 5.1; Figures 5.2, 5.3) between night and day periods during this northern phase. Mean water temperature sampled by the turtles did not differ statistically between day and night and (model estimates: night: 16.7°C; day: 17.0°C; Table 5.1; Figures 5.2, 5.3).
Southward Migration

After leaving northern foraging areas, diel differences in diving behaviour became very pronounced among all 13 turtles. During the day period, turtles spent substantial amounts of time in the top 6 m of the water column (mixed model estimate: 82%, see Table 5.2, Figures 5.2, 5.3). However, turtles also tended to make their deepest dives (often > 400 m) during the day period. These very deep dives were limited to the morning, day and evening periods (13/13 turtles). During the night period, turtles spent significantly less time in the top 6 m (20% of night period) than during the day and showed more concentrated use of depths between 24 and 100 m (night mean depth: 40 m; day mean depth: 18 m; Figures 5.2, 5.3; Table 5.2).

Dive durations during southward migration increased with decreasing latitude, but showed marked diel differences (Figure 5.2). During the night period, turtles made long dives (model estimate for maximum duration: 34 min; Table 5.2; Figures 5.2, 5.3), but with a fairly limited range of dive durations (range: 15 min; Table 5.2; Figures 5.2, 5.3). During the day period, turtles made these long dives, but also made many short dives, such that the range of durations during the day was wider (21 min) and the mean duration lower (13 min, Table 5.2) than the mean duration during the night period (28 min). The differences between the night and day periods presented here were all significantly different (p<0.0001, Wald test on modeled parameters; Table 5.2).

Water temperature sampled by turtles increased as turtles moved south. Mean temperatures during the day and night periods were similar (night: 25.0°C; day: 25.3°C; Table 5.2; Figure 5.3).
Surface Time

Surface time (0-2 m (n=12 tags) or 0-3 m (n=3 tags)), for all 15 turtles corroborate the diel trends outlined above (Figure 5.4). While in shelf and slope waters of the northeastern U.S. and Canada, turtles spent a modeled average of 43% of the night period at the surface (Table 5.3). During the day period, the average surface time was 50%, although these levels were quite variable from day to day within and between turtles (Figure 5.5). Mixed modeling of the mean surface time per period revealed significantly higher surface times in the day and evening periods than in the night and morning periods (Table 5.3; p<0.0001 in pairwise comparisons, Wald test).

During southward migration through pelagic waters, leatherbacks showed much larger differences in surface time between periods. Once turtles had left continental shelf and slope waters, the average percentage of time they spent at or near the surface was very high during the day period (77%), and was much lower during the other periods, particularly during the night (night: 18%; morning: 29%; evening:29%; Table 5.3). Leatherbacks present in temperate waters off Canada and the northeastern United States showed only small diel differences in measures of diving behaviour, and spent more time at or just below the surface during day and evening periods versus during the morning and night. After departing northern waters, diel differences in diving behaviour and surface activity became more pronounced. Mean dive depth and mean dive duration were much greater at night versus during the day (depth: 40 m versus 18 m, duration: 28 min versus 13 min, Table 5.2). Turtles migrating southward also spent far more time at or just below the surface during the day versus during the night (77% versus 18%, Table 3).
Table 5.1. Results of mixed models for turtles during northern foraging
<table>
<thead>
<tr>
<th>Response Variable</th>
<th>Transformation*</th>
<th>n turtles</th>
<th>Period</th>
<th>Estimate</th>
<th>Lower 95% C.I.</th>
<th>Upper 95% C.I.</th>
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</thead>
<tbody>
<tr>
<td>Mean depth (m)</td>
<td>log</td>
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<td>night†</td>
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<td>day†</td>
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<td>7.0</td>
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<td>69</td>
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<tr>
<td>Maximum depth (m)</td>
<td>log</td>
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<td>night†</td>
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<td>37</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
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<td></td>
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<td>(min)</td>
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<td></td>
<td>day</td>
<td>2.4</td>
<td>2.2</td>
<td>2.7</td>
</tr>
<tr>
<td>Percentage of dives</td>
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<td>26</td>
<td>18</td>
<td>36</td>
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<td>0-4 min in duration</td>
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<td>33</td>
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<tr>
<td>Mean duration (min)</td>
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<td>night</td>
<td>4.9</td>
<td>4.3</td>
<td>5.5</td>
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<td></td>
<td></td>
<td>day</td>
<td>4.7</td>
<td>4.2</td>
<td>5.3</td>
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<tr>
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<td>night</td>
<td>16.7</td>
<td>15.0</td>
<td>18.6</td>
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<td>------</td>
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</tr>
<tr>
<td></td>
<td>day</td>
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<td>15.2</td>
<td>18.7</td>
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*Some response variables transformed before fitting models; results presented back-transformed to original units. None of transformations affected inferences. †significantly different between periods at p<0.0001; + p=0.005; others NS.
Table 5.2. Results of mixed models for turtles during southward migration ($36-21^\circ N$)
<table>
<thead>
<tr>
<th>Response Variable</th>
<th>Transformation*</th>
<th>n turtles</th>
<th>Period</th>
<th>Estimate</th>
<th>95% C.I. Lower</th>
<th>95% C.I. Upper</th>
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</thead>
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<td>Mean depth (m)</td>
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<td>14</td>
<td>23</td>
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<tr>
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<tr>
<td>0-6 m</td>
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<td>10</td>
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</tr>
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<td>night</td>
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*Some response variables transformed before fitting models; results presented back-transformed to original units. None of transformations affected inferences. All comparisons between periods significantly different at p<0.0001, with the exception of mean temperature: p < 0.02.
Table 5.3. Results of mixed models estimating the average percentage of time turtles spent at or near the surface (0-2 m).

<table>
<thead>
<tr>
<th>Leg of track*</th>
<th>Transformation</th>
<th>n turtles</th>
<th>Period</th>
<th>Estimate</th>
<th>Lower 95% C.I.</th>
<th>Upper 95% C.I.</th>
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<tbody>
<tr>
<td>Northern foraging</td>
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<td>night</td>
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<td>48</td>
<td>55</td>
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<td>Southward migration</td>
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<td>night</td>
<td>18</td>
<td>13</td>
<td>25</td>
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<td>22</td>
<td>38</td>
</tr>
</tbody>
</table>

*Models fit separately for northern foraging time and southward migration. Values logit back-transformed to original units. Statistical differences: northern foraging: night = morning < day = evening; southward migration: night < morning = day < evening. =:NS; <: significantly smaller at p<0.0001.
Figure 5.1. Satellite-derived positions of turtle A (mature female, CCL = 141.5 cm), tagged on 16 August 2001 off Nova Scotia, Canada. Dashed horizontal lines show latitudinal boundaries of region included in analyses of southward migration (21° and 36° N latitude). Arrow shows direction of movement. Final transmission received 30 March 2002. Inset: enlargement of region marked with dashed box. Track between point 1 (7 days post-tagging) and point 2 (7 days before start of migration behaviour) included in analyses of northern foraging. Dotted line: 1000-m depth contour; x axis: degrees longitude; y axis: degrees latitude.
Figure 5.2. Time at depth, dive duration, water temperature and latitudinal position of turtle B (subadult, CCL = 134.0 cm). Colour panels generated from tag which reported data within 14 user-defined ranges for each variable. Coloured line in each range (separated by dotted lines) indicates percentage of time or dives in that range, for a 6-hr period. Night: 2100-0300; morning: 0300-0900; day: 0900-1500; evening: 1500-2100 hours. Left column: percentage of time (6-hour period) spent at different depth ranges. Depth ranges: 0-6m, 6-12m, 12-18m, ..., >400m. Middle column: percentage of dives (per 6-hour period) of different durations. Duration ranges: 0-4min, 4-8min, 8-12min, ..., >52min. Right column: percentage of time (6-hour period) spent in different temperature ranges (°C). Temperature ranges: <7.9°C, 7.9-10.0°C, 10.0-11.9°C, ..., >31.8°C. Bottom row: latitudinal movement. Dashed lines in each latitude panel show timespans of data used in mixed models (Table 1-3; Fig. 3) for foraging time (left) and southward migration (right); x axis: degrees longitude; y axis: degrees latitude.
Figure 5.3. Back-to-back histograms of measures of diving behaviour and water temperature sampled in night period (dark bars, 2100-0300 hours) and day period (white bars, 0900-1500 hours) for three turtles: B (subadult, CCL=134.0 cm), C (mature female, CCL=155.0 cm), and D (mature male, CCL=168.5 cm). Three left columns show mean data during time spent in northern foraging areas; three right columns show mean data for southward migration as defined for mixed models. * denotes presence of bars between 0.005-0.05. a) Proportion of time (of six-hour period) spent in different depth ranges. Depth ranges: 0-6m, 6-12m, 12-18m, …, >400m. b) Proportion of dives whose maximum depth fell in different depth ranges. Depth ranges: 0-6m, 6-12m, 12-18m, …, >400m. c) Proportion of dives in different duration ranges. Durations: 0-4min, 4-8min, 8-12min, …, >52min. d) Proportion of time (of six-hour period) spent in different temperature ranges. Temperature ranges: <7.9°C, 7.9-10.0°C, 10.0-11.9°C, …, >31.8°C.
Figure 5.4. Median surface time (<2m: n=12 turtles; <3m: n=3 turtles) for (a) night and (b) day periods within hexagonal area bins (width: 0.917 degrees latitude; largest height: 1.001 degrees longitude).
Figure 5.5 Percent time spent at the surface for two turtles during six-hour periods. Left column: turtle B, 0-2m; right column: turtle A, 0-3m). Night: 2100-0300; morning: 0300-0900; day: 0900-1500; evening: 1500-2100 hours. Bottom row: latitudinal movement. Dashed lines in each latitude panel show timespans of data used in mixed models (Table 3) for foraging time (left) and southward migration (right).
Figure 5.6. Dorsal view of leatherback turtle head showing the “pineal spot” or “pink spot”. Maximum head width approximately 24 cm.
5.4 Discussion

Diel vertical migration (DVM) has been interpreted as a means by which organisms avoid predators or maximize feeding efficiency, with a trade-off between these motivations shaping DVM in some species (Loose and Dawidowicz 1994; Bollens 1996). However, in many cases, the adaptive significance of DVM behaviour is still unclear. This is true for leatherback turtles, as there is little information available on where, when and how this species forages. Our results demonstrate that leatherback diving behaviour does not consistently parallel the most common pattern of DVM reported for gelatinous plankton, but may be influenced by it. Moreover, our results show that leatherback diving does not follow a specific diel pattern across the species’ range. Instead, diel diving patterns change as turtles use different habitats, including migratory and temperate feeding areas.

Northern areas

The diving behaviour of turtles in northern foraging areas revealed very minor diel differences, with mean and typical maximum dive depths only several metres different during the night versus during the day (Figure 5.2, 5.3, Table 5.1). In multiple measures of dive duration, no statistical difference was found between day and night periods. Together, these findings support an absence of strong diel changes in northern activity for the leatherbacks in this study (Tables 5.1, 5.3). Foraging behaviour in northern waters has been confirmed through field observations (James and Herman 2001; James and Mrosovsky 2004). We suggest that once leatherbacks locate patches of jellyfish prey in these areas, they can be profitably exploited throughout the day and night.
The relatively shallow depth range used by turtles in northern foraging areas, and particularly shelf waters, suggests that leatherbacks do not have to undertake deep dives to locate jellyfish in these areas. The small overall changes in depth use which we report here may represent turtles tracking diel vertical migrations of their gelatinous planktonic prey, as has been suggested to explain diving behaviour in tropical waters (Eckert et al. 1989; Hays et al. 2004b). However, clearly, if this is the case, diel vertical migration in *Cyanea capillata* and other jellyfish forage species is likely occurring at the scale of metres, or at most, tens of metres, rather than hundreds of metres. This pattern of diving presumably necessitates little additional energy expenditure on the part of the turtles to reach their prey during daylight hours than during the night.

While using northern waters, leatherbacks spent slightly more time near the surface during the night than during the day (0-6 m, not including the surface; Table 5.1). However, surface time itself (0-2 m, including surface time, n=7 turtles) was significantly higher during the day than during the night. At sea off Nova Scotia, we regularly see turtles resting or swimming at the surface from late morning through to dusk. We interpret these activities as basking, behaviour which may be important in digesting large volumes of cold prey in temperate waters. Therefore, while turtles may forage throughout the day and night in northern waters, daytime foraging appears to be punctuated by periods of basking; this may explain the higher daytime and evening surface times we observed. Basking behaviour is likely not necessary during southward migration, as turtles are both generating heat metabolically and are encountering warmer water temperatures associated with lower latitudes.
Southward migration

In contrast to their behaviour in northern foraging areas, leatherbacks showed dramatic diel differences in behaviour while moving southwards. Turtles spent a relatively large proportion of time at and near the surface (0-6 m) during the day; however, the deepest dives also occurred during the day (e.g., Figure 5.2, 5.3). During the night, the amount of time spent at 0-6 m decreased markedly and turtles spent much more time at depths >24 m. At the six-hour resolution of our data, these results are consistent with the diel vertical movements of female leatherbacks in tropical waters (Eckert et al. 1989; Hays et al. 2004b). For example, Hays et al. (2004b) found that leatherbacks spent the most time diving beyond 10 m during the middle of the night and while the deepest dives recorded were exclusively diurnal, these turtles mainly used waters <10 m from the surface during the day. This pattern of diving may represent leatherbacks responding to the diel vertical migrations of their gelatinous prey, with turtles dedicating more time to foraging during the night, when prey have ascended to depths where they can be most profitably exploited. If leatherbacks that forage at northern latitudes continue to feed as they migrate southward, we would predict that corresponding diel dive patterns would be shaped by the costs of searching for and exploiting prey at various depths relative to the energetic benefits to the individual (Hays et al. 2004b).

However, one must be cautious in drawing parallels between the behaviour of female leatherbacks during and in the first several months following their nesting season (Hays et al. 2004b) and that of juvenile and adult leatherbacks of both sexes as they depart northern waters following several months of foraging (as presented here). Nesting leatherbacks are in much leaner body condition than their northern foraging counterparts.
(James et al. 2005c) and would be expected to dedicate more time to foraging versus transiting. In contrast, the high rates of travel characteristic of turtles leaving northern waters (James et al. 2005b), combined with extended foraging prior to departure, suggest that these animals may be primarily focused on promptly returning to breeding and/or foraging areas in distant tropical waters, rather than foraging continuously along the way. As regular deep diving would greatly decrease horizontal movement (Eckert 2002b), we would predict that to maximize migratory speed and energy efficiency, turtles would preferentially forage when prey are presumably at shallower depths (during the night). Swimming long distances at shallow depth by leatherbacks is consistent with maximizing energetic efficiency (Eckert 2002b). Turtles, like other marine vertebrates, maximize swimming efficiency by traveling a minimum of 1.5 times their body diameter just below the surface (Blake 1983), and it has been proposed that leatherbacks use this strategy when traveling long distances. We therefore suggest that in deep waters, migrating turtles may spend little time foraging during the day, in order to maximize energetic efficiency for long distance travel. Relatively infrequent deep dives during daylight hours (Figure 5.2) may represent periodic foraging or may be involved in thermoregulation (James et al. 2005b).

**Navigation**

Differences in leatherback diving behaviour between day and night during migration may also reflect how these turtles access cues that assist in navigation across vast expanses of ocean. While sensitivity to magnetic field intensity and to magnetic inclination angles (which are strongly correlated with latitude) have been proposed to play key roles in the transoceanic migrations of sea turtles (Lohmann and Lohmann 1994,
1996), these animals may use other cues to orient, including a time-compensated sun compass (Avens and Lohmann 2003). This is consistent with results from studies of amphibians showing that when the sun is visible, these organisms obtain directional information from a sun compass, rather than the magnetic compass (e.g., Adler 1976).

Magnetic compass orientation has been shown to be sensitive to the wavelength and/or intensity of ambient light in several species, including some amphibians, insects, and birds (for a review, see Phillips et al. 2001). Moreover, in one species, the eastern red-spotted newt (*Notophthalmus viridescens*), there is evidence for a direct effect of light on the perception of the magnetic field (Deutschlander et al. 1999a). Eckert (2002b) proposed that female leatherbacks may use a sun compass to navigate back to nesting beaches during the internesting interval. If light intensity and/or wavelength are involved in leatherback navigation, these turtles must be able to accurately perceive and evaluate light cues. Visual assessment of light cues is the most obvious mechanism; however, in some amphibians, extraocular photoreceptors located in the pineal gland and associated structures have been found to influence orientation to polarized light (Taylor and Adler 1978). The same photoreceptors believed to mediate magnetic compass orientation of newts (Deutschlander et al. 1999b) are also found in some reptiles (Phillips et al. 2001). Therefore, it is possible that the pineal complex of leatherback turtles may be similarly instrumental in processing directional information for compass orientation.

The pineal complex is well situated for receiving light cues in the leatherback, as it is situated below a conspicuous thin layer of lightly-pigmented skin on the dorsal surface of the head (Figure 5.6). This feature, known as the “pineal spot” or “pink spot” (McDonald et al. 1996) is exposed on each surfacing and is on the same plane as the
ocean's surface while turtles are swimming at or just below the surface. While subadult and adult leatherbacks have pink spots, this feature is not present in any other marine turtle, as the dorsal surface of other turtles' heads is covered with scales rather than skin. The function of the pink spot in leatherbacks is unknown. Experimental studies of newts which have shown that exposure of the dorsal surface of the head facilitates detection of light and subsequent magnetic compass orientation in these animals (Deutschlander et al. 1999b). This appears consistent with our hypothesized role of the pink spot/pineal complex in leatherback navigation.

Beyond the morphological evidence, the diel changes in behavior reported here are consistent with the use of the pineal complex as a migratory guidance mechanism in leatherbacks. During migration, turtles spent more time near the surface during the day versus during the night. This would facilitate continuous reception of sunlight during daylight hours. Moreover, large diel differences in the amount of time spent at or near the surface were not apparent in phases of the migratory cycle when navigation was presumably not as critical, such as during the foraging period in northern waters.

**Diel patterns in ambient temperature**

During both the northern foraging period and southward migration, SLTDRs attached to turtles recorded warmer temperatures during the day versus during the night (Figures 5.2, 5.3). As mean and maximum depth and the proportion of time logged in the shallowest depth range (0-6 m) did not vary much by time of day in northern waters, the warmer daytime temperatures likely mainly represent activity at shallow depths affected by solar warming of the ocean's surface. By spending more time at the surface during the day, southward migrating turtles would similarly experience elevated temperatures
associated with solar warming of the surface layer. However, during migration, SLTDRs also sampled a broader range of ambient temperatures during the day, principally reflecting exploitation of a wider range of depth, and therefore temperature, during the day (Figures 5.2, 5.3).

Implications for aerial surveys

There are considerable challenges inherent in estimating leatherback abundance in foraging areas. Aerial surveys are the most commonly used method for locating turtles over large areas of ocean. However, they are costly and must be limited to those days when both weather and sea conditions are favorable for detecting turtles at or near the surface. Moreover, while large scale aerial survey programs in northwest Atlantic waters have collected observations of leatherbacks over periods of several years, there has been little confidence in the resulting estimates of turtle abundance because surface time correction factors have not been available (Shoop and Kenny 1992).

In a separate analysis, data from a different group of turtles showed that, at 24-hr resolution, leatherbacks spent less time at the surface once they moved from temperate foraging areas to lower latitudes (James et al. 2005b). The current analysis reveals diel changes in diving and surfacing behaviour, which are particularly pronounced during migration (Figures 5.4, 5.5; Table 5.3). Moreover, it shows that important behavioural patterns may be obscured by analysis at larger temporal scales (i.e. 24 versus 6 hr periods). The present results indicate that the highest surface activity actually occurs from 0900-1500 hours during migration through pelagic waters (Table 5.3). Leatherbacks may be most visible during this time. Nonetheless, turtles spend substantial amounts of time at the surface during the day and evening (~50%) in shelf and slope waters off Canada and
northeastern U.S., where aerial surveys are most feasible because turtles aggregate there in the summer and autumn (James et al. 2005c; Eckert et al. in press) and aircraft can operate relatively close to shore (e.g., Shoop and Kenny 1992).

By quantifying diel changes in leatherback behaviour in northern waters, we have provided the first surface time correction factors for aerial survey abundance estimates based on multiple individuals for this species and have identified day and evening (0900-2100 hours) as periods during which leatherbacks spend the most time (C.I. day mean: 46-53%, C.I. evening mean: 48-55%; Table 5.3) at the surface. Our results suggest that there is considerable variability in surface time both within and among turtles. Analysis of surface activity recorded at even finer temporal scales will be key to refining surface time correction factors and thereby improving estimates of abundance from aerial survey data.

The relatively high proportion of time leatherbacks spend at or near the surface in northern foraging areas likely puts them at risk for collisions with vessels, particularly in waters adjacent large urban coastal communities with heavy recreational boat traffic. Corroborating evidence comes from examination of leatherbacks found stranded along the coast of northeastern United States (Dwyer et al. 2003).

5.5 Conclusion

This analysis demonstrates that fundamentally different diel patterns characterize leatherback diving and surface behaviour in northern waters versus during southward migration. While we have compared leatherback biotelemetry data to the most common pattern of diel vertical migration described for gelatinous planktonic organisms, testing hypotheses regarding how leatherback behaviour may be influenced by the distribution
and movements of their prey will require additional research. We must improve our understanding of the diet of leatherbacks in different areas of their range, particularly in those relatively inaccessible pelagic areas where turtles are known to migrate or aggregate, and establish when, at what depths, and on what species, feeding occurs. Faced with similar questions, biologists studying other diving organisms have used various telemetry systems to detect feeding events using drops in stomach or esophageal temperatures (Ancel et al. 1997) and have used animal-borne video systems and data recorders (Davis et al. 1999) to study prey species composition, ingestion rates, and how prey is located and handled.

Given the leatherback’s global status as critically endangered (IUCN 2004), experimental tests of the potential role of the pink spot and pineal complex in the navigational abilities of free-swimming turtles are unlikely. Hence, determining if and when these animals feed during migratory periods will be critical to further clarifying the basis of diel behavioural patterns. Despite recent advances in our knowledge of the at-sea biology of leatherbacks, a poor understanding of the relationship between these predators and their prey persists, presenting a fundamental challenge to explaining the behaviour of these animals. Therefore, beyond identifying and mapping the distributions of organisms that represent the leatherback’s primary prey, their behaviour—including diel migration patterns—must also be studied to enable more quantitative hypothesis testing regarding predator-prey dynamics.
Chapter 6. Migratory and Reproductive Movements of Male Leatherback Turtles (*Dermochelys coriacea*)

6.1. Introduction

Research on the behaviour of leatherback turtles, *Dermochelys coriacea*, has previously focused on the movements of adult females, because they nest on tropical and subtropical beaches and are, therefore, readily available for study. The internesting behaviour of turtles in tropical waters has been studied through the use of electronic archival tags (Eckert et al. 1989, 1996; Southwood et al. 1999b; Eckert 2002b) and radio telemetry (Eckert 2002b). The post-nesting movements of turtles have been revealed using both satellite telemetry (Morreale et al. 1996; Hughes et al. 1998; Luschi et al. 2003; Ferraroli et al. 2004; Hays et al. 2004a, 2004b) and the recovery of conventional flipper tags (Pritchard 1976; Girondot and Fretay 1996; James 2004). These studies have shown that female turtles disperse broadly after nesting and frequently journey to northern waters. In contrast, the behaviour of male leatherbacks has been difficult to study, as males never come ashore and there are formidable challenges associated with locating and humanely capturing this species at sea. Field research in eastern Canada has recently provided access to leatherbacks at sea, including males, to investigate broad movement patterns (James et al. 2005c). However, the spatial and temporal distribution of males is still not well understood.

A lack of data on the movements of males and only rare reports of leatherbacks mating (Carr and Carr 1986; Godfrey and Barreto 1998) have led to contrasting hypotheses about when and where leatherbacks mate. Lazell (1980) speculated that mating occurs in waters adjacent nesting beaches. This is consistent with what is known
about the breeding behaviour of other sea turtles (Limpus 1993; Plotkin et al. 1996; Frick et al. 2000). However, Pritchard (1982) suggested that a paucity of observations of copulation in the vicinity of nesting beaches indicated that leatherbacks do not mate in these areas, and Eckert and Eckert (1988) proposed that females mate prior to entering tropical waters, based on the rate of tropical barnacle (*Chonchodera virgatum*) colonization on turtles nesting at St. Croix (U.S. Virgin Islands). If mating does not occur in waters adjacent nesting beaches, male turtles from temperate foraging grounds might be expected not to travel to these areas. To test this hypothesis, we used satellite telemetry to study the movements of male leatherbacks encountered in waters off eastern Canada.

6.2. Materials and Methods

Fieldwork occurred in two areas off the coast of Nova Scotia. The first area (approximately 47°N, 60°W) includes the northeast portion of the Scotian Shelf and encompasses waters adjacent the Laurentian Channel, a deepwater trench (>400 m) that runs between Cape Breton Island and Newfoundland. The second area (approximately 44°N, 64°W) is larger and is located off the southwest shore of mainland Nova Scotia, including waters inshore from the shelf break.

Turtles were located in these areas with the assistance of the Nova Scotia Leatherback Turtle Working Group, a network of commercial fishers and tour boat operators who voluntarily report sightings of leatherbacks to assist with research on this species (Martin and James 2005).

Turtles were captured while foraging on jellyfish using a breakaway hoop net operated from either an 8.5-m or 10.5-m commercial fishing boat equipped with a stern
ramp. Each turtle was moved up the ramp onto a raised platform where it was measured and sampled for DNA using a skin biopsy punch (6 mm, Acuderm, Ft. Lauderdale, FL, USA). Sex of male turtles was readily confirmed by the presence of an elongated tail with a cloacal vent distant from the tip of the caudal peduncle. Monel tags (style no. 49, National Band and Tag Company, Newport, KY, USA) were applied to the rear flippers and a passive integrated transponder (AVID, Calgary, AB, Canada) was implanted in the right shoulder muscle. A satellite-linked transmitter was attached to the carapace using a harness made of polypropylene webbing and polyvinyl tubing, which incorporates corrodbile links to ensure release (modified after Eckert 2002b). Transmitters included Kiwisats (Sirtrack, Havelock North, New Zealand), Spot 3s (Wildlife Computers, Redmond, WA, USA), and an ST-10 (Telonics Inc., Mesa, AZ, USA). Satellite-linked time-depth recorders (SLTDRs) were also deployed (SDR-SSC3, Wildlife Computers, Redmond, WA, USA).

Turtles were released promptly after satellite tag attachment (usually within 30 min) and their subsequent movements were monitored via the Argos satellite network. Location of the turtle, location class (LC, an index of positional accuracy), and the corresponding date and time were provided daily via e-mail. Argos calculates locations from transmissions received during a satellite pass and categorizes them by LC. Locations designated as LC 3, LC 2, LC 1, or LC 0 are classified as within 150 m, >150–350 m, >350–1,000 m, or >1,000 m, respectively, of the tag’s true position. Locations classified as “A” and “B” are not categorized for positional accuracy by Argos; however, LC A locations have recently been shown to be as accurate as LC 1 locations and more accurate than LC 0 locations (Hays et al. 2001b; Vincent et al. 2002).
An analysis has shown that less than 1% of rates of travel for leatherbacks calculated using only LC 1–3 positions exceed 5 km/h (James et al. 2005c), which closely agrees with data published on leatherback sea turtle swim speeds (Eckert 2002b). Therefore, we filtered positions of poorer reported quality (e.g. LC A, LC B, LC 0) based on a maximum rate of travel of 5 km/h. To maximize positional certainty, we calculated rates of travel (distance/time) between consecutive surface locations (LC 1, 2, 3, and A) that were a minimum of 2 h apart.

SLTDRs reported data on diving behaviour during 6-h periods (four per day: 20:00–01:59, 02:00–07:59, 08:00–13:59, 14:00–19:59; Atlantic Standard Time) in histogram format. SLTDRs specifically recorded the proportion of each 6-h period spent in 14 user-specified depth ranges (time at depth) and the number of dives (>4m, turtle E; >6m, turtle F) with durations that fell within 14 user-specified ranges. These data were compared to corresponding rates of travel associated with turtle migration and residency in different areas. Surface time data from two SLTDRs were also analyzed. In this case, “surface time” values represented the fraction of time in each 6-h period when the depth sensor read less than 2 m (turtle E) or 3 m (turtle F). Diel changes in diving behaviour and surface time were investigated by comparing data collected during periods 20:00–01:59 (night) and 08:00–13:59 (day).

To compare the timing of male leatherback residency in tropical waters to nesting activity on nearby beaches, we considered turtle E and turtle H, as these turtles restricted their movements to waters off relatively large colonies for which there is detailed information on the temporal distribution of nesting.
6.3. Results

Satellite tags were deployed on 11 male leatherback turtles captured off the coast of Cape Breton Island (n=6) and mainland Nova Scotia (n=5) in the summers of 1999 to 2003. All turtles eventually assumed southward migrations from temperate foraging areas, with tags on eight turtles (Table 6.1) transmitting long enough to reveal southerly destinations (Figure 6.1). Two of these animals journeyed to pelagic areas off the coast of South America before swimming northwest (Figure 6.1a, g). The remaining six turtles migrated to waters adjacent nesting beaches; four to the Lesser Antilles (Figure 6.1b–d, f), one to Trinidad (Figure 6.1e), and one to Panama (Figure 6.1h). Migration to waters adjacent nesting beaches was direct: once turtles assumed their southward migration, their rate of travel did not decrease until they arrived in nearshore waters (Figure 6.2).

Turtles did not generally follow common paths on their southward and northward migrations, and even individual turtles utilised different routes while journeying to and from northern waters. However, the tracklines south for turtles C and D, tagged in the same area within 25 h of each other, were remarkably similar (Figure 6.1c, d). While utilising northern coastal waters, these turtles were generally <10 km apart and they simultaneously departed the continental shelf and started migrating south at the beginning of November (Table 6.1). Both turtles then swam to the Lesser Antilles. Turtle C occupied waters between the islands of Grenada, Los Testigos (Venezuela), and Tobago for only 3 weeks (5–23 February 2002) before heading north again (Figure 6.1c). However, turtle D restricted his movements to waters adjacent a string of islands, bordered by St. Lucia to the north and Grenada to the south, for 3 months (15 January to 17 April 2002) before transmissions ceased (Figure 6.3). During this time, the turtle
remained in waters on the eastern side of the islands (where most nesting occurs), only briefly venturing into the Caribbean Sea in the area between St. Lucia and St. Vincent. Turtle D’s tag resumed transmitting 6 months later (11 October to 10 December 2002) in shelf waters of the mid-Atlantic Bight (40.8°N, 70.6°W) where he had resided for a part of the previous summer. Remarkably, transmissions from this tag resumed for a second time in late March 2003, placing turtle D in the same region of the Lesser Antilles he had occupied during the previous winter (Figure 6.3). The intermittent performance of turtle D’s transmitter may have reflected periodic epibiont fouling of the saltwater switch, a conductivity sensor that suppresses transmissions when the tag is submerged.

While four male leatherbacks ranged broadly in the vicinity of nesting beaches and inhabited waters off nesting beaches on multiple islands (Figure 6.1b–d, f), two turtles (turtles E and H) restricted their movements to relatively small areas off specific nesting colonies. Turtle E swam to waters off Trinidad, where he remained resident for 44 days in a nearshore area (approximately 50 km2) off the northeast tip of the island (Figure 6.4) before returning to coastal waters off Atlantic Canada (Figure 6.1e). In the following year, this turtle returned to the same site off Trinidad at the same time (last week of February; Figure 6.4). Turtle H was the only male to venture to a Western Caribbean nesting colony, swimming to waters off the Bocas del Toro Archipelago in Panama where he resided for 96 days (Figure 6.5) before assuming a northward journey.
<table>
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<th>CCL (cm)</th>
<th>Avid microchip ID</th>
<th>Instrument</th>
<th>Area tagged</th>
<th>Date instrument deployed (dd/mm/yyyy)</th>
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</table>

CCL, curved carapace length; Location, location-only satellite tag; SLTDR, satellite-linked time-depth recorder, N.S., waters off mainland Nova Scotia; C.B.I., waters off Cape Breton Island.

Table 6.1. Summary information for eight male leatherback turtles equipped with satellite tags off Nova Scotia, Canada. CCL Curved carapace length; Location location-only satellite tag; SLTDR satellite-linked time-depth recorder; N.S. waters off mainland Nova Scotia; C.B.I. waters off Cape Breton Island.
Figure 6.1. Movements of eight male leatherback turtles (turtles A–H, panels a–h) satellite tagged off Nova Scotia, Canada. *Dashed lines* represent 1,000 m depth contour. Turtle E: *dotted line* corresponds to segment of track for which no positions were received; *solid arrows* indicate direction of travel in 2003; *open arrows* indicate direction of travel in 2004 and 2005. Tracks of turtles C and E from James et al. (2005c); track of turtle E updated to 10 March 2005.
Figure 6.2. Representative plots of rates of travel for male leatherback turtles during migration and while resident in breeding areas. a Turtle D. b Turtle H. Calculations of rate of travel begin 2 months before arrival in breeding area.
Figure 6.3. Male leatherback turtle fidelity for a breeding area adjacent nesting beaches in the Lesser Antilles (turtle D). *Open circles* are positions of turtle D from 12 January to 11 April 2002, when satellite tag transmissions ceased. *Solid circles* are positions from 25 March 2003, when transmissions resumed, to 20 April 2003, when transmissions ceased.
Figure 6.4. Remigration of a male leatherback to a coastal breeding area off Trinidad (turtle E). Solid circles are positions from 2004; open circles are positions from 2005; arrows show direction of travel. Inset shows locations of turtle while resident off the island from 28 February to 12 April 2004 and 26 February to 10 March 2005 (when track was last updated).
Figure 6.5. Male leatherback migration to and departure from coastal waters off the Bocas del Toro Archipelago in Panama (turtle H). Arrows show direction of travel. Inset shows positions of turtle while resident in the area from 26 January to 1 May 2004.
Behaviour in waters off nesting beaches was characterized by slower rates of travel than that associated with long-distance movement (Figure 6.2, Figure 6.6a, b). Diving behaviour varied between two turtles equipped with SLTDRs. After arriving in nearshore waters off Trinidad, turtle E's diving behaviour changed markedly. Dive duration decreased, and more time was spent at shallower depths (Figure 6.6c, e). In contrast, arrival in waters off the nesting beaches was not punctuated by similar changes in the diving behaviour of turtle F (Figure 6.6d, f).

A diel pattern in surface activity during the breeding period was observed in turtle E and turtle F. Turtle E spent more time near the surface (water depth <2 m) during the day than during the night (day mean=21.23%, SD=11.04%; night mean=16.23%, SD=6.47%; P=0.058, Wilcoxon rank-sum test). This difference was more pronounced in turtle F (day mean=65.94%, SD=25.97%; night mean=14.06%, SD=4.52%; P=0.029, Wilcoxon rank-sum test).

Turtle E exhibited distinct diel changes in diving behaviour in the vicinity of the nesting beaches. Diving was shallower during the night than during the day (P<0.05, t test), with a high proportion of time spent during the day at or near the ocean floor (24–50 m, Figure 6.7a). This same pattern was not observed in turtle F. While this male did spend more time diving to depths >12 m during the night versus during the day, a large proportion of time was spent in waters <12 m during the day (Figure 6.7b).

A comparison of when turtle E was resident off Trinidad (29 February to 12 April 2004) relative to the seasonal distribution of nesting activity on Matura Beach, one of the island's largest nesting centres, revealed that this male arrived in coastal waters at the very start of the nesting season and departed prior to peak nesting (Figure 6.8a). A similar
pattern was observed in turtle H, a male that was resident in waters off Panama in 2004. Leatherbacks nesting in Panama are considered part of a larger colony that includes the index beach of Gandoca in adjacent Costa Rica (Chacón et al. 1996; Chacón 1999; Troëng et al. 2004). Turtle H arrived in his residency area in late January, prior to the start of the 2004 nesting season at Gandoca Beach, and departed on 1 May, around the time of peak nesting activity (Figure 6.8b).
Figure 6.6. Behaviour of turtles E (left column) and F (right column) during migration and while resident in breeding areas in tropical waters. a, b Rate of travel. c, d Dive depth. The vertical bars represent the depth range sampled over 6-h periods for which data were received. The deeper limits of 14 depth ranges are identified on the left-hand axis. Diamonds show midpoint of depth range in which daily mean falls. e, f Distribution of dive durations (per 6-h sample). Vertical bars indicate the range for each 6-h period for which data were received. The upper limits of 14 dive duration ranges are identified on the left-hand axis. Diamonds show midpoint of duration range in which daily mean falls. g, h Latitudinal movement.
Figure 6.7 Diel dive patterns of male leatherback turtles during residency periods off nesting beaches: mean proportion of time spent in different depth ranges. *Solid bars* show behaviour at night (20:00–01:59 local time) and *open bars* show behaviour during the day (08:00–13:59 local time). a Turtle E, 28 February to 12 April 2004. b Turtle F, 7–26 January 2002.
Figure 6.8. Timing of male leatherback residency in waters off nesting beaches relative to the temporal distribution of nesting. *Solid bars* indicate residency period. **a** Turtle E. *Solid circles* represent number of females encountered each night from 2 March to 17 July 2004 at Matura Beach, Trinidad. Line fit for normal distribution by least squares after log transformation. **b** Turtle H. *Solid circles* represent nest counts from nightly surveys conducted from 1 January to 3 August 2004 at Gandoca Beach, Costa Rica (D. Chacón, unpublished data). Line fit for normal distribution by least squares after log transformation.
6.4 Discussion

Although Pritchard (1982) suggested that leatherbacks do not mate in the vicinity of nesting beaches and Eckert and Eckert (1988) proposed that mating occurs prior to, or during migration to nesting areas, the results presented here suggest that mating does occur near Caribbean nesting colonies, and that many male turtles migrate directly to breeding areas from temperate foraging grounds.

Courtship behaviour in loggerhead turtles (*Caretta caretta*) has been observed during aerial surveys conducted off the coast of Georgia and Florida, states that support large nesting populations of this species (Frick et al. 2000). If similar aerial surveys were conducted to correspond with peak abundance of leatherbacks in waters adjacent their nesting beaches, it is possible that copulation in this species would be observed more regularly.

It does seem strange, however, that more reports of mating by leatherbacks near large nesting colonies such as Trinidad and Panama have not been recorded. This may reflect that most observations of mating are probably made by fishers who are unlikely to report or formally document their observations. This appears to be the case in Trinidad, where one of us (S.A.E.) has interviewed fishers and confirmed that mating is occasionally observed off the north and east coasts of the island. Infrequent reports of mating may also reflect a true scarcity of observations. While studies of mating in most species of sea turtle have been limited to surface observations (e.g. Frick et al. 2000; Godley et al. 2002b), underwater studies of green turtles (*Chelonia mydas*) have shown that copulation also regularly takes place on the ocean floor (Booth and Peters 1972).
Behavioural data from turtle E raise the possibility that this may also be the case for leatherbacks, at least off those nesting areas where water depths are relatively shallow. While resident off Trinidad, turtle E spent much of his time during the day at or near the bottom (Figure 6.7a), where the water depth was generally <50 m (Figure 6.4).

Turtle E's choice of residence area in nearshore waters off Trinidad deserves special mention. Trinidad supports one of the five largest leatherback nesting colonies in the Atlantic, with an estimated population of 1,800–2,000 females (Eckert 2001). Therefore, waters off the island represent a logical area for male turtles to seek mating opportunities, as encounter rates with females will be relatively high. Moreover, turtle E's highly localized movements off Trinidad are readily explained, as they were limited to an area off Golera Point (Figure 6.4) that constitutes the epicentre of internesting habitat for female turtles from the island's largest nesting beaches (S.A. Eckert, unpublished data). It is likely that breeding ranges of many other males incorporate these waters, as females are concentrated here during the nesting season. Turtle H's localized movements off the Bocas del Toro Archipelago (Figure 6.5), which constitutes part of the fourth-largest leatherback nesting colony in the world (Troëng et al. 2004), provide a comparable example. In contrast, mating opportunities may be relatively scarce for males returning to waters adjacent smaller nesting colonies. Therefore, to maximize mating success, these males may have to range more broadly during the breeding season to find mates than those returning to waters off large nesting colonies. This is precisely the pattern we observed among the four males that migrated to waters off beaches in the Lesser Antilles (turtles B–D, F), where individual nesting populations number in the tens, rather than hundreds or thousands of animals. Rather than positioning themselves off
specific islands, as was the case with turtle E and turtle H, the breeding ranges of these males appeared to include waters off several islands (e.g. Figure 3), where they likely take advantage of mating opportunities with females from different nesting populations.

The four turtles that utilized waters near islands in the Lesser Antilles (turtles B–D, F) may also have been attempting to secure mating opportunities not only with those females using local nesting beaches, but also with females entering the Caribbean Sea en route to insular Caribbean nesting beaches. Therefore, some breeding ranges may facilitate mating with turtles from both proximate and distant colonies.

Male fidelity to courtship areas has been documented in other species of sea turtle (Limpus 1993); however, without detailed information on the movements of male leatherbacks spanning multiple breeding seasons, it is not possible to determine if males have long-term fidelity for particular breeding sites, or if they simply opportunistically seek mates over a broad geographic area. Our results are consistent with fidelity to specific breeding destinations. This suggestion is supported by the migration of several turtles through shelf waters off large nesting colonies, en route to more distant breeding sites. For example, in 2004, turtle E maintained a high rate of travel while swimming through waters off French Guiana and Suriname, countries that support the largest nesting colony in the world (Spotila et al. 1996), and did not stop until he reached coastal Trinidad (Figure 6.6a). Similarly, turtle H rapidly transited between the U.S. and British Virgin Islands, both of which host nesting populations of leatherbacks (Boulon et al. 1996; Hasting 2003), while entering the Caribbean Sea en route to the Bocas del Toro archipelago in Panama (Figure 6.5). Again, his rapid movement through these potential
breeding sites demonstrates that he did not seek mating opportunities there, but instead was destined for an alternative breeding area.

The most convincing evidence for male leatherback fidelity for specific breeding areas comes from long-term telemetry data from two turtles. Our 20-month tracking of turtle D revealed return movements to a breeding range encompassing waters adjacent nesting beaches in the Lesser Antilles (Figure 6.3). Moreover, turtle E, tracked for a similar duration, remigrated to the same area off Golera Point, Trinidad, in 2 consecutive years (Figure 6.4). These results indicate that some male leatherbacks that forage in temperate waters of the northwest Atlantic return to breeding areas annually. This is consistent with males migrating more frequently to breeding grounds than females, a pattern that has been reported for other sea turtle species (Limpus 1993). However, the tracks of turtles A and G suggest that if mating activity is limited to waters adjacent nesting beaches, not all males may breed every year. A return to breeding areas every 2–3 years would parallel the remigration interval between nesting seasons for most female Atlantic leatherbacks (Boulon et al. 1996).

In the absence of conclusive genetic results, it is not known whether male leatherbacks exhibit philopatry to breeding areas in the vicinity of natal beaches; however, such behaviour is likely, as it has been reported in other species of sea turtle (FitzSimmons et al. 1997) and would be consistent with regional homing exhibited by nesting females.

Diving data from turtle E and turtle F reveal variability in male behaviour at breeding sites. During the day, turtle E, occupying shallow (maximum depth <80 m) nearshore waters, spent much of his time at or near the bottom (Figure 6.7a), whereas
turtle F, occupying deeper waters (maximum depth 200 m), spent more time at depths \( \leq 12 \) m (Figure 6.7b). Dive duration also varied between the two males, with turtle E (Figure 6.6e) completing much shorter dives than turtle F (Figure 6.6f) in the vicinity of the nesting beaches. Much of this variability may reflect that these animals were occupying areas characterized by differences in bathymetry, prevailing currents, proximity to nesting beaches, and so forth. Bathymetry has been shown to strongly influence the diving behaviour of female leatherbacks, with turtles in the shallow South China Sea routinely diving near the bottom, while turtles off St. Croix (U.S. Virgin Islands) undertake much deeper dives with virtually no bottom time (Eckert et al. 1996). 

Our results show that male leatherbacks E and H arrived in waters adjacent nesting colonies before the nesting season began (Figure 6.8a, b). This is probably a behavioural adaptation to increase reproductive fitness as males arriving in breeding areas early will maximize their potential for mating with multiple females before their first clutches of eggs are laid. The males in this study also departed breeding areas around the time of peak nesting activity on nearby beaches. This pattern has been observed in other species of sea turtle (Plotkin et al. 1996) and likely reflects a decrease in the number of opportunities for successful mating, as females of some species will reject the advances of males after they have started nesting (Booth and Peters 1972). Moreover, while mating was not observed in this study, the timing of male arrival and departure from residency areas relative to nesting activity on nearby beaches does correspond with the temporal distribution of mating reported for other sea turtles species (Booth and Peters 1972; Godley et al. 2002b).
As foraging opportunities for sea turtles may be very limited in breeding areas and energy expenditure by males during the breeding period is high (Jessop et al. 2004), a rapid return to productive foraging areas following mating is probably important. This suggestion is supported by the tracking data from the males in this study. In all cases, departure from the breeding area was followed by a northward migration (Figure 6.1), characterized by rates of travel higher than those recorded in breeding areas (e.g. Figures 6.2b, 6.6a).

During the internesting interval, female leatherbacks from Caribbean nesting colonies range broadly from their nesting sites (Eckert et al. 1989; Keinath and Musick 1993; Eckert 2002b). By contrast, some of the males we tracked remained in relatively small areas near nesting beaches throughout the breeding period. It may be possible that female leatherbacks move farther offshore to avoid continual pursuit from concentrations of males seeking mating opportunities in nearshore waters.

Entanglement in fishing gear in waters adjacent nesting beaches has recently been identified as an important source of mortality for leatherbacks (Chevalier 2001; Lee Lum 2003). While sex ratios of entangled turtles are not currently available, in addition to mature females, male leatherbacks may be vulnerable to entanglement in these areas, as they appear mainly to restrict their movements during the breeding period to nearshore waters, where fishing effort is highest.
Chapter 7. Conclusions

The leatherback turtle has the most extensive geographic range of any reptile; however, relatively little is known about its biology beyond the nesting beach. Research on this species in foraging areas has traditionally been hindered by logistical challenges associated with locating and capturing free-swimming turtles. I addressed this problem by collaborating with commercial fishers to develop equipment and protocols for field studies of leatherbacks off the coast of Nova Scotia. During five seasons of fieldwork (2000-2004), I collected morphometric and core temperature data from foraging leatherbacks and used satellite telemetry to study the local and long-distance behaviour of 42 individuals. As the first biotelemetry study of leatherbacks tagged at sea, this work has broadened research on this species to include male and subadult turtles.

While nesting is limited to subtropical and tropical nesting beaches, leatherbacks regularly occur at northern latitudes where ocean surface temperatures fall below the lower thermal tolerance limits of all other sea turtles. Study of captive leatherbacks under unnatural conditions has revealed that this species is capable of elevating body temperature above ambient. The extent to which endothermy occurs in free-swimming turtles is not known. In Chapter 2, I presented the results of a study on body temperature of leatherbacks in temperate waters. Foraging turtles were captured and their body temperature recorded within 10 minutes, before such large animals could change temperature appreciably. Mean excess temperature over that of the sea surface averaged 8.2 °C. As leatherbacks do not limit their movements to surface waters, to more accurately assess thermal environment during foraging I considered ocean temperature data collected from a satellite-linked time-depth recorder on another turtle present for
three days in the area where core temperatures were recorded. These data revealed that leatherbacks in this area at the same time of year may spend 40% of their time diving to waters cooler than the surface. Therefore, the point measurements of core temperature versus sea surface temperature I reported confirm, but underestimate, the capacity of free-swimming leatherbacks to keep warm in cold water.

To further explore temperature regulation in leatherbacks, it would be instructive to simultaneously record body and ambient temperature of several turtles during long-distance movement between tropical and temperate waters.

A reliance on fisheries observer data and an absence of behavioural data sets corresponding to a large and diverse sample of animals have focused leatherback conservation efforts on a very limited part of the species’ marine habitat. In Chapter 3, I used the largest satellite telemetry data set for Atlantic leatherbacks to identify previously undescribed high-use habitat for these animals encompassing shelf and slope waters off Canada and the northeastern United States. Annual return migrations to preferred foraging zones, long residency times, and large corresponding increases in body weight demonstrated the importance of these areas to this species. I presented entanglement data that reveals that interactions with fixed gear fisheries represent a greater hazard for turtles using northern waters than was previously recognized. This research has implications for the recovery of leatherbacks in the Atlantic as it identifies areas of seasonal aggregation where turtles have traditionally received little management attention and where conservation efforts could be expanded.

In Chapter 4, I presented broad patterns of leatherback movement and diving behaviour obtained during long-term satellite tracking from northern foraging areas to
tropical waters and back again. These are the first tracklines to demonstrate foraging area fidelity in this species.

While the satellite-linked recorders used in this study did not provide data at the resolution of individual dives, patterns in rate of travel, maximum dive depth, time at depth and dive duration were consistent across turtles of different sexes and sizes. Dietary preferences in all but a few areas of the leatherback’s range remain unknown and the biology of most species of gelatinous plankton—widely considered to be the principal variety of prey exploited by these animals—is poorly described. Therefore, without direct evidence of foraging at depth and dive profile data, it is difficult to interpret diving behaviour. Recognizing this, I reviewed both what is known about leatherback feeding biology, including field observations which confirm foraging in shelf waters off eastern Canada, and what is known about the biology of gelatinous macroplankton that have been confirmed as leatherback prey. I evaluated the movement and diving data I collected in light of this information. The results of this work suggest that patterns in movement and diving behaviour may reflect both foraging and thermoregulatory strategies. Additional research is needed to elucidate the specific ecological bases of these patterns across the species’ range. Confirmation of where and when prey handling and ingestion occurs, identification of the prey species targeted, and corresponding studies of prey dynamics will be key to understanding variability in leatherback foraging behaviour throughout the migratory cycle.

Some studies of female leatherbacks equipped with time-depth recorders on nesting beaches have revealed distinct diel patterns in turtle diving behaviour in tropical waters (Eckert et al. 1989, 1996; Hays et al. 2004b). However, Southwood et al. (1999b)
reported an absence of consistent diel patterns in dive depth and duration among females during internesting intervals off Pacific Costa Rica. In Chapter 5, I used data from satellite-linked time-depth recorders attached to 15 subadult and adult turtles to determine if diel patterns in diving and surfacing were characteristic of behaviour during either residency in northern waters or during southward migration. The results of this work demonstrate diel patterns in diving associated with both periods; however, these patterns were much more pronounced during southward migration.

Stomach contents (Bleichney 1965) and field observations (James and Herman 2001) suggest that two species of jellyfish, *Cyanea capillata* and *Aurelia aurita*, may constitute the leatherback’s principal prey in Canadian waters. I suggest that dive data from the northern turtles in my sample is consistent with turtles foraging throughout the day and night on these species, particularly in temperate shelf and slope waters, where such prey is seasonally abundant, and where it may be captured at depth but regularly ingested at the surface. Unfortunately, while leatherbacks specialize on gelatinous zooplankton, it is not clear which species they exploit during southward migrations, nor is the frequency of foraging during these long-distance movements known. I suggest that diel patterns in diving behaviour during southward movements may reflect turtles tracking the normal pattern of diel vertical migration in gelatinous marine plankton, with turtles mainly feeding at night when prey are closer the surface. I also discuss how diel activity patterns could potentially reflect use of the pineal complex to perceive light cues for navigation across vast areas of ocean.

Biotelemetry been most widely used to study the internesting and post-nesting behaviour of female marine turtles. There are very few studies of males, as they must be
captured at sea and subsequent recovery of instruments is highly unlikely. In the case of leatherback turtles, prior to initiating this research, no information was available on the movements and behaviour of males. Moreover, competing hypotheses existed regarding the timing and location of mating in this species. In Chapter 6, I reported on the first deployments of satellite transmitters on male leatherbacks. The results of this work provide evidence for breeding occurring in coastal waters adjacent nesting beaches, with males arriving in these areas early in the nesting season, and departing around the time of peak nesting. Long-term tracking of two males revealed fidelity for breeding areas in the Caribbean in consecutive years. These findings do not dismiss the possibility that some mating may also occur in offshore areas, however, the telemetry data I present is consistent with the timing and location of mating reported for other sea turtles. There are conservation implications associated with this study. High levels of incidental capture of leatherbacks in artisanal fisheries operating off western Atlantic nesting beaches have recently been reported (Chevalier 2001; Lee Lum 2003). While emphasis has focused on the risk these fisheries pose to mature females, my results suggest that mature males may also be vulnerable to entanglement.

This thesis research has shown that subadult and mature male and female leatherbacks captured on foraging grounds in eastern Canada undertake return migrations between temperate and tropical waters, with turtles largely remaining in pelagic waters outside of their northern foraging and southern breeding periods. This migratory cycle appears to be annual for subadults, mature males and mature females in their internesting years. It may even be possible for females in their nesting years; however, to date, transmitter loss or failure has precluded tracking mature females tagged in northern
waters throughout their subsequent nesting season. Furthermore, all the leatherbacks I tracked exhibited fidelity for northern areas on the western side of the Atlantic, where field measurements of core temperature indicated that they support active foraging by keeping warm in cold water.

Telemetry data from the large and diverse sample of turtles I tagged has facilitated identification of high-use areas in temperate waters where potential future implementation of conservation initiatives offers promise for recovering this species. The platform for at-sea research I have developed in Nova Scotia will provide opportunities for expanding research on the biology of these rare animals.
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