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**MOVEMENTS, DIVE BEHAVIOR AND TROPHIC
ECOLOGY OF LEATHERBACK TURTLES
(*DERMOCHELYS CORIACEA*) IN THE NORTHWEST
ATLANTIC**

BY

KARA DODGE
BA, Harvard College, 1998

DISSERTATION

Submitted to the University of New Hampshire
In Partial Fulfillment of
The Requirements for the Degree of

Doctor of Philosophy
In
Zoology

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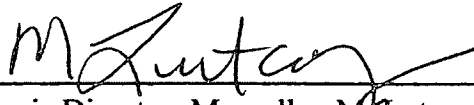
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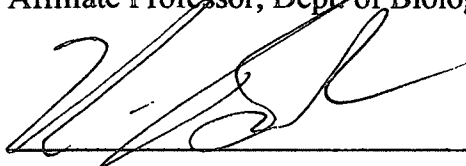


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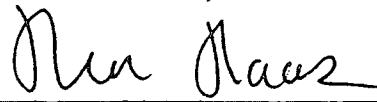
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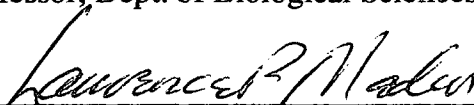
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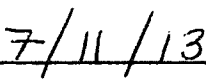
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DEDICATION

For Michael and Skye, who fill my life with joy and love, always. And for those intrepid scientists who first recognized the importance of high latitudes for leatherback turtles, and paved the way for leatherback research in New England.

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ABSTRACT

MOVEMENTS, DIVE BEHAVIOR AND TROPHIC ECOLOGY OF LEATHERBACK TURTLES (*DERMOCHELYS CORIACEA*) IN THE NORTHWEST ATLANTIC

by

Kara Dodge

University of New Hampshire, September 2013

The endangered leatherback turtle is a highly migratory predator that feeds exclusively on gelatinous zooplankton. Leatherbacks spend most of their lives submerged or offshore, and their at-sea biology (particularly that of males and sub-adults) is poorly understood throughout much of their range. I used satellite telemetry to monitor movements and dive behavior of nine adult and eleven sub-adult leatherbacks captured off Massachusetts, USA, and tracked throughout the NW Atlantic. Leatherback movements and environmental associations varied by oceanographic region, with slow, sinuous, area-restricted search behavior and shorter, shallower dives occurring in cool, productive, shallow shelf habitat at temperate latitudes. Leatherbacks were highly aggregated in temperate shelf waters during summer, early fall, and late spring, and more widely dispersed in subtropical and tropical habitat from late fall through early spring. Leatherbacks increased path sinuosity with decreasing water depth in temperate and tropical shelf habitats. This relationship is consistent with increasing gelatinous zooplankton biomass with decreasing depth, and bathymetry may be a key feature in identifying leatherback foraging habitat in neritic regions.

I used satellite-derived turtle tracks to examine migratory orientation cues of fifteen leatherbacks in the North Atlantic subtropical gyre. Individual leatherbacks were significantly oriented with no difference between adult and sub-adult headings, and turtles were significantly oriented with respect to magnetic field inclination, sunrise angle and sunset angle. Leatherbacks may use one or more of these features to orient during their open-ocean migrations between temperate and tropical latitudes.

I analyzed stable isotopes in leatherback tissues and prey to investigate feeding behavior. Leatherback skin and whole blood $\delta^{13}\text{C}$ values and red blood cell $\delta^{15}\text{N}$ values were correlated with body size, while $\delta^{13}\text{C}$ values of red blood cells, whole blood and blood plasma differed by sex. Mixing model results suggest that leatherbacks foraging off Massachusetts primarily consume *Cyanea capillata* and *Chrysaora quinquecirrha*, and ctenophores, while a smaller proportion of their diet comes from holoplanktonic salps and sea butterflies (Cymbuliidae). My results are consistent with historical observations of leatherbacks feeding on scyphozoan prey in this region and offer new insight on size- and sex-related differences in leatherback diet.

INTRODUCTION

Leatherback turtles (*Dermochelys coriacea*) are long-lived, highly migratory reptiles listed as endangered under the U.S. Endangered Species Act and critically endangered worldwide (Miller 1997, IUCN Red List 2012). Their unique life history characteristics include rapid growth to a large body size (Rhodin 1985, Zug & Parham 1996), the ability to elevate their core body temperature (Frair et al. 1972, Paladino et al. 1990), deep diving capability (Eckert et al. 1986, Lutcavage et al. 1992; Doyle et al. 2008), long-distance swimming capacity (Pritchard 1971, Ferraroli et al. 2004, James et al. 2005a, Benson et al. 2011) and an unusual vertebrate diet of gelatinous zooplankton (Bleakney 1965, Davenport 1998, Dodge et al. 2011, Heaslip et al. 2012). These combined adaptations allow leatherbacks to exploit a wide variety of habitats throughout the world's oceans, but their enigmatic lifestyle has prevented us from fully understanding their life history outside of their nesting beaches.

Alarming declines of nesting leatherbacks in the eastern Pacific have raised concerns for the future of this population (Spotila et al. 1996, Spotila et al. 2000, Santidrián-Tomillo 2007, Sarti-Martinez et al. 2007) while leatherback populations in the Atlantic appear to be stable or increasing (Dutton et al. 2005, Girondot et al. 2007, TEWG 2007, Witt et al. 2009). What is driving these population trends in different directions? Leatherbacks in both ocean basins are vulnerable to intentional harvest for their meat and eggs (Eckert & Sarti 1997, Spotila et al. 2000), development of their nesting beaches (Lutcavage et al. 1997), coastal and pelagic fishery interactions (National Research Council 1990, Lewison et al. 2004, Lum 2006, Alfaro-Shigueto et al. 2007), boat strikes (Lutcavage et al. 1997), ingestion and entanglement in marine debris (Balazs

1985, Mrosovsky et al. 2009) and climate change effects on ocean productivity (Wallace et al. 2006a, Saba et al. 2008). The latter may be key to understanding differences in population trends: recent work by Saba et al. (2008) suggests that recruitment and reproductive output of leatherbacks in different ocean basins is linked to resource productivity and stability in migration and forage areas. Regions of consistently high primary production, such as the North Atlantic, may lead to higher reproductive output in western Atlantic leatherback rookeries (Saba et al. 2008).

As large sub-adults and adults, leatherback turtles cross long tracts of ocean between mid and high latitude foraging grounds to low latitude breeding and overwintering grounds (Carr & Ogren 1959, Musick & Limpus 1997, Plotkin 2002). The adaptive function of this long-distance migration strategy, similar to some tunas, sharks, and whales, is driven by the need for seasonal resource exploitation in productive temperate regions and reproduction in warmer latitudes (Lockyer & Brown 1981, Mather et al. 1995, Bonfil et al. 2005). There are steep energetic costs associated with extensive migrations, so the adaptive benefits (rapid accumulation of energy reserves, enhanced reproductive output) must outweigh the costs (Alerstam et al. 2003, Jørgensen et al. 2006, Chapman et al. 2011). The consequences of different migration strategies may directly impact population vulnerability to anthropogenic stressors, and impede recovery (Wallace et al. 2006a). Identification of leatherback migratory routes, forage grounds and environmental associations in the northwest Atlantic are critical to understanding population trends.

The Northeast US continental shelf is an extremely productive marine ecosystem (Sherman & Skjoldal 2002, Longhurst 2007) that seasonally supports a number of large,

highly migratory species such as bluefin tuna (Lutcavage & Kraus 1995, Galuardi et al. 2010), right whales (Wishner et al. 1988), humpback whales (Hain et al. 1981), giant ocean sunfish (Kenney 1996, Potter et al. 2011), basking sharks (Kenney et al 1985, Skomal et al. 2009) and leatherback sea turtles (Shoop & Kenney 1992, James et al. 2005a). James et al. (2005a) identified a portion of the southern New England shelf as high-use habitat for leatherbacks satellite-tagged off of eastern Canada, and there has been a decades-long call for data to evaluate leatherback turtle critical habitat and threats to survival in the New England shelf region (Bleakney 1965, Lazell 1976, Goff & Lien 1988, Prescott 1988, Lutcavage & Goldstein 1996, James et al. 2005a). Despite consistent recognition of the New England shelf as important leatherback turtle habitat, feeding areas and migratory movements to and from New England forage grounds are still largely unknown, hindering protection and recovery efforts for the Atlantic leatherback sea turtle in the US (Turtle Expert Working Group 2007). The proliferation of fixed fishing gear off New England is of particular concern since leatherbacks are vulnerable to entanglement in buoy lines and gillnets (Prescott 1988, Dwyer et al. 2002, Lum 2006), and interactions with surface system and buoy lines of pot gear fisheries may be a key threat to leatherbacks in coastal foraging habitats off eastern Canada and New England (Lazell 1976, Prescott 1988, Dwyer et al. 2002, James et al. 2005a).

The purpose of my dissertation was to investigate the movements, dive behavior, and trophic ecology of adult and sub-adult leatherback turtles found off New England. In order to access leatherbacks in this region, I partnered with commercial fishers and nongovernmental organizations (Provincetown Center for Coastal Studies and New England Aquarium) to capture leatherback turtles off the coast of Cape Cod,

Massachusetts, USA. I used satellite telemetry to collect data on leatherback horizontal and vertical movements in Northeast US continental shelf (bathymetry <200 m) and oceanic (bathymetry >200 m) habitats, and I applied stable isotope analyses to leatherback tissues and gelatinous zooplankton to examine their diet.

My first chapter is a synthesis of leatherback movements, dive behavior and remotely sensed environmental data. I determined leatherback occupancy of distinct oceanographic regions in the North Atlantic and characterized leatherback regional movements, dive behavior, migratory pathways and environmental associations. I identified seasonal, high-use habitat and used generalized linear mixed-effects models to investigate the relationship between leatherback search behavior and ecoregion, surface chlorophyll (chl *a*), sea surface temperature (SST), SST gradient magnitude, chl *a* gradient magnitude, and bathymetry.

My second chapter examines the migratory orientation of adult male, female and sub-adult leatherback sea turtles during their open-ocean movements in the Northwest Atlantic. I determined the orientation of individual turtles and turtles grouped by age class (adults vs. sub-adult), and investigated potential orientation cues used by leatherbacks during their southward migration through the subtropical gyre where limited sensory information is available to aid in navigation. Tracks were corrected for currents to determine the turtles' true orientation relative to potential cues.

My third chapter focuses on the trophic ecology of leatherback turtles captured off Massachusetts. I determined stable isotope ratios of nitrogen and carbon in adult and sub-adult leatherback tissues and potential prey items to test for differences in diet and habitat selection between sexes and ages classes. I used a Bayesian isotopic mixing model to

estimate the contribution of different prey items to the leatherback diet, and compared these findings with results from stomach content analysis studies and surface observations of feeding leatherbacks. This chapter was published in *Marine Biology* in 2011.

My dissertation work combined complementary research tools (satellite telemetry, remotely sensed environmental data and stable isotope analysis) to improve our understanding of leatherback turtle movements, dive behavior, and trophic ecology in the New England region, and throughout the NW Atlantic. Identification of important foraging and other marine habitats, and determination of migratory pathways and distribution are high priority objectives in the Federal Recovery Plan for Leatherback Turtles in the US, Caribbean, Atlantic and Gulf of Mexico (1992). More recently, the Turtle Expert Working Group prioritized the identification of important marine habitats and expansion of in-water research on leatherbacks (TEWG 2007). Data from my study addresses these objectives and will be available for state and federal wildlife action plans and international conservation efforts for the Atlantic leatherback turtle, ultimately benefiting by-catch mitigation and population recovery efforts for this species.

CHAPTER 1

LEATHERBACK TURTLE MOVEMENTS, DIVE BEHAVIOR AND HABITAT CHARACTERISTICS IN ECOREGIONS OF THE NORTHWEST ATLANTIC OCEAN

Introduction

Highly migratory marine predators such as leatherback sea turtles encounter a diversity of habitats during their long-distance movements. Oceanographic processes create regional ecosystems with distinct rates of primary productivity and ecology (Longhurst 2007). Predators may exhibit different behaviors in response to region-specific environmental conditions, with some regions optimal for foraging and (or) breeding while others serve as migratory habitat between breeding and feeding grounds. Obtaining direct measurements of foraging behavior in migratory marine species is challenging since the animals are difficult to observe for extended periods of time. Studies often rely on measures of search behavior to distinguish foraging from transiting, with the underlying assumption that a foraging animal should increase time and search effort in resource-rich areas (i.e., area-restricted search behavior) and decrease search effort in areas with fewer resources (Kareiva & Odell 1987). Marine animal tracking data has been used to measure area-restricted search (ARS) behavior through analyses of speed, turning angle, path straightness and first passage time (Pinaud & Weimerskirch 2007, Robinson et al. 2007, Weng et al. 2008), while switching state-space models have

been used to statistically estimate animal behavioral modes (e.g., foraging vs. transiting) (Jonsen et al. 2007, Bailey et al. 2008, 2012).

Leatherback sea turtles (*Dermochelys coriacea*) are far-ranging marine predators, capable of swimming thousands of kilometers between boreal and tropical latitudes (Carr & Ogren 1959, Musick & Limpus 1997, Plotkin 2002). In recent decades, satellite telemetry has demonstrated that leatherbacks can undertake annual migrations (defined here as the seasonal movement between regions/habitats based on favorable versus unfavorable conditions, after Dingle & Drake 2007) in the Atlantic, Pacific and Indian Oceans (Morreale et al. 1996, Hughes et al. 1998, Ferraroli et al. 2004, James et al. 2005a, Shillinger et al. 2008, López-Mendilaharsu et al. 2009, Benson et al. 2011). These extensive migrations take leatherbacks through a heterogeneous seascape where they experience strong differences in biological and physical oceanographic conditions. Despite an increase in broad-scale tracking studies, the relationship between leatherback behavior and their environment has only recently been explored (Luschi et al. 2003, McMahon & Hays 2006, Hays et al. 2006, Shillinger et al. 2008, 2011, Fossette et al. 2010b, Benson et al. 2011, Witt et al. 2011, Bailey et al. 2012a,b). With the exception of a few studies (Benson et al. 2011), research on leatherback environmental associations has almost exclusively focused on the inter-nesting and post-nesting migrations of adult females, resulting in a paucity of data for males, sub-adults, and females during inter-nesting years.

Leatherback foraging is likely associated with oceanographic processes that favor production and (or) retention of their gelatinous zooplankton prey, since targeting dense prey patches reduces search time and allows predators to maximize energy intake per unit

time (MacArthur & Pianka 1966, Schoener 1971, Charnov 1976). In oceanic habitat, inferred foraging behavior and foraging success of leatherbacks have been linked to fronts, upwelling and downwelling zones, and mesoscale features (Lutcavage 1996, Luschi et al. 2003, Ferraroli et al. 2004, Eckert 2006, Doyle et al. 2008, Benson et al. 2011, Fossette et al. 2011a). Although leatherbacks are most often associated with an oceanic lifestyle, some individuals make seasonal use of highly productive continental shelf and slope habitats (Shoop & Kenney 1992, James et al. 2005a, Houghton et al. 2006, Benson et al. 2007, 2011, Witt et al. 2007), residing in near-shore areas for several months (James et al. 2005b; Eckert et al. 2006, López-Mendilaharsu et al. 2009). Continental shelf and slope waters are productive regions where spring bloom conditions can lead to increased seasonal abundance of plankton (Larson 1976, Houghton et al. 2006, Madin et al. 2006, Mann & Lazier 2006). Increased nutrient input from land, tidal-mixing, and wind-driven upwelling can trigger increases in scyphozoan populations, while physical discontinuities in shelf waters and along ocean fronts promote aggregation and retention of gelatinous organisms (Shenker 1984, Olson et al. 1994, Graham et al. 2001, Purcell et al. 2001, Deibel & Paffenhöfer 2009). Productive water masses and fronts in oceanic and neritic regions are also targeted by commercial fishing operations with fixed and mobile gear, often resulting in incidental captures of sea turtles and other non-target species (Lewison et al. 2004, Lum 2006, Phillips et al. 2006, Alfaro-Shigueto et al. 2007, 2010).

In the present study, we deployed satellite tags on adult male, female and sub-adult leatherbacks turtles captured off Massachusetts, USA. We collected geolocation and dive data to: 1) determine leatherback occupancy of distinct oceanographic regions in the

North Atlantic; 2) characterize leatherback regional movements, dive behavior, and environmental associations; 3) identify seasonal high-use habitat and 4) determine key environmental features associated with leatherback search behavior in the NW Atlantic.

Materials and Methods

Satellite telemetry

Twenty adult and sub-adult leatherback turtles were fitted with Wildlife Computers, Inc. (Redmond, WA, USA) model MK10-A (n=8) and MK10-AF (n=12) ARGOS-linked satellite time depth recorders (STDRs). Leatherbacks were located off the coast of Massachusetts, USA (~41°N, 70°W) from August 2007 to September 2009, and captured with either a breakaway hoopnet (n = 11) (Asper 1975, James et al. 2005a) or accessed through the Massachusetts sea turtle disentanglement network (n = 9) (Fig. 1; Table 1). We brought turtles on board commercial fishing or research vessels using a custom-built stern ramp. Following the methods described in Dodge et al. (in prep), we attached STDRs directly to the carapace medial ridge. Leatherbacks were measured to the nearest 0.1 cm (curved carapace length: CCL and curved carapace width: CCW) with a flexible fiberglass measuring tape, and ranged from 123.0 to 161.5 cm CCL (Table 1). We used CCL to classify turtles as adults (CCL \geq 145 cm) or sub-adults (CCL < 145 cm), and we determined gender based on tail length of adult turtles (James et al. 2007). Five sub-adult turtles were sexed based on presence of a penis, subsequent necropsy or evidence of nesting. We collected samples of blood and skin (Innis et al. 2010, Dodge et al. 2011), and all turtles were photographed, scanned for passive integrated transponder (PIT) tags, and given PIT and flipper tags if none were present.

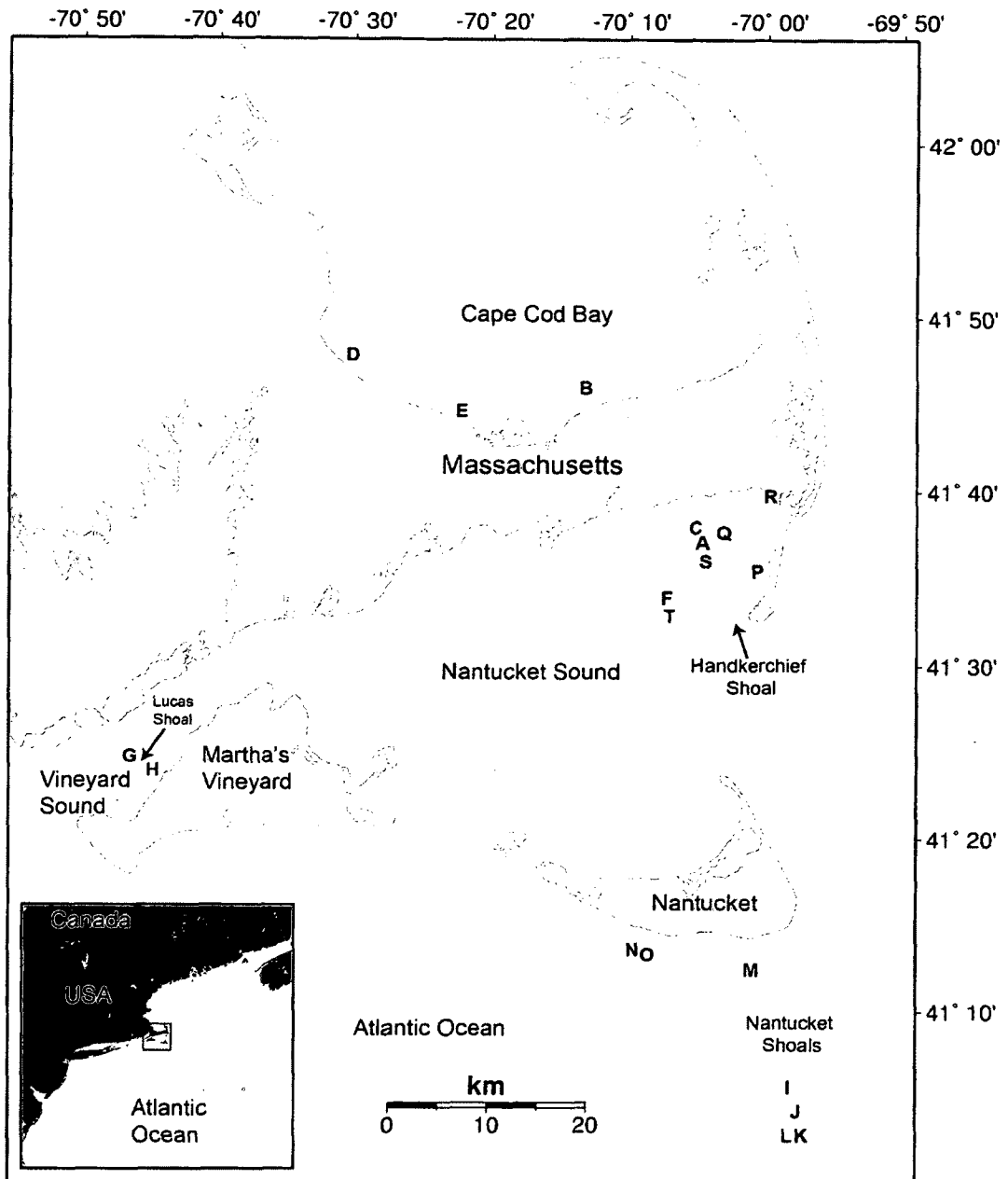


Figure 1. Leatherback turtle tagging locations off Cape Cod, Massachusetts, USA. Letters represent satellite tag deployments from 2007-2009 as listed in Table 1.

Table 1. Summary data for twenty leatherback sea turtles equipped with satellite tags off Massachusetts, USA. PTT: platform transmitter terminal; CCL: curved carapace length; S: sub-adult (<145 cm CCL); A: adult (\geq 145 cm CCL); M: male; F: female, U: unknown sex; MK10-A: Argos-only locations; MK10-AF: Argos and Fastloc GPS locations; N. Sound: Nantucket Sound; CC Bay: Cape Cod Bay; V. Sound: Vineyard Sound; Nantucket: waters south of Nantucket.

Turtle ID	PTT Number	CCL (cm)	Age	Sex	Capture method	Tag Model	Tagging location	Tagging date	Days at liberty	Distance (km)	No. ARGOS locations	No. GPS locations
A	68366	140.7	S	M	Entangled	MK10-AF	N. Sound	19-Aug-07	34	938	137	263
B	68364	143.2	S	M	Entangled	MK10-AF	CC Bay	29-Aug-07	18	461	82	90
C	68369	123.0	S	U	Entangled	MK10-AF	N. Sound	29-Aug-07	16	277	64	89
D	68370	137.5	S	U	Entangled	MK10-AF	CC Bay	22-Sep-07	183	6444	572	777
E	68365	136.0	S	F	Entangled	MK10-AF	CC Bay	1-Oct-07	35	991	109	252
F	68365a	149.5	A	M	Hoopnet	MK10-AF	N. Sound	17-Jul-08	174	8004	1520	1067
G	68364a	146.0	A	F	Hoopnet	MK10-AF	V. Sound	26-Jul-08	199	7920	1407	1498
H	82052	161.5	A	F	Hoopnet	MK10-A	V. Sound	29-Jul-08	272	8435	2114	na
I	76988	152.2	A	M	Hoopnet	MK10-AF	Nantucket	10-Aug-08	214	8878	1932	1469
J	76990	140.4	S	U	Hoopnet	MK10-AF	Nantucket	10-Aug-08	150	5967	1147	593
K	82055	133.8	S	U	Hoopnet	MK10-A	Nantucket	10-Aug-08	152	5792	1306	na
L	82051	153.3	A	M	Hoopnet	MK10-A	Nantucket	10-Aug-08	242	9466	1846	na
M	76989	144.8	A	F	Hoopnet	MK10-AF	Nantucket	21-Aug-08	180	9191	1427	1563
N	85538	154.0	A	M	Hoopnet	MK10-AF	Nantucket	22-Aug-08	183	6528	1707	796
O	85537	138.5	S	M	Hoopnet	MK10-AF	Nantucket	22-Aug-08	181	5883	1722	307
P	82053	146.4	A	M	Entangled	MK10-A	N. Sound	23-Aug-08	234	9765	1095	na
Q	82054	140.0	S	U	Entangled	MK10-A	N. Sound	28-Aug-08	191	5980	1306	na
R	82056	126.5	S	U	Weir	MK10-A	N. Sound	10-Jul-09	414	14168	3570	na
S	82057	127.7	S	U	Hoopnet	MK10-A	N. Sound	27-Aug-09	278	11541	1616	na
T	27579	155.0	A	M	Entangled	MK10-A	N. Sound	3-Sep-09	203	7096	1458	na

The STDRs collected Fastloc® GPS locations (MK10-AF tags only), ARGOS-derived locations (all tags) and dive information (depth resolution ± 0.5 m and temperature resolution $\pm 0.05^\circ\text{C}$) via Service ARGOS (Toulouse, France) (Table 1). Ninety-five percent of Fastloc GPS locations are accurate to ± 55 m (Bryant 2007), while ARGOS-derived location error varies by location class (LC) as follows: LC3 <150 m, LC2 150-350 m, LC1 350-1000 m, and LC0 >1000 m. ARGOS does not provide accuracy estimates for LCA and LCB locations, and LCZ are considered invalid.

We defined a dive as vertical movement below two meters for at least one minute. The number of dives within specified depth and duration ranges and the time spent within depth and temperature ranges were collected as frequency histograms based on preprogrammed bins (Table 2). Histograms were aggregated over four 6-hour periods in GMT: 0:00-5:59, 6:00-11:59, 12:00-17:59, 18:00-23:59. Tags deployed in 2007 and 2008 (n=17) were programmed to transmit daily while tags deployed in 2009 (n=3) were programmed to transmit daily from July to December, every other day from January to April, and every third day from May to June.

Environmental data

We selected environmental data likely to influence production and distribution of gelatinous prey (Graham et al. 2001, Lilley et al. 2011), and thus leatherback movements. Sea surface temperature (SST), surface chlorophyll *a* concentration (chl *a*), SST gradient, chl *a* gradient and bathymetry were used as potential predictors. We used SST and chl *a* gradients as a proxy for the presence of fronts (Belkin & O'Reilly 2009). SST data were obtained as a blended product available at the GHRSSST website (<http://www.ghrsst.org>) as 9km, daily averages. The blended SST product was derived from microwave SST data

from three sources (Advanced Microwave Scanning Radiometer, Tropical Rainfall Measuring Mission Microwave Imager and WindSAT Polarimetric Radiometer) and InfraRed SST data from Aqua Moderate Resolution Imaging Spectroradiometer (MODIS). Chl *a* data were obtained from MODIS data as 2.5km, 8 day averages at the NOAA ERDDAP website (<http://coastwatch.pfeg.noaa.gov/erddap/info/erdMWchla8day/index.html>). Bathymetry was determined using 1-minute gridded global relief data (ETOPO1) from the National Geophysical Data Center (www.ngdc.noaa.gov/mgg/global/). SST and chl *a* gradients were generated using the Belkin-O'Reilly (BOA) oceanic front detection algorithm (Belkin & O'Reilly 2009).

Table 2. Bin ranges of dive parameters from satellite tags deployed on leatherback sea turtles from 2007 to 2009 (dive depth and dive duration) and from 2008 to 2009 (time-at-depth and time-at-temperature).

Years	Number of tags	Depth bin (m)	Duration bin (min)	Years	Number of tags	Time-at-Depth bin (m)	Time-at-Temp bin (°C)
2007-2009	20	2-5	1-4	2008-2009	15	0-2	0-4
2007-2009	20	5-10	4-8	2008-2009	15	2-10	4-6
2007-2009	20	10-15	8-12	2008-2009	15	10-15	6-8
2007-2009	20	15-20	12-16	2008-2009	15	15-20	8-10
2007-2009	20	20-25	16-20	2008-2009	15	20-25	10-12
2007-2009	20	25-30	20-24	2008-2009	15	25-30	12-14
2007-2009	20	30-50	24-28	2008-2009	15	30-40	14-16
2007-2009	20	50-75	28-32	2008-2009	15	40-50	16-18
2007-2009	20	75-100	32-36	2008-2009	15	50-75	18-20
2007-2009	20	100-200	36-40	2008-2009	15	75-100	20-22
2007-2009	20	200-300	40-44	2008-2009	15	100-125	22-24
2007-2009	20	300-400	44-48	2008-2009	15	125-150	24-26
2007-2009	20	400-500	48-52	2008-2009	15	150-200	26-28
2007-2009	20	>500	>52	2008-2009	15	>200	>28

Data analysis

We filtered 30,173 raw ARGOS and GPS locations using Kalman filter methods outlined in Royer & Lutcavage (2008). Since our analysis included GPS data, we extended the original error covariance structure to include this information. Data were interpolated to a three-hour time step and smoothed. Environmental data were then extracted for the 28,253 filtered turtle locations. Rate of travel was determined using the distance function in Matlab (Mathworks, Natick, MA) and a daily straightness index (SI) was calculated as the ratio of straight-line distance to total distance traveled by each turtle per day (in km d^{-1}), resulting in a dimensionless index from 0 (sinuous) to 1 (straight) (Batschelet 1981, Benhamou 2004). Travel rate and straightness were not calculated from January to June for turtles tagged in 2009 since tags were duty-cycled and did not transmit daily during these months. Leatherback positions and dive data were assigned to distinct biogeographic provinces or “ecoregions” defined by Longhurst (2007) (Fig. 2). We calculated the duration of leatherback occupancy in each ecoregion, and assessed variability in leatherback search effort, dive behavior and environmental associations across ecoregions. Averages are shown as mean \pm standard deviation (mean \pm SD) for normally distributed data, and median, interquartile range (Q1-Q3) where data are not normally distributed.

To investigate variation in seasonal habitat use, we created density utilization maps of filtered leatherback positions for pooled data across all turtles by season. Seasons were defined as: July – September (summer), October – December (autumn), January – March (winter), and April – June (spring). Daily locations were summed into hexagonal area bins, with the area of each hexagon approximately 669 km^2 (or 4 hexagons per

degree). These bins are larger than the error associated with our filtered ARGOS and GPS location data, but small enough to identify regional high-use areas. Density utilization maps were produced using R (R Development Core Team 2013) and Generic Mapping Tools (Wessel and Smith 1991).

We applied generalized linear mixed-effects models to investigate the influence of ecoregion, SST, chl *a*, SST gradient magnitude, chl *a* gradient magnitude and bathymetry (fixed effects) on leatherback path straightness while accounting for the correlation of repeated observations from individual turtles (Zuur et al. 2009). Changes in path straightness have been used to identify purported search behavior associated with foraging in leatherbacks (Fossette et al. 2010a), as well as other marine predators (Weimerskirch et al. 2002, Kuhn et al. 2010, McCarthy et al. 2010). Density plots of the environmental data showed that logarithmic transformation was required for SST gradient, chl *a*, chl *a* gradient and bathymetry. We were primarily interested in the influence of SST, SST gradient, chl *a* and chl *a* gradient in regions where these surface features are most variable (least homogenous), and we were mainly interested in the effect of bathymetry in neritic habitats where leatherbacks can access the entire water column. Therefore, we estimated region-specific regression parameters for these variables: SST (Northwest Atlantic Shelves, Gulf Stream), SST gradient (Northwest Atlantic Shelves, Gulf Stream) and bathymetry (Northwest Atlantic Shelves, Guianas Coastal). We compared models where effects of SST, SST gradient, chl *a*, chl *a* gradient and bathymetry on SI are the same for the respective groups of regions with less parsimonious models that allow the effects to differ for each ecoregion (Table 3). As SI ranges between 0 and 1, we assumed a Gaussian error structure for the logit-transformed

SI with continuous AR(1) autocorrelation structure for repeated observations as a function of time between observations (Chi & Reinsel 1989).

We fit the models by maximum marginal likelihood in R (R Core Team 2013) using the lme4 package and compared relative performance using Akaike Information Criterion (AIC) (Akaike 1973) of the fitted models. As a measure of evidence for relative performance of each model that we fit, we used Akaike weights (Burnham and Anderson 1998). We chose to use AIC over a criteria adjusted for sample size (AIC_c) because AIC_c requires a known number of observations, and this is not straightforward for mixed-effects models (see Faes et al. 2009). For AR(1) error structured models as used here, the effective sample size depends on the correlation of the observations within each individual. Since the autocorrelation we estimated for our models is generally low, we had a large effective sample size where differences between AIC and AIC_c are negligible. For the model that provided the best fit, we used restricted maximum likelihood to obtain parameter estimates and predict changes in steepness with various covariates and factors (Pinheiro and Bates 2000).

Results

Satellite telemetry

We received data from all tagged leatherbacks: four tags transmitted for less time than expected and 16 tags met or exceeded predicted battery life. Tags reported between 16 and 414 days, with a median tracking duration of 184 (152 to 219; Q1-Q3) days (Table 1). We pooled the percent frequency distributions of the four dive parameters: dive-depth (n=19), dive-duration (n=17), time-at-depth (n=15), and time-at-temperature (n=15), shown in Fig. 3. Three tags deployed in 2007 reported spurious dive-duration

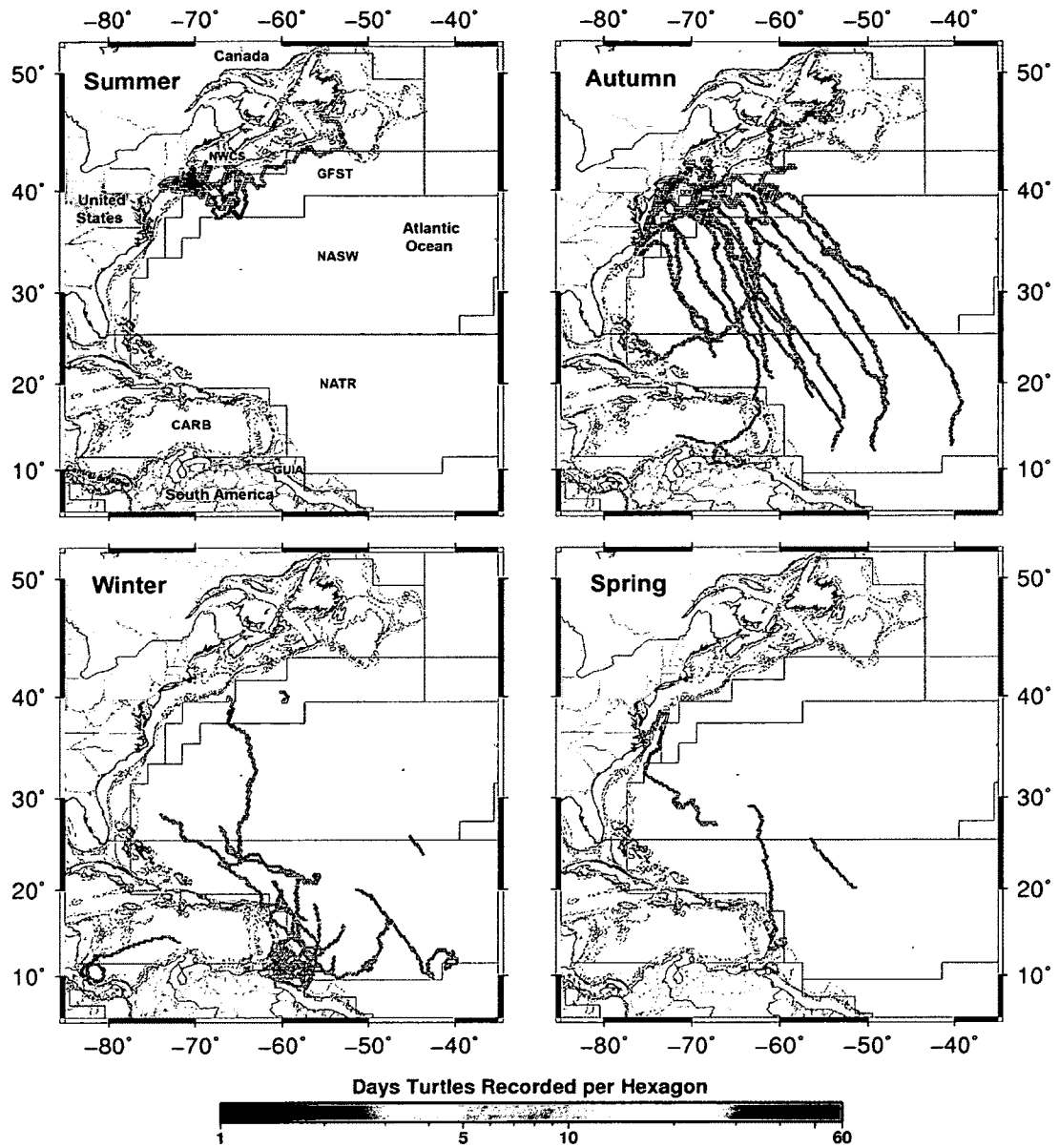


Figure 2. Seasonal habitat use of adult male, female and sub-adult leatherback sea turtles from 2007 to 2010. Summer, July – September (n=19 turtles, autumn, October – December (n=17 turtles), winter, January – March (n=16 turtles), and spring, April – June (n=5 turtles). There are four hexagons per degree; each hexagon represents approximately 669 km². Color scale shows the number of track days per hexagon. Ecoregions from Longhurst (2007): NWCS, Northwest Atlantic Shelves; GFST, Gulf Stream; NASW, North Atlantic Subtropical Gyral West; NATR, North Atlantic Tropical Gyral; CARB, Caribbean; GUIA, Guianas Coastal.

data (i.e., the total number of dives recorded in the >52 min bin exceeded the 6-hour time period) and one 2007 tag recorded insufficient dive-depth data, so these tags were excluded from the dive-duration and dive-depth analysis. We only included time-at-depth and time-at-temperature data for tags with the same lower bin ranges (2008 and 2009).

Of the 210,556 dives reported for the dive-depth parameter, over 28% were to depths less than 5 m and 90% were shallower than 75 m (Fig. 3a). Fifteen turtles dove deeper than 500 m during the study period, with males recording the deepest dives (>1200 m, n = 3). The pooled dive-duration data showed that close to 75% of all leatherback dives were less than 12 min, and more than 90% were shorter than 32 min (Fig. 3b). Sixteen turtles recorded extended dives lasting over 52 minutes, but these represent less than 3% of the total. The pooled frequency distribution of the time-at-depth shows that turtles spent over 25% of their time within 2 m of the surface, and over 50% of their time shallower than 10 m (Fig. 3c). Over 90% of their time was spent in the top 100 m of the water column. The pooled frequency distribution of the time-at-temperature shows that turtles spent 86% of their time between 16°C and 28°C (Fig. 3d).

Habitat use and environmental associations

Leatherbacks ranged widely between 39°W and 83°W, and between 9°N and 47°N (Fig. 4), over six oceanographically distinct ecoregions: the Northwest Atlantic Shelves (NWCS; n=20), the Gulf Stream (GFST; n=16), the North Atlantic Subtropical Gyral West (NASW; n=15), the North Atlantic Tropical Gyral (NATR; n=15), the Caribbean (CARB; n=6) and the Guianas Coastal (GUIA; n=7) (Fig. 2). All leatherbacks were tagged in the NWCS, and 16 turtles were tracked long enough to determine an

average minimum residency of 79 days (\pm 39 days) post-tagging. Fifteen turtles left the NWCS between late September and mid-November, with the majority leaving between mid-October and mid-November ($n=11$). Most turtles spent less than a week in the GFST (median 6 days), but two individuals (Turtles F & D; Table 1 & Fig. 4) made more extensive use of this region (95 and 59 days, respectively). Between October and February, leatherbacks transited rapidly through the NASW (median 29 days), entering the NATR between November and early February. Leatherbacks either remained in the NATR for the remainder of the tracking period ($n=7$) or continued on to breeding and (or) foraging areas in CARB and GUIA (8). Three sub-adults and one small adult male were tracked long enough to observe a complete (32 and 92 days; Turtles D & R) or partial (83 and 56 days; Turtles P & S) overwintering period in the NATR before they returned to the NASW between late March and mid-May. One turtle returned to the NWCS in mid-May, remaining in the region for 96 days before the tag stopped transmitting in late August.

Turtles modified their movements and dive behavior while occupying different ecoregions. Leatherbacks in the NWCS had the lowest travel rates and path straightness of all regions (Fig. 5a,b), and they combined slow, sinuous swimming with short, shallow dives (Fig. 6a,b). They spent most of their time in the top 10 m of the water column at temperatures between 16°C and 20°C (Fig. 6c,d). Outside of the NWCS, turtles increased their travel rate and path straightness (Fig. 5a,b). Leatherbacks continued making shallow dives (< 5 m), but increasingly made deeper, longer dives as they traveled south (Fig. 6a,b). As turtles moved into subtropical and tropical ecoregions, they began spending more time at temperatures over 22°C and at depths over 50 m, experiencing the warmest

Table 3. Definition of fitted mean logit straightness models for observation j of turtle i . Turtle i is in ecoregion r_{ij} at observation j , $I(x)$ is an indicator function equaling 1 when x is true and 0 otherwise. There are K ecoregions, and K_{SST} , K_{SSTg} , K_{chla} , K_{chlag} , and K_{bathy} are the number of ecoregions where SST, SSTg, chla, chlag, and bathy effects are allowed. The variance structure is the same for all models.

Model	$E\left[\log\left(\frac{SI_{ij}}{1-SI_{ij}}\right)\right]$
null	β_0
ecoregion	$\sum_{k=1}^K \beta_{0,i} I(r_{ij} = k)$
ecoregion + SST ^a	$\sum_{k=1}^K \beta_{0,i} I(r_{ij} = k) + \beta_1 \sum_{l=1}^{K_{SST}} I(r_{ij} = l) SST_{ij}$
ecoregion x SST ^b	$\sum_{k=1}^K \beta_{0,i} I(r_{ij} = k) + \sum_{l=1}^{K_{SST}} \beta_{1,i} I(r_{ij} = l) SST_{ij}$
ecoregion + chla ^a	$\sum_{k=1}^K \beta_{0,i} I(r_{ij} = k) + \beta_1 \sum_{l=1}^{K_{chla}} I(r_{ij} = l) chla_{ij}$
ecoregion x chla ^b	$\sum_{k=1}^K \beta_{0,i} I(r_{ij} = k) + \sum_{l=1}^{K_{chla}} \beta_{1,i} I(r_{ij} = l) chla_{ij}$
ecoregion + SSTg ^b	$\sum_{k=1}^K \beta_{0,i} I(r_{ij} = k) + \beta_1 \sum_{l=1}^{K_{SSTg}} I(r_{ij} = l) SSTg_{ij}$
ecoregion x SSTg ^b	$\sum_{k=1}^K \beta_{0,i} I(r_{ij} = k) + \sum_{l=1}^{K_{SSTg}} \beta_{1,i} I(r_{ij} = l) SSTg_{ij}$
ecoregion + chlag ^b	$\sum_{k=1}^K \beta_{0,i} I(r_{ij} = k) + \beta_1 \sum_{l=1}^{K_{chlag}} I(r_{ij} = l) chlag_{ij}$
ecoregion x chlag ^b	$\sum_{k=1}^K \beta_{0,i} I(r_{ij} = k) + \sum_{l=1}^{K_{chlag}} \beta_{1,i} I(r_{ij} = l) chlag_{ij}$
ecoregion + bathymetry ^a	$\sum_{k=1}^K \beta_{0,i} I(r_{ij} = k) + \beta_1 \sum_{l=1}^{K_{bathy}} I(r_{ij} = l) bathy_{ij}$
ecoregion x bathymetry ^b	$\sum_{k=1}^K \beta_{0,i} I(r_{ij} = k) + \sum_{l=1}^{K_{bathy}} \beta_{1,i} I(r_{ij} = l) bathy_{ij}$
ecoregion + SST ^a + bathymetry ^a	$\sum_{k=1}^K \beta_{0,i} I(r_{ij} = k) + \beta_1 \sum_{l=1}^{K_{bathy}} I(r_{ij} = l) bathy_{ij} + \beta_2 \sum_{m=1}^{K_{SST}} I(r_{ij} = m) SST_{ij}$

ecoregion x SST ^b + bathymetry ^a *	$\sum_{k=1}^K \beta_{0,k} I(r_{ij} = k) + \beta_1 \sum_{l=1}^{K_{bathy}} I(r_{ij} = l) bathy_{ij} + \sum_{m=1}^{K_{SST}} \beta_{2,m} I(r_{ij} = m) SST_{ij}$
ecoregion + chla ^a + bathymetry ^a	$\sum_{k=1}^K \beta_{0,k} I(r_{ij} = k) + \beta_1 \sum_{l=1}^{K_{bathy}} I(r_{ij} = l) bathy_{ij} + \beta_2 \sum_{m=1}^{K_{chla}} I(r_{ij} = m) chla_{ij}$
ecoregion x chla ^b + bathymetry ^a	$\sum_{k=1}^K \beta_{0,k} I(r_{ij} = k) + \beta_1 \sum_{l=1}^{K_{bathy}} I(r_{ij} = l) bathy_{ij} + \sum_{m=1}^{K_{chla}} \beta_{2,m} I(r_{ij} = m) chla_{ij}$
ecoregion + SSTg ^a + bathymetry ^a	$\sum_{k=1}^K \beta_{0,k} I(r_{ij} = k) + \beta_1 \sum_{l=1}^{K_{bathy}} I(r_{ij} = l) bathy_{ij} + \beta_2 \sum_{m=1}^{K_{SSTg}} I(r_{ij} = m) SSTg_{ij}$
ecoregion x SSTg ^b + bathymetry ^a	$\sum_{k=1}^K \beta_{0,k} I(r_{ij} = k) + \beta_1 \sum_{l=1}^{K_{bathy}} I(r_{ij} = l) bathy_{ij} + \sum_{m=1}^{K_{SSTg}} \beta_{2,m} I(r_{ij} = m) SSTg_{ij}$
ecoregion + chlag ^a + bathymetry ^a	$\sum_{k=1}^K \beta_{0,k} I(r_{ij} = k) + \beta_1 \sum_{l=1}^{K_{bathy}} I(r_{ij} = l) bathy_{ij} + \beta_2 \sum_{m=1}^{K_{chlag}} I(r_{ij} = m) chlag_{ij}$
ecoregion x chlag ^b + bathymetry ^a	$\sum_{k=1}^K \beta_{0,k} I(r_{ij} = k) + \beta_1 \sum_{l=1}^{K_{bathy}} I(r_{ij} = l) bathy_{ij} + \sum_{m=1}^{K_{chlag}} \beta_{2,m} I(r_{ij} = m) chlag_{ij}$

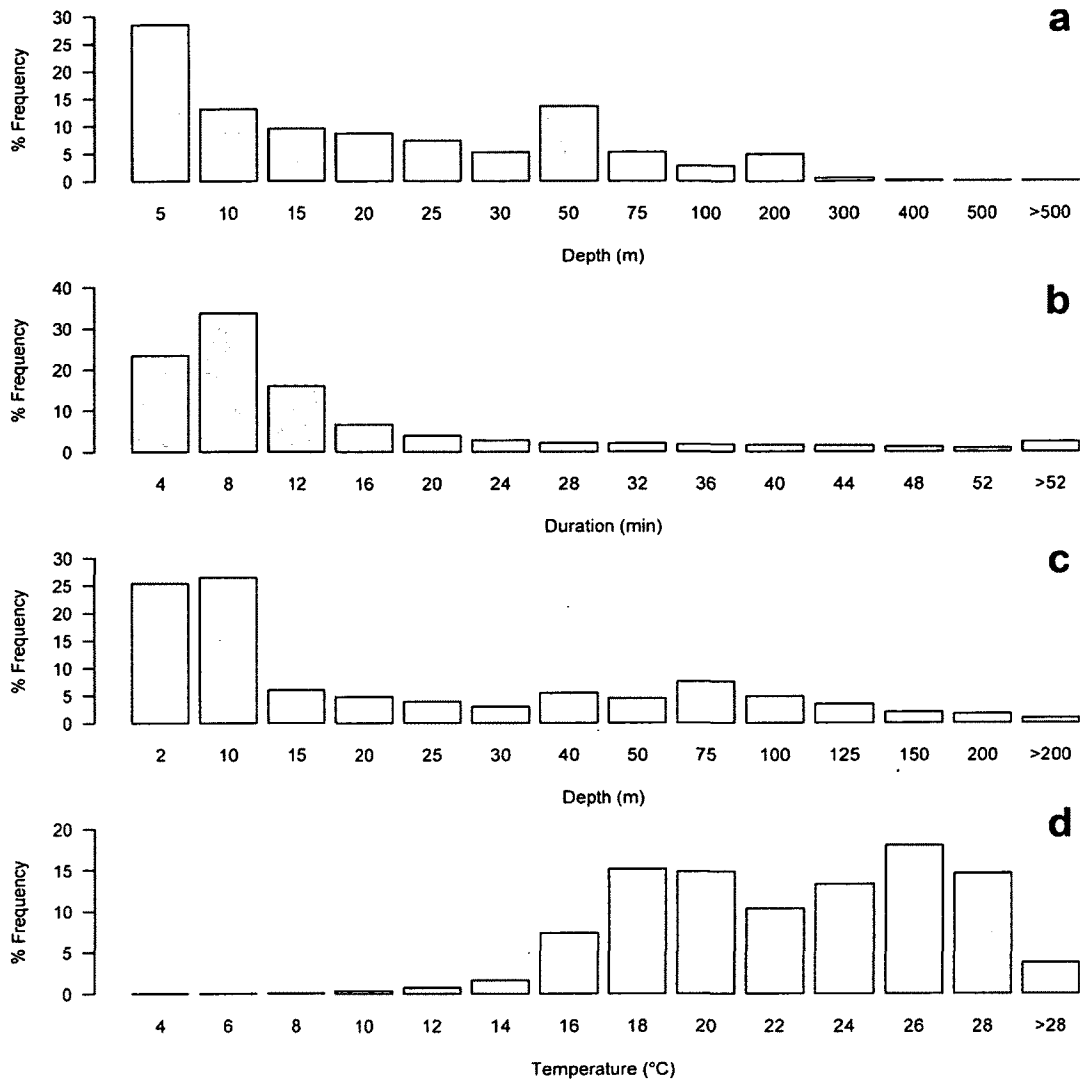


Figure 3. Frequency distributions of a) dive-depth, b) dive-duration, c) time-at-depth and d) time-at-temperature collected from satellite tags on leatherback sea turtles in the North Atlantic Ocean. Dive-depth (n = 19) and dive-duration (n = 17) from turtles tagged from 2007 to 2009. Time-at-depth (n = 15) and time-at-temperature (n=15) from turtles tagged from 2008 to 2009.

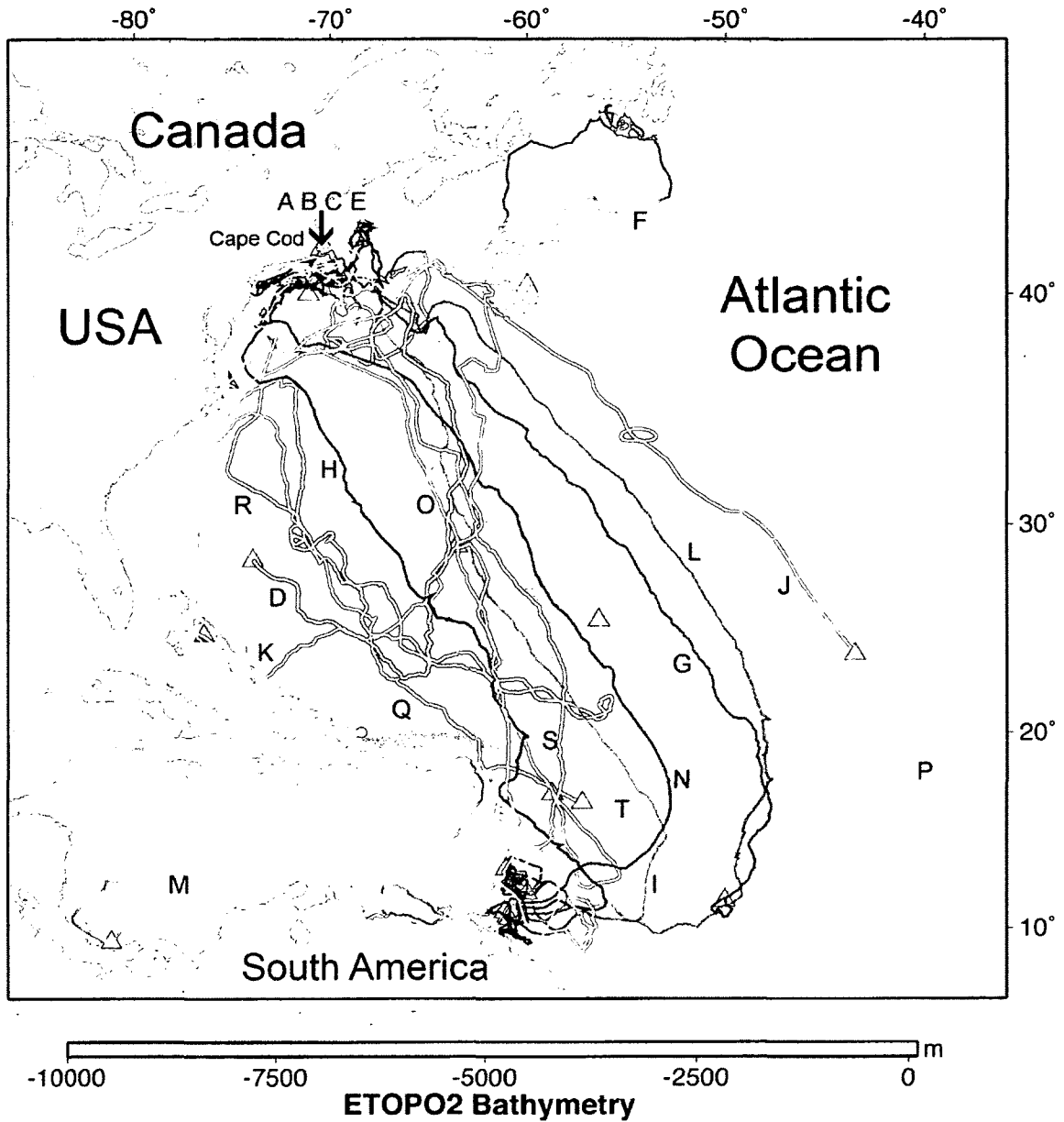


Figure 4. Reconstructed movements of 20 satellite-tagged leatherback sea turtles from point of release (Cape Cod) to point of last Argos transmission (red triangles) in the North Atlantic Ocean from 2007 to 2010. Tags were deployed on adult males (F, I, L, N, P, T), adult females (G, H, M), and sub-adults (A, B, C, D, E, J, K, O, Q, R, S).

temperatures and making the deepest, longest dives in the NATR and CARB (Fig. 6c,d). Diving patterns in the primarily shelf waters of GUIA were distinct from other tropical regions: leatherbacks spread their diving effort throughout the top 200 m and most dives were less than 24 min (Fig. 6a,b). Leatherback surface times (0-2 m) were similar across most regions, with the greatest surface times recorded in the NASW (mean 30%), NWCS (mean 27%), CARB (mean 26%) and GFST (mean 25%). Leatherbacks spent the least amount of time at the surface in GUIA (mean 14%) and NATR (mean 21%).

Turtles experienced highly variable environmental conditions across ecoregions, where bathymetry ranged from shallow bays and sounds on the continental shelf to deep oceanic waters, SST from 9.6°C to 28.9°C and chl *a* from near zero to 64.36 mg m⁻³ (Fig. 5). Leatherbacks occupied areas with SST and chl *a* gradients of varying magnitudes, with SST gradients of 0 to 1.85 °C km⁻¹ and chl *a* gradients of 1.052 to 1.144 (Fig. 5). Turtles in the NWCS used relatively shallow habitat on the shelf, staying mostly within the 80 m isobath and associating with the highest chl *a* of all regions (Fig. 5e,g). Turtles experienced the coolest, most variable sea surface temperatures and strongest SST gradients in the NWCS and the GFST (Fig. 5c,d). While the chl *a* gradients were similar across ecoregions, leatherbacks in the GUIA used areas with the most variable and strongest chl *a* gradients (Fig 5f).

Based on AIC values, the most well supported model showed that differences in leatherback search behavior (represented by logit-transformed SI) were best explained by ecoregion and effects of bathymetry and SST, with effects of SST depending on the ecoregion (Table 4). In the mainly neritic ecoregions (NWCS and GUIA), there was a positive relationship between SI and bathymetry, with leatherback movements becoming

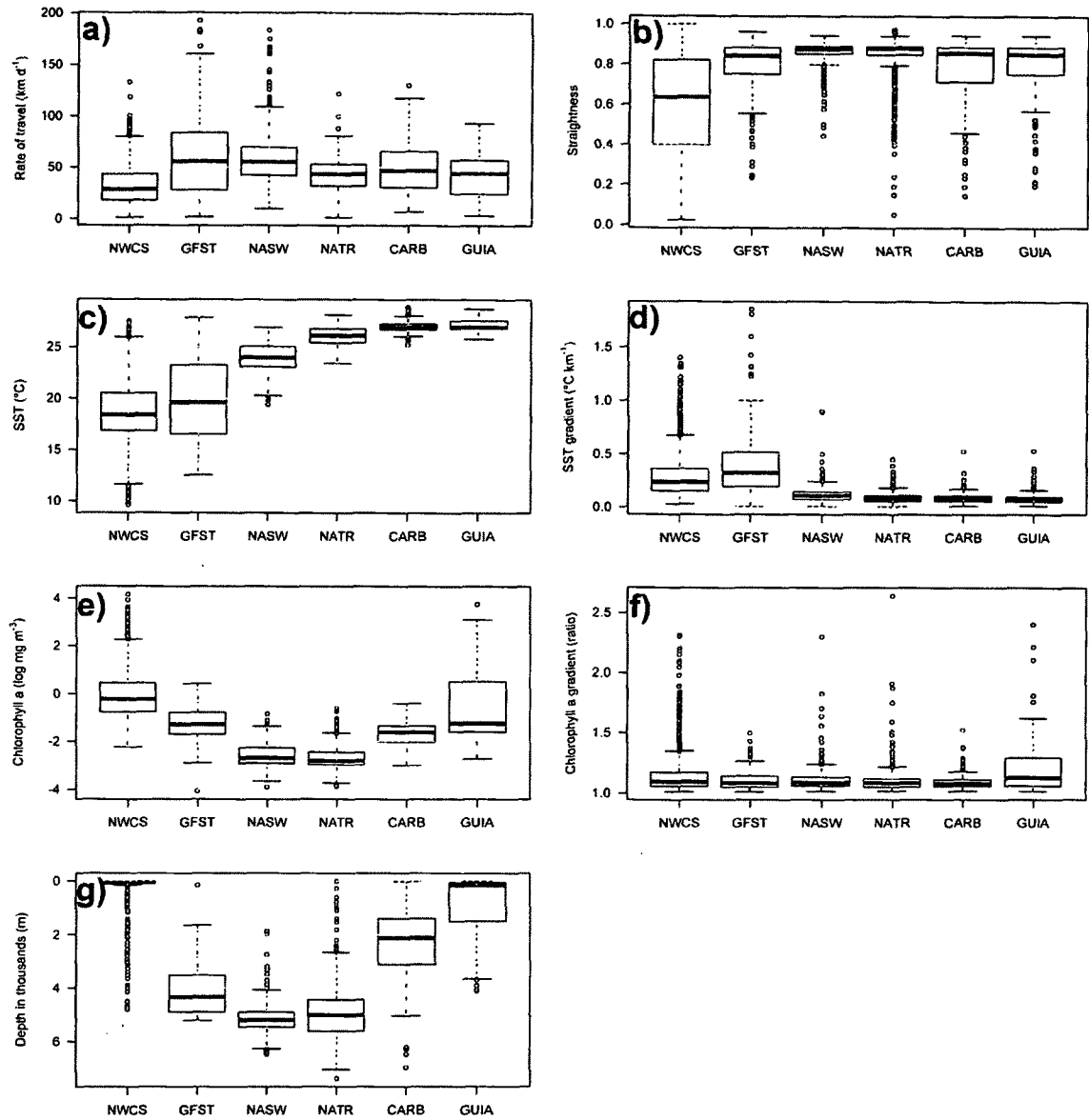


Figure 5. Leatherback behavioral indices: a) rate of travel, b) straightness, c) SST, d) SST gradient magnitude, e) chl *a*, f) chl *a* gradient magnitude, and g) bathymetric depth in Longhurst regions of the North Atlantic Ocean. NWCS, Northwest Atlantic Shelves; GFST, Gulf Stream; NASW, North Atlantic Subtropical Gyral West; NATR, North Atlantic Tropical Gyral; CARB, Caribbean; GUIA, Guianas Coastal. Boxplots: centerline, median; edges of box, 1st and 3rd quartiles; whiskers, data points within the range $Q1 - 1.5(Q3 - Q1)$ to $Q3 + 1.5(Q3 - Q1)$.

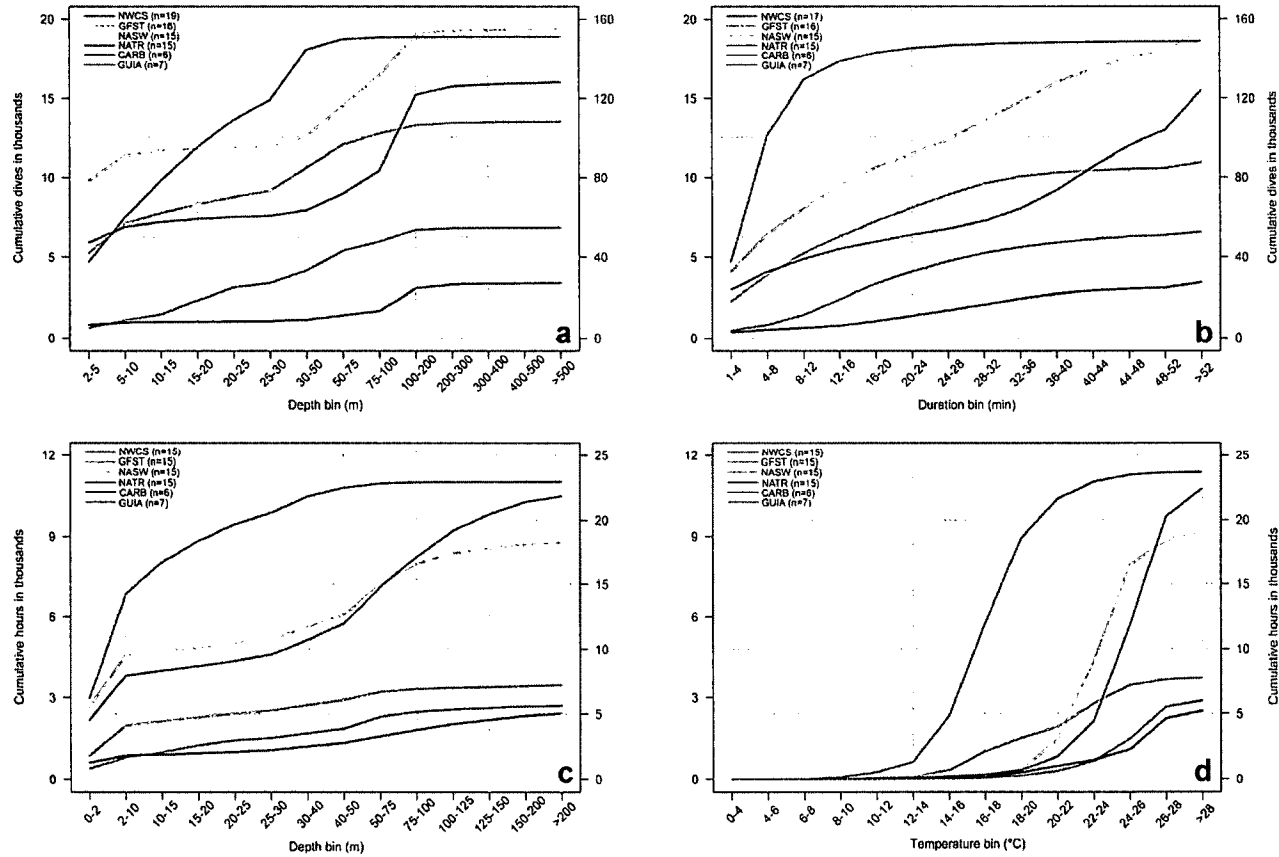


Figure 6. Cumulative frequency plots of leatherback dives in depth and duration bins (top panels) and leatherback hours in depth and temperature bins (bottom panels) in Longhurst regions of the North Atlantic Ocean. NWCS, Northwest Atlantic Shelves; GFST, Gulf Stream; NASW, North Atlantic Subtropical Gyral West; NATR, North Atlantic Tropical Gyral; CARB, Caribbean; GUIA, Guianas Coastal. The second y-axis (red) corresponds to NWCS (red line) while all other regions reference the first y-axis (black). This highlights the increased dive activity of tagged turtles in the NWCS region.

more sinuous as water depth decreased (Table 5; Fig. 7a). In the regions where SST was most variable (NWCS and GFST), the relationship between SI and SST differed. In the GFST, the relationship between SI and SST was positive, with leatherback path sinuosity increasing with decreasing SST. In the NWCS, the relationship between SI and SST was negative, with leatherback sinuosity increasing with increasing SST (Table 5; Fig. 7b). The relationship between SI and SST in the Gulf Stream region was slightly positive, reflecting the fact that this slope parameter was not significant in the model.

Seasonal density utilization maps showed leatherback movements were the least extensive during summer, with turtles tagged off Massachusetts showing a strong preference for the Northeast US continental shelf, concentrating movements off southern New England and Virginia/North Carolina (Fig. 2 ‘Summer’). Leatherbacks expanded their range in autumn, increasing their use of the Mid-Atlantic Bight and Gulf Stream before initiating a rapid, directed southward migration, following widely dispersed pathways through the subtropical and tropical gyral regions (Fig. 2 ‘Autumn’). Winter movements were restricted to tropical oceanic habitat and neritic waters of the Antilles, South America, and Central America, with the exception of two sub-adults and one small adult male that occupied subtropical oceanic waters for part of the season. Densely occupied winter habitat occurred off breeding beaches in the Windward Islands, particularly the north/northeast coast of Trinidad and the western half of the Tobago Basin (Fig. 2 ‘Winter’). Our limited tracking data for the spring showed that leatherbacks either remained in tropical breeding areas in the Windward Islands or began northward migrations, with one individual occupying the North Carolina shelf (Fig. 2 ‘Spring’).

Table 4. AIC results for linear mixed-effects models where mean logit-transformed path straightness is a function of ecoregion, sea surface temperature (SST), logarithm of surface chlorophyll a concentration (chla), logarithm of SST gradient (SSTg), logarithm of surface chla gradient (chlag), and logarithm of bathymetry (bathy). p: number of parameters in the model; Δ AIC: difference in AIC value between best fitting model and other models; ω : Akaike weight. ^a Slopes held constant in regions of interest. ^b Slopes and intercepts allowed to vary in regions of interest. *Best fitting model.

Model	p	AIC	Δ AIC	ω
null	4	7258.06	390.51	0
ecoregion	9	6927.63	60.08	0
ecoregion + SST ^a	10	6927.26	59.71	0
ecoregion x SST ^b	11	6921.62	54.07	0
ecoregion + chla ^a	10	6908.31	40.76	0
ecoregion x chla ^b	15	6908.97	41.42	0
ecoregion + SSTg ^a	10	6928.73	61.18	0
ecoregion x SSTg ^b	11	6929.90	62.35	0
ecoregion + chlag ^a	10	6923.94	56.39	0
ecoregion x chlag ^b	15	6922.50	54.95	0
ecoregion + bathymetry ^a	10	6871.17	3.62	0.07
ecoregion x bathymetry ^b	11	6873.15	5.60	0.03
ecoregion + SST ^a + bathymetry ^a	11	6871.52	3.97	0.06
ecoregion x SST ^b + bathymetry ^a *	12	6867.55	0.00	0.42
ecoregion + chla ^a + bathymetry ^a	11	6871.76	4.21	0.05
ecoregion x chla ^b + bathymetry ^a	16	6868.89	1.34	0.21
ecoregion + SSTg ^a + bathymetry ^a	11	6873.13	5.58	0.03
ecoregion x SSTg ^b + bathymetry ^a	12	6874.93	7.38	0.01
ecoregion + chlag ^a + bathymetry ^a	11	6871.61	4.06	0.05
ecoregion x chlag ^b + bathymetry ^a	16	6870.84	3.29	0.08

Table 5. Fixed effects parameter estimates of final model. Random effect parameter estimate intercept was 0.196 and residual was 0.960, and estimated autocorrelation was 0.306.

Effect	Estimate	Standard Error
Intercept	1.563	0.119
GFST	-0.723	0.522
GUJA	-1.312	0.235
NASW	0.303	0.125
NATR	0.337	0.121
NWCS	-1.467	0.321
log(bathy)	0.231	0.030
sst_NWCS	-0.032	0.014
sst_GFST	0.034	0.024

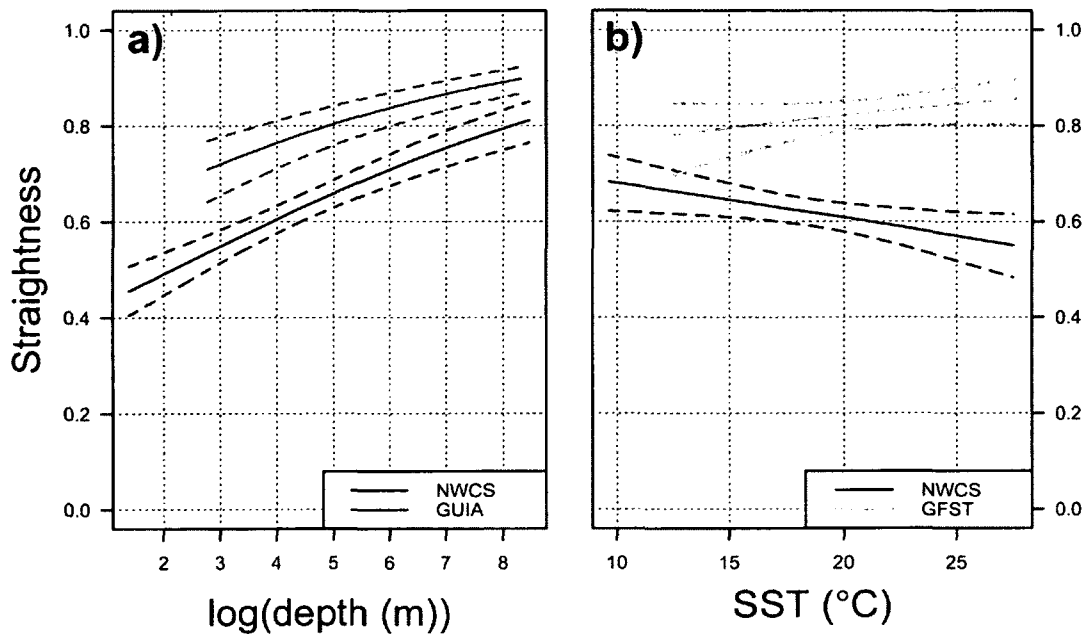


Figure 7. Predicted straightness (solid lines) and 95% confidence intervals (dashed lines) from the best performing model in Table 4 for leatherback movements in relation to: a) observed log-transformed bathymetry (m) in each of two distinct ecoregions of the northwest Atlantic and b) observed sea surface temperature (SST) in each of two distinct ecoregions of the northwest Atlantic; Northwest Atlantic Shelves (NWCS); Gulf Stream (GFST); Guianas Coastal (GUIA). Mean SST value in each region was used to create the bathymetry plot and mean bathymetry value in each region was used to create the SST plot.

Overall, dispersal patterns differed between adult and sub-adult leatherbacks.

Most adults followed widely spaced but highly oriented south/southeast headings during their southward migration until they reached latitudes between 10°N and 13°N (Fig. 4).

Sub-adult leatherbacks had more variable headings and did not disperse as far south, with most turtles remaining north of 15°N (Fig. 4). Two sub-adults were tracked near land (the Bahamas and the Lesser Antilles) during a portion of their migrations, but most sub-adults occupied offshore tropical and subtropical habitat during winter and early spring.

The four largest adult males and two adult females traveled to areas off nesting beaches

in the Lesser Antilles and Central America where they remained until tag transmissions ceased. Two smaller adult males and one adult female did not travel to known breeding areas; one male remained in the Gulf Stream into early January and the other two turtles overwintered in a tropical region near the convergence of the North Equatorial Current and North Equatorial Counter-Current.

Discussion

We deployed a mix of GPS-linked and conventional ARGOS STDs to simultaneously collect data on movements and dive behavior of adult and sub-adult leatherbacks in the North Atlantic. This study is one of the first to obtain highly accurate GPS locations from leatherback turtles, allowing us to identify high use habitat, movement patterns and environmental associations with less observation error. We also used novel design and direct attachment techniques to deploy low profile, hydrodynamic tags. We believe our methods minimized impacts to the turtles' natural behavior, resulting in a more accurate portrayal of leatherback behavior than telemetry studies employing harness attachments (Lutcavage et al. 2001, Fossette et al. 2007, Jones et al. 2011, Witt et al. 2011).

Dispersal patterns and seasonal habitat use

Leatherbacks tagged off Massachusetts showed a strong affinity to the Northeast US continental shelf before dispersing widely throughout the northwest Atlantic. One individual tracked for >1 year exhibited site fidelity to the US shelf, returning in late spring and remaining through late summer. Surprisingly, only one Massachusetts-tagged leatherback moved onto the eastern Canada shelf, an important and well-documented leatherback foraging ground (Bleakney 1965, James et al. 2005a,b, Heaslip et al. 2012).

In contrast, leatherbacks tagged off eastern Canada spent extended periods in both Canadian and Northeast US shelf waters within a single foraging season (James et al. 2005a). Over half of the turtles tagged off Massachusetts were classified as sub-adults (55%) whereas sub-adults were the minority in the Canada tagging study (16%, $n = 38$). The sub-adults in our study may have been at the northern part of their foraging range. Migration distance depends partly on an animal's body size and their capacity to store energy (e.g., adipose tissue) (Alerstam et al. 2003). Larger animals are able to swim longer distances at lower energetic cost (Schmidt-Nielsen 1972), as has been predicted for cod (Jørgensen et al. 2006) and bluefin tuna (Chapman et al. 2011). Smaller body size and lower lipid stores may limit the migratory range of some sub-adult leatherbacks. Alternatively, resources may have been sufficient on the Northeast US shelf during the years of our study, precluding a longer migration to more northerly foraging areas. Adult female leatherbacks tagged on nesting beaches in the northwest Atlantic showed different habitat utilization patterns than those tagged in temperate foraging grounds: high-use habitat tended to occur close to the nesting beaches where turtles were tagged or turtles were more widely distributed in oceanic and neritic regions throughout the North Atlantic (TEWG 2007). Although there is inherent bias in determining habitat utilization from tracking data from one deployment location, bias is reduced with increasing deployment time, and alternative methods may be used to address this in the future (Walli et al. 2009, Whitehead & Jonsen 2013).

There was a strong seasonal component to habitat selection, with most leatherbacks remaining in temperate latitudes in the summer and early autumn and moving into subtropical and tropical habitat in the late autumn, winter and spring. This

latitudinal shift is consistent with previous studies of leatherbacks tracked from foraging grounds in the North Atlantic (James et al. 2005b, Doyle et al. 2008) and similar to seasonal migration patterns of other sea turtle species (Polovina et al. 2004, McClellan & Read 2007) and large pelagic species such as ocean sunfish *Mola mola* (Potter et al. 2011), basking sharks *Cetorhinus maximus* (Skomal et al. 2009), bluefin tuna *Thunnus thynnus* (Sibert et al. 2006, Galuardi et al. 2010), and swordfish *Xiphias gladius* (Neilson et al. 2009). Latitudinal shifts in habitat-use likely reflect seasonal changes in temperature and productivity at high latitudes, and, for some species, the necessity to spawn or nest in tropical regions.

While most adult leatherbacks make seasonal migrations to the tropics to breed, sub-adults and reproductive females in inter-nesting years could remain at higher latitudes to forage. Yet the majority of these non-reproductive individuals still migrated to tropical latitudes. Their choice of overwintering habitat may be tied to minimizing energy expenditure for thermoregulation while maximizing prey encounter-rates in the patchier, less productive environment of the tropics. Sub-adults, small adult males, and a single inter-nesting-year female primarily remained in oceanic habitat, while large adult males and two reproductive females moved into coastal breeding areas. Little is known about the demographics of male leatherbacks, but there may be a size constraint whereby smaller males are unable to compete for females, and are effectively displaced from breeding areas by larger, more dominant individuals (Alerstam et al. 2003). Smaller males may direct energy toward growth rather than reproduction, and select overwintering habitat to maximize limited foraging opportunities in the tropics. Adult females in an inter-nesting year are likely to avoid breeding areas where they would be subject to

aggressive mating attempts by males (Reina et al. 2005); by overwintering offshore, they can save energy and accumulate fat stores for return migration and future reproductive effort. Sub-adults also largely avoided breeding areas and most did not travel as far south as adults. The highly oriented paths taken by adult leatherbacks suggests movement toward a goal (e.g., specific breeding and/or foraging areas), while the more variable headings taken by sub-adults may indicate an opportunistic overwintering strategy, or lack of experience locating consistent resource patches in oceanic habitat.

Regional movements, dive behavior, and habitat characteristics

Temperate neritic habitat

Our density utilization maps demonstrate that the Northeast US shelf, particularly southern New England, provides important seasonal habitat for leatherback turtles tagged of Massachusetts. The Northeast US shelf is one of the most well-studied and productive large marine ecosystems in the world (Sherman & Skjoldal 2002, Longhurst 2007). South of Cape Cod, peak depth-integrated primary production rates tend to occur toward the end of summer (Longhurst 2007), overlapping spatially and temporally with the highest density of leatherback locations. Waters south and east of Long Island, New York, including the eastern portion of the New York Bight, were heavily used by leatherbacks in late summer and autumn; the New York Bight has consistently high primary production rates associated with nitrogen input from urban sewage, strong tidal fronts and mixing (Longhurst 2007). Temperature and productivity decrease in late autumn and winter, coinciding with leatherbacks' departure from the region. One turtle extensively frequented an area north of Cape Hatteras, North Carolina; anomalously high chlorophyll values have been measured in this region during midsummer, associated with penetration

of high nutrient slope water onto the shelf and close proximity to Gulf Stream meanders (Longhurst 2007).

Leatherback search behavior (slow, sinuous swimming) in the Northwest Atlantic Shelves (NWCS) is consistent with area-restricted search (ARS), affirming the importance of this region for foraging leatherbacks (Bleakney 1965, Lazell 1980, James et al. 2005a, Eckert et al. 2006, Dodge et al. 2011). Leatherback locations in the NWCS coincided with stronger SST gradients and higher chl *a* than that found in other regions, and most dives were in the euphotic zone within the average seasonal mixed layer depth on the Northeast US shelf (10-20 m) (Longhurst 2007). Highly productive water masses and frontal zones influence the spatial distribution and movements of some top predators, aggregating them in relatively small areas or “hotspots” on the shelf, shelf break, slope, offshore and at depths where prey is concentrated (Olson et al. 1994, Schick et al. 2004, Mann & Lazier 2006, Bost et al. 2009). Other sea turtle species associated with enhanced frontal activity (Polovina et al. 2000, Seminoff et al. 2008), though some cheloniids may face thermal constraints, limiting their access to cooler temperate frontal zones (Seminoff et al. 2008). Leatherback movements coincided spatially and temporally with the persistent Shelf-Slope Front and tidal-mixing fronts north of Nantucket Shoals, in the Gulf of Maine, and around Georges Bank (Belkin et al. 2009). The tidal-mixing fronts occur during peak leatherback presence in summer and early autumn, and may play an important role in consolidating seasonally abundant patches of the leatherback’s gelatinous prey. Our model results showed that leatherbacks increased path sinuosity at shallower depths and warmer surface temperatures within the NWCS region. Decreasing water depth has been linked to increases in epipelagic gelatinous zooplankton biomass on

a global scale, with greatest biomass found in shallow locations (< 10 m average depth) (Lilley et al. 2011). Shallow shelf habitat such as shoals, banks, and ledges may be important for leatherback prey searching and (or) foraging in this region, and is consistent with our field observations of leatherbacks feeding in shoal habitat off Massachusetts (Dodge et al. 2011) (Fig. 1).

The average mixed layer depth on the Northeast US shelf is also shallowest (10-20 m) during the summer and early autumn (Longhurst 2007), potentially aggregating gelatinous prey at or above the pycnocline (Graham et al. 2003, Rakow & Graham 2006). This would reduce ascent and descent times for foraging leatherbacks, and minimize time spent in cool waters below seasonal thermoclines. The relatively high chl *a* associated with leatherback locations in the NWCS could be attributed to a preference for habitat with a high biomass of gelatinous zooplankton. Gelatinous predators can drastically reduce local zooplankton biomass, decreasing grazing pressure on phytoplankton populations and resulting in localized phytoplankton blooms (Durbin & Durbin 1996). This has been demonstrated on the Northeast US shelf, specifically in Narragansett Bay, Rhode Island, where the ctenophore *Mnemiopsis leidyi* can control zooplankton biomass, resulting in diatom blooms (Durbin & Durbin 1996). Mean leatherback surface time in the NWCS (27%) was much lower than that observed by James et al. (2006) for turtles tagged off eastern Canada (mean 43% night and 50% day, n=12 (0-2 m) and n=3 (0-3 m)). The Canada-tagged turtles used habitat off the Northeast US as well as eastern Canada, so the disparity in surface times is somewhat surprising, but the colder water temperatures experienced by leatherbacks off eastern Canada may contribute to increased surface times in that region. James et al. (2005b, 2006) described regular observations of

leatherbacks basking at the surface off Nova Scotia, a behavior that we rarely observed off Massachusetts. It is possible that leatherbacks off eastern Canada spend greater time at the surface for thermoregulation (James et al. (2005b) but this behavior is less important in the comparatively warm waters of the Northeast US shelf.

Subtropical oceanic habitat

We observed marked behavioral changes as leatherbacks left continental shelf habitat and began their southward migrations through subtropical oceanic habitat. As turtles moved through the Gulf Stream (GFST) and North Atlantic Subtropical Gyral West (NASW), they showed rapid, directed travel and began spending more time at depths >50 m. Most turtles spent minimal time in these ecoregions, suggesting that these are less important feeding areas for Massachusetts-tagged leatherbacks and are primarily used for transiting between temperate (i.e., foraging) and tropical (i.e., breeding) habitat. However, two individuals did make more extensive use of the GFST during summer, fall and early winter. The Gulf Stream's strong horizontal SST gradient, particularly in fall and winter, is evident in the strong SST fronts encountered by leatherbacks there, and chl *a* was high compared to other subtropical and tropical oceanic regions. Leatherback movements in the GFST became slightly more sinuous at lower SST, possibly associated with upwelling along the Gulf Stream front, but this relationship was weak in our model. The GFST has been previously identified as probable foraging habitat for leatherback turtles (Lutcavage 1996, Fossette et al. 2010a,b), and turtles exploiting this area may take advantage of the enhanced productivity of energetic, mesoscale eddies characteristic of this region (Longhurst 2007).

Leatherback movement patterns and dive behavior in the subtropical gyral region were consistent with other studies of this species in the North Atlantic (James et al. 2005b, 2006, Eckert 2006, Fossette et al. 2010a,b). Observed changes in dive behavior in the NASW may be partially explained by cycles of seasonal stratification and depth of the mixed layer and (or) deep chlorophyll maximum (DCM). In the NASW, the mixed layer deepens in the fall and winter when leatherbacks are present, and average mixed layer depth is over 50 m (Longhurst 2007). If leatherbacks target the pycnocline to search for prey, they would increase their diving activity to depth strata >50 m, with longer durations associated with increasing ascent and descent times. Leatherbacks in NASW may also be exploiting the intense trophic activity associated with the deep chlorophyll maximum (DCM), which occurs at about 100 m (Longhurst 2007). Consumption at the DCM follows a strong diel cycle (Longhurst 2007), and leatherbacks may be capitalizing on enhanced nighttime prey availability in the vicinity of the DCM by making deeper, longer dives (James et al. 2006). However, the rapid transit rate and limited time spent in the NASW suggests that foraging in this region is not as profitable for leatherbacks as in tropical regions. Reproductive adults would have additional incentive to move quickly through the NASW to reach breeding and nesting areas in the tropics.

Leatherback surface times in the GFST and the NASW were similar to the surface times recorded by James et al (2006) in the morning (06:00 – 12:00 GMT; mean 29%) and evening (18:00 – 0:00 GMT; mean 29%) periods of the southern migration, but much lower than their day surface time (12:00 – 18:00 GMT; mean 77%). Considering only the day period in our data set (12:00 - 18:00 GMT), the average surface time is still much lower (44%). Turtles tagged off eastern Canada and Massachusetts had similar dispersal

and migratory patterns in the subtropical gyre, so the observed difference in surface times may be due to other factors such as different demographics (e.g., sex and body size) of our turtle sample or tagging technique (harness vs. direct attachment). Comparisons of these techniques showed that leatherbacks had lower travel rates (Fossette et al. 2007, Witt et al. 2011) and shorter dive durations (Fossette et al. 2007) when wearing a harness. While surface time was not directly addressed in these comparisons, it's possible that leatherbacks wearing harnesses increase their surface time to recover from the energetic costs of increased drag caused by the harness (78 – 112 % increase in drag coefficient, Jones et al. 2011).

Tropical oceanic and neritic habitats

Leatherbacks overwintered in tropical ecoregions, with reproductively active adults primarily occupying the Guianas Coastal (GUIA) and Caribbean (CARB) while non-reproductively active individuals mainly used oceanic habitat in the North Atlantic Tropical Gyral (NATR). Turtles slowed down in the tropics compared to the subtropical gyre but travel was still directed compared to the sinuous movements we observed in the NWCS, suggesting a mix of behaviors that may include foraging, transiting and breeding. The GUIA and CARB regions encompass important breeding and nesting habitat for leatherbacks (TEWG 2007). Two adult females in our study nested in GUIA (Trinidad and Costa Rica/Panama) while tracked (Dodge et al. 2011), and two adult males remained in coastal waters off Trinidad. In the primarily shallow, shelf region of GUIA, leatherback movements became more sinuous in response to decreasing water depth, probably linked to breeding activity (James et al. 2005a,c, Eckert 2006) although some

leatherbacks do forage during the nesting season (Myers & Hays 2006, Casey et al. 2010, Fossette et al. 2012).

The average mixed layer depth varies throughout the tropics, with deepest depths occurring in winter when leatherbacks are present (Longhurst 2007). Leatherbacks occupied the western side of the NATR where average winter mixed layer depths are 70-80 m (Longhurst 2007). This could explain the deeper, longer dives that leatherbacks made there if prey accumulates near the pycnocline and (or) nutricline (Eckert et al. 1989, Hays et al. 2004a). In the NATR, the night-time depths of diel migrants is consistently within the upper 50-75 m (Longhurst 2007), and leatherbacks may target prey aggregated in this layer (James et al. 2006), though nocturnal foraging may be light-limited based on studies of leatherback ocular morphology (Brudenall et al. 2008) and feeding behavior (Casey et al. 2010).

The convergence of the North Equatorial Current, North Equatorial Counter-Current and the North Brazil Current appears to play an important role for overwintering leatherbacks in the southern part of their range. From June to January, the upper North Brazil Current joins the meandering North Equatorial Counter-Current at a retroflexion zone near 5-10°N, where large, anti-cyclonic eddies are formed (Johns et al. 1990). The eddies, known as North Brazil Current rings, have loop diameters of hundreds of kilometers, with a lifespan on the order of months, and they propagate northwest along the Brazil coast towards the Lesser Antilles (Johns et al. 1990, Fratantoni & Richardson 2006). North Brazil Current rings, and the convergence of the westward-flowing North Equatorial Current and eastward-flowing North Equatorial Counter-Current at 10-12°N, are associated with enhanced wintertime productivity (Longhurst 2007). Three

leatherbacks resided in this region during winter months, associating with meanders from the North Equatorial Current and Counter-Current convergence and mesoscale eddies (Fig. 8). Fossette et al. (2010a) inferred high foraging success year-round for leatherbacks at the southern boundary of the NATR, while a single tagged leatherback resided in this area for several months (Hays et al. 2004b). Since overall production in open tropical oceans is low compared to temperate and boreal latitudes (Longhurst 2007), leatherbacks may rely on enhanced productivity there to maximize foraging opportunities during overwintering periods in the tropics.

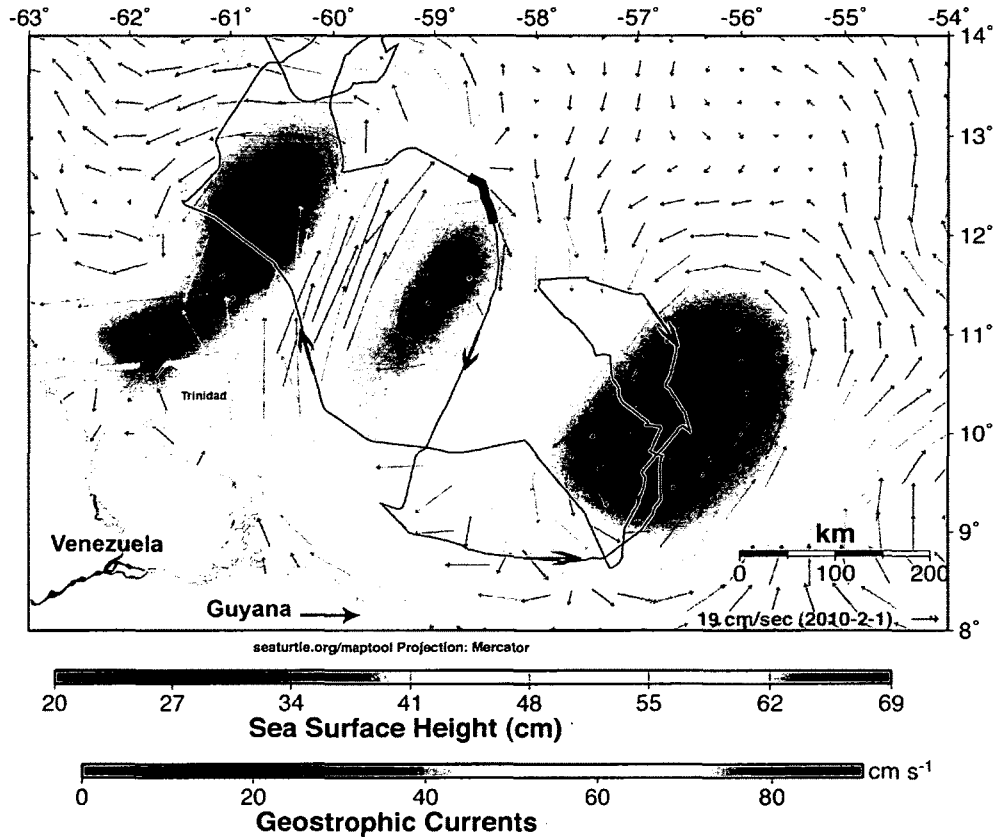


Figure 8. Reconstructed track of a sub-adult leatherback turtle (Turtle S) interacting with two mesoscale eddies that were moving NW from the GUIA toward the CARB region. The track represents the turtle's movements from 23 January to 7 April. The darkened track segment shows the turtle's movements on 1 February, concurrent with the AVISO sea surface height and geostrophic current maps (<http://www.aviso.oceanobs.com>). The arrows indicate the turtle's direction of travel.

River outflows have a significant impact on sea surface salinity (SSS) and productivity in the GUIA, CARB, and southern NATR. Fresh nutrient-rich discharge from the Amazon and Orinoco rivers creates large river plumes and offshore lenses of fresh water, with surface salinities as low as 32 ppt (Hu et al. 2004). Low SSS plumes extend north or northwest during the first half of the calendar year when leatherbacks are present. It is unknown whether leatherbacks can sense strong salinity gradients, but five turtles made sharp westward turns between 49°W and 57°W and 10°N and 13°N, overlapping with the winter extent of the plume (Hu et al. 2004). The river's plume may provide orientation cues for reproductive leatherbacks navigating towards nesting beaches in the Lesser Antilles.

Both adult and sub-adult leatherbacks in our study adjusted their movements and dive behavior in response to regional differences in environmental features. Leatherbacks increased their path sinuosity with decreasing water depth in temperate and tropical shelf habitats. This relationship is consistent with increases in gelatinous zooplankton biomass with decreasing water depth (Lilley et al. 2011), and bathymetry may be a key feature in identifying leatherback foraging habitat in neritic regions. Coastal ecosystems are under intense pressure worldwide, with some of the highest predicted cumulative impact in the North American eastern seaboard and the eastern Caribbean (Halpern et al. 2008). Parts of these regions constituted high-use habitat for leatherbacks in our study, putting turtles at heightened risk from both land- and ocean-based human activities.

CHAPTER 2

ORIENTATION CUES OF LEATHERBACK SEA TURTLES IN THE NORTH ATLANTIC SUBTROPICAL GYRE

Introduction

Sea turtles show remarkable orientation and navigation abilities over long tracts of seemingly featureless open ocean, but how they accomplish these feats is still not well understood (Carr 1962, 1967, Schmidt-Koenig 1975, Papi et al. 1995, Sale & Luschi 2009). Studies have revealed a myriad of cues that turtles may use to navigate in their coastal and oceanic environments. Extensive research on sea turtle hatchlings' ocean-finding abilities demonstrates the importance of visible light (Carr & Ogren 1960, Mrosovsky & Shettleworth 1968) and slope elevation (Salmon et al. 1992), while hatchling orientation in coastal waters relies primarily on wave direction (Salmon & Lohmann 1989, Lohmann et al. 1990, Lohmann et al. 1995) and can be light-independent (Lohmann et al. 1990, Wyneken et al. 1990). In deep water beyond the reach of shoreward-propagating waves, hatchlings switch to other cues that may include the earth's magnetic field (Light et al. 1993, Lohmann & Lohmann 1994, 1996a, Goff et al. 1998).

Magnetic orientation has been demonstrated in many long distance migrants including fin whales (Walker et al. 1992), yellowfin tuna (Walker 1984), birds (Wiltschko & Wiltschko 1996), salmon (Quinn 1980), blue sharks (Carey & Scharold

1990), and sea turtles (Lohmann & Lohmann 1996a). Sea turtle hatchlings are capable of detecting magnetic inclination angle (Lohmann & Lohmann 1994) and magnetic field intensity (Lohmann & Lohmann 1996b), and they appear to use these features to aid in migration (Lohmann et al. 2001). Juvenile sea turtles subjected to magnetic conditions found north and south of their capture location demonstrated orientation back to the capture site, further supporting a magnetic map sense (Lohmann et al. 2004). Although lab experiments on adult sea turtles are lacking, field studies by Luschi et al. (2007) demonstrated the potential importance of geomagnetic cues during open-sea homing of adult sea turtles.

Although magnetic features are a promising source of global positional information for long distance migrations, sea turtles are unlikely to rely on them exclusively. Experimental evidence suggests that sea turtles still navigate effectively in the presence of distorted magnetic fields (Papi et al. 2000, Benhamou et al. 2011), though results of Papi et al. (2000) failed to account for the effect of currents. Pacific leatherbacks have been hypothesized to travel along “persistent corridors” using topographic features (Morreale et al. 1996; Shillinger et al. 2008), but in the Atlantic no evidence of migratory corridors has been found (Ferraroli et al. 2004; Hays et al. 2004b; James et al 2005a). Travel adjacent to oceanic fronts has also been hypothesized (Olson et al. 1994, Lutcavage 1996). Additional studies point to a “multifactor navigation system” in turtles (Rozhok 2008) that may include a combination of visual and magnetic cues (Avens & Lohmann 2003), currents (Luschi et al. 2003) and possibly olfactory cues over shorter distances (Hays et al. 2003; but see Girard et al. 2006). Sea turtles likely rely on a combination of orientation cues in different situations (i.e., navigation over long

distances versus localized movements) (Lohmann et al. 2008, Benhamou et al. 2011).

Since the ability to navigate will impact migration distance and duration, identification of potential orientation cues is an important step toward understanding how leatherbacks optimize travel routes and minimize the energetic costs of migration.

We examined the migratory orientation of adult male, female and sub-adult leatherback sea turtles (*Dermochelys coriacea*) during their open-ocean movements in the Northwest Atlantic between 2008 and 2009 by analyzing satellite-derived tracks. In this region, leatherbacks make extensive migrations between temperate feeding and tropical breeding and (or) over-wintering grounds (Bleakney 1965, Ferraroli et al. 2004, Hays et al. 2004b, James et al. 2005a, Eckert 2006). We investigated potential orientation cues that leatherbacks use during their southward migration through the subtropical gyre, where limited sensory information is available to aid in their navigation.

Materials and Methods

Twenty adult and sub-adult leatherback turtles were fitted with Wildlife Computers, Inc. (Redmond, WA, USA) model MK10-A (n=8) and MK10-AF (n=12) ARGOS-linked satellite time depth recorders (STDRs). Leatherbacks were located off the coast of Massachusetts, USA (~41°N, 70°W) from August 2007 to September 2009, and captured with either a breakaway hoopnet (n = 11) (Asper 1975, James et al. 2005a) or accessed through the Massachusetts sea turtle disentanglement network (n = 9). We brought turtles on board commercial fishing or research vessels using a custom-built stern ramp. Following the methods described in Dodge et al. (in prep), we attached STDRs directly to the carapace medial ridge. Leatherbacks were measured to the nearest 0.1 cm (curved carapace length: CCL and curved carapace width: CCW) with a flexible

fiberglass measuring tape, and ranged in size from 123.0 to 161.5 cm CCL (Table 6). We used CCL to classify turtles as adults ($CCL \geq 145$ cm) or sub-adults ($CCL < 145$ cm), and we determined gender based on tail length of adult turtles (James et al. 2007). Five sub-adult turtles were sexed based on presence of a penis, subsequent necropsy or nesting.

The STDRs collected Fastloc GPS locations (MK10-AF tags only) and ARGOS-derived locations (all tags) via Service ARGOS (Toulouse, France). Ninety-five percent of Fastloc GPS locations are accurate to ± 55 m (Bryant 2007), while ARGOS-derived location error varies by location class (LC) as follows: LC3 < 150 m, LC2 150-350 m, LC1 350-1000 m, and LC0 > 1000 m. ARGOS does not provide accuracy estimates for LCA and LCB locations, and LCZ are considered unreliable. We filtered 30,173 raw ARGOS and GPS locations using Kalman filter methods outlined in Royer & Lutcavage (2008). Since our analysis included GPS data, we extended the original error covariance structure to include this information. Data were interpolated to a three-hour time step and smoothed, resulting in 28,253 filtered turtle locations. We limited our analysis to track segments that occurred in the North Atlantic Subtropical Gyral West province defined by Longhurst (2007), hereafter referred to as the subtropical gyre, where leatherback behavior was characterized by rapid, highly-directed travel consistent with migration (Dodge et al. submitted). The reconstructed track segments in the subtropical gyre included 3,904 filtered turtle locations for fifteen turtles.

To determine the turtles' true headings at each time step, we corrected the reconstructed tracks for current drift. We subtracted an estimate of the surface current velocity from the observed turtle velocity at each location, following the methods described in Gaspar et al. (2006) and Fossette et al. (2012). To calculate the surface

Table 6. Summary data for fifteen leatherback sea turtles equipped with satellite tags during the migratory period in the North Atlantic Subtropical Gyral West region. ID: turtle ID; PTT: platform transmitter terminal; CCL: curved carapace length; S: sub-adult (< 145 CCL); A: adult (\geq 145 CCL); M: male; F: female; U: unknown sex.

ID	PTT Number	Latitude (start/end)	Longitude (start/end)	CCL (cm)	Age	Sex	Tagging date	Duration (days)	Distance (km)	Mean travel rate (km/d)
A	68364a	37.4/25.7	-63.7/-52.9	149.5	A	F	26-Jul-08	26	1755	68
B	82052	35.7/25.5	-71.2/-63.8	161.5	A	F	29-Jul-08	34	1508	44
C	76988	38.3/26.0	-67.1/-61.3	152.2	A	M	10-Aug-08	29	1591	55
D	82051	37.4/26.2	-61.2/-50.7	153.3	A	M	10-Aug-08	27	1616	60
E	76989	37.6/25.6	-69.6/-64.0	144.8	A	F	21-Aug-08	23	1540	67
F	85538	37.7/25.6	-69.7/-57.9	154.0	A	M	22-Aug-08	27	1841	68
G	82053	39.4/25.7	-58.6/-44.1	146.4	A	M	23-Aug-08	38	2159	57
H	27579	37.6/25.8	-69.2/-58.9	155.0	A	M	3-Sep-09	27	1768	68
I	68370	36.7/24.6	-64.7/-65.0	137.5	S	U	22-Sep-07	31	1497	48
J	76990	37.8/26.0	-59.1/-45.3	140.4	S	U	10-Aug-08	64	2293	36
K	82055	37.9/25.7	-61.5/-66.2	133.8	S	U	10-Aug-08	46	1945	42
L	85537	37.5/25.8	-70.0/-62.1	138.5	S	M	22-Aug-08	28	1599	57
M	82054	33.4/25.6	-72.4/-67.7	140.0	S	U	28-Aug-08	22	1086	49
N	82056	33.8/25.8	-71.7/-68.3	126.5	S	U	10-Jul-09	35	1148	33
O	82057	37.8/25.6	-67.6/-59.2	127.7	S	U	27-Aug-09	30	1724	57

current velocity, we extracted surface geostrophic and Ekman current data from the NOAA Environmental Research Division's Data Access Program website. The geostrophic component was available as a 0.25-degree, daily product (<http://coastwatch.pfeg.noaa.gov/erddap/info/erdTAgeo1day/index.html>) and the Ekman component was available as a 0.125-degree, weekly product (<http://coastwatch.pfeg.noaa.gov/erddap/info/erdQSekm8day/index.html>). We calculated turtle orientation angles (e.g., headings) for the observed and current-corrected tracks using the `gzAzimuth` function in R (R Core Team 2013).

To assess potential orientation cues in the subtropical gyre, we selected environmental features most likely to be detectable by and available to sea turtles migrating in this region: magnetic inclination angle (Lohmann & Lohmann 1994), magnetic field intensity (Lohmann & Lohmann 1996b) and solar azimuth (Avens & Lohmann 2003). We used the International Geomagnetic Reference Field model (IGRF-11) to determine magnetic inclination angle and total magnetic field intensity at a 0.1-degree spatial resolution at filtered turtle locations. Estimated values of the Earth's magnetic field (typically accurate to 30 minutes of arc) were extracted from the NOAA National Geophysical Data Center using the Magnetic Field Calculator (<http://www.ngdc.noaa.gov/geomag-web/#igrfgrid>). Time at sunrise and sunset, and solar azimuth at sunrise and sunset were calculated using AstroCalc4R (Jacobson et al. 2011).

All statistical analyses were carried out using the program "circular" in R (R Core Team 2013) and Oriana 4.0 (Kovach Computing). For the distribution of angles for each leatherback, we determined a mean vector that included the mean vector length (r), ranging from 0 (uniformly scattered distribution) to 1 (fully concentrated distribution),

and the mean vector angle (θ). Since adult leatherbacks might be expected to navigate more efficiently than sub-adults, due to greater experience or goal-orientation (e.g., travel to specific breeding areas), we also grouped turtles by age class and used Watson's two-sample test of homogeneity to test for significant differences in orientation between adults and sub-adults (Mardia 1972, Batschelet 1981). We calculated the grand mean vector, including grand mean angle, vector length and 95% confidence limits, for all turtles and turtles grouped by age class for both observed and current-corrected tracks (Batschelet 1981). We used the Hotelling's one sample second order test to determine if the turtles had a significant mean direction during migration. To understand how leatherbacks oriented relative to potential environmental cues, we calculated the differences between turtle angle of orientation and the three angular environmental parameters: magnetic inclination angle, sunrise angle and sunset angle. We assessed the distribution of angular differences in individual turtles, and calculated the grand mean vector of angular differences for all turtles and turtles grouped by age class. We used the Hotelling's one sample second order test to determine if leatherbacks showed a significant mean direction relative to these features. We also overlaid turtle tracks on maps of isoclinics (lines of equal magnetic field inclination) and isodynamics (lines of equal magnetic field intensity) to visually assess turtle orientation relative to these field lines.

Results

Fifteen of the twenty turtles were tracked for sufficient duration to observe migration from temperate to tropical latitudes. Leatherbacks migrated through the subtropical gyre for an average of 32 (± 11) days, covering distances of 1093 to 2301 km

(Table 6). Adult leatherbacks had a higher average rate of travel (mean 60.9 km d⁻¹, sd 8.7 km d⁻¹) than sub-adult leatherbacks (46.0 km d⁻¹, sd: 9.5 km d⁻¹) (Table 6). Twelve track segments were successfully corrected for currents, while three track segments could not be corrected due to limited temporal coverage of the satellite-derived surface current products in 2009. There were negligible differences between the current-corrected turtle tracks and the observed turtle tracks in the subtropical gyre (Fig. 9), with most mean current-corrected turtle headings within 1° of observed mean turtle headings, but there was greater overall variability in current-corrected turtle headings (Table 7, Fig. 10).

Individual leatherbacks were significantly oriented in the subtropical gyre with a grand mean heading of 153° (observed) and 154° (current-corrected) (Table 8, Fig. 10) for all turtles. When analyzed by age class, adult and sub-adult leatherback groups were both significantly oriented with a grand mean angle of 148° (adults, observed and current-corrected) and 161° (sub-adults, observed) and 164° (sub-adults, current-corrected) (Table 8, Fig. 10). Although adult leatherbacks maintained similar within-group headings and showed greater overall precision in orientation (Table 7, Fig. 10), adult and sub-adult distributions were not significantly different (Watson test, $U^2 = 0.041$, $P > 0.10$). When we analyzed the distributions of angular differences between turtle headings and environmental features, we found that leatherbacks were significantly oriented with respect to all tested features (Table 8, Fig. 10). The distributions of angles were highly concentrated for all parameters (r values > 0.7), with the highest concentrations in the adult groups (r values > 0.86). Most adult leatherbacks in our study maintained mean headings that were approximately orthogonal to isoclinics (Table 7), with a grand mean angle of 93° for both observed and current-corrected tracks (Table 8).

Table 7. Summary statistics. Circular mean headings (\pm circular standard deviation) for individual turtles and angular differences (\pm circular standard deviation) between turtle headings and environmental features. Observed data are from the reconstructed turtle tracks (n=15); Corrected data are from the current-corrected turtle tracks (n=12).

ID	Observed turtle heading (\pm SD)	Corrected turtle heading (\pm SD)	Observed turtle- inclination diff (\pm SD)	Corrected turtle- inclination diff (\pm SD)	Observed turtle- sunrise diff (\pm SD)	Corrected turtle- sunrise diff (\pm SD)	Observed turtle- sunset diff (\pm SD)	Corrected turtle- sunset diff (\pm SD)
A	142.4 (19.9)	141.7 (33.6)	88.5 (21.0)	87.5 (33.1)	28.0 (19.0)	37.4 (25.3)	101.2 (14.3)	106.5 (29.5)
B	148.9 (27.6)	148.5 (38.0)	91.9 (26.1)	91.5 (36.4)	38.7 (18.7)	43.0 (23.7)	96.6 (26.9)	98.0 (29.5)
C	162.4 (26.4)	161.8 (32.4)	104.9 (26.0)	104.5 (32.2)	51.2 (25.4)	51.7 (42.1)	91.3 (21.7)	84.9 (22.8)
D	141.3 (11.8)	141.6 (18.7)	87.4 (13.5)	87.7 (19.8)	32.6 (10.9)	31.5 (14.4)	108.2 (14.1)	113.0 (21.6)
E	160.7 (20.8)	161.2 (24.1)	103.2 (21.3)	103.6 (24.6)	55.2 (20.4)	57.4 (22.4)	94.3 (24.0)	95.3 (27.9)
F	145.7 (18.6)	145.3 (25.5)	89.9 (20.7)	89.5 (26.2)	32.2 (15.4)	35.5 (16.9)	101.2 (17.6)	101.3 (20.2)
G	138.2 (19.1)	137.0 (25.0)	85.5 (19.9)	84.1 (25.6)	36.1 (21.6)	36.4 (17.1)	112.8 (20.0)	119.7 (20.9)
H	146.1 (22.4)	NA	90.3 (23.5)	NA	32.3 (23.2)	NA	99.0 (16.7)	NA
I	180.1 (26.0)	181.7 (34.4)	124.8 (28.4)	126.5 (36.2)	66.3 (30.7)	74.3 (35.3)	66.2 (21.7)	70.6 (23.7)
J	133.3 (45.4)	130.5 (43.7)	80.1 (44.1)	77.3 (42.2)	29.1 (39.7)	28.8 (36.7)	109.3 (36.7)	111.2 (32.3)
K	204.3 (48.6)	204.1 (52.5)	147.3 (48.1)	147.0 (52.2)	95.5 (40.7)	95.1 (46.9)	52.8 (38.0)	53.4 (42.5)
L	155.5 (18.7)	155.9 (28.3)	98.5 (20.2)	98.9 (28.0)	38.1 (20.0)	42.8 (28.4)	87.5 (17.7)	85.7 (27.6)
M	149.7 (26.7)	149.8 (38.8)	93.1 (25.1)	93.3 (35.9)	39.0 (21.5)	44.0 (33.7)	98.1 (29.4)	96.8 (23.9)
N	157.8 (40.1)	NA	100.4 (35.9)	NA	57.1 (32.5)	NA	86.7 (33.2)	NA
O	150.1 (25.7)	NA	94.2 (26.9)	NA	38.2 (32.2)	NA	92.8 (19.9)	NA

When we overlaid the observed and current-corrected turtle tracks on maps of isoclinics and isodynamics, we found that the majority of leatherbacks traveled approximately orthogonally to both of these field lines, which are almost parallel throughout most of our study area (Fig. 11).

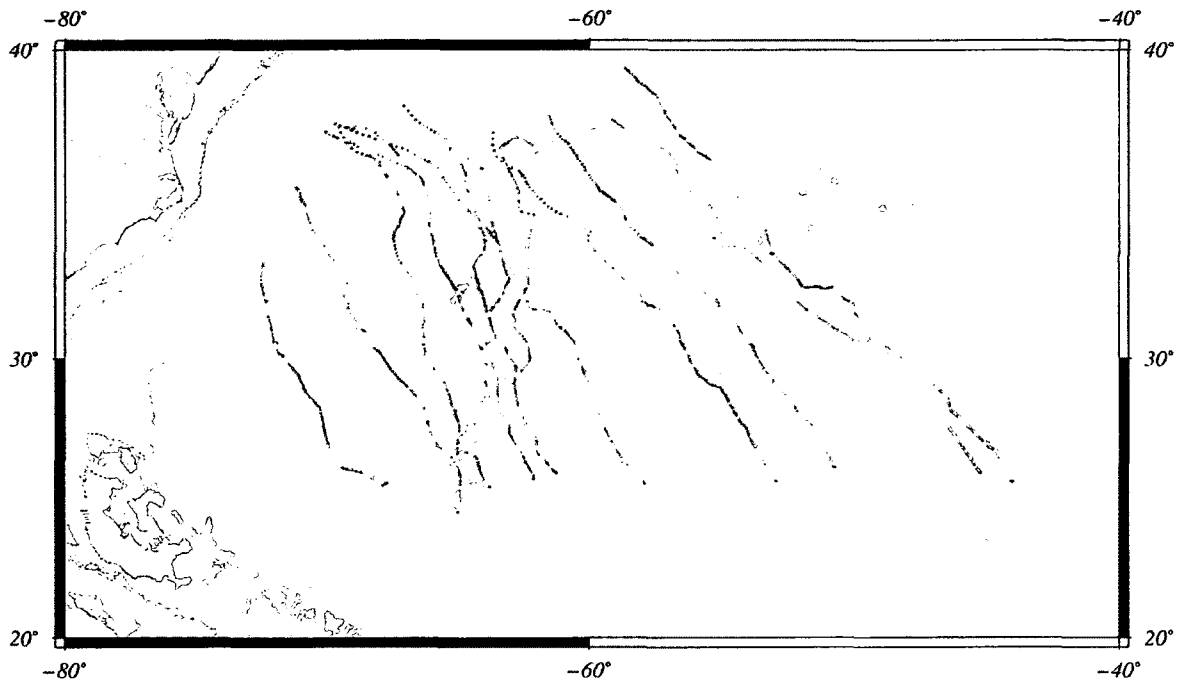


Figure 9. Filtered locations of 12 satellite-tagged leatherback sea turtles in the North Atlantic Subtropical Gyral West province (defined by Longhurst 2007). Green dots represent observed turtle locations and red dots represent current-corrected turtle locations.

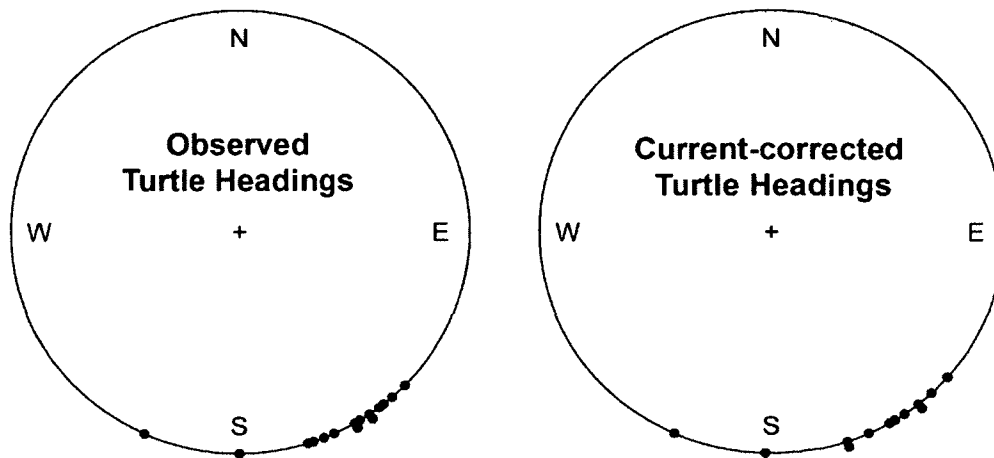


Figure 10. Observed (left) and current-corrected (right) orientation of adult (red dots) and sub-adult (blue dots) leatherback turtles in the North Atlantic Subtropical Gyral West region (defined by Longhurst 2007). The position of each dot indicates the mean angle of a single turtle. Data are plotted relative to geographic north ($N = 0^\circ$ true).

Discussion

Navigation over thousands kilometers of open ocean requires an ability to orient with limited sensory information. With the exception of the island platform of Bermuda, the North Atlantic subtropical gyre is characterized by deep water where leatherbacks cannot use bathymetric features to guide them. Weak ocean currents due to light and variable winds, and lack of stationary reference points render hydrodynamic cues as improbable guidance mechanisms within the subtropical gyre interior (Sargasso Sea); this was substantiated by the negligible differences we found between the turtles' observed tracks and their current-corrected tracks. Wind- or current-borne cues disperse rapidly over the long distances (> 1000 km) recorded in our study and would be unlikely to keep leatherbacks on course (reviewed by Lohmann et al. 2008). Sea turtles' poor eyesight above water likely negates the utility of celestial cues such as stars (Ehrenfeld &

Koch 1967, Bartol et al. 2002, Lohmann et al. 2008). Lacking bathymetric, hydrodynamic, celestial (star patterns) and chemosensory guidance, leatherbacks migrating through the subtropical gyre are most likely to orient to some aspect of the earth's geomagnetic field (magnetic compass) and (or) the position of the sun on the horizon (sun compass).

Most leatherbacks in our study, particularly adults, maintained mean orientation angles that were approximately orthogonal to both isoclinics and isodynamics in the subtropical gyre. To accomplish this, leatherbacks would have to be highly sensitive to very small gradients in magnetic inclination angle and (or) magnetic field intensity. Little is known about the location of magnetoreceptors in any animal (reviewed by Johnsen & Lohmann 2008) or the degree of sensitivity of sea turtles to these two magnetic field parameters (Lohmann et al. 2008), but some birds (Semm & Beason 1990), bees (Walker & Bitterman 1989) and lobsters (Boles & Lohmann 2003) may be capable of detecting small gradients in magnetic parameters. Local anomalies in the magnetic field could mask small gradients over short (100s of m to a few 10s of km) distances (Walker & Dennis 2005), but the strength of local anomalies decreases quickly with distance (Lohmann et al. 2007), and the leatherbacks in our study had high daily rates of travel (Table 1).

Isoclinics and isodynamics are almost parallel in our study region, and unlikely to provide the grid necessary for position fixing based on an entirely bicoordinate magnetic map (Lohmann & Lohmann 1996). The features we tested varied by latitude and cues for longitudinal guidance are less apparent, but it's possible that turtles may use a bicoordinate magnetic map once they enter tropical latitudes where isolines have larger

Table 8. Second order statistics. Distribution of angles and Hotelling's one sample test results for grouped turtles. *N*: sample size; *r*: vector length; *F*: Hotelling's test statistic; *p*: probability level; CI: confidence interval.

Group	Number of means (<i>N</i>)	Grand mean heading	Lower limit 95% CI	Upper limit 95% CI	Mean resultant length (<i>r</i>)	Hotelling's test statistic (<i>F</i>)	Hotelling's test probability level (<i>p</i>)
All turtles (observed/corrected)	15 / 12	153.4 / 153.6	142.8 / 139.5	165.5 / 170.4	0.85 / 0.80	432.99 / 271.181	<0.001 / <0.001
Adults (observed/corrected)	8 / 7	148.0 / 148.0	137.6 / 134.6	159.1 / 162.1	0.92 / 0.87	6151.27 / 1007.00	<0.001 / <0.001
Sub-adults (observed/corrected)	7 / 5	160.5 / 163.2	135.1 / 117.4	192.0 / 218.9	0.79 / 0.71	90.37 / 47.16	<0.001 / <0.01
All – Inclination (observed/corrected)	15 / 12	97.6 / 97.9	87.7 / 84.7	109.1 / 113.8	0.86 / 0.81	553.61 / 339.77	<0.001 / <0.001
Adults – Inclination (observed/corrected)	8 / 7	92.6 / 92.6	84.0 / 81.4	101.7 / 104.2	0.92 / 0.86	8827.12 / 1276.47	<0.001 / <0.001
Sub-adults – Inclination (observed/corrected)	7 / 5	104.3 / 107.0	79.9 / 64.0	135.5 / 163.0	0.79 / 0.72	116.94 / 60.16	<0.001 / <0.001
All – Sunrise (observed/corrected)	15 / 12	43.6 / 46.6	32.7 / 33.4	56.3 / 63.0	0.87 / 0.83	777.10 / 528.93	<0.001 / <0.001
Adults – Sunrise (observed/corrected)	8 / 7	38.2 / 41.4	26.7 / 29.2	50.3 / 55.5	0.93 / 0.90	6259.37 / 785.96	<0.001 / <0.001
Sub-adults – Sunrise (observed/corrected)	7 / 5	50.8 / 55.4	25.5 / 14.4	83.3 / 110.7	0.80 / 0.75	208.85 / 120.30	<0.001 / <0.01
All – Sunset (observed/corrected)	15 / 12	93.8 / 95.5	82.4 / 79.4	104.1 / 109.9	0.88 / 0.85	1014.77 / 609.82	<0.001 / <0.001
Adults – Sunset (observed/corrected)	8 / 7	100.7 / 102.7	91.9 / 86.3	109.2 / 118.8	0.94 / 0.89	4222.36 / 4135.88	<0.001 / <0.001
Sub-adults – Sunset (observed/corrected)	7 / 5	85.0 / 84.3	59.2 / 39.4	108.8 / 123.5	0.84 / 0.82	227.78 / 117.49	<0.001 / <0.01

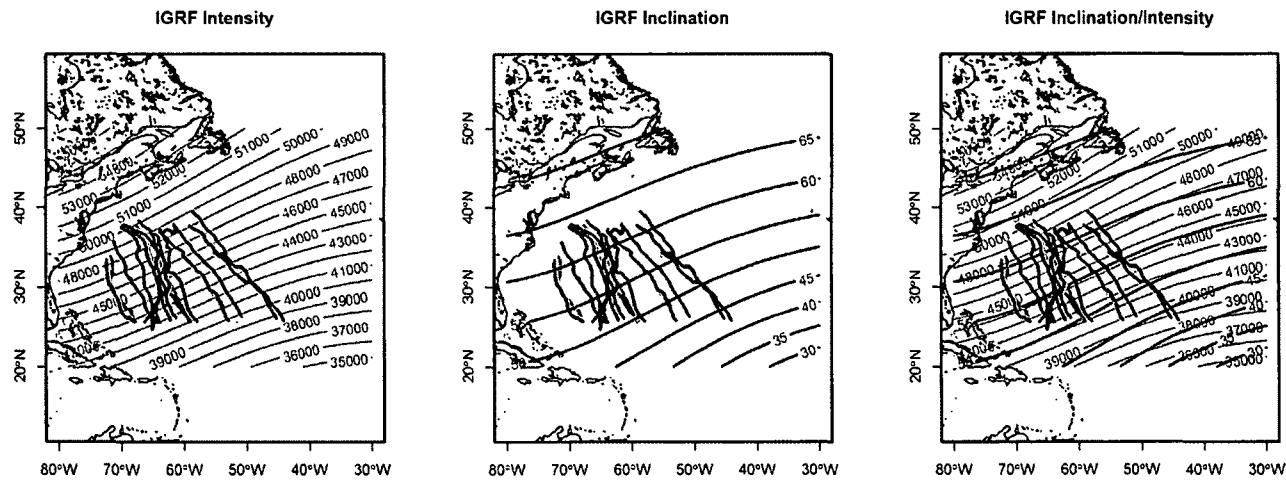


Figure 11. Maps of reconstructed leatherback turtle track segments overlaid on international geomagnetic reference field (IGRF) isodynamics (left panel), isoclinics (middle panel) and both magnetic field parameters (right panel) in the Northwest Atlantic Subtropical Gyral region. Adjacent isoclinics differ by 5° and adjacent isodynamics differ by 1,000 nT. Green dots represent observed turtle locations (n=15 turtles) and black dots represent current-corrected turtle locations (n=12 turtles). For the twelve turtles where both observed and current-corrected track data were available, the lines are almost indistinguishable.

angular differences (Putman et al. 2011). We found most adult leatherbacks in our study maintained SSE headings into the tropics, and made westward turns toward Caribbean breeding areas south of 15°N where isolines form a non-orthogonal grid, but that region was also characterized by potential hydrodynamic (North Equatorial Current) and olfactory (low sea surface salinity plumes) orientation cues (Dodge et al. submitted). Declination (the difference between true north and magnetic north) could be a potential longitudinal cue in this region, and some leatherbacks in our study closely followed isogonics (lines of equal declination) (Fig. 12). Navigation by declination is improbable, however, since leatherbacks would have to know the direction of true geographic north to use this magnetic parameter, and no animals are currently known to detect declination (Gould 2008; but see Åkesson et al. 2005).

We expected adult leatherbacks to show greater precision in orientation since a proportion of this group must travel to specific beaches to breed and (or) nest. Although not statistically different, the mean orientation angles of adult leatherbacks were more concentrated (*r* value range: 0.86 to 0.94) than the mean orientation angles of sub-adult leatherbacks (*r* value range: 0.71 to 0.84). Our statistical power would be improved by larger samples sizes for both groups and by verification of age (e.g., reproductive status). Our age classification was based on curved carapace length, and leatherbacks show considerable variability in size at nesting (Stewart et al. 2007), so it's possible that a proportion of the turtles classified as sub-adults were of reproductive age.

Since the parameters we tested are confounded, it is difficult to assess the relative importance of the different cues, and leatherbacks may use one or more of these features to orient. For example, during controlled experiments where juvenile loggerheads were

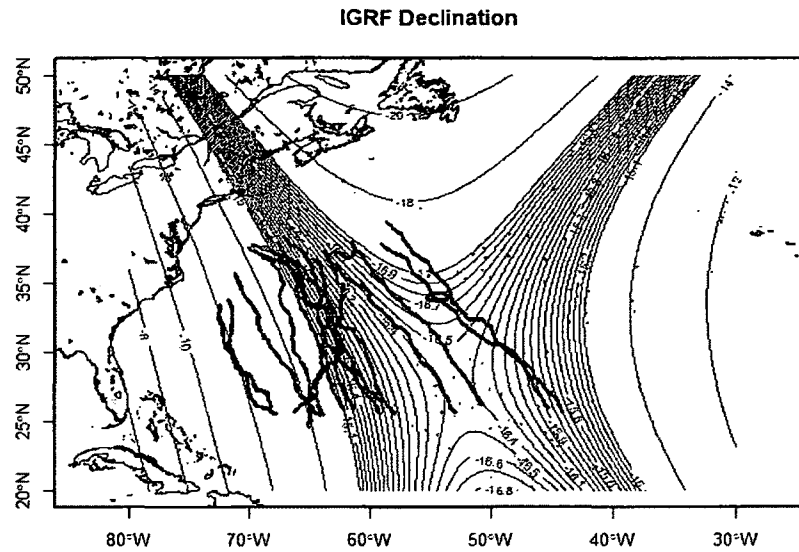


Figure 12. Map of reconstructed leatherback turtle track segments ($n=15$) overlaid on international geomagnetic reference field (IGRF) isogonics in the Northwest Atlantic Subtropical Gyral region. Adjacent isogonics differ by 0.1° in the map center and by 2° elsewhere.

deprived of magnetic cues, the turtles were still able to orient based on visual cues alone (Arens & Lohmann 2003), and leatherbacks may also be able to interchangeably use magnetic and visual (e.g., sun) compasses. Other long-distance migrators, such as the sharp-tailed sand piper (Grönroos et al. 2010), may use both solar and magnetic cues during their extensive migrations. Some birds (Cochran et al. 2004, Muheim et al. 2006) and bats (Holland et al. 2010) calibrate their magnetic compasses by the sun, specifically using sunrise/sunset for directional reference. Leatherbacks in our study were significantly oriented to isolines as well as the position of the sun on the horizon at sunset and sunrise, so it's feasible that leatherbacks are also calibrating their magnetic compasses using sunrise/sunset cues to reduce orientation errors over their long-distance migration. James et al. (2006) found that leatherbacks spent a greater proportion of time

at and near the surface during the day during their southward migrations in Northwest Atlantic, and we recorded the highest leatherback surface (0-2 m) time in the subtropical gyre (30%) compared to other oceanographic regions (Dodge et al. submitted). Higher surface time during the day may be related to partial reliance on a sun compass for orientation (Eckert 2002a, James et al. 2006).

Our tracks recorded the leatherback turtles' natural journeys and we could not control the availability of all possible environmental cues, so we can only infer the importance of the tested features. Our results were also obtained from small sample sizes, and additional leatherback tracks from the North Atlantic subtropical gyre would greatly improve our statistical power and help confirm our results. We also cannot rule out the possibility of alternative cues that have yet to be discovered and were not considered in this study. However, given the limited number of known available cues in the subtropical gyre, and the remarkable consistency of individual leatherback headings over such a broad swath of ocean, our results strongly support the importance of ubiquitous magnetic and (or) solar cues during open ocean migrations of leatherback sea turtles in the Northwest Atlantic Ocean.

CHAPTER 3

FORAGING ECOLOGY OF LEATHERBACK SEA TURTLES IN THE WESTERN NORTH ATLANTIC DETERMINED THROUGH MULTI-TISSUE STABLE ISOTOPE ANALYSES

Introduction

The leatherback sea turtle, *Dermochelys coriacea*, occurs in temperate and tropical oceans worldwide, exploiting prey in shelf, slope and oceanic habitats and at several hundred meters depth (Pritchard 1973, Eckert et al. 1989, Ferraroli et al. 2004, James et al. 2005a, Shillinger et al. 2008). Although studies of leatherback movements and habitat use have increased in recent years, its unique, gelatinous diet remains poorly defined throughout much of its range. Trophic research on leatherback turtles consistently indicates a diet of scyphomedusae (genera *Aurelia*, *Chrysaora*, *Cyanea*, *Pelagia*, *Rhizostoma*, *Stomolophus*), hydromedusae (*Physalia*), tunicates and siphonophores (*Pyrosoma*) (Bjorndal 1997). Few vertebrates specialize in low energy gelatinous prey and the only large vertebrate species associated with a gelatinous diet are leatherback turtles and ocean sunfishes (family Molidae) (MacGintie 1938, Fraser-Brunner 1951, Hooper et al. 1973, Desjardin 2005; but see Pope et al. 2010).

Unbiased, long-term leatherback diet data are often difficult to obtain using conventional approaches. Most leatherback diet studies to date have been based on stomach content analysis (SCA) of dead turtles (Bleakney 1965, Brongersma 1969, den Hartog & van Neiroop 1984, Frazier et al. 1985, Davenport & Balazs 1991) or rare

observations of leatherbacks feeding at the surface (e.g., Duron 1978, Eisenberg & Frazier 1983, Grant & Ferrell 1993, James & Herman 2001). These studies describe recent ingestion events, and reveal diet in coastal ecosystems where live or dead leatherbacks are readily accessible. Leatherbacks in the North Atlantic are seldom exploited and are now largely protected by international agreements and national laws (TEWG 2007). Leatherbacks incidentally captured at sea are rarely brought on board vessels so most sampling opportunities come from stranded specimens that may not be representative of healthy turtles. Furthermore, SCA of a gelatinovore is of limited utility unless the prey is undigested (Arai 2005) or the digested prey has identifiable parts (e.g., nematocysts in cnidarians).

An alternative approach for elucidating leatherback turtle feeding habits is stable carbon ($^{13}\text{C}/^{12}\text{C}$; $\delta^{13}\text{C}$) and nitrogen ($^{15}\text{N}/^{14}\text{N}$; $\delta^{15}\text{N}$) isotope analysis (SIA). Due to selectivity of heavier isotopes during metabolic processes, stable isotope ratios of nitrogen ($^{15}\text{N}/^{14}\text{N}$) and carbon ($^{13}\text{C}/^{12}\text{C}$) in consumer tissues tend to be elevated relative to their diet. Discrimination factors, the difference in isotopic values between consumer and prey tissues (Martínez del Rio & Wolf 2004), reflect relatively predictable changes (i.e., generally between 0-2‰ for $\delta^{13}\text{C}$ and 2-4‰ for $\delta^{15}\text{N}$) for each trophic level (DeNiro & Epstein 1978, 1981, Minagawa & Wada 1984, Vanderklift & Ponsard 2003, Sweeting et al. 2007a,b), although values can vary across species and tissue types (Hobson & Clark 1992, Vanderklift & Ponsard 2003, Reich et al. 2008, Caut et al. 2009). Since nitrogen isotope ratios tend to have greater discrimination factors than carbon isotope ratios (DeNiro & Epstein 1978, Fry & Sherr 1984, Minagawa & Wada 1984, Peterson & Fry 1987), $\delta^{15}\text{N}$ measurements are often used as a proxy for an animal's trophic position.

Stable isotope values reflect a time-integrated diet, with the time scale determined by the metabolic activity of the tissue and species analyzed (Peterson & Fry 1987). Dietary information can be estimated over a broad temporal scale by using multiple tissue types with different turnover rates (Tieszen et al. 1983). Liver and plasma tend to have faster turnover rates (reflecting recent diet) while slower rates in muscle and whole blood (Tieszen et al. 1983, Hobson et al. 1993, Hobson et al. 1999) indicate feeding patterns on longer time scales. In turtles, reported plasma turnover rates were weeks to months, while whole blood, red blood cells, and skin required months or longer (Seminoff et al. 2007, Reich et al. 2008).

In addition to trophic studies, stable isotope analyses are used to investigate the origin and broad movement patterns of migratory species (Hobson 1999). In marine ecosystems, $\delta^{13}\text{C}$ varies between inshore versus offshore regions or benthic versus pelagic environments (Hobson et al. 1994, France 1995). Carbon isotope ratios tend to decrease from low to high latitudes due to oceanographic parameters such as water temperature and CO_2 concentration effects on carbon fixation by phytoplankton (Rau et al. 1982). Nitrogen stable isotopes also vary across oceanographic regions due to spatial differences in nitrogen sources (Saino & Hattori 1987).

SIA is particularly useful for diet studies of highly migratory, pelagic species like sea turtles (Reich et al. 2007), and has been used to investigate sea turtle feeding ecology among species (Godley et al. 1998), within species (Hatase et al. 2002, Hatase et al. 2006, Reich et al. 2007, Caut et al. 2008, Reich et al. 2009, McClellan et al. 2010) and in populations occupying different ocean basins (Wallace et al. 2006b). Size-related differences in feeding habitats have been found in loggerhead sea turtles in Japan (Hatase

et al. 2002) and the Cape Verde Islands (Hawkes et al. 2006), suggesting habitat selection may be a function of body size in this species. Although SIA has revealed a dichotomy in habitat selection and nutrient sourcing in leatherback sea turtles (Wallace et al. 2006b, Caut et al. 2008), studies to date have been limited to adult females. We collected samples from sub-adult and adult leatherbacks of different sexes in US east coast foraging grounds. Based on estimated turnover rates for turtles (Seminoff et al. 2007, Reich et al. 2008), we selected leatherback tissues that represented long-term (whole blood, red blood cells and skin) and recent (blood plasma) diet. We conducted carbon and nitrogen stable isotope analyses of leatherback tissues and potential prey items to 1) test for differences in diet and habitat selection between sexes and size classes and 2) estimate contribution of different prey items to the leatherback diet, and to compare these findings with results from diet studies.

Materials and Methods

Sampling

Tissue samples (skin (n=26), whole blood (n=15), red blood cells (n=15), and blood plasma (n=13)) were collected from live leatherback turtles captured off Massachusetts, USA (~41°N, -70°W) from July to October, 2007-2009 (Fig. 14), and northern Florida, USA (30° 35'N, -80° 57'W) during March, 2007. Skin (n=6), muscle (n=7), and liver (n=8) were collected from freshly dead leatherbacks stranded in Massachusetts (Fig. 14) and Florida, USA between 2005 and 2010. Samples from dead leatherback turtles were taken with sterile scalpels and samples from live leatherbacks were taken via sterile syringes (blood) and disposable 4-6 mm biopsy punches (skin). Whole blood was centrifuged within 5 to 900 min after collection at 1500 × g for 5 min to harvest red blood

cells and blood plasma solutes (Innis et al. 2010). Tissues were stored on ice during sampling and frozen until preparation for analysis. At the time of sample collection, all turtles were measured to the nearest 0.1 cm (curved carapace length, CCL, and curved carapace width, CCW) with a flexible fiberglass measuring tape. Measurements were obtained from 31 turtles, ranging in size from 13 to 161.5 cm CCL (mean \pm SD: 139 \pm 26 cm). For live turtles larger than 145 cm CCL, we determined gender based on tail length (James et al. 2007). Five turtles < 145 cm CCL were sexed based on presence of a penis (James 2004), subsequent necropsy or evidence of nesting..

We collected likely prey items off northern Florida in March, 2007, and off Massachusetts from August to October, 2007 and July to September, 2008 (Table 9, Fig. 13). Gelatinous prey were collected from the surface with a dip net or at depth by towing a 1m² multiple opening/closing net (335- μ m mesh size) and environmental sensing system (MOCNESS) in Massachusetts only (Wiebe et al. 1976, 1985). We collected prey where we observed leatherbacks foraging or in regions we identified as potential foraging habitat based on feeding behavior (i.e., diving patterns) of leatherbacks monitored via satellite tags (Dodge et al. submitted). Potential foraging habitat was sampled within 24 - 72 hours of receiving satellite telemetry data. All samples were stored frozen until analysis.

Table 9. Stable isotope signatures of leatherback sea turtles and potential prey items. $\delta^{13}\text{C}$ values are lipid-corrected. Values are means (\pm SD) and n = sample size. ^a Combined sample(s) of multiple individuals; ^b N. Lysiak, unpublished data; ^c McClellan et al. 2010; ^d Wallace et al. 2009.

Sample	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)
Coastal waters of Massachusetts, USA		
Leatherback		
Blood plasma (n=12)	11.33 (1.78)	-19.19 (0.39)
RBC (n=15)	10.39 (1.12)	-18.45 (0.25)
Whole blood (n=15)	10.61 (1.03)	-18.51 (0.44)
Skin (n=27)	11.13 (1.29)	-17.84 (0.67)
Muscle (n=4)	11.32 (0.87)	-18.40 (0.83)
Liver (n=5)	11.99 (1.34)	-18.03 (1.43)
Potential prey		
<i>Cyanea capillata</i> (n=16)	10.90 (1.39)	-20.31 (0.82)
<i>Chrysaora quinquecirrha</i> (n=9)	10.83 (0.82)	-19.30 (0.53)
<i>Pelagia noctiluca</i> (n=1)	7.59	-20.81
<i>Beroe ovata</i> (n=2 ^a)	9.65 (1.61)	-20.55 (2.12)
<i>Mnemiopsis leidyi</i> (n=1 ^a)	9.48	-18.37
<i>Pleurobrachia pileus</i> (n=1 ^a)	8.82	-20.83
<i>Thalia democratica</i> (n=1 ^a)	6.34	-21.04
Cymbuliidae (n=1 ^a)	5.36	-20.33
Coastal waters of Florida & Georgia, USA		
Leatherback		
Blood plasma (n=1)	11.13	-19.27
Skin (n=4)	11.65 (0.56)	-17.87 (0.45)
Muscle (n=2)	11.74 (0.23)	-18.39 (0.04)
Liver (n=2)	11.86 (0.74)	-17.81 (0.39)
Potential prey		
<i>Stomolophus meleagris</i> (n=1)	8.90	-18.89
<i>Stomolophus meleagris</i> (n=3 ^b)	9.01 (0.38)	-20.44 (0.92)
Gulf Stream off North Carolina, USA		
Potential prey		
<i>Cyanea capillata</i> (n=1 ^c)	5.29	-17.46
<i>Chrysaora quinquecirrha</i> (n=6 ^c)	5.19 (0.25)	-17.20 (0.68)
<i>Pelagia noctiluca</i> (n=8 ^c)	4.61 (0.68)	-17.95 (0.51)
<i>Aurelia aurita</i> (n=5 ^c)	8.52 (0.55)	-19.50 (0.58)
Coastal waters of North Carolina, USA		
Potential prey		
<i>Stomolophus meleagris</i> (n=5 ^d)	7.92 (0.22)	-18.85 (0.08)

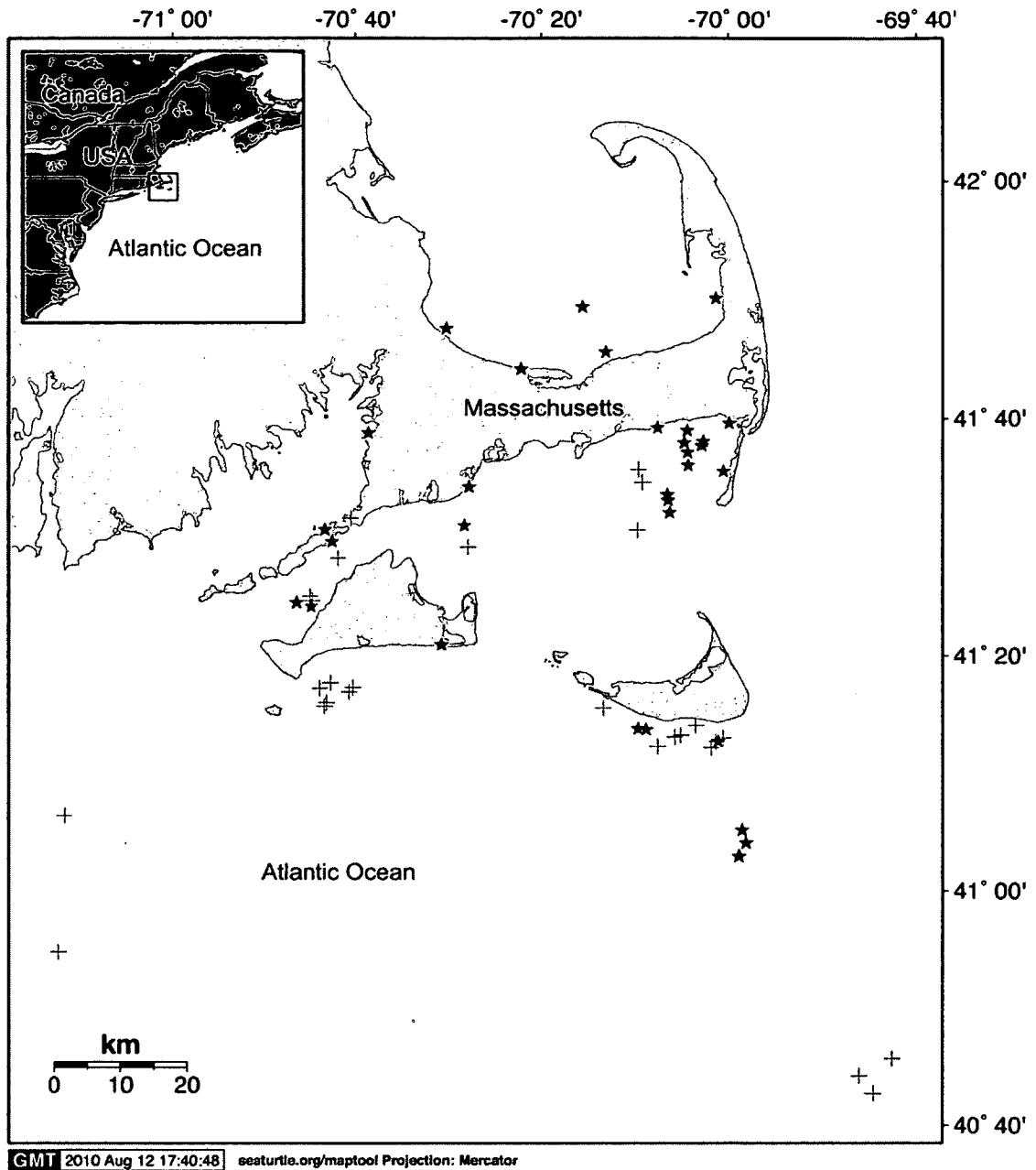


Figure 13. Locations of tissue collection for stable isotope analysis off Cape Cod, Massachusetts, USA. Stars represent leatherback sampling locations from 2005-2009 and crosses represent gelatinous zooplankton sampling locations from 2007-2008.

Sample preparation

Leatherback tissue samples and whole prey items were used for isotopic analyses. Multiple individuals of some prey items (salps, pteropods, and ctenophores; Table 9) were combined when necessary to produce sufficient dry material for measurements. Samples were thawed and dried at 65°C for a minimum of 48 hours and homogenized with a mortar and pestle (gelatinous zooplankton) or with a Mixer/Mill® (SPEX SamplePrep, LLC, Metuchen, New Jersey, USA) with stainless steel vials (leatherback tissues). Aliquots of homogenized sample (0.6 – 1.2 mg for leatherback tissues, 0.6 – 3 mg for gelatinous zooplankton) were packed into 4 x 6 mm tin cups and analyzed for $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, % carbon, and % nitrogen by continuous flow using a Costech EDS4010 elemental analyzer (Costech Analytical Technologies, Inc, Valencia, California, USA) coupled with a DELTA_{plus} XP isotope ratio mass spectrometer (Thermo Scientific, Bremen, Germany) at the University of New Hampshire Stable Isotope Laboratory (UNH). Because of the high salt content of gelatinous zooplankton, the cups containing prey samples were nested into a second silver cup in order to prevent potential damage to the mass spectrometer. Lipids can cause a negative bias in $\delta^{13}\text{C}$ values (Abelson & Hoering 1961, Park & Epstein 1961), requiring correction through chemical extraction or mathematical models. In place of lipid extraction, we used a *post hoc* lipid correction factor on carbon isotope ratios for all samples with C:N \geq 3.5 (Post et al. 2007). Correction models derived from different species or tissue types can produce inaccuracies in $\delta^{13}\text{C}$ estimates (Kiljunen et al. 2006, Logan et al. 2008), so our results likely contained some error.

Stable carbon and nitrogen isotope ratios are reported in conventional notation as parts per thousand (‰) differences from a standard according to the following equation:

$$\delta X = [(R_{\text{sample}} / R_{\text{standard}}) - 1] * 1000$$

where X is ^{13}C or ^{15}N and R is the corresponding ratio $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$ (Peterson & Fry 1987). Vienna Pee Dee belemnite (VPDB) and atmospheric nitrogen (AIR) were used as the carbon and nitrogen standards, respectively. At UNH, two internal standards (tuna and turtle white muscle), the NIST standard 1515 (apple leaves), and Acetanilide A were analyzed throughout each run to assess analytical precision, which was within 0.2‰ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for all four reference materials. Samples run in duplicate had SD $\leq 0.2\text{‰}$ for $\delta^{15}\text{N}$ and SD $\leq 0.3\text{‰}$ for $\delta^{13}\text{C}$ (n=13).

Statistical analyses

All statistical analyses were carried out using the program R (R Development Core Team 2008). Blood plasma, red blood cells, whole blood, and skin were grouped by sex, and comparisons were made among groups for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ (Table 10). Homogeneity of variance among groups was tested with Levene's test. Where variances were homogenous, we made comparisons with a one-way analysis of variance (ANOVA), and where heterogeneous, a one-way test was used. Student's *t*-tests were used to compare $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values among grouped samples, and a Holm adjustment was applied to *P* values to account for multiple comparisons. Simple linear regressions were performed for tissue $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ relative to curved carapace length (CCL) to examine potential effects of body size (CCL) on tissue $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. Significance level was set at alpha = 0.05 unless otherwise noted.

Isotope mixing models are used to infer diet composition by estimating proportional contributions of potential prey isotope values to values observed in consumers (Phillips & Gregg 2003). We used a Bayesian isotopic mixing model available as the open source package 'SIAR' (Parnell et al. 2010) in the program R (R Development Core Team 2008). The SIAR mixing model produces posterior distributions that represent true probability densities for the parameters of interest (e.g., prey contribution to diet), and the probability estimates are robust since the model incorporates uncertainty and variability in isotope signatures of fractionation factors, consumers, and prey (Parnell et al. 2010). Eight prey species were collected off Massachusetts for use in the mixing model (Table 9). Before running SIAR, we grouped species with similar functional significance and isotopic values (Phillips et al. 2005). The model consisted of one sea turtle group and four prey groups (group 1 = *Chrysaora quinquecirrha* (sea nettle), and *Cyanea capillata* (lion's mane); group 2 = *Beroe ovata*, *Mnemiopsis leidyi*, and *Pleurobrachia pileus* (ctenophores); group 3 = *Pelagia noctiluca* (mauve stinger); and group 4 = *Thalia democratica* (salps) and sea butterflies (Cymbuliidae) (Fig. 16). We used blood plasma values of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ from leatherback turtles captured off Massachusetts during late summer (29 July – 3 September, n = 9) in order to obtain isotope values likely equilibrated to local diet. The model was only run for all turtles pooled because of limited sample sizes and minimal differences in isotope values by sex for the subset of samples used in the model. Discrimination factors for plasma from juvenile leatherback turtles reared in captivity ($\Delta_{\text{dt}} \delta^{13}\text{C}$: $-0.58 \pm 0.53\text{‰}$, $\Delta_{\text{dt}} \delta^{15}\text{N}$: $2.86 \pm 0.82\text{‰}$) were included in the mixing model (Seminoff et al. 2009).

Results

Linear regression showed $\delta^{13}\text{C}$ was correlated with body size for skin (Fig. 14a) and whole blood (Fig. 14c), and $\delta^{15}\text{N}$ was correlated with body size for red blood cells (Fig. 14b). Although not significant in all cases, the general trend in most tissues showed increasing values of $\delta^{15}\text{N}$ and decreasing values of $\delta^{13}\text{C}$ with body size (Fig. 14a-d).

While not included in our analysis, the skin values from a single small juvenile (CCL = 13 cm) were also consistent with this trend ($\delta^{15}\text{N} = 6.87\text{‰}$, $\delta^{13}\text{C} = -16.64\text{‰}$). For $\delta^{13}\text{C}$, female leatherback red blood cell values were significantly higher than males ($F_{2,5} = 12.09$, $P = 0.01$) (Fig. 15b, Table 10), and female whole blood values were significantly higher than males and turtles of unknown gender ($F_{2,12} = 7.26$, $P < 0.01$) (Fig. 15c, Table 10). Turtles of unknown gender had higher blood plasma $\delta^{13}\text{C}$ values than female turtles ($F_{2,6} = 6.89$, $P < 0.03$) (Fig. 15d, Table 10). There were no significant differences in $\delta^{13}\text{C}$ values of leatherback skin among male, female, and unknown gender turtles ($F_{2,28} = 1.86$, $P = 0.17$) (Fig. 15a, Table 10), and no significant differences in $\delta^{15}\text{N}$ values were detected between sexes for any tissue type (Fig. 15a-d, Table 10).

Based on the results of the SIAR mixing model, leatherback turtles foraging off Massachusetts primarily consumed lion's mane (*C. capillata*) and sea nettles (*C. quinquecirrha*) (95th% credibility interval: 5-59%) and ctenophores (*B. ovata*, *M. leidyi*, and *P. pileus*) (95th% credibility interval: 0.4-61%) (Fig. 16). They foraged to a lesser extent on mauve stingers (*P. noctiluca*) (95th% credibility interval: 0-38%), salps (*T. democratica*) and sea butterflies in the family Cymbuliidae (95th% credibility interval: 0-36%) (Fig. 16).

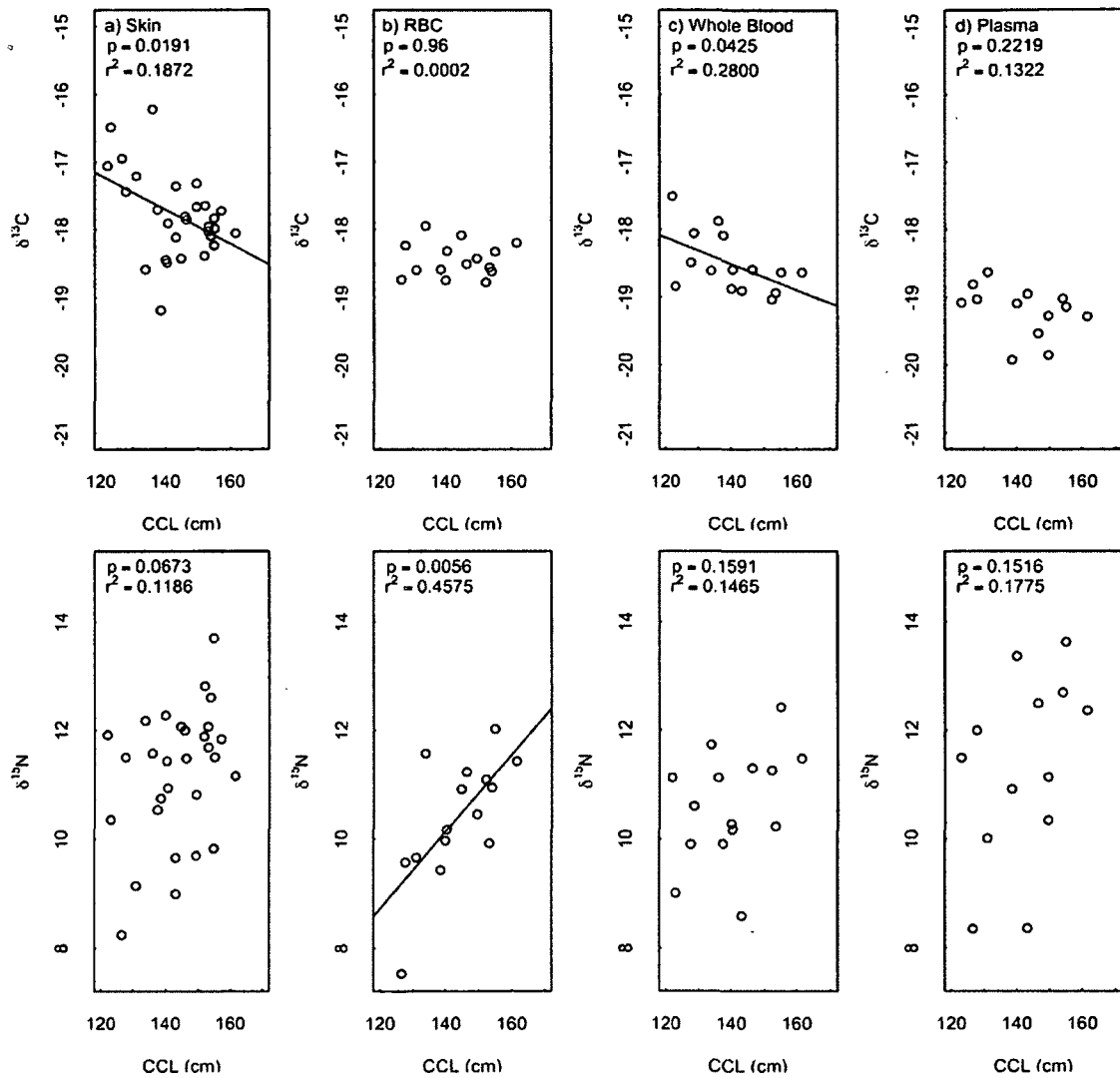


Figure 14. Linear regressions of a) skin, b) RBC, c) whole blood and d) blood plasma $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values relative to curved carapace length (CCL) for leatherback turtles.

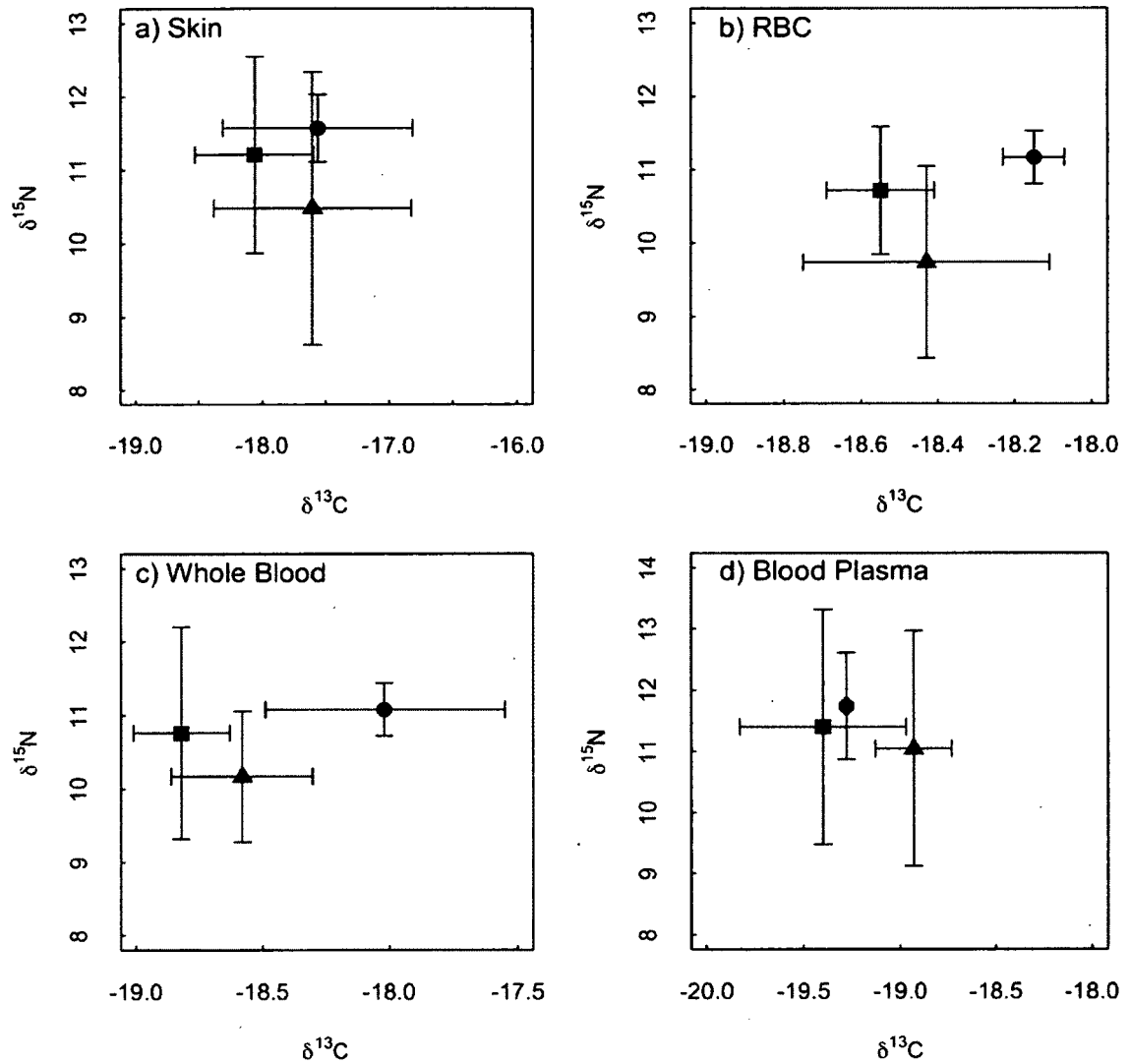


Figure 15. Dual stable isotope plots of nitrogen-carbon showing isotopic signatures (mean \pm SD) of leatherback tissues grouped by sex. Males square, females circle, and unknown sex triangle.

Discussion

Multi-tissue isotopic analysis revealed that leatherback turtles of different size and gender had dissimilar diets. Less metabolically active tissues like skin have slower isotopic turnover (Reich et al. 2008), so higher $\delta^{13}\text{C}$ values in the skin of smaller

leatherbacks may reflect a dietary history of feeding primarily on a food web characterized by high $\delta^{13}\text{C}$. There are few observations of juvenile leatherbacks (CCL < 100 cm), and their distribution is largely unknown, but existing distribution data and physiological attributes (Musick & Limpus 1997, Witt et al. 2007, Bostrom et al. 2010) indicate that they are restricted to warmer waters ($>26^\circ\text{C}$) during the first years of life (Eckert 2002b). Stable isotope values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in the skin of smaller leatherbacks in our study reflected a food web depleted in ^{15}N and enriched in ^{13}C , characteristic of offshore food webs associated with *Sargassum* (Rooper et al. 2006) and *Trichodesmium* (Wada & Hattori 1991). Organic matter derived from these sources is enriched in ^{13}C (and depleted in ^{15}N) compared to phytoplankton.

Notably, gelatinous zooplankton sampled from the Gulf Stream revealed isotopic values enriched in ^{13}C and depleted in ^{15}N relative to the same species collected off coastal Massachusetts in our study (McClellan et al. 2010) (Table 9). Warm, *Sargassum*-rich waters of the Gulf Stream and central North Atlantic provide important developmental habitat for juvenile loggerhead sea turtles and may serve a similar function in juvenile stages of other sea turtle species (Musick & Limpus 1997, Reich et al. 2007). We found high $\delta^{13}\text{C}$ and low $\delta^{15}\text{N}$ values in the skin of the small juvenile leatherback relative to larger turtles in our dataset, providing additional evidence that offshore food webs may be important for early life stages. Sub-adult and juvenile leatherbacks may spend a larger proportion of time feeding on prey from the Gulf Stream recirculation region, retaining higher $\delta^{13}\text{C}$ and lower $\delta^{15}\text{N}$ values in their skin as they transition to subsequent foraging habitats such as the northeast US continental shelf. Observations of these early life stages and characterization of juvenile habitat remain an

area of important research in leatherback ecology, and collection of additional skin samples from juvenile leatherbacks is needed to better understand size-related differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

Table 10. Stable isotope signatures of leatherback sea turtle tissues grouped by sex. Values in the same column for a given tissue type with different superscript letters are significantly different ($P < 0.05$).

Group	Sample size (n)	$\delta^{15}\text{N}$ (‰) Mean (SD)	$\delta^{13}\text{C}$ (‰) Mean (SD)
Skin			
Female	7	11.57 (0.46) ^a	-17.56 (0.75) ^a
Male	15	11.21 (1.34) ^a	-18.06 (0.47) ^a
Unknown	9	10.88 (1.45) ^a	-17.71 (0.74) ^a
Whole Blood			
Female	4	11.08 (0.36) ^a	-18.02 (0.47) ^a
Male	5	10.76 (1.44) ^a	-18.82 (0.19) ^b
Unknown	6	10.17 (0.89) ^a	-18.58 (0.28) ^b
Red Blood Cells			
Female	2	11.17 (0.36) ^a	-18.15 (0.08) ^a
Male	7	10.72 (0.87) ^a	-18.55 (0.14) ^b
Unknown	6	9.74 (1.31) ^a	-18.43 (0.32) ^{ab}
Blood plasma			
Female	2	11.74 (0.87) ^a	-19.28 (0.01) ^a
Male	6	11.40 (1.92) ^a	-19.40 (0.43) ^{ab}
Unknown	5	11.04 (1.92) ^a	-18.93 (0.20) ^b

The trend in whole blood was similar to that in skin, with $\delta^{13}\text{C}$ values decreasing as turtles increased in body size (Fig. 14a,c). The lack of significant correlation between $\delta^{13}\text{C}$ and body size in the other two tissues may be explained by several factors: 1) difference in turnover rate between tissues 2) no difference in habitat use and diet between turtles sampled for RBCs and plasma, and 3) small sample sizes. Assuming that blood plasma has fast turnover and reflects local diet, we would not expect to find size-related differences in this tissue. Most samples were taken from similar locations, and

there is probably overlap in prey selected by leatherbacks of different sizes feeding off Massachusetts. Red blood cells in sea turtles have a slower turnover rate than blood plasma (Reich et al. 2008). Since whole blood is a combination of RBCs and plasma, we would expect RBCs to have a slower turnover rate than whole blood. In this case, turnover rate would not explain why we did not detect a size effect in $\delta^{13}\text{C}$. A more likely explanation is that small leatherbacks (< 130 cm CCL) were under-represented in our RBCs group (n=2) relative to our whole blood group (n=4).

When leatherbacks were grouped by gender, the general trend was elevated $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in female tissues relative to males (Fig. 15a-d, Table 10). In contrast, the blood plasma values of $\delta^{13}\text{C}$ were significantly higher in turtles of unknown gender than females (Fig. 15d, Table 10). Although we and others have documented that adult male, female, and sub-adult leatherbacks mix on their temperate foraging grounds in the northwest Atlantic (James et al. 2007; this study), satellite telemetry studies have revealed different migratory patterns among these groups (James et al. 2005b; Dodge et al. submitted). Most sub-adult and female leatherbacks in their inter-nesting years spend winter offshore in the pelagic realm, whereas adult males and nesting females spend several months in coastal waters adjacent to nesting beaches (James et al. 2005b; Dodge et al. submitted). Red blood cell samples in females (Fig. 15b, Table 10) came from two females that nested the following spring after we had sampled them (one confirmed nesting, one unconfirmed but probable based on satellite telemetry data). Given the 2-3 year remigration interval between nesting seasons for the majority of Atlantic leatherbacks (Boulon et al. 1996, TEWG 2007), these two turtles likely spent the previous winter/spring offshore before we sampled them off the Massachusetts coast.

Whole blood samples in females (Fig. 15c, Table 10) were taken from one adult turtle that likely nested nine months after sampling and three sub-adults (sampled alive, later died and sexed during necropsy). All of these turtles likely over-wintered offshore during the winter/spring before we sampled them off Massachusetts. The elevated $\delta^{13}\text{C}$ values in the red blood cells and whole blood of these females therefore most likely reflects time spent foraging in offshore open ocean habitat during the over-wintering period.

Blood plasma $\delta^{13}\text{C}$ differences between females and those with unassigned sex can be attributed to two samples with higher $\delta^{13}\text{C}$ values from the latter group. Both samples, taken in early July, 2009, were the earliest we had acquired samples from Massachusetts leatherbacks, and our results suggest that recent migrants had not yet equilibrated to local diet, rather than a foraging dichotomy between female and sub-adult turtles. The overall trend of elevated $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in female samples relative to males (Table 10) could also be explained by the energetic demands of nesting. Nutritional stress from migration, egg production and deposition, and starvation during reproduction could lead to elevated $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in female leatherbacks relative to males (Hobson et al. 1993). Another factor to consider is isotopic routing, the process in which isotopes of different dietary components are preferentially distributed to specific tissues or compounds (Gannes et al. 1997, Gannes et al. 1998, Wolf et al. 2009). Differences in routing between sexes or maturity stages could explain observed isotopic differences, although diet items were all gelatinous prey composed mainly of protein (Clarke et al. 1992, Doyle et al. 2007). Given that leatherback turtles are highly migratory and the various tissues sampled vary widely in isotopic turnover rates (Seminoff et al. 2007, Reich et al. 2008), the different timescales of dietary and migratory information

represented by these tissues is a more likely explanation for observed differences than condition or routing. Comprehensive sampling across a range of tissues is warranted to better understand sex-related differences in $\delta^{13}\text{C}$ values.

The Bayesian two-isotope mixing model showed that leatherback turtles off Massachusetts primarily consume some scyphozoan species (lion's mane and sea nettle) and ctenophores (Fig. 16). Supplementary prey may include mauve stingers, salps, and sea butterflies (Table 9, Fig. 16). Leatherback turtles feed on lion's mane on the western North Atlantic shelf off eastern Canada (Bleakney 1965, James & Herman 2001) and New England (Lazell 1980). Lion's mane jellyfish are common worldwide in Arctic and boreal waters where they reach their maximum size and abundance, and medusae can be found off New England in late winter through summer (Johnson & Allen 2005). Leatherbacks in the Pacific feed on several species of sea nettle (Benson et al. 2007), and we have observed leatherbacks swimming in mixed patches of sea nettles and lion's mane jellyfish off New England. Multiple species of ctenophore also occur regularly off New England during summer and fall when leatherbacks are present. The most common and abundant near-shore ctenophore in our study area is *M. leidyi*, which can reach extremely high densities ($> 100/\text{m}^3$) given the right conditions (Johnson & Allen 2005). Tidal-mixing fronts north of Nantucket Shoals, in the Gulf of Maine, and around Georges Bank occur in summer and early fall (Belkin et al. 2009), and may provide enhanced foraging opportunities by consolidating patches of these gelatinous species. The combination of abundant medusae and ctenophores and seasonally persistent fronts makes the New England shelf reliable foraging habitat for leatherbacks and justifies their energetically costly migrations from lower latitudes and forays into cold water.

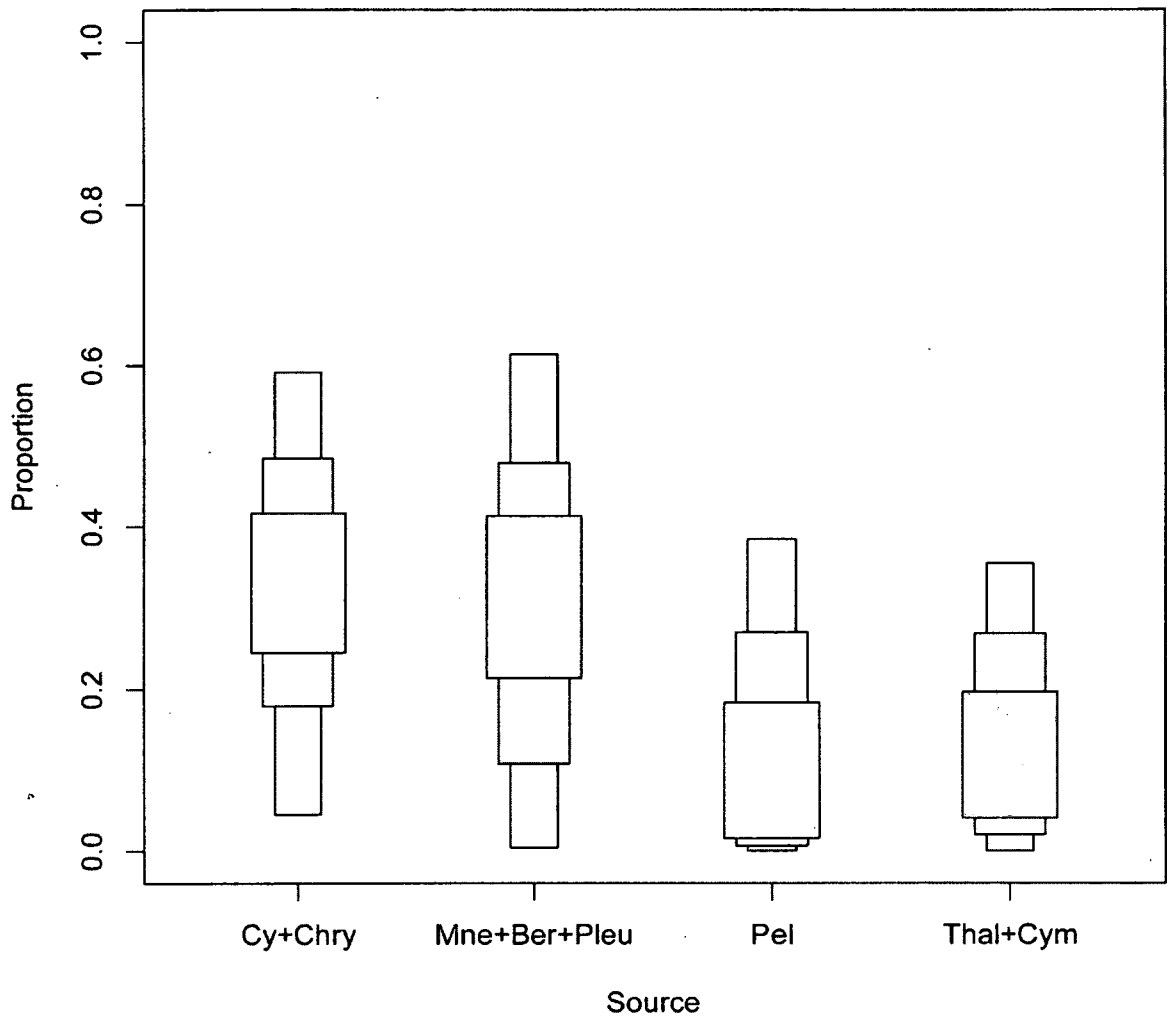


Figure 16. Results of the SIAR (95, 75 and 50% credibility intervals) mixing model showing estimated prey contributions to leatherback turtle diet off Massachusetts, USA. Cy *Cyanea capillata*; Chry *Chrysaora quinquecirrha*; Mne *Mnemiopsis leidyi*; Ber *Beroe ovata*; Pleu *Pleurobrachia pileus*; Pel *Pelagia noctiluca*; Thal *Thalia democratica*; Cym *Cymbuliidae* spp.

Mixing model results should be interpreted with caution because of unknowns in our discrimination factors, the large number of prey sources analyzed with similar isotope values, and the relatively large credibility intervals for our estimates and associated uncertainty (e.g., 95% credibility intervals included zero for mauve stingers and salps/sea butterflies). While our mixing model included species- and tissue-specific discrimination

factors for leatherback turtles, these discrimination factors were derived from juveniles raised in captivity and without any lipid corrections for plasma (Seminoff et al. 2009). Discrimination factors for nitrogen and carbon likely vary for sea turtles raised on different diets and during different developmental stages, as growth contributes significantly to the rate of isotopic incorporation in hatchlings and juveniles (Reich et al. 2008). We also assumed that blood plasma collected in late summer/fall was equilibrated with local diet, and that leatherbacks consume whole prey rather than select body parts (e.g., gonads and oral arms) with higher nutritional value (Doyle et al. 2007). Although most late season plasma samples showed similar isotope values, one turtle had a lower $\delta^{15}\text{N}$ value that likely reflected previous offshore feeding and recent arrival to the coastal foraging grounds. While diet segregation cannot be ruled out as an alternative explanation for this outlier, this turtle would have had to feed nearly two trophic levels below co-occurring turtles to derive the observed plasma value. Biases associated with past feeding in regions with different isotopic baselines are difficult to completely avoid when studying highly migratory species, although compound specific analyses may provide a mechanism for distinguishing between baseline and trophic shifts in future studies (Popp et al. 2007).

This is the first study to report stable isotope values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for male, female, and sub-adult leatherback turtles in their feeding areas. Previously published studies included only nesting females (Wallace et al. 2006b, Caut et al. 2008). By sampling multiple tissues across gender and age class, we were able to examine the effect of size and sex on stable isotope values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in leatherback turtles foraging in the northwest Atlantic. Concurrent sampling of gelatinous prey species at the surface and

at depth allowed for a realistic mixing model and diet characterization of leatherbacks feeding off Massachusetts, USA. Interestingly, we found a large disparity in isotope values of gelatinous zooplankton collected on the shelf (this study) and the Gulf Stream (McClellan et al. 2010). This emphasizes the importance of using local prey in isotopic mixing models rather than relying on published isotope data. Highly migratory predators like the leatherback turtle occupy multiple “ecoregions” within an annual migratory cycle (Longhurst 2007), and interpretation of their isotope values requires an understanding of the different food webs and prey isotope values within those ecoregions and “isotope provinces” (Hobson 1999).

Western North Atlantic shelf and slope waters are productive regions where spring bloom conditions can lead to increased seasonal abundance of the leatherback’s gelatinous zooplankton prey (Larson 1976, Madin et al. 2006, Mann & Lazier 2006, Deibel & Paffenhöfer 2009). Based on the mixing model, leatherbacks in our study area appear to focus on ctenophores and coastal species of scyphomedusae. This type of foraging may have several advantages. Prey on the shelf is closer to the surface, allowing leatherbacks to make shorter, shallower dives and search for prey more efficiently. If leatherbacks are primarily visual predators, abundant prey in shallow, well-lit shelf waters may also be easier to locate and capture, and allow greater time to be spent in warm surface layers above seasonal thermoclines. Although gelatinous zooplankton are generally considered nutrient-poor, coast-occurring scyphozoans such as *C. capillata* have a higher energy density than other “jellies” (Doyle et al. 2007). If leatherbacks feed preferentially on the gonads and oral arms of *Cyanea* and *Chrysaora*, they can derive higher energy content than feeding on salps and ctenophores (Doyle et al. 2007). It may

also be easier and more efficient for leatherbacks to catch and manipulate larger medusae and ctenophores than smaller gelatinous zooplankton like *T. democratica*. Thus a coastal feeding strategy, focusing on the highest energy prey available, would allow leatherbacks to accumulate the energy reserves necessary for migration and reproduction (Casey et al. 2010).

Juvenile and small sub-adult leatherbacks appear to spend more time in oligotrophic, open ocean habitat where prey is more elusive. Recent work on leatherback ocular morphology and offshore diving behavior suggests that leatherback turtles are not well equipped for prey searching in dim light (Brudenall et al. 2008) and may forage primarily during day-time hours (Casey et al. 2010). Many species of gelatinous zooplankton are vertically dispersed or remain at depth in the deep scattering layer (DSL) during daylight hours (Graham et al. 2001, Madin et al. 2006), requiring leatherbacks to dive deeper and search more extensively in oceanic habitat (Eckert et al. 1989, Eckert 2002a, Sale et al. 2006, Houghton et al. 2008). Lutcavage (1996) hypothesized that leatherbacks in pelagic habitats may associate with oceanic fronts, filaments, and Gulf Stream meanders in order to maximize foraging opportunities. The relatively high $\delta^{13}\text{C}$ and low $\delta^{15}\text{N}$ values found in smaller leatherbacks suggest a foraging strategy that includes Gulf Stream prey (McClellan et al. 2010) for part of the year. Although juvenile leatherbacks must consume sufficient prey to support their rapid growth (Jones et al. 2011), they are not yet burdened by the high energetic demands of reproduction (Wallace et al. 2006a) and may be able to meet their energetic requirements in the less productive oceanic realm.

Interpretation of isotopic values depends on knowing where and when leatherbacks feed throughout their life cycle, and the species of prey targeted. Long-term satellite tracking of adults and juveniles of both sexes can reveal migratory patterns and distant feeding grounds over an annual cycle. Integration of satellite telemetry and stable isotope analysis can identify key foraging habitats and food webs that support leatherbacks at different life stages, information critical for protection and recovery of this endangered species.

CONCLUSIONS

Leatherback turtles have been plying the seas for over 100 million years (Zangerl 1980) but their obscure lifestyle and failure to thrive in captivity have made them challenging to study. We are still trying to answer basic questions about their life history; this is especially true for males and life stages that occur exclusively at sea (juveniles, sub-adults and adult females during the inter-nesting interval). Pressing questions remain about leatherback growth rates, age-at-maturity, longevity, distribution and habitat use, stock structure, health (condition) and mortality rates (TEWG 2007). The goal of my dissertation was to collect empirical data on leatherback movements, dive behavior and habitat use in the NW Atlantic and to characterize their environmental associations. I was particularly interested in expanding our knowledge of leatherback behavior in the New England region where there is a long history of leatherback presence and bycatch in fixed gear (pot/trap) fisheries. I also sought to collect information on leatherback migratory pathways (including distance, travel rate and migratory orientation cues) between high latitude forage grounds and low latitude breeding/overwintering grounds. Lastly, I hoped to improve our understanding of leatherback diet off Massachusetts and determine if there were differences in diet and habitat selection between sexes and size classes.

By combining satellite telemetry and remotely sensed environmental data, I found that leatherback movements and environmental associations varied by oceanographic region, with slow, sinuous, area-restricted search (ARS) behavior and shorter, shallower dives occurring in shelf habitat characterized by relatively cool temperatures (median SST: 18.4 °C), high productivity (median chl a : 0.80 mg m⁻³), shallow depths (median

bathymetry: 57 m) and strong sea surface temperature fronts (median SST gradient: $0.23\text{ }^{\circ}\text{C km}^{-1}$) at temperate latitudes. I observed less ARS behavior in subtropical and tropical latitudes, but three individuals used areas of enhanced productivity near the convergence of the North Equatorial Current and North Equatorial Counter-Current, and North Brazil Current rings. Leatherbacks were highly aggregated in temperate shelf and slope waters during summer, early fall, and late spring, with the highest density of turtle locations on the southern New England shelf. Turtles were more widely dispersed in subtropical and tropical oceanic and neritic habitat during late fall, winter and early spring. Using generalized linear mixed-effects models, I found that differences in leatherback search behavior (represented by path sinuosity) were best explained by ecoregion and regional differences in bathymetry and SST. Within the NW Atlantic Shelves region, leatherback path sinuosity increased with increasing SST, but this relationship reversed within the Gulf Stream region. Leatherbacks increased path sinuosity with decreasing water depth in temperate and tropical shelf habitats. This relationship is consistent with increasing epipelagic gelatinous zooplankton biomass with decreasing water depth, and bathymetry may be a key feature in identifying leatherback foraging habitat in neritic regions.

I used satellite telemetry data to determine the migratory pathways of leatherbacks in the NW Atlantic, and found that all leatherbacks that initiated a southward migration showed similar orientation when moving through the subtropical gyre. Leatherbacks transited rapidly through this region and paths were highly directed, suggesting that this region was used primarily for migration (versus foraging or other activities). I determined that there were negligible differences between the turtles' observed and current-corrected paths and there was no significant difference between

adult and sub-adult orientation. I found that turtles were significantly oriented to magnetic field inclination angle, sunrise angle and sunset angle, suggesting leatherbacks may be able to rely on a magnetic and (or) solar compass during this portion of their migration. Turtles moved approximately orthogonally to isoclinics and isodynamics in the subtropical gyre, raising interesting questions about leatherback sensitivity to very small gradients in those magnetic field parameters. All tested cues provided latitudinal guidance, and a sensory mechanism for determining longitude remains obscure.

Using multi-tissue stable isotope analyses, I found that leatherback turtles of different size and gender had dissimilar diets. Stable isotope values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in the skin of smaller leatherbacks in our study reflected a food web depleted in ^{15}N and enriched in ^{13}C , characteristic of offshore food webs associated with *Sargassum* and *Trichodesmium*. Warm, *Sargassum*-rich waters of the Gulf Stream and central North Atlantic provide important developmental habitat for juvenile loggerhead sea turtles and may serve a similar function in juvenile and sub-adult stages of other sea turtle species such as leatherbacks. I found similar differences between male and female turtles, with isotopic signatures of some female tissues more consistent with an offshore food web enriched in ^{13}C . The apparent differences in foraging habitat selectivity between these groups were supported by my observations of their divergent migratory strategies. Satellite telemetry showed that most sub-adult and female leatherbacks in their inter-nesting years spent the winter offshore in the pelagic realm, whereas adult males and nesting females overwintered in coastal waters near nesting beaches. Mixing model results suggested that leatherbacks foraging off Massachusetts primarily consume the scyphozoan jellyfishes, *Cyanea capillata* and *Chrysaora quinquecirrha*, and ctenophores,

while a smaller proportion of their diet comes from holoplanktonic salps and sea butterflies (Cymbuliidae). My diet results are consistent with historical observations of leatherback turtles feeding on scyphozoan prey in this region.

Although I achieved my primary dissertation objectives, I had hoped to analyze leatherback habitat use and environmental associations in the New England shelf region on a finer scale. The main limitations for achieving a fine-scale spatial analysis were tag technology, spatial resolution of remotely sensed environmental data and turtle behavior. My project was one of the first to deploy GPS-linked satellite tags developed by Wildlife Computers and these first generation tags transmitted fewer GPS locations than expected. This limited my ability to reconstruct fine-scale leatherback movements with minimal observation error. Remotely sensed environmental data was unavailable at spatial scales needed for a fine-scale analysis (e.g., 1 km), and leatherbacks were concentrated in coastal areas where satellite remote sensing of chl *a* is subject to large errors due to the presence of colored dissolved organic matter (CDOM) and suspended sediment. Fortunately, GPS tags have become more reliable over the past five years and I hope to eventually tackle a fine-scale analysis of leatherbacks movements and environmental associations in the New England region through collaboration with Northeast Fisheries Science Center, using 1-km Pan converted chl *a* data (Pan et al. 2008).

One of the weaknesses of my results is the assumption that area restricted search behavior represents foraging, and path straightness is good proxy for search behavior. We lack contemporaneous data on prey (gelatinous zooplankton) and the physical and biological forces driving regional prey dynamics. In the absence of such data, our understanding of leatherback turtle movements and dive behavior is incomplete. New

technologies, such as stomach temperature telemetry, will help define the relationship between leatherback spatial movements and feeding events (e.g., Casey et al. 2010, Casey et al. in prep). Small-scale tracking studies using high-resolution time-depth recorders and concurrent oceanographic and prey sampling would give a more complete picture of leatherback behavior relative to prey fields and help characterize gelatinous zooplankton assemblages and the physical and biological processes that lead to gelatinous zooplankton aggregations.

LIST OF REFERENCES

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- Abelson PH, Hoering TC (1961) Carbon isotope fractionation in formation of amino acids by photosynthetic organisms. *Proc Natl Acad Sci U S A* 47:623-632
- Akaike H (1973) Information theory and an extension of the maximum likelihood principle. In *International Symposium on Information Theory*, Ed. BN Petrov and F Csaki, pp. 267-281. Budapest: Akademia Kiado
- Åkesson S, Morin J, Muheim R, Ottosson U (2005) Dramatic orientation shift of white-crowned sparrows displaced across longitudes in the high Arctic. *Curr Biol* 15:1591-1597
- Alerstam T, Hedenström, Åkesson S (2003) Long-distance migration: evolution and determinants. *Oikos* 103:247-260
- Alfaro-Shigueto J, Dutton PH, Van Bressemer M, Mangel, J (2007) Interactions between leatherback turtles and Peruvian artisanal fisheries. *Chelonian Conserv Biol* 6:129-134
- Alfaro-Shigueto J, Mangel JC, Pajuelo M, Dutton PH, Seminoff JA, Godley BJ (2010) Where small can have a large impact: structure and characterization of small-scale fisheries in Peru. *Fish Res* 106:8-17
- Arai MN (2005) Predation on pelagic coelenterates: a review. *J Mar Biol Assoc UK* 85:523-528
- Asper ED (1975) Techniques of live capture of smaller cetacea. *J Fish Res Board Can* 32:1191-1196
- Avens L, Lohmann KJ (2003) Use of multiple orientation cues by juvenile loggerhead sea turtles, *Caretta caretta*. *J Exp Biol* 206:4317-4325

- Bailey H, Shillinger G, Palacios D, Bograd S, Spotila J, Paladino F, Block B (2008) Identifying and comparing phases of movement by leatherback turtles using state-space models. *J Exp Mar Biol Ecol* 356:128-135
- Bailey H, Benson SR, Shillinger GL, Bograd SJ, Dutton PH, Eckert SA, Morreale SJ, Paladino FV, Eguchi T, Foley DG, Block BA, Piedra R, Hitipeuw C, Tapilatu RF, Spotila JR (2012) Identification of distinct movement patterns in Pacific leatherback turtle populations influenced by ocean conditions. *Ecol App* 22:735-747
- Bailey H, Fossette S, Bograd SJ, Shillinger GL, Swithenbank AM, Georges JY, Gaspar P, Strömberg KHP, Paladino FV, Spotila JR, Block BA, Hays GC (2012) Movement patterns for a critically endangered species, the leatherback turtle (*Dermochelys coriacea*), linked to foraging success and population status. *PLoS ONE* 7(5): e36401. doi:10.1371/journal.pone.0036401
- Balazs GH (1985) Impact of ocean debris on marine turtles. In: Shomura RS, Godfrey ML (compilers) *Proceedings of the workshop on the fate and impact of marine debris*. NOAA Tech Memo NMFS-SEFSC-54, p 580
- Bartol SM, Musick JA, Ochs AL (2002) Visual acuity thresholds of juvenile loggerhead sea turtles (*Caretta caretta*): an electrophysiological approach. *J Comp Phys A* 187:953-960
- Batschelet E (1981) *Circular Statistics in Biology*. New York: Academic Press.
- Belkin IM, O'Reilly JE (2009) An algorithm for oceanic front detection in chlorophyll and SST imagery. *J Mar Sys* 78:319-326
- Belkin IM, Cornillon PC, Sherman K (2009) Fronts in large marine ecosystems. *Prog Oceanogr* 81:223-236
- Benhamou S (2004) How to reliably estimate the tortuosity of an animal's path: straightness, sinuosity, or fractal dimension? *J Theor Biol* 229:209-220

- Benhamou S, Sudre J, Bourjea J, Ciccione S, De Santis A, Luschi P (2011) The role of geomagnetic cues in green sea turtle open sea navigation. PLoS ONE 6(10): e26672. doi:10.1371/journal.pone.0026672
- Benson SR, Forney KA, Harvey JT, Carretta JV, Dutton PH (2007) Abundance, distribution, and habitat of leatherback turtles (*Dermochelys coriacea*) off California, 1990-2003. Fish Bull 105:337-347
- Benson, SR, Eguchi T, Foley DG, Forney KA, Bailey H, Hitipeuw C, Samber BP, Tapilatu RF, Rei V, Ramohia P, Pita J, Dutton PH (2011) Large-scale movements and high-use areas of western Pacific leatherback turtles, *Dermochelys coriacea*. Ecosphere 2(7):art84. doi:10.1890/ES11-00053.1
- Bjorndal KA (1997) Foraging ecology and nutrition of sea turtles. In: Lutz PL, Musick JA (eds) The biology of sea turtles, CRC Press, Boca Raton, FL, pp 199-231
- Bleakney JS (1965) Reports of marine turtles from New England and Eastern Canada. Can Field Nat 79:120-128
- Boles LC, Lohmann KJ (2003) True navigation and magnetic maps in spiny lobsters. Nature 421:60-63
- Bost CA, Cotté C, Bailleul F, Cherel Y, Charrassin JB, Guinet C, Ainley DG, Weimerskirch H (2009) The importance of oceanographic fronts to marine birds and mammals of the southern oceans. J Mar Sys 78:363-376
- Bostrom BL, Jones TT, Hastings M, Jones DR (2010) Behavior and physiology: the thermal strategy of leatherback turtles. PLoS ONE 5(11): e13925. doi:10.1371/journal.pone.0013925
- Boulon RH, Dutton PH, McDonald DL (1996) Leatherback turtles (*Dermochelys coriacea*) on St. Croix, U.S. Virgin Islands: fifteen years of conservation. Chelon Conserv Biol 2:141-147
- Brongersma LD (1969) Miscellaneous notes on turtles, IIA, IIB. Proceedings. Koninklijke Nederlandse Akademie van Wetenschappen (ser. C) 72:76-102

- Brudenall DK, Schwab IR, Fritsches KA (2008) Ocular morphology of the Leatherback sea turtle (*Dermochelys coriacea*). *Vet Ophthalmol* 11:99-110
- Bryant E (2007) 2D location accuracy statistics for Fastloc ® cores running firmware versions 2.2 and 2.3. Technical Report TR01. Wildtrack Telemetry Systems, Leeds, UK.
http://www.wildtracker.com/results_files/Technical%20Report%20TR01.pdf
- Burnham KP, Anderson DR (1998) Model selection and inference: A practical information-theoretic approach. Springer-Verlag, New York, USA 353 p
- Carey FG, Scharold JV (1990) Movements of blue sharks (*Prionace glauca*) in depth and course. *Mar Biol* 106:329-342
- Carr AF (1962) Guideposts of animal navigation. *Am Inst Biol Sci*
- Carr AF (1967) So excellent a fish: a natural history of sea turtles. The Natural History Press, Garden City, NY
- Carr AF, Ogren, LH (1959) The ecology and migrations of sea turtles. 3. *Dermochelys* in Costa Rica, 1955. *Am Mus Novit* 1835
- Carr AF, Ogren LH (1960) The ecology and migrations of sea turtles. 4. The green turtle in the Caribbean Sea. *Bull Am Mus Nat Hist* 121:7-48
- Casey J, Garner J, Garner S, Williard A (2010) Diel foraging behavior of gravid leatherback sea turtles in deep water of the Caribbean Sea. *J Exp Biol* 213:3961-3971
- Caut S, Guirlet E, Angulo E, Das K, Girondot M (2008) Isotope analysis reveals foraging area dichotomy for Atlantic leatherback turtles. *PLoS Biol* 3(3): e1845
- Caut S, Angulo E, Courchamp F (2009) Variation in discrimination of factors ($\Delta^{15}\text{N}$ and $\Delta^{13}\text{C}$): the effect of diet isotopic values and applications for diet reconstruction. *J Appl Ecol* 46:443-453

- Chapman EW, Jørgensen C, Lutcavage ME (2011) Atlantic bluefin tuna (*Thunnus thynnus*): a state-dependent energy allocation model for growth, maturation, and reproductive investment. *Can J Fish Aquat Sci* 68:1934-1951
- Charnov EL (1976) Optimal foraging, the marginal value theorem. *Theor Popul Biol* 9:129-136
- Chi EM, Reinsel GC (1989) Models for longitudinal data with random effects and AR(1) errors. *Journal of the American Statistical Association* 84:452-459
- Clarke A, Holmes LJ, Gore DJ (1992) Proximate and elemental composition of gelatinous zooplankton from the Southern Ocean. *J Exp Mar Biol Ecol* 155:55-68
- Cochran WW, Mouritsen H, Wikelsi M (2004) Migratory songbirds recalibrate their magnetic compass daily from twilight cues. *Science* 304:405-408
- Davenport J (1998) Sustaining endothermy on a diet of cold jelly: energetics of the leatherback turtle *Dermochelys coriacea*. *Brit Herp Soc Bull* 37:33-38
- Davenport J, Balazs GH (1991) Fiery bodies - are pyrosomas important items in the diet of leatherback turtles? *Brit Herp Soc B* 37:33-38
- Deibel D, Paffenhöfer GA (2009) Predictability of patches of neritic salps and doliolids (Tunicata, Thaliacea). *J Plankton Res* 31:1571-1579
- DeNiro MJ, Epstein S (1978) Influence of diet on the distribution of carbon isotopes in animals. *Geochim Cosmochim Acta* 42:495-506
- DeNiro MJ, Epstein S (1981) Influence of diet on the distribution of nitrogen isotopes in animals. *Geochim Cosmochim Acta* 45:341-351
- Desjardin NA (2005) Spatial, temporal, and dietary overlap of leatherback sea turtles (*Dermochelys coriacea*) and ocean sunfishes (family Molidae). Master Thesis, Florida Atlantic University, Boca Raton

- Dingle H, Drake VA (2007) What is migration? *BioScience* 57:113-121
- Dodge KL, Logan JM, Lutcavage ME (2011) Foraging ecology of leatherback sea turtles in the Northwest Atlantic determined through multi-tissue stable isotope analyses. *Mar Biol* 158:2813-2824
- Doyle TK, Houghton JDR, McDevitt R, Davenport J, Hays GC (2007) The energy density of jellyfish: estimates from bomb calorimetry and proximate-composition. *J Exp Mar Biol Ecol* 343:239-252
- Doyle TK, Houghton JDR, O'Suilleabhain PF, Hobson VJ, Marnell F, Davenport J, Hays GC (2008) Leatherback turtles satellite-tagged in European waters. *Endang Species Res* 4:23-31
- Durbin EG, Durbin AG (1996) Zooplankton dynamics in the Northeast shelf ecosystem. In: Sherman K, Jaworski NA, Smayda TJ (eds) *The Northeast Shelf Ecosystem: Assessment, Sustainability, and Management*. Blackwell Science, Cambridge, MA, USA p 129-152
- Duron M (1978) Contribution à l'étude de la biologie de *Dermochelys coriacea* (Linné) dans les Pertuis Charentais. *Thèse Université Bordeaux 3me cycle* 1465
- Dutton DL, Dutton PH, Chaloupka M, Boulon RH (2005) Increase of a Caribbean leatherback turtle *Dermochelys coriacea* nesting population linked to long-term nest protection. *Biol Conserv* 126:186-194
- Dwyer KL, Ryder CE, Prescott R (2002) Anthropogenic mortality of leatherback turtles in Massachusetts waters. In: Seminoff JA (compiler) *Proceedings of the 22nd annual symposium on sea turtle biology and conservation*. NOAA Tech Memo NMFS-SEFSC-503, p 260
- Eckert SA (2002a) Swim speed and movement patterns of gravid leatherback sea turtles (*Dermochelys coriacea*) at St. Croix, US Virgin Islands. *J Exp Biol* 205:3689-3697
- Eckert SA (2002b) Distribution of juvenile leatherback sea turtle *Dermochelys coriacea*

sightings. Mar Ecol Prog Ser 230 :289-293

- Eckert SA (2006) High-use oceanic areas for Atlantic leatherback sea turtles (*Dermochelys coriacea*) as identified using satellite telemetered location and dive information. Mar Biol 149:1257-1267
- Eckert SA, Sarti LM (1997) Distant fisheries implicated in the loss of the world's largest leatherback nesting population. Marine Turtle Newsletter 78:2-7
- Eckert SA, Nellis DW, Eckert KL, Kooyman GL (1986) Diving patterns of two leatherback sea turtles (*Dermochelys coriacea*) during inter-nesting intervals at Sandy Point, St. Croix, US Virgin Islands. Herpetologica 42:381-388
- Eckert SA, Eckert KL, Ponganis P, Kooyman GL (1989) Diving and foraging behavior by leatherback sea turtles. Can J Zool 67:2834-2840
- Eckert S, Bagley D, Kubis S, Ehrhart L, Johnson C, Stewart K, DeFresse D (2006) Internesting and postnesting movements and foraging habitats of leatherback sea turtles (*Dermochelys coriacea*) nesting in Florida. Chelonian Conserv Biol 5:239-248
- Ehrenfeld DW, Koch AL (1967) Visual accommodation in the green turtle. Science 155:827-828
- Eisenberg JF, Frazier J (1983) A leatherback turtle (*Dermochelys coriacea*) feeding in the wild. J Herpetol 17(1):81-82
- Faes C, Molenbergh G, Aerts M, Verbeke G, Kenward MG (2009) The effective sample size and an alternative small-sample degrees-of-freedom method. The American Statistician 63:389-399
- Ferraroli S, Georges JY, Gaspar P, Maho YL (2004) Endangered species: where leatherback turtles meet fisheries. Nature 429:521-522
- Fossette S, Corbel H, Gaspar P, LeMaho Y, Georges JY (2007) An alternative technique for the long-term satellite tracking of leatherback turtles. Endang Species Res

- Fossette S, Hobson VJ, Girard C, Calmettes B, Gaspar P, Hays GC (2010a) Spatio-temporal foraging patterns of a giant zooplanktivore, the leatherback turtle. *J Mar Sys* 81:225-234
- Fossette S, Girard C, López-Mendilaharsu M, Miller P, Domingo A, Evans D, Kelle L, Plot V, Prosdocimi L, Verhage S, Gaspar P, Georges JY (2010b) Atlantic leatherback migratory paths and temporary residence areas. *PLoS ONE* 5(11): e13908. doi:10.1371/journal.pone.0013908
- Fossette S, Gleiss AC, Casey JP, Lewis AR, Hays GC (2012) Does prey size matter? Novel observations of feeding in the leatherback turtle (*Dermochelys coriacea*) allow a test of predator-prey size relationships. *Biol Lett* 8:351-354
- Fossette S, Putman NF, Lohmann KJ, Marsh R, Hays GC (2012) A biologist's guide to assessing ocean currents: a review. *Mar Ecol Prog Ser* 457:285-301
- Frair W, Ackman RG, Mrosovsky N (1972) Body temperature of *Dermochelys coriacea*: warm turtle from cold water. *Science* 177:791-793
- France RL (1995) C-13 Enrichment in benthic compared to planktonic algae- foodweb implications. *Mar Ecol Prog Ser* 124:307-312
- Fraser-Brunner A (1951) The ocean sunfishes (family Molidae). *Bull Br Mus* 1:89-121
- Fratantoni DM, Richardson PL (2006) The evolution and demise of North Brazil current rings. *J Phys Oceanogr* 36:1241-1264
- Frazier J, Meneghel MD, Achaval F (1985) A clarification on the feeding habits of *Dermochelys coriacea*. *J Herpetol* 19(1):159-160
- Fry B, Sherr EB (1984) $\delta^{13}\text{C}$ measurements as indicators of carbon flow in marine and freshwater ecosystems. *Contrib Marine Sci* 27:13-47

- Galuardi B, Royer F, Golet W, Logan J, Neilson J, Lutcavage M (2010) Complex migration routes of Atlantic bluefin tuna (*Thunnus thynnus*) question current population structure paradigm. *Can J Fish Aquat Sci* 67:966-976
- Gannes LZ, O'Brien DM, Martínez del Rio C (1997) Stable isotopes in animal ecology: assumptions, caveats, and a call for more laboratory experiments. *Ecology* 78:1271-1276
- Gannes LZ, Martínez del Rio C, Koch P (1998) Natural abundance variations in stable isotopes and their potential uses in animal physiological ecology. *Comp Biochem Physiol* 119:725-737
- Gaspar P, Georges J, Fossette S, Lenoble A, Ferraroli S, LeMaho Y (2006) Marine animal behavior: neglecting ocean currents can lead us up the wrong track. *Proc R Soc Lond B* 273:2697-2702
- Girard C, Sudre J, Benhamou S, Roos D, Luschi P (2006) Homing in green turtles *Chelonia mydas*: ocean currents act as a constraint rather than as an information source. *Mar Ecol Prog Ser* 322:281-289
- Girondot M, Godfrey MH, Ponge L, Rivalan P (2007) Modeling approaches to quantify leatherback nesting trends in French Guiana and Suriname. *Chelonian Conserv Biol* 6:37-46
- Godley BJ, Thompson DR, Waldron S, Furness RW (1998) The trophic status of marine turtles as determined by stable isotope analysis. *Mar Ecol Prog Ser* 166:277-284
- Goff GP, Lien J (1988) Atlantic leatherback turtles, *Dermochelys coriacea*, in cold waters off Newfoundland and Labrador. *Can Field Nat* 102:1-5
- Goff M, Salmon M, Lohmann KJ (1998) Hatchling sea turtles use surface waves to establish a magnetic compass direction. *Anim Behav* 55:69-77
- Gould JL (2008) Animal navigation: the longitude problem. *Curr Biol* 18:R214-R216
- Graham WM, Pages F, Hammer WM (2001) A physical context for gelatinous

zooplankton aggregations: a review. *Hydrobiologia* 451:199-212

Graham WM, Martin DL, Martin JC (2003) *In situ* quantification and analysis of large jellyfish using a novel video profiler. *Mar Ecol Prog Ser* 254:129-140

Grant GS, Ferrell D (1993) Leatherback turtle, *Dermochelys coriacea* (Reptilia, Dermochelidae) - notes on near-shore feeding behavior and association with Cobia. *Brimleyana* 19:77-81

Grönroos J, Muheim R, Åkesson S (2010) Orientation and autumn migration routes of juvenile sharp-tailed sandpipers at a staging site in Alaska. *J Exp Biol* 213:1829-1835

Hain JHW, Carter GR, Kraus SD, Mayo CA, Winn HE (1981) Feeding behavior of the humpback whale, *Megaptera novaeangliae*, in the western North Atlantic. *Fish Bull* 80:259-268

Halpern BS, Walbridge S, Selkoe KA, Kappel CV, Micheli F, D'Agrosa C, Bruno JF, Casey KS, Ebert C, Fox HE, Fujita R, Heinemann D, Lenihan HS, Madin EMP, Perry MT, Selig ER, Spalding M, Steneck R, Watson R (2008) A global map of human impact on marine ecosystems. *Science* 319:948-952

den Hartog JC, Van Nierop MM (1984) A study on the gut contents of six leathery turtles *Dermochelys coriacea* (Linnaeus) (Reptilia: Testudines: Dermochelyidae) from British waters and from the Netherlands. *Zool Verhandl* 209:1-36

Hatase H, Takai N, Matsuzawa Y, Sakamoto W, Omuta K, Goto K, Arai N, Fujiwara T (2002) Size-related differences in feeding habitat use of adult female loggerhead turtles *Caretta caretta* around Japan determined by stable isotope analyses and satellite telemetry. *Mar Ecol Prog Ser* 233:273-281

Hatase H, Sato K, Yamaguchi M, Takahashi K, Tsukamoto K (2006) Individual variation in feeding habitat use by adult female green sea turtles (*Chelonia mydas*): are they obligately neritic herbivores? *Oecologia* 149:52-64

Hawkes LA, Broderick AC, Coyne MS, Godfrey MH, Lopez-Jurado LF, Lopez-Suarez P, Merino SE, Varo-Cruz N, Godley BJ (2006) Phenotypically linked dichotomy in

sea turtle foraging requires multiple conservation approaches. *Curr Biol* 16:990-995

Hays GC, Åkesson S, Broderick AC, Glen F, Godley BJ, Papi F, Luschi P (2003) Island-finding ability of marine turtles. *Proc R Soc B* 270:S5-S7

Hays GC, Houghton DJ, Issacs C, King RS, Lloyd C, Lovell P (2004a) First records of oceanic dive profiles of leatherback turtles, *Dermochelys coriacea*, indicate behavioral plasticity associated with long-distance migration. *Anim Behav* 67:733-743

Hays GC, Houghton JD, Myers AE (2004b) Pan-Atlantic leatherback turtle movements. *Nature* 429:522

Hays GC, Hobson VJ, Metcalf JD, Righton D, Sims DW (2006) Flexible foraging movements of leatherback turtles across the North Atlantic Ocean. *Ecology* 87:2647-2656

Heaslip SG, Iverson SJ, Bowen WD, James MC (2012) Jellyfish support high energy intake of leatherback sea turtles (*Dermochelys coriacea*): video evidence from animal-borne cameras. *PLoS ONE* 7(3): e33259.
doi:10.1371/journal.pone.0033259

Hobson KA (1999) Tracing origins and migration of wildlife using stable isotopes: a review. *Oecologia* 120:314-326

Hobson KA, Clark RG (1992) Assessing avian diets using stable isotopes II: factors influencing diet-tissue fractionation. *Condor* 94:189-197

Hobson KA, Alisauskas RT, Clark RG (1993) Stable-nitrogen isotope enrichment in avian tissues due to fasting and nutritional stress-implications for isotopic analyses of diet. *Condor* 95:388-394

Hobson KA, Piatt JF, Pitocchelli J (1994) Using stable isotopes to determine seabird trophic relationships. *J Anim Ecol* 63:786-798

Holland RA, Borissov I, Siemers B (2010) A nocturnal mammal, the greater mouse-eared

bat, calibrates a magnetic compass by the sun. Proc Natl Acad Sci USA 107:6941-6945

Hooper SN, Paradis M, Ackman RG (1973) Distribution of trans-6-hexadecenoic acid, 7-methyl-7-hexadecenoic acid and common fatty acids in lipids of ocean sunfish *Mola mola*. Lipids 8:509-516

Houghton JDR, Doyle TK, Wilson MW, Davenport J, Hays GC (2006) Jellyfish aggregations and leatherback turtle foraging patterns in a temperate coastal environment. Ecology 87:1967-1972

Houghton JDR, Doyle TK, Davenport J, Wilson RP, Hays GC (2008) The role of infrequent and extraordinary deep dives in leatherback turtles (*Dermochelys coriacea*). J Exp Biol 211:2566-2575

Hu C, Montgomery ET, Schmitt RW, Muller-Karger FE (2004) The dispersal of the Amazon and Orinoco River water in the tropical Atlantic and Caribbean Sea: Observations from space and S-PALACE float. Deep-Sea Res II 51:1151-1171

Hughes GR, Luschi P, Mencacci R, Papi F (1998) The 7000-km journey of a leatherback turtle tracked by satellite. J Exp Mar Biol Ecol 229:209-217

Innis C, Merigo C, Dodge K, Tlusty M, Dodge M, Sharp B, Myers A, McIntosh A, Wunn D, Perkins C, Herdt T, Norton T, Lutcavage M (2010) Health evaluation of leatherback turtles (*Dermochelys coriacea*) in the Northwestern Atlantic during direct capture and fisheries gear disentanglement. Chelonian Conserv Biol 9:205-222

IUCN (2012) IUCN Red List of Threatened Species. Version 2012.2. www.iucnredlist.org. Downloaded on 15 May 2013.

Jacobson L, Seaver A, Tang J (2011) AstroCalc4R: software to calculate solar zenith angle; time at sunrise, local noon, and sunset; and photosynthetically available radiation based on date, time, and location. US Dept of Commer, Northeast Fish Sci Cent Ref Doc. 11-14; 10p.

- James MC (2004) *Dermochelys coriacea* (leatherback sea turtle) penis display. *Herpetol Rev* 35(3):264
- James MC, Herman TB (2001) Feeding of *Dermochelys coriacea* on medusae in the Northwest Atlantic. *Chelonian Conserv Biol* 4:202-205
- James MC, Ottensmeyer CA, Myers RA (2005a) Identification of high-use habitat and threats to leatherback sea turtles in northern waters: new directions for conservation. *Ecol Lett* 8:195-201
- James MC, Myers RA, Ottensmeyer CA (2005b) Behavior of leatherback sea turtles, *Dermochelys coriacea*, during the migratory cycle. *Proc R Soc B* 272:1547-1555
- James MC, Eckert SA, Myers RA (2005c) Migratory and reproductive movements of male leatherback turtles (*Dermochelys coriacea*). *Mar Biol* 147:845-853
- James MC, Ottensmeyer CA, Eckert SA, Myers RA (2006) Changes in diel diving patterns accompany shifts between northern foraging and southward migration in leatherback turtles. *Can J Zool* 84:754-765
- James MC, Sherrill-Mix SA, Myers RA (2007) Population characteristics and seasonal migrations of leatherback sea turtles at high latitudes. *Mar Ecol Prog Ser* 337:245-254
- Johns WE, Lee TN, Schott FA, Zantopp RJ, Evans, RH (1990) The North Brazil current retroflection: seasonal structure and eddy variability. *J Geophys Res* 95:22103-22120
- Johnsen S, Lohmann KJ (2008) Magnetoreception in animals. *Phys Today* 61:29-35
- Johnson WS, Allen DM (2005) Zooplankton of the Atlantic and Gulf coasts : a guide to their identification and ecology. The John Hopkins University Press, Baltimore, MD
- Jones TT, Bostrom B, Carey M, Imlach B, Mikkelsen J, Ostafichuk P, Eckert S, Opat P, Swimmer Y, Seminoff J, Jones DR (2011) Determining transmitter drag and best-

practice attachment procedures for sea turtle biotelemetry. NOAA Tech Memo NMFS-SWFSC-480, 58 p

Jones TT, Hastings MD, Bostrom BL, Pauly D, Jones DR (2011) Growth of captive leatherback turtles, *Dermochelys coriacea*, with inferences on growth in the wild: Implications for populations decline and recovery. J Exp Mar Biol Ecol 399:84-92

Jonsen ID, Myers RA, James MC (2007) Identifying leatherback turtle foraging behaviour from satellite telemetry using a switching state-space model. Mar Ecol Prog Ser 337:255-264

Jørgensen C, Ernande B, Fiksen Ø, Dieckmann U (2006) The logic of skipped spawning in fish. Can J Fish Aquat Sci 63:200-211

Kareiva P, Odell G (1987) Swarms of predators exhibit "preytaxis" if individual predators use area-restricted search. Am Nat 130:233-270

Kenney RD (1996) Preliminary assessment of competition for prey between leatherback sea turtles and ocean sunfish in northeast shelf waters. In: Keinath JA, Barnard DE, Musick JA, Bell BA (eds) Proceedings of the 15th annual workshop on sea turtle biology and conservation. NOAA Tech Memo NMFS-SEFSC-387, pp 144-147

Kenney RD, Owen RE, Winn HE (1985) Shark distributions off the Northeastern United States from marine mammal surveys. Copeia 1985:220-223

Kuhn CE, Tremblay Y, Ream RR, Gelatt TS (2010) Coupling GPS tracking with dive behavior to examine the relationship between foraging strategy and fine-scale movements of northern fur seal. Endang Species Res 12:125-139

Larson RJ (1976) Marine flora and fauna of the northeastern United States. Cnidaria:Scyphozoa. NOAA Tech Rep NMFS Circ 397

Lazell JD (1976) This broken archipelago. Quadrangle Press (Harper and Row), New York, NY

- Lazell JD (1980) New England waters: critical habitat for marine turtles. *Copeia* 1980:290-295
- Lewison RL, Freeman SA, Crowder LB (2004) Quantifying the effects of fisheries on threatened species: the impact of pelagic longlines on loggerhead and leatherback sea turtles. *Ecol Lett* 7:221-231
- Light P, Salmon M, Lohmann KJ (1993) Geomagnetic orientation of loggerhead sea turtles: evidence for an inclination compass. *J Exp Biol* 182:1-10
- Lilley MKS, Beggs SE, Doyle TK, Hobson VJ, Stromberg KHP, Hays GC (2011) Global patterns of epipelagic gelatinous zooplankton biomass. *Mar Biol* 158:2429-2436
- Logan J, Jardine T, Miller T, Bunn S, Cunjak R, Lutcavage M (2008) Lipid corrections in carbon and nitrogen stable isotope analyses: comparison of chemical extraction and modelling methods. *J Anim Ecol* 77:838-846
- Lohmann KJ, Lohmann CMF (1994) Detection of magnetic inclination angle by sea turtles: a possible mechanism for determining latitude. *J Exp Biol* 194:23-32
- Lohmann KJ, Lohmann CMF (1996a) Orientation and open-sea navigation in sea turtles. *J Exp Biol* 199:73-81
- Lohmann KJ, Lohmann CMF (1996b) Detection of magnetic field intensity by sea turtles. *Nature* 380:59-61
- Lohmann KJ, Salmon M, Wyneken J (1990) Functional autonomy of land and sea orientation systems in sea turtle hatchlings. *Biol Bull* 179:214-218
- Lohmann KJ, Swartz AW, Lohmann CMF (1995) Perception of wave direction by sea turtles. *J Exp Biol* 198:1079-1085
- Lohmann KJ, Cain SD, Dodge SA, Lohmann CMF (2001) Regional magnetic fields as navigational markers for sea turtles. *Science* 294:364-366

- Lohmann KJ, Lohmann CMF, Ehrhart LM, Bagley DA, Swing, T (2004) Geomagnetic map used in sea-turtle navigation. *Nature* 428:909-910
- Lohmann KJ, Lohmann CMF, Putman NF (2007) Magnetic maps: nature's GPS. *J Exp Biol* 210: 3697-3705
- Lohmann KJ, Lohmann CMF, Endres CS (2008) The sensory ecology of ocean navigation. *J Exp Biol* 211:1719-1728
- Longhurst AR (2007) *Ecological geography of the sea*. Second edition. Academic Press, Burlington, Massachusetts, USA
- López-Mendilaharsu M, Rocha CFD, Miller P, Domingo A, Prosdocimi L (2009) Insights on leatherback turtle movements and high use areas in the Southwest Atlantic Ocean. *J Exp Mar Biol Ecol* 378:31-39
- Lum LL (2006) Assessment of incidental sea turtle catch in the artisanal gillnet fishery in Trinidad and Tobago, West Indies. *Appl Herp* 3:357-368
- Luschi P, Sale A, Mencacci R, Hughes GR, Lutjeharms JRE, Papi F (2003) Current transport of leatherback sea turtles (*Dermochelys coriacea*) in the Ocean. *Proc R Soc Lond B (Suppl)* 270:S129-S132
- Luschi P, Benhamou S, Girard C, Ciccione S, Roos D, Sudre J, Benvenuti S (2007) Marine turtles use geomagnetic cues during open-sea homing. *Curr Biol* 17:126-133
- Lutcavage ME (1996) Planning your next meal: leatherback travel routes and ocean fronts. In: Keinath JA, Barnard DE, Musick JA, Bell BA (eds) *Proceedings of the 15th annual workshop on sea turtle biology and conservation*. NOAA Tech Memo NMFS-SEFSC-387, p 355
- Lutcavage ME, Kraus S (1995) The feasibility of direct photographic assessment of giant bluefin tuna, *Thunnus thynnus*, in New England waters. *Fish Bull* 93:495-503
- Lutcavage M, Goldstein J (1996) North Atlantic leatherback sea turtle workshop.

Workshop Reader. November 22, 1996, Dalhousie Univ. Halifax, NS

Lutcavage ME, Bushnell PG, Jones DR (1992) Oxygen stores and aerobic metabolism in the leatherback sea turtle. *Can J Zool* 70:348-351

Lutcavage ME, Plotkin P, Witherington B, Lutz PL (1997) Human impacts on sea turtle survival. In: Lutz PL, Musick JA (eds) *The biology of sea turtles*, CRC Press, Boca Raton, FL, pp 387-409

Lutcavage M, Rhodin AGJ, Sadove SS, Conroy CR (2001) Direct carapacial attachment of satellite tags using orthopedic bioabsorbable mini-anchor screws on leatherback turtles in Culebra, Puerto Rico. *Mar Turt Newsl* 95:9-12

Lynam CP, Gibbons MJ, Axelsen BE, Sparks CAJ, Coetzee J, Heywood BG, Brierley AS (2006) Jellyfish overtake fish in a heavily fished ecosystem. *Curr Biol* 16:R492-R493

MacArthur RH, Pianka ER (1966) On optimal use of a patchy environment. *Am Nat* 91:603-609

MacGintie GE (1938) Notes on the natural history of some marine animals. *Am Midl Nat* 19:207-219

Madin LP, Kremer P, Wiebe PH, Purcell JE, Horgan EH, Nemazie DA (2006) Periodic swarms of the salp *Salpa aspera* in the slope waters of the NE United States: biovolume, vertical migration, grazing, and vertical flux. *Deep-Sea Res* 53:804-819

Mann KH, Lazier JRN (2006) *Dynamics of marine ecosystems: biological-physical interactions in the oceans* (3rd ed). Blackwell Science Inc., Cambridge, MA

Mardia KV (1972) *Statistics of directional data*. Academic Press, London

Martínez del Rio C, Wolf BO (2004) Mass-balance models for animal isotopic ecology. In: Starck JM, Wang T (eds) *Physiological consequences of feeding*. Springer, Berlin Heidelberg New York

- McCarthy AL, Heppell S, Royer F, Freitas C, Dellinger T (2010) Identification of likely foraging habitat of pelagic loggerhead sea turtles (*Caretta caretta*) in the North Atlantic through analysis of telemetry track sinuosity. *Prog Oceanogr* 86:224-231
- McClellan CM, Read AJ (2007) Complexity and variation in loggerhead sea turtle life history. *Biol Lett* 3:592-594
- McClellan CM, Braun-McNeill J, Avens L, Wallace BP, Read AJ (2010) Stable isotopes confirm a foraging dichotomy in juvenile loggerhead sea turtles. *J Exp Mar Biol Ecol* 387:44-51
- McMahon CR, Hays GC (2006) Thermal niche, large-scale movements and implications of climate change for a critically endangered marine vertebrate. *Global Change Biol* 12:1330-1338
- Miller JD (1997) Reproduction in sea turtles. In: Lutz PL, Musick JA (eds) *The biology of sea turtles*, CRC Press, Boca Raton, FL, pp 51-82
- Mills CE (2001) Jellyfish blooms: are populations increasing globally in response to changing ocean conditions? *Hydrobiol* 451:55-68
- Minagawa M, Wada E (1984) Stepwise enrichment of $\delta^{15}\text{N}$ along food chains: further evidence of the relation between $\delta^{15}\text{N}$ and animal age. *Geochim Cosmochim Acta* 48:1135-1140
- Morreale SJ, Standora EA, Spotila JR, Paladino FV (1996) Migration corridor for sea turtles. *Nature* 384:319-320
- Mroskovsky N, Shettleworth SJ (1968) Wavelength preferences and brightness cues in the water finding behavior of sea turtles. *Behaviour* 32:211-257
- Mrosovsky N, Ryan GD, James MC (2009) Leatherback turtles: the menace of plastic. *Marine Pollution Bulletin* 58: 287-289.

- Muheim R, Phillips JB, Åkesson S (2006) Polarized light cues underlie compass calibration in migratory songbirds. *Science* 313:837-839
- Musick JA, Limpus CJ (1997) Habitat utilization and migration in juvenile sea turtles. In: Lutz PL, Musick JA (eds) *The biology of sea turtles*, CRC Press, Boca Raton, FL, pp 137-163
- Myers AE, Hays GC (2006) Do leatherback turtles *Dermochelys coriacea* forage during the breeding season? A combination of data-logging devices provide new insights. *Mar Ecol Prog Ser* 322:259-267
- National Research Council (1990) *Decline of the sea turtles: causes and prevention*. National Academy Press, Washington, D.C., 259 Pp
- NMFS and USFWS (1992) *Recovery plan for leatherback turtles in the US Caribbean, Atlantic and Gulf of Mexico*. National Marine Fisheries Service, Washington, DC
- Neilson JD, Smith S, Royer F, Paul SD, Porter JM, Lutcavage M (2009) Investigations of horizontal movements of Atlantic swordfish using pop-up satellite archival tags. *Tagging and Tracking of Marine Animals with Electronic Devices*. Available: http://dx.doi.org/10.1007/978-1-4020-9640-2_18
- Olson DB, Hitchcock GL, Mariano AJ, Ashjian CJ, Peng G, Nero RW, Podesta GP (1994) Life on the edge: marine life and fronts. *Oceanography* 7:52-59
- Paladino FV, O'Connor MP, Spotila JR (1990) Metabolism of leatherback turtles, gigantothermy, and thermoregulation of dinosaurs. *Nature* 344:858-860
- Pan X, Mannino A, Russ ME, Hooker SB (2008) Remote sensing of the absorption coefficients and chlorophyll a concentration in the United States southern Middle Atlantic Bight from SeaWiFS and MODIS-Aqua. *J Geophys Res* 113:C11022, doi:10.1029/2008JC004852
- Papi F, Liew HC, Luschi P, Chan EH (1995) Long-range migratory travel of a green turtle tracked by satellite: evidence for navigational ability in the open ocean. *Mar Biol* 122:171-175

- Papi F, Luschi P, Akesson S, Capogrossi S, Hays GC (2000) Open-sea migration of magnetically disturbed sea turtles. *J Exp Biol* 203:3435-3443
- Park R, Epstein S (1961) Metabolic fractionation of C¹³ & C¹² in plants. *Plant Physiol* 36:133-138
- Parnell AC, Inger R, Bearhop S, Jackson AL (2010) Source partitioning using stable isotopes: coping with too much variation. *PLoS ONE* 5(3):e9672.doi:10.1371/journal.pone.0009672
- Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. *Ann Rev Ecol Syst* 18:293-320
- Phillips DL, Gregg JW (2003) Source partitioning using stable isotopes: coping with too many sources. *Oecologia* 136:261-269
- Phillips DL, Newsome SD, Gregg JW (2005) Combining sources in stable isotope mixing models: alternative methods. *Oecologia* 144:520-524
- Phillips RA, Silk JRD, Croxall JP, Afanasyev V (2006) Year-round distribution of white-chinned petrels from South Georgia: relationships with oceanography and fisheries. *Biol Conser* 129:336-347
- Pinaud D, Weimerskirch H (2007) At-sea distribution and scale-dependent foraging behaviour of petrels and albatrosses: a comparative study. *J Anim Ecol* 76:9-19
- Pinheiro JC, Bates DM (2000) *Mixed-effects models in S and S-PLUS*. Springer-Verlag, New York, USA 353 p
- Plotkin P (2002) Adult migrations and habitat use. In: Lutz PL, Musick JA, Wyneken J (eds) *The Biology of Sea Turtles Volume II*. CRC Press, Boca Raton, FL, p 225-233
- Polovina JJ, Kobayashi DR, Parker DM, Seki JP, Balaz GH (2000) Turtles on the edge: movements of loggerhead turtles (*Caretta caretta*) along oceanic fronts, spanning

longline fishing grounds in the central North Pacific, 1997-1998. *Fish Oceanogr* 9:71-82

Polovina JJ, Balaz GH, Howell EA, Parker DM, Seki MP, Dutton PH (2004) Forage and migration habitat of loggerhead (*Caretta caretta*) and olive ridley (*Lepidochelys olivacea*) sea turtles in the central North Pacific. *Fish Oceanogr* 13:36-51

Pope EC, Hays GC, Thys TM, Doyle TK, Sims DW, Queiroz N, Hobson VJ, Kubicek L, Houghton JDR (2010) The biology and ecology of the ocean sunfish *Mola mola*: a review of current knowledge and future research perspectives. *Rev Fish Biol Fish* 20:471-487

Popp B, Graham B, Olson R, Hannides C, Lott M, L López-Ibarra G, Galván-Magaña F, Fry B (2007) Insight into the trophic ecology of yellowfin tuna, *Thunnus albacares*, from compound-specific nitrogen isotope analysis of proteinaceous amino acids. In: Dawson T, Seigwolf R (eds) *Isotopes as tracers of ecological change*. Elsevier Academic Press, San Diego, CA, pp 173-190

Post DM, Layman CA, Arrington DA, Takimoto G, Quattrochi J, Montaña CG (2007) Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia* 152:179-189

Potter IF, Galuard B, Howell WH (2011) Horizontal movement of ocean sunfish, *mola mola*, in the northwest Atlantic. *Mar Biol* 158:531-540

Prescott RL (1988) Leatherbacks in Cape Cod Bay, MA, 1977-1987. Abstract. Proc. 8th Annual Workshop on Sea Turtle Biology and Conservation, Feb, 1988

Pritchard PCH (1973) International migrations of South American sea turtles (*Cheloniidae* and *Dermochelyidae*). *Anim Behav* 21:18-27

Purcell JE, Graham WM, Dumont HJ (2001) *Jellyfish blooms: ecological and societal importance*. Kluwer Academic Publishers

Putman NF, Endres CS, Lohmann CMF, Lohmann KJ (2011) Longitude perception and biocoordinate magnetic maps in sea turtles. *Curr Biol* 21:1-4

- Quinn TP (1980) Evidence for celestial and magnetic compass orientation in lake migrating sockeye salmon fry. *J Comp Physiol* 137:243-248
- R Core Team (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>
- Rakow KC, Graham WM (2006) Orientation and swimming mechanics by the scyphomedusa *Aurelia* sp. in shear flow. *Limnol Oceanogr* 51:1097-1106
- Rau GH, Sweeney RE, Kaplan IR (1982) Plankton ^{13}C : ^{12}C ratio changes with latitude: differences between northern and southern oceans. *Deep-Sea Res* 29:1035–1039
- Reich KJ, Bjorndal KA, Bolten AB (2007) The ‘lost years’ of green turtles: using stable isotopes to study cryptic lifestages. *Biol Lett* 3:712-714
- Reich KJ, Bjorndal KA, Martínez del Rio C (2008) Effects of growth and tissue type on the kinetics of ^{13}C and ^{15}N incorporation in a rapidly growing ectotherm. *Oecologia* 155:651-663
- Reich KJ, Bjorndal KA, Frick MG, Witherington BE, Johnson C, Bolten AB (2009) Polymodal foraging in adult female loggerheads (*Caretta caretta*). *Mar Biol* 157:113-121
- Reina RD, Abernathy KJ, Marshall GJ, Spotila JR (2005) Respiratory frequency, dive behaviour and social interactions of leatherback turtles, *Dermochelys coriacea* during the inter-nesting interval. *J Exp Mar Biol Ecol* 316:1-16
- Rhodin AGJ (1985) Comparative chondro-osseous development and growth of marine turtles. *Copeia* 1983:752-771
- Robinson PW, Tremblay Y, Crocker DE, Kappes MA, Kuhn CE, Shaffer SA, Simmons SE, Costa DP (2007) A comparison of indirect measures of feeding behaviour based on ARGOS tracking data. *Deep-Sea Res II* 54:356-368

- Rooker JR, Turner JP, Holt SA (2006) Trophic ecology of *Sargassum*-associated fishes in the Gulf of Mexico determined from stable isotopes and fatty acids. *Mar Ecol Prog Ser* 313:249-259
- Royer F, Lutcavage M (2008) Filtering and interpreting location errors in satellite telemetry of marine animals. *J Exp Mar Biol Ecol* 359:1-10
- Rozhok A (2008) Orientation and navigation in vertebrates. Springer-Verlag, Berlin
- Saba VS, Spotila, JR, Chavez FP, Musick JA (2008) Bottom-up and climatic forcing on the worldwide population of leatherback turtles. *Ecology* 89:1414–1427
- Saino T, Hattori A (1987) Geographic variation of the water column distribution of suspended particulate nitrogen and its ^{15}N natural abundance in the Pacific and its marginal seas. *Deep-Sea Res* 34:807–827
- Sale A, Luschi P, Mencacci R, Lambardi P, Hughes GR, Hays GC, Benvenuti S, Papi F (2006) Long-term monitoring of leatherback turtle dive behaviour during oceanic movements. *J Exp Mar Biol Ecol* 328:197-210
- Sale A, Luschi P (2009) Navigational challenges in the oceanic migrations of leatherback sea turtles. *Proc R Soc B* doi: 10.1098/rspb.2009.0965
- Salmon M, Lohmann KJ (1989) Orientation cues used by hatchling loggerheads (*Caretta caretta*) during their offshore migration. *Ethology* 83:215-228
- Salmon M, Wyneken J, Fritz E, Lucas M (1992) Sea finding by hatchling sea turtles: role of brightness, silhouette, and beach slope as orientation cues. *Behaviour* 122:56-77
- Santidrián Tomillo P, Veléz E, Reina RD, Piedra R, Paladino FV, Spotila JR (2007) Reassessment of the leatherback turtle (*Dermochelys coriacea*) nesting population at Parque Nacional Marino Las Baulas, Costa Rica: effects of conservation efforts. *Chelonian Conserv Biol* 6:54-62

- Sarti Martínez L, Barragán AR, Muñoz DG, García N, Huerta P, Vargas F (2007) Conservation and biology of the leatherback turtle in the Mexican Pacific. *Chelonian Conserv Biol* 6:70–78.
- Schick RS, Goldstein J, Lutcavage ME (2004) Bluefin tuna (*Thunnus thynnus*) distribution in relation to sea surface temperature fronts in the Gulf of Maine (1994-96). *Fish Oceanogr* 13: 225-238
- Schmidt-Nielsen K (1972) Locomotion: energy cost of swimming, flying, and running. *Science* 177:222-228
- Schmidt-Koenig K (1975) Migration and homing in animals. *Zoophysiology Ecol* 6:47-40
- Schoener TW (1971) Theory of feeding strategies. *Annu Rev Ecol Syst* 2:369-404
- Seminoff JA, Bjorndal KA, Bolten AB (2007) Stable carbon and nitrogen isotope discrimination and turnover in Pond Sliders *Trachemys scripta*: insights for trophic study of freshwater turtles. *Copeia* 2007:534-542
- Seminoff JA, Zárate P, Coyne M, Foley DG, Parker D, Lyon BN, Dutton PH (2008) Post-nesting migrations of Galápagos green turtles *Chelonia mydas* in relation to oceanographic conditions: integrating satellite telemetry with remotely sensed ocean data. *Endang Species Res* 4:57-72
- Seminoff JA, Jones TT, Eguchi T, Hastings M, Jones DR (2009) Stable carbon and nitrogen isotope discrimination in soft tissues of the leatherback turtle (*Dermochelys coriacea*): insights for trophic studies of marine turtles. *J Exp Mar Biol Ecol* 381:33-41
- Semm P, Beason RC (1990) Responses to small magnetic variations by the trigeminal system of the bobolink. *Brain Res Bull* 25:735-740
- Shenker JM (1984) Scyphomedusae in surface waters near the Oregon coast, May-August, 1981. *Estuar Coast Shelf Sci* 19:619-632

- Sherman K, Skjoldal HR (2002) Large marine ecosystems of the North Atlantic: changing states and sustainability. Elsevier Science, Amsterdam, The Netherlands
- Shillinger GL, Palacios DM, Bailey H, Bograd SJ, Swithenbank AM, Gaspar P, Wallace BP, Spotila JR, Paladino FV, Peidra R, Eckert SA, Block BA (2008) Persistent leatherback turtle migrations present opportunities for conservation. PLoS Biol 6(7): e171
- Shillinger GL, Swithenbank AM, Bailey H, Bograd SJ, Castelton MR, Wallace BP, Spotila JR, Paladino FV, Piedra R, Block BA (2011) Vertical and horizontal habitat preferences of post-nesting leatherback turtles in the South Pacific Ocean. Mar Ecol Prog Ser 422:275-289
- Shoop CR, Kenney RD (1992) Seasonal distributions and abundances of loggerhead and leatherback sea turtles in the waters of the northeastern United States. Herp Monogr 6:43-67
- Sibert JR, Lutcavage ME, Nielsen A, Brill RW, Wilson SG (2006) Inter-annual variation in large-scale movement of Atlantic bluefin tuna (*Thunnus thynnus*) determined from pop-up satellite archival tags. Can J Fish Aquat Sci 63:2154-2166. doi:10.1139/F06-114
- Skomal GB, Zeeman SI, Chisholm JH, Summers EL, Walsh HJ, McMahon KW, Thorrold SR (2009) Transequatorial migrations by basking sharks in the western Atlantic Ocean. Curr Biol 19: 1019-1022
- Spotila JR, Dunham AE, Leslie AJ, Steyermark AC, Plotkin PT, Paladino FV (1996) Worldwide population decline of *Dermochelys coriacea*: are leatherback turtles going extinct? Chelonian Conserv Biol 2:209-222
- Spotila JR, Reina RD, Steyermark AC, Plotkin PT, Paladino FV (2000) Pacific leatherback turtles face extinction. Nature 405:529-530
- Stewart K, Johnson C, Godfrey MH (2007) The minimum size of leatherbacks at reproductive maturity, with a review of sizes for nesting females from the Indian, Atlantic and Pacific Ocean basins. Herp J 17:123-128

- Sweeting CJ, Barry J, Barnes C, Polunin NVC, Jennings S (2007a) Effects of body size and environment on diet-tissue $\delta^{15}\text{N}$ fractionation in fishes. *J Exp Mar Biol Ecol* 340:1-10
- Sweeting CJ, Barry J, Polunin NVC, Jennings S (2007b) Effects of body size and environment on diet-tissue $\delta^{13}\text{C}$ fractionation in fishes. *J Exp Mar Biol Ecol* 352:165-176
- Tieszen LL, Boutton TW, Tesdahl KG, Slade NA (1983) Fractionation and turnover of stable carbon isotopes in animal tissues: implications for $\delta^{13}\text{C}$ analysis of diet. *Oecologia* 57:32-37
- TEWG (Turtle Expert Working Group) (2007) An assessment of the leatherback turtle population in the Atlantic Ocean. NOAA Tech Memo NMFS-SEFSC-555
- Vanderklift MA, Ponsard S (2003) Sources of variation in consumer-diet $\delta^{15}\text{N}$ enrichment: a meta-analysis. *Oecologia* 136:169-182
- Wada E, Hattori A (1991) Nitrogen in the sea: forms, abundances, and rate processes. CRC Press, Boca Raton, FL
- Walker MM (1984) Learned magnetic field discrimination in yellowfin tuna, *Thunnus albacares*. *J Comp Physiol A* 155:673-679
- Walker MM, Kirschvink JL, Ahmed G, Diction AE (1982) Evidence that fin whales respond to the geomagnetic field during migration. *J Exp Biol* 171:67-78
- Walker MM, Bitterman ME (1989) Honeybees can be trained to respond to very small changes in geomagnetic field intensity. *J Exp Biol* 145:489-494
- Walker MM, Dennis TE (2005) Role of the magnetic sense in the distribution and abundance of marine animals. *Mar Ecol Prog Ser* 287:295-33
- Wallace BP, Kilham SS, Paladino FV, Spotila JR (2006a) Energy budget calculations indicate resource limitation in eastern Pacific leatherback turtles. *Mar Ecol Prog Ser* 318:263-270

- Wallace BP, Seminoff JA, Kilham SS, Spotila JR, Dutton PH (2006b) Leatherback turtles as oceanographic indicators: stable isotope analyses reveal a trophic dichotomy between ocean basins. *Mar Biol* 149:953–960
- Wallace BP, Avens L, Braun-McNeill J, McClellan CM (2009) The diet composition of immature loggerheads: insights on trophic niche, growth rates, and fisheries interactions. *J Exp Mar Biol Ecol* 373:50-57
- Walli A, Teo SLH, Boustany A, Farwell CJ, Williams T, Dewar H, Prince E, Block BA (2009) Seasonal movements, aggregations and diving behavior of Atlantic bluefin tuna (*Thunnus thynnus*) revealed with archival tags. *PLoS ONE* 4(7):e6151. doi:10.1371/journal.pone.0006151
- Weimerskirch H, Bonadonna F, Bailleul F, Mabile G, Dell’Omo G, Lipp H (2002) GPS tracking of foraging albatrosses. *Science* 295:1259
- Weng KC, Foley DG, Ganong JE, Perle C, Shillinger GL, Block BA (2008) Migration of an upper trophic level predator, the salmon shark *Lamna ditropis*, between distant ecoregions. *Mar Ecol Prog Ser* 372:253-264
- Wessel P, Smith WHF (1991) Free software helps map and display data. *EOS Trans AGU* 72:441
- Whitehead H, Jonsen ID (2013) Inferring animal densities from tracking data using Markov Chains. *PLoS ONE* 8(4):e60901. doi:10.1371/journal.pone.0060901
- Wiebe PH, Burt KH, Boyd SH, Morton AW (1976) A multiple opening/closing net and environmental sensing system for sampling zooplankton. *J Mar Res* 34:313-326
- Wiebe PH, Morton AW, Bradley AM, Backus RH, Craddock JE, Barber V, Cowles TJ, Flierl GR (1985) New developments in the MOCNESS, an apparatus for sampling zooplankton and micronekton. *Mar Biol* 87:313-323
- Wiltschko W, Wiltschko R (1996) Magnetic orientation in birds. *J Exp Biol* 199:29-38

- Wishner K, Durbin E, Durbin A, Macaulay M, Winn H, Kenney R (1988) Copepod patches and right whales in the Great South Channel off New England. *Bull Mar Sci* 43:825-844
- Witt MJ, Broderick AC, Johns DJ, Martin C, Penrose R, Hoogmoed MS, Godley BJ (2007) Prey landscapes help identify potential foraging habitats for leatherback turtles in the NE Atlantic. *Mar Ecol Prog Ser* 337:231-244
- Witt MJ, Baert B, Broderick AC, Formia A, Fretey J, Gibudi A, MOUNGUENGUI GAM, MOUSSOUNDA C, NGOUSSONO S, PARNELL R, ROUMET D, SOUNGUET G, VERHAGE B, ZOGO A, Godley BJ (2009) Aerial surveying the world's largest leatherback turtle rookery: a more effective methodology for large-scale monitoring. *Biol Conserv* 142:1719-1727
- Witt MJ, Bonguno EA, Broderick AC, Coyne MS, Formia A, Gibudi A, MOUNGUENGUI GAM, MOUSSOUNDA C, NSAFOU M, NOUGUSSONO S, PARNELL RJ, SOUNGUET GP, VERHAGE S, Godley BJ (2011) Tracking leatherback turtles from the world's largest rookery: assessing threats across the South Atlantic. *Proc R Soc B* 278:2338-2347
- Wolf N, Carleton SA, Martínez del Río C (2009) Ten years of experimental animal isotopic ecology. *Funct Ecol* 23:17-26
- Wyneken J, Salmon M, Lohmann KJ (1990) Orientation by hatchling loggerhead sea turtles, *Caretta caretta*, in a wave tank. *J Exp Mar Biol Ecol* 139:43-50
- Zangerl R (1980) Patterns of phylogenetic differentiation in the Toxochelyid and Chelonid sea turtles. *Am Zool* 20:585-596
- Zug GR, Parham JF (1996) Age and growth in leatherback turtles, *Dermochelys coriacea*: a skeletochronological analysis. *Chelonian Conserv Biol* 2:244-249
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York, NY

APPENDICIES

APPENDIX A



UNIVERSITY of NEW HAMPSHIRE

June 14, 2006

Lutcavage, Maryellen M
Zoology, Spaulding Life Sciences Bldg
Durham, NH 03824

IACUC #: 060501
Approval Date: 05/19/2006
Review Level: B
Project: Satellite tagging of the leatherback sea turtle, *Dermochelys coriacea*

The Institutional Animal Care and Use Committee (IACUC) reviewed and approved the protocol submitted for this study under Category B on Page 4 of the Application for Review of Vertebrate Animal Use in Research or Instruction - *the study involves either no pain or potentially involves momentary, slight pain, discomfort or stress.*

Approval is granted for a period of three years from the approval date above. Continued approval throughout the three year period is contingent upon completion of annual reports on the use of animals. At the end of the three year approval period you may submit a new application and request for extension to continue this project. Requests for extension must be filed prior to the expiration of the original approval.

Please Note:

1. All cage, pen, or other animal identification records must include your IACUC # listed above.
2. Use of animals in research and instruction is approved contingent upon participation in the UNH Occupational Health Program for persons handling animals. Participation is mandatory for all principal investigators and their affiliated personnel, employees of the University and students alike. A Medical History Questionnaire accompanies this approval; please copy and distribute to all listed project staff who have not completed this form already. Completed questionnaires should be sent to Dr. Gladi Porsche, UNH Health Services.

If you have any questions, please contact either Roger Wells at 862-2726 or Julie Simpson at 862-2003.

For the IACUC,

A handwritten signature in cursive script that reads "Jessica Bolker".

Jessica A. Bolker, Ph.D.
Chair

cc: File

Research Conduct and Compliance Services, Office of Sponsored Research, Service Building,
51 College Road, Durham, NH 03824-3585 * Fax: 603-862-3564

APPENDIX B

University of New Hampshire

Research Integrity Services, Office of Sponsored Research
Service Building, 51 College Road, Durham, NH 03824-3585
Fax: 603-862-3564

28-May-2009

Lutcavage, Maryellen M
Biological Sciences, Rudman Hall
Durham, NH 03824

IACUC #: 090402

Project: Satellite Tagging of the Leatherback Sea Turtle, *Dermochelys coriacea*

Category: D

Approval Date: 20-May-2009

The Institutional Animal Care and Use Committee (IACUC) reviewed and approved the protocol submitted for this study under Category D on Page 5 of the Application for Review of Vertebrate Animal Use in Research or Instruction - *Animal use activities that involve accompanying pain or distress to the animals for which appropriate anesthetic, analgesic, tranquilizing drugs or other methods for relieving pain or distress are used.*

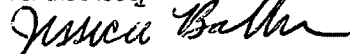
Approval is granted for a period of three years from the approval date above. Continued approval throughout the three year period is contingent upon completion of annual reports on the use of animals. At the end of the three year approval period you may submit a new application and request for extension to continue this project. Requests for extension must be filed prior to the expiration of the original approval.

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1. All cage, pen, or other animal identification records must include your IACUC # listed above.
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If you have any questions, please contact either Dean Elder at 862-4629 or Julie Simpson at 862-2003.

For the IACUC,



Jessica A. Bolker, Ph.D.
Chair

cc: File
Toppin, Becca