Behavior, Ecology, and Conservation of Sea Turtles in the North Atlantic Ocean

by

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Dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Department of Environment in the Graduate School of Duke University

2009
ABSTRACT

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Abstract

Sea turtles have experienced dramatic population declines during the last century as a consequence of direct harvest, by-catch in fisheries, and habitat loss. Despite almost 50 years of partial international protection, several populations of sea turtles are still at imminent risk of extinction. Our knowledge of their complex life histories is still far from complete; these knowledge gaps hinder our ability to provide scientific advice regarding their conservation and management. It is the very complexity of their life histories, which allows them to exploit widely separated habitats during development, often over the course of decades, which makes them inherently difficult to study. I used satellite telemetry (n=60) to investigate the movements and habitat use patterns of juvenile loggerhead (Caretta caretta), green (Chelonia mydas), and Kemp’s ridley (Lepidochelys kempii) sea turtles on their summer feeding grounds in North Carolina estuaries. These turtles migrate into and out of the estuarine waters each spring and autumn, encountering a gauntlet of fishing gear on each journey. The by-catch of sea turtles is an important conservation issue in North Carolina, and throughout the world’s oceans. I evaluated conservation measures established to reduce the by-catch of sea turtles in Pamlico Sound’s autumnal large-mesh gill net fishery for southern flounder (Paralichthys lethostigma), using a spatially explicit predator/prey model. My findings indicated that species-specific habitat preferences contributed to a turtle’s risk
of encountering fishing gear and that areas of high by-catch are predictable from patterns of overlap between sea turtle habitat use and flounder fishing effort. I then examined how the behavior of green turtles affected their vulnerability to incidental capture in estuarine commercial fisheries. Individual green turtles interact with multiple gears per season as a result of strong site fidelity to habitats also preferred by fishers. Telemetry also allowed me to examine individual variation in movements, habitat use, and site fidelity patterns of juvenile loggerhead turtles, both within the estuary and as the turtles migrated out into the North Atlantic. I used these observations to test the hypothesis of a discrete ontogenetic shift in habitat and diet in juvenile loggerheads. Approximately one-third of large juvenile loggerheads tagged in North Carolina estuaries return to oceanic habitat, sometimes for several years, where they are vulnerable to by-catch in pelagic fisheries. This led me to conclude that the long held notion of a discrete ontogenetic habitat shift between the oceanic and neritic habitat was incorrect for juvenile loggerheads (and possibly also for green turtles). Finally, I explored variation in migratory destinations in these animals through multivariate analyses of carbon and nitrogen stable isotope ratios in blood plasma and red blood cells, and through analysis of sex, genetic, haplotype, body size, and remigration records, and described the trophic niche of these turtles with Bayesian isotope mixing models. Variation in migratory destination (oceanic or neritic habitat) was best described by stable isotope ratios of nitrogen and remigration tendency. Turtles that
returned to the open ocean had significantly lower nitrogen ratios than those animals that remained in the neritic zone and their diets retained a substantial contribution of epipelagic prey items. The diet composition of neritic turtles, on the other hand, consisted primarily of estuarine benthic invertebrates during the summertime and autumn foraging season but shifted toward pelagic jellyfish, fish, and *Sargassum* during the overwintering period. Oceanic turtles likely came from open ocean regions prior to entering the summer foraging grounds while neritic turtles likely overwintered at the edge of the Gulf Stream. The agreement between the dietary compositions and migration patterns between the two groups of turtles suggest that these feeding and habitat use strategies were persistent characteristics in the turtles I sampled. My work has improved our understanding of sea turtle habitats in North Carolina estuaries and identified their migratory destinations and overwintering habitats. I hope that this work lays the groundwork for future studies that will explore how variation in habitat use and feeding strategies are manifested in life history traits that affect fitness directly, such as survivorship, growth rates, stage durations, and fecundity.
Dedication

To my husband, Michael, and our menagerie, for enveloping me with love throughout this journey.
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Introduction

One of the fundamental goals of ecology is to understand organisms’ relationships to their environment. This relationship shapes an animal’s life history and is reflected through a montage of foraging, habitat selection, and reproductive strategies. In the marine realm, these strategies are often obscured by their inherent spatial and temporal scales (Lima & Zollner 1996, Fritz et al. 2003, Pinaud & Weimerskirch 2007, Wilson et al. 2007). Many long-lived marine vertebrates exhibit life histories that allow them to exploit widely separated habitats during development, often over the course of decades (Musick 1999). Throughout the journey to and from these disparate habitats, the movements and behavior of an individual animal are influenced by environmental and resource heterogeneity (Morales et al. 2005, Eckert et al. 2008, Mueller & Fagan 2008).

Sea turtles are classic examples of animals with complex life histories that span multiple habitats. Despite decades of research, however, we still have only a rudimentary understanding of their ecology. Most of our knowledge is derived from snapshots of their lives when they occur on land, either as nesting females, eggs and hatchlings, or after death as stranded carcasses. Yet most of their life history is spent at sea below the ocean surface, far from the shore and out of the sight of human observers. It may take as long as four decades before a female loggerhead (*Caretta caretta*) hatchling
returns to her natal beach to nest (NMFS SEFSC 2001). What happens between this gap is largely a mystery. Recently, some parts of this story have been unveiling through in-water research (Mendonça & Ehrhart 1982, Avens et al. 2003, Heithaus et al. 2005, Bowen & Karl 2007) and satellite telemetry (reviewed in Godley et al. 2008) programs.

The focus of my dissertation was to explore the behavior and movements of three species of hard-shelled sea turtles - the loggerhead (*Caretta caretta*), the green (*Chelonia mydas*), and the Kemp’s ridley (*Lepidochelys kempii*) – during their juvenile life stages in the Atlantic Ocean. Loggerhead, green, and Kemp’s ridley sea turtles are all members of the family Cheloniidae and occur throughout the temperate and tropical waters of the Atlantic.

Loggerheads are considered “anti-tropical” (Pritchard 1979). In the northwest Atlantic juvenile loggerheads range geographically from Venezuela to Canada (reviewed in Ehrhart et al. 2003). Their coastal distribution is best known in the United States (US) between southern Florida and Gulf of Mexico to Virginia. In these areas individuals make seasonal migrations to inshore foraging grounds (Shoop & Kenney 1992, Lutcavage & Musick 1985, Epperly et al. 1995a, b, Hopkins-Murphy et al. 2003, Braun-McNeill & Epperly 2004). Loggerheads found along the US southeast coast originate from at least four western Atlantic rookeries (Yucatan, south Florida, northeast Florida-North Carolina, and northwestern Florida; Bowen et al. 1993, Encalada et al.
1998, Bass et al. 2004) and a few Mediterranean rookeries (Greece, Turkey; Bass et al. 2004). In the northeastern Atlantic, juvenile loggerheads occur along the West African coast from Senegal to Spain and inhabit waters surrounding the archipelagos of Cape Verde, the Canaries, Madeira, and the Azores (reviewed in Ehrhart et al. 2003). Eastern Atlantic juvenile loggerheads originate from the southeastern US and Yucatan nesting rookeries (Brongersma 1982, Carr 1986, Bolten et al. 1993).

Green sea turtles are primarily tropical (Pritchard 1997), although juveniles are found seasonally as far north as North Carolina in the western Atlantic (Epperly et al. 1995a, b) and Morocco in the eastern Atlantic (Brongersma 1982). Green turtles have at least seven rookeries in the Atlantic: Costa Rica, Mexico, Ascension Island, Florida, Aves Island, Suriname, and Guinea Bissau (reviewed in Hirth 1997, Bass et al. 2006).

Kemp’s ridley turtles have one of the most restricted distributions of any sea turtle in the world (USFWS & NMFS 1992). Nearly all nesting of this species occurs on a single beach near Rancho Nuevo, Tamaulipas, Mexico (Musick & Limpus 1997). Juveniles occur primarily along coastal areas of the Gulf of Mexico and extend their distribution seasonally into the northwestern Atlantic Ocean as far north as New England (reviewed in Musick & Limpus 1997). A few records exist from northeastern Atlantic waters as well: Western Europe (Brongersma 1982); Madeira and the Azores (Bolten & Martins 1990).
All three species exhibit a “type two” life history pattern (Bolten 2003) in which they spend their early development in the oceanic zone (past the continental shelf and in waters greater than 200 m in depth) feeding in the epipelagic zone. Later they undergo an ontogenetic shift and enter the neritic zone (within the continental shelf and in waters less than 200 m in depth) and begin feeding demersally, although there is considerable variation in the timing of this ontogenetic shift between species. In the 1980s, Archie Carr proposed the current life history model by piecing together bits and pieces of anecdotal information. Carr (1986) suggested that loggerhead hatchlings leaving southeastern US beaches were entrained into the Gulf Stream and passively swept along in the North Atlantic gyre eventually returning to their natal origins (Figure 1). This idea, coined “the mystery of the lost year,” was supported by the presence of small juvenile loggerheads in the Azores and large juveniles in Florida (Carr 1986). Carr believed that post-hatchling and juvenile turtles could survive by feeding on prey aggregated in oceanic convergence zones and by finding refuge amongst patches of floating Sargassum (Carr 1986). A decade later his trans-Atlantic migration hypothesis was supported by genetic evidence which confirmed that Azorean turtles originated in the western Atlantic (Bolten et al. 1998). Carr soon recognized that loggerheads must spend several years in the gyre to achieve the sizes found in US estuaries and he believed this was true for green turtles as well (Carr 1987, Carr & Meylan 1980).
Recently, the frontal convergences that intrigued Carr have been demonstrated as important habitat for larger juvenile turtles in other ocean basins (Luschi et al. 2003, Polovina et al. 2000, Polovina et al. 2004).

Figure 1: Currents of the North Atlantic gyre symbolizing Archie Carr’s sea turtle life history model (modified from Carr 1986).

In the past, and in some areas still today, marine turtles were harvested, resulting in dramatic population declines in some areas. These declines have resulted in their protection through national and international legislation and regulation, although this
protection is by no means universal. Declines in loggerhead populations resulted from fisheries by-catch and habitat loss/degradation (Witherington 2003). Loggerheads were listed as threatened under the US Endangered Species Act (ESA) in 1978 (NMFS & USFWS 2008) and were initially listed as vulnerable on the World Conservation Union’s (IUCN) Red List (Groombridge 1982) but now appear as endangered (IUCN 2008). Recovery efforts are complicated by their complex life history and hindered by continued anthropogenic mortality. In the US, each sub-population has been evaluated recently based on trends in nesting; all were considered to be either without a detectable trend or in decline (NMFS & USFWS 2008). In fact, the Atlantic northern sub-population is being considered as a potential Distinct Population Segment (DPS) and its status may be changed from threatened to endangered (Federal Register 2008). In a pivotal paper by Crouse et al. (1987), the survivorship of large juveniles was identified as the most critical stage on which to focus recovery efforts.

Past declines to green turtle populations have been attributed primarily to direct harvest and, although they are protected throughout most of their range today, they continue to face a variety of threats (Witherington 2003). Green turtles were listed on the ESA in 1978; the Florida and Pacific Mexican stocks are currently listed as endangered (US NMFS & FWS 1991) and all other populations are listed as threatened. The species appeared on the IUCN Red List as endangered in 1982 (Groombridge 1982; IUCN 2008).
The status of green turtles has not been reviewed in the US since 1991, at which time their populations were considered to be stable or increasing.

Kemp’s ridley sea turtles suffered major declines caused by poaching of their eggs, direct harvest of juveniles and adults, and by-catch in fisheries (Witherington 2003). Kemp’s ridleys were listed as endangered in the US in 1970 (prior to establishment of the current ESA) (US NMFS & FWS 1992). The species began receiving protection on its sole nesting beach by the Mexican government in the 1960s, but continued to experience incidental losses in fishing gear (TEWG 2000). They are currently listed as critically endangered by the IUCN (IUCN 2008), after being initially listed as endangered in 1982 (Groombridge 1982). Their status in the US was reviewed in 2000 (TEWG 2000) and their population appears to be recovering, although this prognosis is guarded.

The purpose of my dissertation was to: (1) deepen our knowledge of sea turtle ecology by studying their movements and use of marine habitats; and (2) in the light of this new information, evaluate management measures established to reduce sea turtle by-catch in commercial gill net fisheries. Migratory large marine vertebrates, such as sea turtles, are inherently difficult to study. However, technological advances in biotelemetry and remote sensing have opened up avenues for studying their movements and patterns of habitat use over a variety of spatial and temporal scales (Godley et al. 2008). My approach was to track individuals via satellite telemetry (Figure 2) and to
integrate these movement data with biological and oceanographic observations, together
with information on the distribution of fishing effort, to make ecological and
conservation inferences. North Carolina was an ideal setting for my research; it is an
important seasonal foraging habitat for migrating juvenile sea turtles, it has an active in-
water research program established by the National Marine Fisheries Service (NMFS), it
is positioned along the edge of one of the world’s most dynamic oceanographic features
– the Gulf Stream, and it has a series of coastal and estuarine fisheries that have both
lethal and non-lethal interactions with sea turtles. Working with commercial fishers
and management agencies allowed me to gain access to the turtles and to obtain insight
into the conflicts between turtles and fisheries.

Figure 2: Loggerhead sea turtle with satellite transmitter.
My first chapter is a case study on sea turtle by-catch in North Carolina’s large-mesh gill net fishery for flounder in Pamlico Sound. Some parts of this autumnal fishery have been closed due to high levels of sea turtle mortality. These closures created a contentious climate among fishers, turtles, scientists, and managers. I employed a spatially explicit predator/prey model to investigate the real-time overlap between sea turtle habitats and fishing effort. My objective was to evaluate the efficacy of the current suite of management measures and demonstrate how applying animal movement data can enhance conservation efforts in a proactive manner. This chapter is currently in press in *Ecological Applications*.

My second chapter follows this theme by focusing on the habitat use of green sea turtles. I examined habitat preferences of both turtles and gill net fishers and identified particular behaviors that put green turtles at risk of encountering fishing gear. This chapter is currently in press at *Endangered Species Research*.

In Chapter Three, I described the migratory behaviors of juvenile loggerhead turtles, highlighting variability in life history strategies and challenging the long held notion of a discrete ontogenetic habitat shift between the oceanic and neritic environments. This chapter was published in the journal *Biology Letters* in 2007.

In Chapter Four I explored potential explanatory factors for the behavioral polymorphisms described in the previous chapter, using stable isotope analysis, genetic,
morphometric, sex, and recapture information as potential predictors of the various migratory strategies. Also in this chapter I defined the spatial and trophic niche of loggerheads using isotope mixing models.

My final chapter synthesizes important aspects of my animal movement research and looks at the way forward for these kinds of conservation-oriented ecological studies.

I had a unique opportunity to study a rather large number of these protected marine turtles in the wild. The results of my research contribute new information on the ecology of juvenile sea turtles and have direct implications for their conservation. With that in mind, I have endeavored to always share my data, techniques, and findings freely along the way. As a result these data are already being applied not only to the conservation efforts of these species, but to the further development of analytical aides to study marine vertebrates and to attract the interest of the general public of all ages to marine conservation issues.
Chapter 1: Using telemetry to mitigate the by-catch of long-lived marine vertebrates

In Press in *Ecological Applications*

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**Introduction**

Gill net fisheries capture vast numbers of large marine vertebrates as by-catch (Read et al. 2006, Peckham et al. 2007, Davoren 2007). Current research is directed at reducing by-catch through gear modifications, but so far management that includes regional time-area closures is the most effective for reducing by-catch in gill nets (Young 2001).

In this chapter I describe a method of addressing the by-catch problem from the view of the by-caught species. As a case study I describe a spatially explicit approach that combines data on the distribution of fishing effort and observations of the distribution of the by-catch species derived from satellite telemetry. By merging information on the behavior of by-catch species with fisheries data I can determine whether there are times and areas where fishing overlaps with the habitat of the animal (i.e., assess risk). I hypothesize that by-catch is predictable because of the habitat preferences of fishers and marine vertebrates.

I suggest that much like predator/prey encounters, risk of incidental capture in fishing gear can be predicted based on the distribution and density of predators (fishing gear) and prey (by-catch species) in a given region. When both predators and prey are patchily distributed, the overall predation risk increases significantly when there is a high degree of spatial overlap (Williamson 1993). In order to predict, and therefore avoid, by-catch we must first understand the scale dependent patterns of how fishers
and by-catch species use habitat all under the guise of a highly dynamic environment. I used a predator/prey model called the Williamson Spatial Overlap Index (SOI) (Williamson 1993) to identify areas of high by-catch risk in a case study on the incidental capture of sea turtles in a gill net fishery in Pamlico Sound, North Carolina. The model describes the degree to which the spatial correlation of gill nets and sea turtles deviates from a random expectation under uniform spatial distributions. The SOI, \( O_{ij} \), is calculated as:

\[
O_{ij} = \frac{\sum_{z} (N_{iz} N_{jz}) m}{\sum_{z} (N_{iz}) \sum_{z} (N_{jz})}
\]

Where \( z \) is a sample location, \( m \) is the total number of samples, \( N_i \) is the density of species \( i \) (gill nets), and \( N_j \) is the density of species \( j \) (by-catch species). A value <1 indicates less than expected overlap, while a value >1 indicates a greater than expected overlap, with the upper bound determined by the number of locations sampled and the lower bound theoretically zero (Williamson 1993). While any value greater than zero indicates opportunities for by-catch, values greater than one were used in this study to identify areas with a high risk for entanglement.

**Case Study**

In November 1999 the North Carolina Sea Turtle Stranding Network documented a significant increase in strandings (\( n = 69 \)) along the southeastern shore of
Pamlico Sound (Boettcher 2000). Field necropsies performed on animals implicated incidental capture in fishing gear (Boettcher 2000). By December, the number of strandings in this area reached 97 individuals. In response, the National Marine Fisheries Service (NMFS) and North Carolina Division of Marine Fisheries (NCDMF) investigated fishing activities in the area (shrimp trawling, large- and small-mesh gill netting) and identified the flounder gill net fishery as the likely cause of these strandings after two Kemp’s ridley turtles (Lepidochelys kempii) were observed in large-mesh gear (Gearhart 2001). The fishery was closed by the NMFS on 10 December 1999 (Federal Register 1999, NMFS 1999). The decision was decidedly unpopular with flounder fishers, many of whom believed that there was not enough evidence to support a closure (Santora 2003).

In 2000, the fishery resumed in a restricted fashion under a state held Incidental Take Permit (ITP) authorized by Section 10 of the ESA (Federal Register 2000). The initial management measures obliged the state to develop a conservation plan and to establish a zone where fishing was allowed from September 1 through December 15 each year; this zone was called the Pamlico Sound Gill Net Restricted Area (PSGNRA). The permit also established mandatory requirements for gill net fishers in the PSGNRA including: registering for a permit; using a limited length of net; weekly self-reporting of fishing activity and incidental takes; and allowing an observer to accompany fishing trips. The ITP stipulated five percent observer coverage (based on total effort (net length
x soak time)), set a goal of a 50% reduction in strandings from the previous year, and established a turtle take limit.

Many fishers opposed the restrictions included in the ITP (Santora 2003). Despite adoption of these measures, however, portions of the fishery were closed again in 2000, 2001, and in 2002 because sea turtle strandings and observed incidental takes exceeded limits set by the National Marine Fisheries Service (Proclamations M-14-2000, October 27th, 2000; M-14-2001, September 29th, 2001; M-12-2002, October 20th, 2002). In 2002, the deepwater gill net fishery was permanently closed to large-mesh nets (> 11 cm) from 1 September to 15 December (Federal Register 2002).

The three sources of data used in management of the gill net fishery have been: sea turtle strandings; fishing effort; and observed by-catch. The state, in consultation with the NMFS, has since worked to manage the Pamlico Sound gill net fishery by limiting fishing effort, making adjustments to restricted areas, and closing sections of the fishery when by-catch rates of sea turtles approach or exceed incidental take limits. An important component lacking in these management measures, however, is consideration of sea turtle habitat and behavior. The Pamlico Sound Gill Net Restricted Areas (PSGNRAs) were initially designated on the basis of spatial and temporal patterns of sea turtle strandings (Bianchi 2002). Later PSGNRAs were delineated using the distribution of traditional shallow water fishing grounds (Gearhart 2002), which encompassed the most productive flounder habitat.
Much of the past criticism aimed at the Pamlico Sound gill net fishery management system was based on the lack of scientific information required to justify management actions and a lack of stakeholder participation (Santora 2003). I worked with fishers to study sea turtle movements using satellite telemetry in Pamlico Sound and compared these movements to the designated management areas. I explored both pattern and variation in the movements of turtles. The data I provide here contribute to an understanding of how sea turtles use the Sound and may be used to refine or modify future management measures, such as time-area closures.

**Methods**

**Study Area**

Pamlico Sound is a shallow, meso-haline estuary connected to the Atlantic Ocean by a series of small inlets (Figure 3a). The estuary is an important nursery habitat for a wide variety of estuarine species and supports more than 90% of North Carolina’s commercial finfish and shellfish catch (Copeland & Gray 1991). Sea turtles are present in the Sound on a seasonal basis (Epperly et al. 1995a, b, Avens et al. 2003).

**Field Sampling**

I collected 50 sea turtles from commercial pound nets in and around Pamlico Sound between September 2002 and November 2004; 21 in 2002, 24 in 2003, and 5 in 2004 (Figure 3b). Sea turtles are commonly captured in flounder pound nets – passive
Figure 3: A. Map of North Carolina’s inshore waters where my study was conducted. The blue stippled area indicates the traditional shallow water gill net fishing grounds and the orange area indicates the traditional deepwater gill net fishing grounds. In between these two lay a shallow “reef.” B. The current Pamlico Sound Gill Net Restricted Areas (PSGNRAs) with capture locations of turtles overlaid with orange circles. OIC = Oregon Inlet corridor; SGNRA = southern gill net restricted areas 1, 2, 3, and 4; HC = Hatteras Inlet corridor; OC = Ocracoke Inlet corridor; Deepwater Closure = federal closure (September 1 – December 15); MGNRA = mainland gill net restricted areas 1 and 2. C. Filtered locations of sea turtles in North Carolina estuarine waters overlaid on the PSGNRAs. Red = loggerhead; green = green; yellow = Kemp’s ridley. Circles are locations from turtles tagged in 2002, squares are from 2003, and triangles are from 2004.
traps that lead turtles into a corral where they are free to swim and breathe. I tagged 36 loggerhead turtles (Caretta caretta), ranging in size from 59.2 – 82.2 cm straight carapace length (SCL); seven green turtles (Chelonia mydas), ranging in size from 32.2 – 72.3 cm SCL; and seven Kemp’s ridleys, ranging in size from 38.6 – 52.2 cm SCL. My sample is representative of sea turtles in North Carolina, both in species diversity and size (Epperly et al. 1995b, Sasso et al. 2006, Epperly et al. 2007).

Fisher participation was voluntary and I endeavored to arrange trips throughout the fishing season (September – December) and to stratify my efforts in space and time. However, no turtles were collected from the western side of Pamlico Sound, as no pound net fishers were operating in that area. Over my three year study, I worked with 20 fishermen and conducted 33 sampling trips. Fishers operated from small wooden vessels approximately 7 m in length to fish their nets while I followed in a similar sized research vessel. If turtles were present in their nets, they passed them to my boat.

Once turtles were brought on board the research vessel, I secured them into foam-padded plastic tubs and followed a standard NMFS sampling protocol (NMFS SEFSC 2008). I applied the satellite transmitter, antenna frontward, on the first and second vertebral scutes using a combination of PowerFast® epoxy and fiberglass cloth and resin (NMFS SEFSC 2008). I used Wildlife Computers’ SPOT2 (n = 45) and SPOT4 (n = 5) satellite transmitters (Redmond, WA) in two sizes (small 73.8 x 50.8 x 21 mm, 80 g;
large 128 x 49 x 36 mm, 185 g), to accommodate a range of sea turtle sizes. Turtles were then released into the water near their capture location.

**Satellite Telemetry Data**

Location and water temperature data were transmitted from each tagged turtle to National Oceanic and Atmospheric Administration (NOAA) satellites when the animals surfaced to breathe. The satellite tags were programmed to transmit daily over an 8-hour period beginning from just before dawn to near mid-day. A few of the smaller tags (n = 7) were duty cycled to transmit every other day to extend the life of the transmitters.

Satellite-linked location data were converted and de-coded using Wildlife Computers’ SPOT2 (2002 – 2003) and SATPACK (2004) software (Redmond, WA) and imported into a geographic information system (GIS) for analysis (ArcView 3.2, ESRI 1999, with Animal Movement, (Hooge & Eichenlaub 2000) and Spatial Analyst extensions and ArcGIS 8.3, ESRI 2002). These data were analyzed in Albers Equal Area projection, with a 2 km resolution. The Albers Equal Area projection is a conic, equal area map projection that uses two standard parallels to reduce distortions in shape and linear scale and is best suited for areas oriented east-to-west (ArcGIS 8.3, ESRI 2002).

Estimates of the position of satellite-linked tags are coded by location accuracy classifications (LC) by Service Argos, Inc. (hereafter referred to as ARGOS) (Appendix A). I independently evaluated these estimates of positional accuracy by placing each
transmitter in a known location on shore for 24 hours and verifying its position with a GPS receiver before deployment. These satellite positions were then compared with the known location. I found that the reported accuracy from Service Argos underestimated the true error (Appendix A), a finding similar to the results of investigations by Vincent et al. (2002) and Hays et al. (2001). I recognize that the estimated locations of sea turtles do not represent their exact positions. Nevertheless, I have taken great care to measure and consider the errors associated with each positional estimate. To ensure that I did not include erroneous positional estimates, I employed a three-stage filtering algorithm (McConnell et al. 1992, Austin et al. 2003) to reject implausible locations. After using this filtering method I was left with approximately 80% of the initial locations.

To determine how the habitat use of sea turtles in Pamlico Sound related to the active gill net fishing areas, I examined all filtered location data (including multiple locations per day) for turtles that entered the Pamlico Sound Gill Net Restricted Areas (PSGNRAs) during the period of the fishery (September – December). I calculated the proportion of time each animal spent in every management area in the PSGNRA by week and over the entire season. This allowed me to assess the habitat use of sea turtles in the context of current management measures.

To examine potential interactions between sea turtles and gill nets, I calculated a density function of positions for each turtle during each week of the fishery period and corrected for the number of days without transmissions. I chose a radius of 1 km
because that is the maximum error estimate provided by ARGOS. Individual densities were then added together. I was interested in relative comparisons; because the densities were extremely small, I multiplied densities by 1000.

Sea turtle movements were reconstructed by plotting the best received location per day of the filtered location data and used to estimate distance traveled. I used these tracks to determine the points of exit the turtles used from the sounds during their fall migration. Chi-square analyses were used to test for differences in direction of movement out of the sounds. Site fidelity of loggerheads was measured by comparing distance between initial capture locations and re-migration locations the following year and tested using a $t$-test.

**Fisheries Data**

I obtained coordinates for the boundaries of the PSGNRAs for each year (Figure 3b) from DMF Proclamations (Proclamations M-10-2002, August 14th, 2002; M-10-2003, August 15th, 2003; M-8-2004, August 20th, 2004). Management areas changed between years as DMF refined fisheries restrictions based on observed sea turtle by-catch and fishing effort. The deepwater fishing grounds were closed to large-mesh gill nets during the entire fall flounder fishing season (September – December) in all years. Shallow water areas were open on the mainland side (MGNRA1, MGNRA2) and along the Outer Banks (SGNRA1, SGNRA2, SGNRA3). After 2002, SGNRA3 was divided into two areas,
creating SGNRA4. There were also three migratory corridors designated at the Oregon, Hatteras, and Ocracoke Inlets, where no fishing with large-mesh gill nets was allowed.

The NCDMF has observed a sample of the fall flounder gill net fishing trips in Pamlico Sound since 2000 (Gearhart 2001, 2002, 2003, Price 2004, 2005). Their objective is to observe 10% of the fishing effort in each restricted area (using stratified ratio sampling methods). Observer coverage is adjusted weekly based on the previous week’s landings. Actual observer coverage based on logbook reports was 7.5% of fishing effort in 2002, 6.2% in 2003, and 8.5% in 2004 (Gearhart 2003, Price 2004, 2005). Observers recorded: location, mesh size, net length, number of hauls, soak duration, pounds of flounder caught, and sea turtle by-catch. I obtained the large-mesh gill net observer data for 2002 - 2004 from NCDMF.

Flounder gill nets are made of monofilament, ranging from 14 to 18 cm stretched mesh set on the bottom overnight (Steve et al. 2001, Gearhart 2001, 2002, 2003, Price 2004, 2005). There is a 1,829 m limit to large-mesh gill nets, but many nets are only 91 m and are typically set in a string comprised of several nets set a short distance apart in a parallel fashion. Each string of nets is referred to as a “haul.” I calculated fishing effort as a function of net length per haul (m) and soak duration (days). I then calculated probability density functions based on fishing effort with a 2 km radius for each week of the fishery. This distance was chosen on the basis of the maximum allowed net length; in addition, observers only recorded one end of each net hauled, so I was not able to
determine the actual orientation of the set. The observed gill net densities were relatively small, so I multiplied these densities by 100. These values were later analyzed in conjunction with the observed distribution of sea turtles.

Figure 4: Cartoon depiction of the spatially explicit predator/prey model used in my study. Spatial Overlap Index (SOI) (Williamson 1993).

Spatial Analyses

I calculated the Williamson (1993) spatial overlap index (SOI) for every PSGNRA for each week of the fishery in 2002 - 2004, using the probability density functions described above for turtles and nets after Cox (2003). I used the model to evaluate the interaction potential of sea turtles and large-mesh gill nets in Pamlico Sound (i.e., SOI > 1) within 4 km² grid cells (Figure 4). I assume that my sample of sea turtle distribution was representative of the sea turtle population in the area and, furthermore, that the observed distribution of gill nets represented the distribution of fishing effort in each
PSGNRA. Actual by-catches of sea turtles were then used to evaluate the performance of the model.

**Sea Turtle Stranding Data**

I obtained sea turtle stranding data from the NC Wildlife Resources Commission (WRC) for 1999 – 2004. Stranding data for Pamlico Sound are used with reservation in this assessment, as observer effort is opportunistic and spatially disjoint, due to the remoteness of the shoreline and its extensive marsh. Moreover, stranded sea turtles are widely subject to wind, tides, and currents and conclusive determination of their cause of death is rare (Epperly et al. 1996, Hart et al. 2006). I include the observations here because they have been used previously in cases of fisheries interactions (Crowder et al. 1995, Epperly et al. 1996, Lewison et al. 2003) and contributed to the instigation of the PSGNRA in the first place. These data were used to make qualitative comparisons of whether the SOI would predict strandings in the PSGNRAs in the same manner as by-catch.

**Environmental Data**

Most of the observed sea turtle interactions with gill nets prior to my study were reported in the deepwater fishery (which ultimately led to its closure). However, an increased number of turtle interactions were observed in shallow water when the deepwater fishery was closed (J. Gearhart, DMF, personal communication). I obtained a bathymetric digital elevation model (DEM) at 30 m resolution from the NOAA’s
National Ocean Service (NOAA NOS 1998) and sampled sea turtle locations. These analyses do not tell me the precise depths used by the turtles, because they are subject to LC errors, but they do allow me to evaluate the general water depths occupied by the turtles.

**Results**

**Satellite Telemetry**

I tracked turtles for periods ranging from 13 to 660 days as they traveled between 60 and 12,418 km (Table 1). Two transmitters failed immediately, one from a loggerhead in 2002 and the other from a Kemp’s ridley in 2003. I cannot be certain about the cause of transmitter failure but possible reasons include attachment failure, battery failure, damage to the transmitter, or death of the turtle. All but two other transmitters functioned until turtles migrated out of the sound or until the end of the fishery period.

During September – December (the fishery period) in all years sea turtles were distributed from Albemarle Sound through Bogue Sound; these locations are presented in Figure 3c. My tagging efforts were restricted to the eastern side of Pamlico Sound, including the Croatan and Albemarle Sounds and in Core and Back Sounds. I tagged only nine turtles initially encountered along the Outer Banks, although a large number of estimated locations from many turtles were recorded from this area.
Table 1: Satellite tagging summary of sea turtles tracked from North Carolina between 2002 - 2004. Values for size, track duration, and distance traveled are means (± 1 standard deviation). Number of turtles deployed by year are indicated in parentheses.

<table>
<thead>
<tr>
<th>Species</th>
<th>Size (cm SCL)</th>
<th>Year Deployed</th>
<th>Track Duration (days)</th>
<th>Net Distance Traveled (km)</th>
<th>Number Re-migrated</th>
</tr>
</thead>
<tbody>
<tr>
<td>Loggerhead</td>
<td>63.0 (6.9)</td>
<td>2002 (14)</td>
<td>234 (120)</td>
<td>3,043 (3,471)</td>
<td>14</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2003 (17)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>2004 (5)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Green</td>
<td>50.5 (19.6)</td>
<td>2002 (2)</td>
<td>80 (52)</td>
<td>1,753 (2,170)</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2003 (5)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Kemp’s ridley</td>
<td>45.1 (6.1)</td>
<td>2002 (5)</td>
<td>33 (44)</td>
<td>325 (611)</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2003 (2)</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The directionality of turtle movements was bi-modally distributed as they made their fall migration out of the sounds (Figure 5). Sea turtles tagged in Albemarle Sound, Pamlico, and Core/ Back Sounds did not display a preferential migratory orientation between the north-east and south-west directions ($\chi^2$, $0.1 < P < 0.05$). The turtles left the sounds most frequently through Barden’s Inlet at Cape Lookout followed by Hatteras, Drum, Oregon, Ocracoke, and Beaufort inlets. Only 30% of the turtles left through the nearest inlet; others passed by one or more inlets before selecting a distant inlet from which to leave. I was able to determine the point of re-entry for 12 of the 14 loggerheads that re-migrated into the sounds the following year. Half of these animals used the
same inlets to enter and leave the estuary. In the six cases where the turtles used a
different inlet, five chose an adjacent inlet to the north (1) or south (4). One animal was
tracked long enough to capture its fall migration in two consecutive years and both
times this individual used Hatteras Inlet; its remigration had been through Ocracoke
Inlet. Fourteen of the thirty-five loggerheads re-entered the sounds the year after
capture. Core Sound turtles had significantly stronger site fidelity than those captured
in Pamlico Sound (P = 0.047).

Figure 5: Rose diagram showing a northeast/southwest bimodal distribution of
turtles’ migratory orientation. Direction measured from capture location to outlet.
I calculated the proportion of time turtles spent in each PSGNRA by fishery week for 2002, 2003, and 2004 (Figure 6). Considering only the turtles that entered the PSGNRA complex (n = 15 in 2002, 6 in 2003, and 5 in 2004), most time was spent in the deepwater closed area in 2002 and 2003 (64% and 70% respectively). In 2004, the deepwater area ranked second in importance (23%) and Southern Gill Net Restricted Area (SGNRA) 2 was occupied most frequently (54%), but my tracking began late in the season (week 11 of the fishery) and all turtles left the Sound within three weeks. In 2002, all PSGNRAs were inhabited by turtles at some point during the fishery. In 2003, only the Ocracoke Corridor (OC) and Mainland Gill Net Restricted Areas (MGNRAs) were not used by sea turtles during the fishery period. On 18 September 2003, week 3 of the fishery, Hurricane Isabel passed directly over Pamlico Sound, modifying our sampling efforts, fishing effort, and probably the behavior of the turtles. In 2004, the turtles occupied all PSGNRAs except SGNRA 1 and the MGNRAs.
Figure 6: Graphical summary of the percent of time turtles spent in each PSGNRA over all weeks in the fishery for each year (2002-2004). Turtles spent the majority of time in the NMFS deepwater closed area. ● indicates the number of individual satellite tagged turtles that occupied the PSGNRAs each year.
Fishery

The greatest large-mesh gill net fishing effort consistently occurred in SGNRA 3 followed by SGNRAs 4, 2, 1, and the MGNRAs (Figure 7). Twelve observed takes were documented in 2002, four in 2003, and nine in 2004. Seventy-two percent of the turtles were caught in SGNRA 3 (Figure 7). Most (17) observed by-caught turtles were released alive. All three species of sea turtle were caught in gill nets, but green turtles comprised by far the largest proportion in each year. In the three years of our study, 270 turtles were estimated to be taken by this fishery (221 live, 49 lethal) (Gearhart 2003, Price 2004, 2005).

Figure 7: Map of large-mesh gill nets (blue circles) and sea turtle by-catch (stars) observed by NCDMF (September – December 2002-2004). Red = loggerhead; green = green; yellow = Kemp’s ridley.
Strandings

Fourteen stranded turtles were observed in the PSGNRA in 2002, 10 in 2003, and 38 in 2004 during the fishery period (Figure 8). Fifty-eight percent of these stranded turtles were found in the inlet corridors followed by 15% in SGNRA3, 13% in SGNRA2, 6% in SGNRA4, 5% in SGNRA1, 2% in MGNRA1, and 2% in the deepwater closure. The spatial distribution of strandings was similar to that of observed by-catch, but a large proportion was located near inlets. The species dominating the strandings shifted from loggerhead (50% in 2002) to green (55% in 2004) during the three year period. Only in two cases were large-mesh gill nets conclusively implicated in the strandings over the three year period.

Spatial Analyses

Overlap of fishing effort and satellite tagged turtles was rare, and occurred on only a few occasions in SGNRA 2, SGNRA 3, and SGNRA 4. The number of satellite tagged turtles moving through Pamlico Sound in any given year was low and the majority occupied the deepwater area closed to fishing where overlap would have been greatest prior to the closure (Figure 6). The SOI revealed by-catch opportunities in SGNRA2 during weeks 7 and 10 of 2002, week 8 of 2003, and weeks 11, 12, and 13 of 2004, in SGNRA3 in week 6 of 2002 and week 9 of 2003, in SGNRA4 in weeks 6, 8, 10, and 11 in 2002, week 9 in 2003, and week 11 of 2004. These values < 1 essentially say that nets and turtles co-occurred, but were not clustered within the analysis unit. The SOI
showed the highest potential for entanglement in SGNRA 2 during week 9 of 2002, in SGNRA 3 during week 7 of 2002 and week 11 of 2004. SGNRA 3, in particular, had the most observed by-catch (Figure 9) as predicted by the SOI. SOI values for all years, weeks, and GNRA s are available in Appendix B. These values are conservative predictions based on the spatial and temporal scales at which I analyzed the data because I modeled only a portion of the fishery (as available through observer coverage) and turtle locations were limited by an 8 hour/day time window and foraging behavior which reduces surface intervals.

Figure 8: Map of sea turtle strandings observed in the PSGNRA by NCWRC (September – December 2002-2004). Red = loggerhead; green = green; yellow = Kemp’s ridley; white = unidentified species.
Figure 9: Top panel - Changes in predator (gill net) and prey (satellite tagged sea turtles) relative densities in SGNRA 3 during the fishery weeks of my study. Weeks indicate week of the fishery beginning September 1st. Lower panel - By-catch and strandings are denoted by large, open and small, solid circles respectively. SOI values >1 are indicated by upward arrows and values <1 indicated by downward arrows.

Environmental Correlates

In Pamlico Sound, sea turtles were found in water depths from 0 – 6 m. Greens occurred primarily in shallow water (mean 0.5 m, range 0 – 5 m) while loggerheads and Kemp’s ridleys occupied a wider range of depths (mean 3 m, range 0 – 5 m and mean 3 m, range 0 – 6 m respectively). Most estuarine locations outside the PSGNRA occurred
in Core Sound, which is shallow. Here, all turtles occupied average depths of 0.5 m (range greens 0 – 2 m, loggerheads 0 – 5 m, Kemp’s 0 – 2 m).

**Discussion**

My study of marine turtles in Pamlico Sound allowed me to identify areas of high use during the fall large-mesh gill net fishery period and to evaluate the current constellation of restricted areas intended to reduce turtle by-catch. The seasonal closure of the deepwater fishing grounds during the past seven years has been controversial and criticized by fishery participants (Santora 2003). Despite this criticism, I found the closure to be well placed based on the turtles’ distribution in the Sound, particularly for loggerheads and Kemp’s ridleys. This result concurs with the reduction in by-catch in the PSGNRA since the implementation of the closure. If the deepwater area were to re-open, it is likely that by-catches of loggerheads and Kemp’s ridleys would increase as in the past (2000, 2001 gear testing only). My data further suggest that many turtles use the traditional deepwater fishing grounds along the “reef” (Figure 3a). Interactions in the shallow water PSGNRAs may, therefore, occur along the boundaries of current management areas.

My results were consistent with the spatial and temporal distributions reported by Epperly et al. (1995a, b) and with anecdotal reports of fishers participating in this study, but more importantly they allowed me to determine how long individual animals remained in the PSGNRAs. I was also able to document seasonal changes in habitat use
and highlight areas that have been under appreciated as turtle habitat. For example, the
turtles in my study primarily used the eastern portion of Pamlico Sound, but I tracked
some animals to the western side, particularly during the summer and early fall. Aerial
surveys and reports from fishers in the late 1980s and early 1990s also noted the
presence of turtles in the western Pamlico during the summer and fall months (Epperly
et al. 1995a, b). DMF observers documented only one Kemp’s ridley in large-mesh gill
nets set in the Mainland Gill Net Restricted Areas between 2002 and 2004 and as a result
the state is considering reducing or eliminating observer coverage in this area. Fishing
effort is currently low, however changes in regulations to other areas in the sounds
could induce displacement of effort as this region historically had much more fishing
activity.

My approach, using a spatially explicit predator/prey model (Williamson 1993),
accurately predicted areas where by-catch occurred on several occasions, allowing me to
independently identify high risk fishing areas. This success is quite remarkable given
my relatively small sample of turtles (50) and limited observations (7.6%) of actual
fishing effort. This technique was also successful at predicting by-catch in a post-hoc
analysis of harbor porpoise (*Phocoena phocoena*) telemetry data and gill net fishing in the
Gulf of Maine (Cox 2003). Both studies found that the greatest risk of by-catch occurred
in areas of high spatial overlap. While this conclusion is a simple one, it demonstrates
that information on habitat use and fisheries effort can predict the locations of by-catch
at appropriate scales. Obviously, incidental capture is possible any time gear and turtles co-occur; therefore an understanding of behaviors that lead to entanglement would be additionally valuable.

Stranding levels in the PSGNRA have not shown the same decline as the observed by-catches and, although species composition has shifted towards green turtles, the yearly proportions are dissimilar to those of the observed by-catch. Similar to the findings of other studies on the distribution of stranded sea turtles (Epperly et al. 1996, Hart et al. 2006) I found that wind, tides, and currents likely influenced the location of strandings; namely clustered in the inlets. Strandings data remain a blunt instrument for drawing attention to potential problem areas – such as the initial suggestion of fisheries interactions in Pamlico Sound in 1999 and with regard to shrimp trawls and Turtle Excluder Devices (TEDs) (Epperly & Teas 2002, Crowder et al. 1994, Crowder et al. 1995) – but they are less useful in defining specific management areas and are unreliable indicators of actual by-catch levels. Currently, nothing can replace observer programs for monitoring by-catch.

During the period when the deepwater area remained open (2000), the by-catch was comprised mostly of loggerheads and Kemp’s ridleys. Recent takes, although few in number, are nearly all green turtles. This result could also be predicted by understanding the habitat preference of marine turtles and overlaying them on the habitat mosaic of Pamlico Sound. My analysis of depth data shows that, although
loggerheads and Kemp’s ridleys use a wide variety of habitat, greens are restricted to shallow waters. These depth preferences are similar to those reported by Byles (1988) for loggerheads and Kemp’s ridleys in Chesapeake Bay, Virginia and by Mendonça (1983) for greens in Mosquito Lagoon, Florida. My results are also consistent with observations of the by-catches of sea turtles in Pamlico Sound; loggerheads and Kemp’s ridleys in deeper water and greens in shallower water (Gearhart 2001, 2002, 2003, Price 2004, 2005). Green turtles are closely associated with seagrass, which is their primary diet in neritic environments (Bjorndal 1980, Mendonça 1983). Pamlico Sound is relatively turbid, so light attenuation constrains the distribution of seagrass to the shallows. Freshwater outflow from the Neuse and Tar-Pamlico rivers produce lower salinities and muddier substrates on the western side of the Sound (Woodruff et al. 1999). In contrast, the area behind the Outer Banks is adjacent to inlets that exchange clear, high salinity sea water, and has sandy bottoms that are more favorable to seagrasses. This is also the region where the highest fishing effort now occurs. Green turtles are particularly vulnerable to entanglement in these areas. Therefore, the current management measures unwittingly selected for green turtle by-catch, albeit in small numbers.

A review of historic green turtle fisheries along the southeastern U.S. documents how large-mesh gill nets were very effective in catching turtles and were used widely
from North Carolina to the Florida Keys (True 1887). True (1887) describes the capture technique:

“On arriving on the grounds the boat or vessel is kept beating back and forth until signs of turtles are noticed… the nets are set out near them and in a straight line parallel with the course of the tide. The turtles come to surface every few minutes to breathe, and while rising and sinking near the net are very apt to become entangled in it. Only one flipper may be caught at first, but when the animal turns the other is entrapped and, shortly, the whole body is securely wrapped in the cords.”

It is not surprising that this same manner of fishing, targeting flounder, catches turtles inhabiting the same area. Fisheries observer data suggest that by-catch peaks in the first few weeks of the flounder gill net fishery. This trend has been noted in other fisheries, such as the trawl fishery off South Carolina (Crowder et al. 1995). High numbers of takes and strandings were observed coinciding with the start of the fishery. This may reflect interactions between the inaugurate fishery and turtles which have established patterns of seasonal residency.

Work by Avens et al. (2003) suggests that juvenile loggerheads exhibit strong site fidelity within Core Sound. These researchers found that turtles were re-captured multiple times within a season in the same area and that recaptures occurred between seasons in the same location. Furthermore, loggerheads displaced from the capture location and tracked with radio telemetry displayed homing behavior and were able to
navigate back to particular sites (Avens et al. 2003). The pound net fishers I worked with told me that they recognized particular turtles in their nets day after day. I also noted strong site fidelity, especially in Core Sound, and nearly half the turtles in this study re-migrated into the sounds the following year which could affect their risk to incidental capture.

Results from an experimental study on juvenile loggerhead and green turtles from North Carolina estuaries describe a southerly orientation during the autumn consistent with the onset of migration seen in the field (Avens & Lohmann 2004). However, about 30% of the turtles I satellite tagged did not exhibit a southern orientation in the sounds, but moved out of inlets to the north-east of their capture location. These results suggest that behavioral differences exist between turtles in North Carolina sounds. Furthermore, many turtles in my study used distant inlets to exit the sounds suggesting there may be individual preferences for these corridors, but clearly more work is necessary to assess inlet fidelity. Movements within the Sound affect encounters with fishing gear, especially in narrow areas such as Core Sound where gear is highly likely to intercept the large number of animals migrating through the area.

Most by-caught sea turtles in the shallow water fishing grounds are released alive. The average estimated lethal take of turtles based on fisheries effort in the PSGNRA between 2002 and 2004 was 16 animals - three percent of the direct harvest that took place over a century earlier. Gill netting occurs throughout North Carolina
sounds at various times of the year, but so far only the Pamlico Sound fall large-mesh fishery is regulated with respect to sea turtle by-catch under a Section 10 permit. The DMF maintains proclamation authority, however, which allows establishment and/or modification of restrictions in areas/times when known problems exist such as the seasonal net attendance requirement in the lower Cape Fear River which began in 2005 (Proclamation M-7-2005, June 13th, 2005). Information on the post-release mortality and sub-lethal effects related to by-catch is required to fully assess fisheries related impacts on these populations. Gill nets are only one of several gears that turtles encounter in the sounds, so identification of turtle habitat preferences is valuable to the management of these other fisheries as well.

Catch rates of juvenile loggerheads in North Carolina have increased in the past decade, but trends on nesting beaches in other juvenile foraging grounds along the southeast US provide conflicting messages as to whether or not sea turtle populations are increasing, decreasing, or stable (Epperly et al. 2007). Variability in capture rates has complicated estimation of the number of turtles present in North Carolina (Sasso et al. 2007), although fishers assert that they are seeing an increasing number of turtles. The current lack of abundance estimates hinders our ability to manage fisheries and allocate take. Estuarine fisheries are declining in North Carolina. Most fishers operate alone, fish multiple gears, and an increasing number are supplementing their income with other employment (Crosson 2007). Restrictions to fisheries administer an additional toll
to an already struggling heritage. Some fishers are leaving the business, while others switch to fishing more affordable gears, like gill nets, which are cheaper to buy, require smaller boats and fewer (if any) additional crew, and allow them to move their gear as the fish move. Therefore, it is imperative that we understand and mitigate the by-catch of protected species in gill net fisheries.

**Concluding Remarks**

My case study demonstrated that satellite telemetry is an excellent tool for evaluating the spatially explicit nature of fisheries interactions and for evaluating specific conservation measures. This approach could be accomplished with traditional survey data, but in my case diving behaviors of the turtles and turbid waters of the sounds limit wide applicability of this method. Satellite telemetry allows identification of important habitat without many of the biases that survey data contain and allows quantification of the time individuals spend within particular habitats. I suggest that spatially explicit studies, such as this one, can be used to develop effective by-catch reduction measures in many situations, particularly if the telemetry studies are conducted prior to the establishment of time-area closures.
Chapter 2: Confronting the gauntlet: Understanding incidental capture of green turtles through fine-scale movement studies

In Press in *Endangered Species Research*

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**Introduction**

The by-catch of protected species including marine birds, mammals and turtles, is a significant conservation issue for some fisheries. Sea turtles, protected in US waters under the 1973 Endangered Species Act (ESA), are particularly vulnerable to incidental capture in fishing gear (Crouse et al. 1987, Epperly et al. 1995c, Lewison et al. 2004, Peckham et al. 2007). In some cases, time-area restrictions of fishing effort are the most effective means of reducing or eliminating the threat of by-catch (Young 2001). For example, the by-catch of loggerhead (*Caretta caretta*) and Kemp’s ridley (*Lepidochelys kempii*) turtles resulted in the seasonal closure of a gill net fishery in Pamlico Sound, North Carolina (Santora 2003, Chapter 1). However, the by-catch of green sea turtles (*Chelonia mydas*) persists in the shallow water areas that remain legally open to fishing under a Section 10 permit (Chapter 1).

Juvenile green turtles forage on seagrass in the sounds of North Carolina during summer and autumn (May – November) (Epperly et al. 1995b, Epperly et al. 2007), their primary diet item in neritic habitats along the coasts of the western Atlantic (Bjorndal 1980, Mendonça 1983). Gill net fishers operate a variety of gear (large and small mesh, sink and float set nets, run around nets, drift nets) throughout North Carolina sounds in all seasons targeting a variety of fish species (Steve et al. 2001). The large-mesh (> 11 cm) bottom-set sink gill net has been identified as a primary concern with respect to sea turtle by-catch (STAC 2006), particularly in the deepwater areas of Pamlico Sound.
Since 2000, the North Carolina Division of Marine Fisheries (NCDMF) has held a Section 10 ESA permit to authorize Pamlico Sound’s autumn flounder fishery (September – December) under a set of restrictions designed to reduce the frequency of sea turtle by-catch. The permit allows the fishery to operate unattended in shallow water areas, provided that the by-catch does not exceed species-specific limits. A variety of management measures were implemented in 2000 (Santora 2003), but in 2002, the National Marine Fisheries Service (NMFS) permanently closed the deepwater portion of the fishery due to persistent by-catch, mostly of loggerheads and Kemp’s ridleys (Federal Register 2002). The fishery is now restricted to shallow water areas of the Sound (Figure 10). Green turtles are the species caught most frequently in the remaining open fishing areas. Most turtle by-catch occurs in areas of high fishing effort along the sound side of the Outer Banks.

In the Caribbean, green turtles tend gardens of seagrass, exhibit extreme site fidelity, and enrich the nutrient content of vegetation through grazing (Bjorndal 1980). There are striking exceptions to this association with seagrass in the literature, however, as post-pelagic green turtles have been documented with a variety of algae and invertebrates in their diet (reviewed in Bjorndal 1997). Therefore, I was interested in studying the relationship between green turtles and seagrass meadows in North Carolina and determining whether or not this relationship could inform us about their vulnerability to by-catch in shallow-water gill net fisheries. In particular, I examined the
habitat preferences and behavior of green turtles which could increase their risk of incidental capture in fisheries.

**Methods**

**Study area**

My study was conducted in a North Carolina estuary (~76° W x 35° N) comprised of a series of shallow coastal lagoons separated from the Atlantic Ocean by barrier islands (Figure 10). I focused on two shallow water regions – Core/Back Sound (373 km²) and the Outer Banks portion of the Pamlico Sound Gill Net Restricted Area (PSGNRA) (712 km²) (Figure 10). Green sea turtles are seasonal (April – December) residents of these waters (Epperly et al. 1995a, b, Epperly et al. 2007). Large-mesh (14 – 18 cm stretch mesh) gill nets are fished in both areas throughout the year.

Seagrass beds are common inside the chain of barrier islands that delimit North Carolina’s lagoonal estuaries (Ferguson et al. 1993). The distribution of seagrass is limited by several factors, including light, depth, current velocities, shifting sediments, and nutrient runoff from the land (Ferguson et al. 1980, Fonseca et al. 1983, Thayer et al. 1984). In North Carolina, seagrasses primarily include eelgrass (*Zostera marina*) and shoalgrass (*Halodule wrightii*) (Thayer et al. 1984). Seagrass meadows occur in homogeneous or mixed stands, dominated by *Zostera* in the winter and spring, which then dies off in the heat of the summer and gives way to *Halodule* (Thayer et al. 1984).
Figure 10: Map of two shallow-water study sites: Core/Back Sound and the Outer Banks portion of the Pamlico Sound Gill Net Restricted Area (PSGNRA). Capture locations of green turtles are denoted by a star.

Green turtles have been documented to feed on these genera in several parts of the world (reviewed in Bjorndal 1997). Meadows of seagrass vary in size from small isolated patches to continuous expanses, both of which can be exposed during portions
of the tidal cycle (Thayer et al. 1984). These meadows are important habitat, structure,
and/or food for many marine organisms (Thayer et al. 1984, Venitia et al. 2006).

Field sampling

I relied on the help of commercial pound net, long haul seine, and gill net fishers
to collect green turtles during the months May – October of 2005 and 2006. I arranged
trips to accompany fishers during normal fishing operations in areas where green turtle
by-catch has been documented, most notably in the sound area behind Cape Hatteras
(Figure 10). However, few fishers were operating in this region during the summer
months (May – August) and I collected only one green turtle in 2005. My effort
consisted of three pound net and one gill net trips with commercial fishers and seven
days of gill netting on my own. In 2006 I expanded my capture area to Core and Back
Sounds. After eight long haul seine and 21 pound net trips I was able to collect the
remaining nine turtles in this study. Most turtles in 2006 were collected in conjunction
with trips observed by NMFS biologists; all but one turtle (2005) were brought back to
the Duke Marine Laboratory.

I processed each turtle according to standard NMFS techniques (NMFS SEFSC
2008). This entailed measuring the straight and curved carapace lengths and widths of
each turtle, weighing them with a Pelosa® macro-spring scale, drawing a 5 cc blood
sample from the dorsal cervical sinus, and collecting a 3 mm skin biopsy from a rear
flipper. I also applied INCONEL tags to each rear flipper and a Passive Integrated
Transponder (PIT) in the front left flipper. I attached a satellite transmitter (SPOT5, Wildlife Computers, Redmond, WA) and an ultrasonic transmitter (CHP-87-S, Sonotronics, Tucson, AZ) to the carapace of each turtle using a cool-setting two-part epoxy (PowerFast®) (NMFS SEFSC 2008). The total weight of both transmitters and epoxy did not exceed 5% of the turtle’s body weight. I minimized the epoxy footprint due to the small size of the turtles in my study. Transmitters are loosened and shed with pealing scutes as the turtles grow; retention can vary significantly throughout the year (i.e., rapid growth seasons like summer risk shorter tag retention than slower growth seasons like winter).

Ultrasonic acoustic (hereafter “sonic”) transmitters emit a sound at regular intervals and may be detected underwater with the aid of a directional hydrophone and receiver. Individual tags are identified with separate frequencies by unique codes that emit signals at different intervals. I used frequencies from 70 – 80 kHz, well above the hearing capabilities of green sea turtles (200-700 Hz) (Bartol & Musick 2003). The manufacturer estimated a detectable range for my transmitters at 3+ km, but my field testing yielded ranges of only 800 m in deep open water, 500 m in shallow open water, and < 100 m near seagrass beds and sandbars. I followed the direction of the strongest signal until the received signal was equally strong in all directions, indicating that I was in close proximity to the tagged turtle and recorded these coordinates as the turtle’s location. I held the animals overnight in flow-through sea water tanks and released
them the following day either in the SGNRA 3 in the PSGNRA study site (2005) or at the southern end of the Core/Back Sound study site (2006) at a maximum of 42 km from their capture location (minimum 4 km). I tracked turtles by hydrophone for as long as possible that day.

After release, I conducted daily surveys of the study areas to relocate tagged animals. If I did not find an animal, I executed an extensive search in a grid pattern at 100 m intervals as long as daylight and weather conditions permitted. When an animal was located, I recorded water depth, water temperature, whether or not seagrass was present, notes on signal strength, and whether or not I was able to see the turtle. I typically observed turtles from a distance and waited for a surfacing, or took one location record and moved on to search for other animals. I estimated my sonic location error in the field at each location based on signal strength, tracking conditions, and visual observation. My mean, median, and range of estimated error for my best locations per day (i.e., those used in habitat analyses) were 32m, 0m, and 0 – 650m, respectively. If I was able to visually relocate the turtle, I noted the turtle’s appearance and behavior. I also documented the location and approximate length of any large-mesh gill nets that I found opportunistically during my surveys.

The satellite transmitters recorded daily water histories experienced by the turtles in user-defined bins (2° C) and were programmed with a continuous duty cycle (i.e., to function continuously in air). Location and water temperature data were
uplinked to satellites when the turtles surfaced to breathe. I received daily updates from each transmitting turtle.

I converted and de-coded satellite-linked positional data using Wildlife Computers’ SatPak software (Redmond, WA) and imported these data into a geographic information system (GIS) for movement analysis. Satellite location data have potentially large errors (Hays et al. 2001, Vincent et al. 2002), so I filtered all the data to remove implausible locations using a three-stage algorithm parameratized with biologically appropriate speed and distance thresholds (McConnell et al. 1992, Austin et al. 2003).

I reconstructed sea turtle movements by plotting the best received location per day (based on Argos location quality classifications) of the filtered location data in an Albers Equal Area projection and created poly-lines between points in ArcView 3.2 (ESRI 1999) with Animal Movement Extension (Hooge & Eichenlaub 2000). The location error structure of satellite data is complicated and generally not reported in absolute terms (Vincent et al. 2002). However, based on the empirical location class specific deviations from true reported in Hayes et al. (2001) and the distribution of location classes received during my study, my satellite data have an estimated mean, median, and range error of 3 km, 1 km, and 0.01 – 10 km, respectively. The data filtration process I employed (above) serves to minimize these errors by removing those locations which are implausible. I estimated distance traveled in ArcInfo (ESRI 2006, ArcGIS 9.2). I summarized the area of habitat use for each turtle by constructing fixed kernel
utilization distributions (UDs) from telemetry positions by season. I restricted the habitat analyses that follow to the summer months (May – August) when turtles had established foraging sites in order to avoid biases associated with behavioral changes induced by seasons. UDs were calculated in ArcGIS with Hawth’s Tools (Beyer 2004) with a fixed ad hoc smoothing factor of H = 2,000 (units in meters) using all filtered locations for each turtle. When faced with the trade-off between sample size and serial autocorrelation in calculating UDs, I sided with sample size as it is more important than independence in estimating home ranges (Kernohan et al. 2001). UDs are non-parametric analyses which do not require independence and reducing data to independent locations to avoid serial autocorrelation has been criticized for its removal of important biological information from an animal’s movements (de Solla et al. 1999). My selection of a fixed 2 km bandwidth was optimal for the aquatic turtles in my study area (Silverman 1986). UD area was corrected by clipping out portions that encompassed any land and I used the 95th percent density contour values for consistency with other studies (Laver & Kelly 2008). I recognize that the UD estimates do not represent the turtles’ true home ranges (Worton 1989), but rather their summertime habitat use within a 2 – 5 week period. Preliminary asymptote analysis (Laver & Kelly 2008) of cumulative core UDs (50th percent density contour) calculated at daily intervals suggested a minimum sample period of 4 days was necessary to estimate a UD for turtles in this study.
Fisheries data

I obtained coordinates for the boundaries of the PSGNRA for each year from DMF Proclamations (Proclamations M-8-2005, August 3rd, 2005; M-9-2006, August 11th, 2006) (Figure 10). DMF observes approximately 10% of the autumn flounder gill net fishing trips (based on log book reports of effort) in the PSGNRA between September 1st and December 15th each year (Price 2006, 2007a). DMF also observes a small number of trips in other regions and times (Price 2007b). I obtained gill net fishing effort data (2005 and 2006) and sea turtle by-catch records (2000 – 2007) from DMF to evaluate the distribution and habitat characteristics of the shallow water fishery and to assess the spatial distribution of overlap between green turtle habitat use and gill net fishing effort.

Habitat analyses

I used three variables to evaluate habitat selection: water depth, distance to seagrass beds, and distance to shore. I obtained a bathymetric digital elevation model (DEM) at 30 m resolution from the National Oceanic and Atmospheric Administration’s National Ocean Service (NOAA-NOS 1998) to identify (mean low) water depths (1 m resolution) used by turtles and gill nets. I also recorded water depth and temperature (± 0.1° C) of turtles tracked with sonic telemetry in the field using a Garmin 250C depth finder.

I obtained digitized polygons of seagrass beds interpreted from aerial photography (scale 1:20,000 – 1:50,000) from the NOAA-NOS Applied Spatial Ecology
and Habitat Characterization Division. The polygons represent a mosaic of aerial surveys conducted in 1985, 1988, 1991, and 1992 (Ferguson et al. 1993). These surveys have demonstrated seagrass meadows in my study site are relatively stable through time (Ferguson & Korfmacher 1997). I used point locations of seagrass beds recorded during tracking to assess the accuracy of these polygons at the time of the study. Assessment of seagrass polygons with in situ observations showed that 3/164 records were misclassified as seagrass when the bottom was sand (error of commission), whereas 11/164 records were misclassified as not being seagrass when seagrass was present (error of omission). The true nature of seagrass patches in the field cannot be captured by the GIS polygons, but the misclassification was low and the polygons generally represented the spatial extent of seagrass in this area quite well. The shoreline I used in my analysis was NOAA’s Medium Resolution Digital Vector US Shoreline (scale 1:70,000). I created distance layers in GIS for seagrass and shoreline to 100 m resolution using the Euclidean Distance function in ArcInfo (ESRI 2006, ArcGIS 9.2).

I defined habitat availability at two spatial scales proposed by Johnson (1980); second-order habitat selection occurs within the study site while third-order selection occurs within the animal’s UD. In each case the individual turtle was my experimental unit. Identity of gill net fishers, however, was confidential and I could not generate UD for individual fishers. Comparisons between green turtles and gill net fishers’ sets were therefore restricted to second-order selection comparisons.
To characterize available habitat at the study site scale, I generated 250 random points in ArcGIS using Hawth’s Tools (Beyer 2004) in each study region (Core/Back Sound and PSGNRA) for a total of 500 points over an area of 1,125 km². I assume that these random points represent the habitat available in the study site based on accumulation curves of increasing sample size. Within the UD scale, I generated 50 random points in each turtle’s unique UD. I sampled the locations of sea turtles (best per day), gill nets, and random points in GIS for my three habitat metrics (see above) in ArcGIS using Marine Geospatial Ecology Tools (Roberts et al. 2009).

I tested the null hypothesis that turtles used habitat randomly (i.e., no selection) with a Euclidean distance approach, treating water depth also as a distance category. For each animal I created vectors of mean use/mean availability ratios for each habitat metric (depth and distance to features) (see Conner & Plowman 2001). I then used a multivariate analysis of variance (MANOVA) to determine if the overall mean vector ($\rho_{\text{habitat}}$) significantly differed from a vector of 1s (i.e., if significant then selection). Univariate $t$-tests were used to determine which habitat types (if any) were used disproportionally. MANOVAs and $t$-tests were performed in SAS 9.1 (SAS Institute 2003).

I also calculated the proportion of use for each habitat type for turtles, gill net sets, and random points. The proportion of habitat available (random points) was subtracted from the proportion of use (turtles and fishers’ nets) to assess habitat
preference (positive values) (Johnson 1980). I assumed that the turtles could use all areas in my study region. I also assumed that the sample of gill nets observed represent the true distribution of fishing effort and that fishing could take place and be observed anywhere within the study site. I used raster calculation in ArcGIS to extract preferred habitat type (bathymetry, distance to shore, and distance to seagrass) from available habitat surfaces. I also used raster calculation to produce composite habitat preference grids for turtles and gill net fishers and to identify areas of overlap where conflict is likely to occur.

**Results**

**Telemetry in the sounds**

I collected one green turtle in August 2005 from the PSGNRA region and nine turtles between May and October 2006 from the Core/Back Sound region (Figure 10). During my study I worked with eight fishers from the pound net, gill net, and long haul seine communities. The 2005 turtle was incidentally captured with hook and line by a recreational fisher.

Turtles ranged in size from 27.9 – 42.5 cm SCL (Table 2), typical for green turtles in North Carolina estuaries (Epperly et al. 1995b, Epperly et al. 2007). Eight turtles were tracked with both sonic and satellite telemetry and two other individuals produced satellite locations only because of the turtles’ immediate departure from the estuary
Table 2: Summary of green turtle telemetry tracking in North Carolina between 2005 and 2006. ‡ indicates turtle died within one month post-release of its incidental capture in a large-mesh gill net during my study (see text for details).

<table>
<thead>
<tr>
<th>Turtle ID</th>
<th>Size (cm) SCL</th>
<th>Date Deployed (d/m/y)</th>
<th>Latitude °N</th>
<th>Longitude °W</th>
<th>Track Duration (days) Satellite/Sonic</th>
<th>Net Distance Traveled (km) Satellite/Sonic</th>
<th>N Locations Satellite/Sonic</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>27.9</td>
<td>4/8/2005</td>
<td>35.22648</td>
<td>75.69933</td>
<td>65/12</td>
<td>207/3</td>
<td>21/27</td>
</tr>
<tr>
<td>B</td>
<td>33.5</td>
<td>23/5/2006</td>
<td>34.6904</td>
<td>76.52854</td>
<td>36/74</td>
<td>21/5</td>
<td>7/13</td>
</tr>
<tr>
<td>C</td>
<td>29.8</td>
<td>23/5/2006</td>
<td>34.6904</td>
<td>76.52859</td>
<td>33/9</td>
<td>9/8</td>
<td>7/8</td>
</tr>
<tr>
<td>D</td>
<td>32.7</td>
<td>5/6/2006</td>
<td>34.69503</td>
<td>76.52773</td>
<td>71/26</td>
<td>246/11</td>
<td>159/30</td>
</tr>
<tr>
<td>E‡</td>
<td>32.6</td>
<td>6/6/2006</td>
<td>34.69553</td>
<td>76.52746</td>
<td>60/60</td>
<td>17/6</td>
<td>23/24</td>
</tr>
<tr>
<td>F</td>
<td>30.9</td>
<td>12/6/2006</td>
<td>34.69566</td>
<td>76.52759</td>
<td>154/54</td>
<td>158/4</td>
<td>165/32</td>
</tr>
<tr>
<td>G</td>
<td>31.1</td>
<td>28/7/2006</td>
<td>34.68428</td>
<td>76.52629</td>
<td>17/18</td>
<td>20/2</td>
<td>93/18</td>
</tr>
<tr>
<td>H</td>
<td>42.5</td>
<td>16/8/2006</td>
<td>34.67284</td>
<td>76.54298</td>
<td>75/8</td>
<td>117/2</td>
<td>138/12</td>
</tr>
<tr>
<td>I</td>
<td>31.6</td>
<td>6/10/2006</td>
<td>34.68428</td>
<td>76.52629</td>
<td>137/NA</td>
<td>1558/NA</td>
<td>20/0</td>
</tr>
<tr>
<td>J</td>
<td>28.4</td>
<td>6/10/2006</td>
<td>34.68428</td>
<td>76.52629</td>
<td>29/NA</td>
<td>90/NA</td>
<td>38/0</td>
</tr>
</tbody>
</table>
(Table 2). Thirty-seven percent of the sonic locations were confirmed with visual observations of the turtles. The duration of satellite tracks ranged from 17 – 154 days with net distances traveled ranging from 9 – 1,558 km (Table 2). Sonic tracks lasted from 0 – 74 days with net distances traveled ranging from 2 – 11 km (Table 2). Turtles occurred from Bogue to Pamlico Sounds with the greatest concentration of records in Back Sound (Figure 11). In general, each turtle used a very restricted area and showed little movement during the summer followed by increased movement rates during the autumn, consistent with an onset of migratory behavior (Figure 12). Mean (± 1 standard deviation) summertime UDs for greens were 39.7 km² (12.3) based on sonic tracking, and 84.6 km² (48.3) based on satellite tracking (Table 3). UDs derived from satellite tracking encompassed the UDs obtained from sonic tracking and characterized the general area occupied by the turtles.

Sonic tracking was particularly difficult because aquatic vegetation and sand bars baffled the signal, reducing detectability and causing signals to bounce. Noise from boat traffic, wind and waves, and occasional dolphin echolocation exacerbated these problems. When animals settled into a foraging site, I obtained relatively few satellite uplinks, typically of poor location class. My visual observations of tagged turtles indicated that the animals raised only their heads out of the water to breathe, not surfacing high enough to trigger activation of the saltwater switch on the transmitter, located on their carapace. This behavior precluded systematic comparisons of satellite
Figure 11: Maps of 10 green turtles tracked during my study. Individual IDs are in the lower right hand corner of each panel. Open circles indicate best daily locations derived from satellite telemetry, filled circles are best daily locations from sonic telemetry.
and sonic locations. Tracking durations were short compared to my experience in the autumn (September – December) months (Chapter 1). Water clarity varied throughout the summer, but on 17 occasions I was able to watch turtles underwater.

![Graph showing mean movement rate by season](image)

**Figure 12:** Plot of mean movement rate (km/d) of turtles by season based on satellite locations. Bars are ± 1 standard deviation. Numbers above bars indicate number of turtles.

Turtles were disturbed by the presence of motorized vessels and often moved short distances upon my approach. Disturbance was also related to weather events, fishing activity or curious loggerhead turtles that I twice observed approaching and circling the green turtle I was tracking. The degree of displacement appeared to be related to the nature of disturbance. When animals moved great distances, they were difficult to find with sonic methods.

I relocated all turtles either in or adjacent to seagrass. On one occasion I was able to witness a turtle foraging on *H. wrightii*. Five animals (turtles C, D, E, F, J) occupied
Table 3: Estuarine green turtle habitat use metrics. Superscript indicates season (S = summer (May – August), A = autumn (September – November), W = winter (December – January)). N indicates the number of locations used; mpd = multiple locations per day and bpd = best location per day. 95th percentile density utilization distributions (UD) are reported as seasonal home range areas (mpd). Habitat metric values are means of the bpd (± 1 standard deviation).

<table>
<thead>
<tr>
<th>Turtle ID</th>
<th>N (mpd/bpd)</th>
<th>UD (km²)</th>
<th>Temp. (°C)</th>
<th>Depth (m)</th>
<th>Dist. Seagrass (km)</th>
<th>Dist. Shore (km)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Satellite</td>
<td>Sonic</td>
<td>Satellite</td>
<td>Sonic</td>
<td>Satellite</td>
<td>Sonic</td>
</tr>
<tr>
<td>A</td>
<td>14/7</td>
<td>27/8</td>
<td>171.6</td>
<td>28 (2)</td>
<td>29.6 (1.8)</td>
<td>1.9 (2.4)</td>
</tr>
<tr>
<td>A</td>
<td>15/6</td>
<td></td>
<td>106.1</td>
<td>25 (1)</td>
<td>2 (1.2)</td>
<td>0.01 (0.04)</td>
</tr>
<tr>
<td>B</td>
<td>12/3</td>
<td>13/7</td>
<td>97.6</td>
<td>24 (3)</td>
<td>26.9 (3)</td>
<td>0.03 (0.06)</td>
</tr>
<tr>
<td>C</td>
<td>8/3</td>
<td>8/2</td>
<td>60.8</td>
<td>24 (3)</td>
<td>25.4 (4)</td>
<td>0.03 (0.06)</td>
</tr>
<tr>
<td>D</td>
<td>121/25</td>
<td>30/4</td>
<td>140.3</td>
<td>25 (2)</td>
<td>25.6 (2.4)</td>
<td>0.08 (0.1)</td>
</tr>
<tr>
<td>E</td>
<td>35/6</td>
<td>24/7</td>
<td>71.1</td>
<td>25 (1)</td>
<td>28.2 (2.8)</td>
<td>0.02 (0.08)</td>
</tr>
<tr>
<td>F</td>
<td>225/40</td>
<td>31/11</td>
<td>40.2</td>
<td>25 (1)</td>
<td>28.3 (2.5)</td>
<td>0.03 (0.1)</td>
</tr>
<tr>
<td>G</td>
<td>94/15</td>
<td>18/4</td>
<td>45.2</td>
<td>26 (1)</td>
<td>28.7 (0.8)</td>
<td>0.06 (0.1)</td>
</tr>
<tr>
<td>H</td>
<td>89/15</td>
<td>12/4</td>
<td>49.8</td>
<td>26 (1)</td>
<td>26.7 (0.8)</td>
<td>0.08 (0.1)</td>
</tr>
<tr>
<td>H</td>
<td>55/20</td>
<td></td>
<td>94.8</td>
<td>22 (3)</td>
<td>1 (0.9)</td>
<td>0.05 (0.1)</td>
</tr>
<tr>
<td>I</td>
<td>38/12</td>
<td></td>
<td>171.8</td>
<td>13 (1)</td>
<td>1.5 (2.4)</td>
<td>0.4 (0.5)</td>
</tr>
<tr>
<td>J</td>
<td>59/18</td>
<td></td>
<td>174.7</td>
<td>18 (4)</td>
<td>1.1 (2)</td>
<td>0.3 (0.3)</td>
</tr>
<tr>
<td>mean</td>
<td>75/14</td>
<td>21/6</td>
<td>84.6</td>
<td>26 (1.5)</td>
<td>27.8 (2.5)</td>
<td>0.2 (0.7)</td>
</tr>
</tbody>
</table>
tidal creeks, two set up residence along marshy shorelines (A) or marsh islands (B), and two inhabited seagrass beds in open water (G, H) (Figure 11). The latter two animals were observed in water approximately 4 m deep; the others were consistently found in water less than 1 m deep and typically within a few meters from the shore (Table 3). In mid-summer, turtles were found in waters exceeding 28° C. Two turtles moved regularly with the tide. Turtle E traveled in and out of a creek with the flood and ebb tide, while turtle B swam around a marsh island relative to the tide.

Six animals initially established residence relatively near their release location, two moved northward up Core Sound, and two left the estuary immediately via Barden’s Inlet (Figure 11). The last two animals were released late in the field season (October), although both later re-entered the estuary.

Three of ten turtles were subsequently re-captured in fishing gear after release: one in a gill net, one in a long haul seine, one in a pound net. It is important to note that all turtles were initially captured in fishing gear, so these re-captures represent multiple occurrences of by-catch within a single season. The turtle caught in a gill net (E) was released alive, but confirmed dead one month later when I recovered its bones and transmitters from the sea floor. The turtle caught in the long haul seine (B) had lost both of its transmitters, but was in good condition. This animal had grown 2.6 cm in 3.5 months. I did not examine the turtle re-captured in the pound net (H), as the satellite tag was retrieved (11 weeks after deployment) but the turtle was not present. Three of
the sonic transmitters were found on the sea floor several weeks after deployment (B in week 10, F in week 8, H in week 3) presumably due to rapid growth spreading the scutes resulting in shedding of the transmitters. Five of the turtles were tracked out of the sounds (Figure 11), but only one of these turtles (I) was followed for a significant period of time (4 months) (Figure 11).

**Turtle by-catch in shallow water fishery**

The NCDMF observed 522 gill net sets in Core, Back, and Pamlico Sounds between May and December of 2005 and 2006 (Figure 13). In the PSGNRA observer coverage was 11.9% and 9.6% for 2005 and 2006, respectively (Price 2006, 2007a). Four (live) by-caught green turtles were documented in the PSGNRA in 2005 (Price 2006) (Figure 13) and five (2 live, 3 dead) were observed in the PSGNRA in 2006 (Price 2007a) (Figure 13); all were small juveniles < 36 cm SCL. The estimated combined numbers of turtles caught in large-mesh gill nets in the PSGNRA was 48 live and 17 dead green turtles during these two years (Price 2006, 2007a). Eighty percent of the observed green turtle by-catch during this time occurred in SGNRA 3 and the remaining 20 percent in SGNRA 1 (Figure 13). Outside the PSGNRA, one green turtle was observed dead in large-mesh gear in Back Sound (2005) and one green turtle was observed alive in large-mesh gear in Pamlico Sound (2006) (Price 2007b) (Figure 13). Since the initiation of the PSGNRA in 2002, the estimated by-catch based on fishing effort of all sea turtles in large-mesh gill nets in the PSGNRA has declined except for green turtles (Figure 14).
I noted 58 large-mesh gill net sets opportunistically while tracking turtles during the summer (Figure 13). As mentioned above, I found one of my tagged turtles in a large-mesh gill net. I also witnessed long haul seine activity on at least four occasions and one of my tagged turtles was also re-captured in this gear.

**Habitat analyses**

Habitat metrics of green turtles sampled during the summer from satellite and sonic tracking were similar, although satellite-derived locations occurred in slightly deeper water and at greater distances to features (Table 3). In general, turtles occupied mean temperatures between 26 – 28 °C and water depths < 1 m (Table 3). Turtles were found close to the shoreline (mean < 1 km) and near seagrass meadows (mean < 200 m) (Table 3). Ninety-four percent of the sonic locations occurred directly in seagrass (direct observation) while 67% of the satellite locations fell within seagrass (as determined by GIS).

Similarly, large-mesh gill nets occurred in mean depths < 1 m and within 500 m from seagrass meadows (Table 4). Nets observed by DMF were found at a greater range
of distances from shore (mean 2.3 km) than those I found serendipitously while searching for turtles (mean < 1 km) (Table 4). These latter nets were most often placed on the barrier island side of the sounds and across small tidal creeks or in front of marsh islands and were unattended by fishers.

Table 4: Estuarine gill net fishers’ habitat use and available habitat (random) metrics. Superscript indicates season (*S* = summer (May – August), *A* = autumn (September – November)). Values are means (± 1 standard deviation).

<table>
<thead>
<tr>
<th>Locations in Study Sites</th>
<th>Depth (m)</th>
<th>Distance from Seagrass (km)</th>
<th>Distance from Shore (km)</th>
</tr>
</thead>
<tbody>
<tr>
<td>DMF Observed Large-mesh Gill Nets <em>S,A</em></td>
<td>0.6 (0.3)</td>
<td>0.5 (1.5)</td>
<td>2.3 (1.9)</td>
</tr>
<tr>
<td>Opportunistic Large-mesh Gill Nets <em>S</em></td>
<td>0.5 (0.2)</td>
<td>0.01 (0.04)</td>
<td>0.7 (0.9)</td>
</tr>
<tr>
<td>Random</td>
<td>0.8 (0.7)</td>
<td>0.7 (1)</td>
<td>1.4 (1.5)</td>
</tr>
</tbody>
</table>

The available habitat at the study site scale was determined through sampling 500 randomized point locations, approximately three times the total number of daily turtle locations. Mean (± 1 standard deviation) values are reported in Table 4.

Use/availability ratios indicated that, during summer, the locations of green turtles differed from random locations at both the second (study site) and third (UD) order selection scales (*F*<sub>3,5</sub> = 61.95, *P* < 0.001; *F*<sub>3,5</sub> = 10.94, *P* < 0.05 respectively). There was no significant difference between turtles and random points with regard to water depth.
(\rho_{\text{depth}} = -0.14 \pm 0.12 \text{ (mean \pm 1 standard deviation)}, t_7 = -1.13, P = 0.297), but turtles were found closer to seagrass and closer to shore than expected (\rho_{\text{seagrass}} = -0.77 \pm 0.15, t_7 = -5.04, P = 0.001; \rho_{\text{shore}} = -0.50 \pm 0.13, t_7 = -3.74, P = 0.007). Within the turtles’ UD s, there was no difference between turtles and random points with regard to either water depth or distance to shore (\rho_{\text{depth}} = -0.14 \pm 0.07, t_7 = -2.08, P = 0.076, \rho_{\text{shore}} = 0.008 \pm 0.22, t_7 = 0.04, P = 0.972), but turtles were closer to seagrass than expected (\rho_{\text{seagrass}} = -0.57 \pm 0.09, t_7 = -6.17, P < 0.001).

I used habitat selection indices (i.e., use – availability) to identify areas in which one would expect to find green turtles and/or large-mesh gill nets within the shallow waters of North Carolina estuaries. Within my study site I found that turtles preferred water depths < 1 m, distances from shore between 0.1 and 2 km, and proximities to seagrass < 0.5 km based on the availability of habitat (Figure 15). Turtles G and H were exceptions to this pattern, preferring depths between 1 – 2 m and areas up to 2 km from shore in Back Sound (Figure 11). Turtle A was found on single occasions in deep water far from both the shore and seagrass, as it moved between two foraging sites in Pamlico Sound (Figure 11). Habitat preferences were reasonably similar within the animals’ UD s. All turtles preferred depths < 1 m and within 0.1 km of seagrass beds (Figure 15), but turtles were split with respect to distance to shore. Turtles A, B, C, E, and F preferred areas < 1 km from shore, while D, G, and H preferred areas 1 – 2 km from shore (Figure 15).
Figure 15: Plots of summertime habitat selection for green turtles and large-mesh gill net flounder fishery with respect to water depth (m), distance to shore (km), and distance to seagrass (km). Positive values indicate preference (i.e., use > availability). Panels on the left are based on analysis within the turtles’ UDs where the letter identifies the individual. Panels on the right are mean (± 1 standard deviation) values based on analysis at the scale of the study area.

Gill nets were preferentially set in depths less than 1 m, distances from shore between 4 and 7 km, and within 0.1 km, from 5.0 – 6.5 km, and > 7 km from seagrass based on availability of habitat within the study area (Figure 15). I combined the ranges of values for preferred habitat above for both turtles and gill net fishers (Figure 16). The
Figure 16: Top two panels represent the habitats preferred by green turtles and gill net fishers. Values indicate areas where a number of the habitat parameters were preferred (see Figure 15). The value 3 is the highest combined preference ranking. The bottom panel indicates the spatial region where habitat use may conflict between fishers and turtles. Stars are locations of green sea turtle by-catch in large-mesh gill nets documented by DMF between 2000 and 2007.
Discussion

Individual juvenile green turtles exhibited strong site fidelity during the summer months and were tightly tied to seagrass habitat. The habitat selection of turtles was similar at two scales of availability likely due, in part at least, to the shallow water nature of my study area. The summer home ranges of green turtles were extremely small and individual turtles could be found each day in the same bay or tidal creek, a pattern that is consistent with other studies of green turtles in the southeastern US (Mendonça 1983). Such fidelity is masked, to some degree, in location error from satellite-derived positional estimates, but my sonic tracking allowed me to document the exact positions of individual turtles. In her Florida lagoonal work, Mendonça (1983) reported that individuals returned to sleeping sites within 3 m of their previous night’s location. I did not conduct nocturnal tracking, but my work suggests that animals show similar fidelity especially to tidal creeks along the barrier islands and marsh islands.

Green turtles occurred most frequently at the edge of seagrass beds and often retreated into the beds when disturbed. Seven out of ten turtles settled into tidal creeks or near marsh islands. These areas are sheltered, calm, shallow, and limit access from large predators (i.e., sharks) or boats. When turtles were found farther from shore they...
were usually near persistent sandbars or marsh islands; perhaps any type of structure, submerged or emergent, may be equally appealing to small green turtles.

Similar to the results of Mendonça (1983), the turtles in my study moved very little during the warm months. Most individuals returned to a particular foraging area even after short forays. My findings, therefore, suggest that incidental capture of green turtles during summer is mediated by gear deployed in their foraging or sleeping site. I was able to track each turtle for only a few weeks, so it is unclear how long this site fidelity lasts within a season, or whether disturbance may cause a turtle to abandon its preferred habitat.

Proximity to seagrass was clearly important for the green turtles in my study. Ninety-four percent of my sonic observations were made directly in seagrass. Only 67% of the satellite records fell in seagrass, but the location error associated with this method likely resulted in an underestimate of the time spent in this patchy habitat. Despite their strong site fidelity and association with seagrass I did not observe the cropped “lawns” described in Bjorndal (1980). Small round bare patches were occasionally observed in the seagrass but were more likely the result of fish grazing, in which the whole plant is torn out of the ground, than clipping by green turtles. The UDs of turtles in my study were much larger than Bjorndal’s study site (0.03 km$^2$) and as mentioned above, my monitoring lasted only a few weeks at any given site. Therefore, I may not have been able to capture this behavior or perhaps the turtles in my study may have selectively
foraged on new growth throughout the seagrass meadows, rather than maintaining individual gardens.

Seventy percent of the observed gill net sets occurred within seagrass, suggesting these areas are important fishing grounds. Fish assemblages have been shown to be more abundant and diverse in seagrass beds than adjacent sandy areas (Venitia et al. 2006). As estuarine predators, flounder are likely to be distributed greater where prey resources are most profitable (MacArthur & Pianka 1966, Wright et al. 1993, Harter & Heck 2006). Seagrass is restricted to shallow areas and, as expected, both turtles and nets were mainly located in water depths less than 1 m deep. All shallow water, however, does not contain seagrass, so it is the combination of these two habitat parameters that is important to the co-occurrence of green turtles and nets. Distance from shore was highly variable among gill net sets. Fishers often placed their nets perpendicular to submerged shoals or near marsh islands as these features serve as natural leads which direct fish towards their nets. A notable local example is the long series of shoals that run along the inside of the Outer Banks behind Hatteras and Ocracoke and is a highly popular fishing area in the PSGNRA (SGNRA2 & SGNRA 3) (Chapter 1).

Disturbance, whether anthropogenic (boats, incidental capture) or natural (interspecific interactions, weather), may also play a role in the encounters between turtles and fishing gear. Despite two intensive field seasons, lasting for eight months
over two years, I made very few observations of non-telemetered turtles. I observed loggerheads and diamondback terrapins (*Malaclemys terrapin*), but no green turtles other than those which I had tagged. Studies examining the catch rate of sea turtles in these waters show that greens are much less common than loggerheads (Sasso et al. 2007). During my tracking efforts, I found green turtles to be extremely wary of boats and my tagged turtles darted away when approached. Their surfacings were quick and inconspicuous. Balazs et al. (1987), Renaud et al. (1995), and Seminoff et al. (2002) also reported that green turtles may alter their behavior to avoid human activity. Thus their wariness and surfacing behavior, combined with their small size, appears to be responsible for my lack of green turtle sightings. I hypothesize that disturbance leads turtles to move and that the distance they move is a function of the degree of disturbance. Minor disturbances may result in temporary retreats into seagrass beds, as was the case when a green turtle was too closely investigated by a loggerhead turtle.

I found that movement rates increased predictably during the autumn, consistent with the onset of migration triggered by falling temperatures (Mendonça 1983). Even while making longer distance movements in my study area (*i.e.*, 7 km/day), green turtles traveled through areas of seagrass. Therefore, during estuarine migration, fishers setting nets in close proximity to seagrass meadows are likely to encounter green turtles. Because the turtles are covering greater distances, the rate of encounter with gill nets increases as they move through a gauntlet of fishing gear.
The behaviors of turtles B and E suggest that greens may conserve energy by drifting in and out of creeks with the tide. Turtle B was tracked in an area where the current flow was strong, and this animal moved around the marsh island so as not to be transported away from the area, whereas E moved back and forth in a creek with the tide (Figure 11). These findings are similar to those of Byles (1988) and Mansfield (2006) who documented tidal-related movements of loggerhead and Kemp’s ridley turtles in Chesapeake Bay. Therefore, tidal cycle may be an important factor in the probability of encountering nets set in a foraging site. Fishers often set nets overnight and over tidal cycles. Flounder have been shown to move in and out of creeks with the tide during the night (Szedlmayer & Able 1993, Roundtree & Able 1997).

While the management of the gill net fishery in Pamlico Sound is considered successful overall, it has not reduced the number of interactions between green turtles and gill nets in shallow water seagrass habitats that are still open to fishing. Spatial and temporal overlap in itself does not necessarily lead to entanglement, as evidenced by the frequency with which I witnessed fishing activity in locations where I tracked turtles. By-catch, however, cannot occur without spatial and temporal overlap. The more gill nets there are in an area, the greater the chance for a turtle to encounter a net. I estimate that 32% of the PSGNRA is preferred green sea turtle habitat. When observed by-catches were superimposed on the overlap of preferred turtle habitat and preferred fishing areas, there was an almost perfect match (Figure 16). The permitted by-catch
authorized by NMFS to the PSGNRA fishery implies by definition that the current level of by-catch is sustainable to the green turtle population. A full assessment of the impact of these by-catches has yet to be conducted, however.

In addition to the high degree of overlap between green turtles and gill nets, one of the most striking results of my study was the high rate of interactions between green turtles and other fisheries in the sounds of North Carolina. All turtles were initially caught in pound nets, long haul seines, or by hook and line. At least three turtles were confirmed to be caught a second time in a large-mesh gill net, long haul seine, or pound net. Two of these turtles may have been caught a third time, based on an unusual series of high quality satellite uplinks. Fortunately, most of these interactions were non-lethal. In fact, the vast majority of green turtles captured in North Carolina fisheries and observed by state or federal observers are released alive (Epperly et al. 2007, Price 2007b), likely due to the ability of turtles to reach the surface and breathe. To my knowledge, this is the first paper to describe multiple incidental capture rates for individuals in different gears in this region.

The potential for multiple live captures raises the question of capture stress and delayed mortality. Few studies have been conducted on post-release mortality of sea turtles. Harms et al. (2003) demonstrated that incidental capture resulted in adverse changes in loggerhead turtle blood chemistry and that these changes were greater in animals that had been forcibly submerged. Turtles can drown during forced
submergences in as little as ten minutes (Sasso & Epperly 2006) and repeated capture may reduce submergence endurance (Lutcavage & Lutz 1991). High survival rates (> 0.8) have been reported for sea turtles hooked in longline gear (Swimmer et al. 2006; Sasso & Epperly 2007), but questions still remain as to the sub-lethal effects of incidental capture and the potential for increased susceptibility to other threats such as boat strikes, predators, cold stunning, or infection post-release. Recapture rates of green turtles (based on flipper and PIT tags) are low in pound nets (Epperly et al. 2007) and have not been observed in gill nets in the PSGNRA (B. Price, DMF, personal communication), although gill net fishers in the PSGNRA are instructed to escort by-caught turtles to inlets during the autumn. Therefore, it is uncertain whether re-captures are low because disturbed turtles leave the area, whether their survivorship is low, or whether they leave the estuary after being released near inlets. Research is currently underway on the post-release survival of green and Kemp’s ridley turtles in North Carolina and preliminary data shows increased stress levels of animals entangled in large-mesh nets in four hours or less (J. Snoddy, UNCW, personal communication), similar to the findings of Harms et al. (2003) for trawls and pound nets. Snoddy’s preliminary research suggests post-release mortality occurs in less than one month as a result of physiological stress (specifically, a Kemp’s ridley mortality one week post-release); mortality rates may be as high as 7 – 29%. As noted above, I documented a
post-release mortality within one month of capture in a shallow water gill net. No other studies have been published on the post-release mortality of turtles in gill nets.

Current management practices in the PSGNRA restrict the use of flounder gill nets to the shallow water fishing grounds along the margins of Pamlico Sound. This restriction has the intended effect of greatly reducing the by-catch of (mostly) loggerhead turtles, but concentrates fishing effort into shallow waters, where green turtles are captured frequently. DMF now monitors the shallow-water fishery in Pamlico Sound with a dedicated observer program to ensure that by-catch does not exceed permitted removal levels. But in fact, the shallow water fishery was closed one month early in 2007 when green turtle takes surpassed the allowable threshold (Proclamation M-19-2007, November 13th, 2007). My research indicates that by-catches of green turtles also occur in gill nets (and other fishing gears) in the shallow water habitats in Back and Core Sounds, outside the current PSGNRA. I conclude that similar conservation measures, including dedicated observer programs, are required in these shallow habitats used intensively by both green turtles and commercial fishers. Without such measures it will not be possible to fully assess the extent of green turtle by-catch in North Carolina’s estuarine fisheries. I also recommend that further research be conducted into the post-release condition of by-caught turtles to allow estimation of total mortality. The potential for adverse ecological effects in these shallow water areas
is exacerbated by the very small home ranges exhibited by green turtles during the foraging season.
Chapter 3: Complexity and variation in loggerhead sea turtle life history


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Introduction

Throughout their development loggerhead sea turtles (*Caretta caretta*) undergo abrupt developmental changes in habitat, behavior, and resource use (Bjorndal et al. 2000, Snover 2002, Bolten 2003). In the western North Atlantic, hatchlings leave their natal beaches, swim offshore, and become entrained into the Gulf Stream, eventually inhabiting the oceanic waters of the Atlantic. Their whereabouts during this oceanic phase of life was termed the “lost year” by Archie Carr (Carr 1986). We now know that this “lost year” actually lasts for more than a decade, during which the turtles remain in oceanic waters and consume epipelagic prey (Carr 1987, Bjorndal et al. 2000, Snover 2002).

After this oceanic phase, juvenile loggerheads return to neritic waters to forage on benthic prey, in what has assumed to be a discrete ontogenetic shift. In the North Atlantic, this shift occurs when individuals are 42 – 59 cm straight carapace length (SCL) (Bjorndal et al. 2000, Snover 2002). Once these large juveniles have entered a benthic life stage, they inhabit coastal waters and make seasonal latitudinal migrations between neritic feeding (and later breeding) grounds (Carr 1987, Musick & Limpus 1997, Hopkins-Murphy et al. 2003). This shift is believed to allow maximization of growth potential while minimizing predation risk in ecologically distinct stages (Werner & Gilliam 1984).
Discrete ontogenetic niche shifts are common in vertebrates (Mittelbach 1981), but in some species such shifts are not hard wired (Persson & Greenberg 1990). The timing of these shifts may have profound consequences for survivorship (Olson 1996) and, in a world that is increasingly modified by human activities, may mediate risk to sources of anthropogenic mortality.

I tested the hypothesis that loggerheads exhibit a permanent ontogenetic shift and that, once juveniles have returned to neritic waters, they remain in this habitat. Loggerhead sea turtle populations are threatened by mortality in both coastal and oceanic fisheries, so it is critical to understand variation in their life histories (Crouse et al. 1987; Crowder et al. 1994) so that we can assess the demographic impacts of these fisheries.

**Methods**

I used satellite telemetry to track the movements of 30 large juveniles captured in the estuaries of North Carolina, USA in the summers of 2002 and 2003. I attached satellite transmitters (Wildlife Computers SPOT2, Redmond, Washington, USA) to loggerhead turtles collected incidentally in a commercial pound net fishery in North Carolina. Turtle size was measured to the nearest 0.1 cm and reported as straight carapace length (SCL). Transmitters were affixed to the turtle’s carapace using a hybrid technique of a cool setting two-part epoxy (Power Fast®) (Mitchell 1998) and fiberglass cloth and resin (Balazs et al. 1996). Animals were released near their capture location.
The satellite tags were programmed to transmit daily over an 8-hour period beginning from just before dawn to near mid-day. Position estimates and associated location accuracy were provided by Service Argos, Inc. I employed a three-stage filtering algorithm (Austin et al. 2003; McConnell et al. 1992) to reject implausible locations. Sea turtle movements were reconstructed by plotting the best location estimate per day of the filtered location data. To test for significant differences in the size of turtles with different migratory destinations, I conducted a one-way analysis of variance (ANOVA). Migratory destination was classified as oceanic if a turtle moved off the continental shelf, as defined by the 200 meter isobath, or neritic if it remained on the shelf. Seven turtles tracked for less than 1 month and showing no clear destination after leaving the estuaries were excluded from the analysis.

Results

Turtles were tracked for up to 660 days (mean 274; SD 108) and exhibited two discrete behavioral patterns. Thirteen turtles remained in neritic waters as expected; some traveled as far south as Florida, although most remained off North Carolina (Figure 17a). The following year, ten of these loggerheads returned to North Carolina estuaries. The three remaining individuals stopped transmitting prior to or around the time re-migration typically occurs; one in January off Florida and two in April off North Carolina.
Figure 17: Two discrete life history patterns observed in juvenile loggerhead sea turtles tracked via satellite from a summer estuarine foraging area: neritic and oceanic. (a) Neritic animals (N = 13) remained over the continental shelf (in grey). (b) Oceanic turtles (N = 10) ventured past the shelf break into the open ocean.

After leaving the estuaries, however, a group of ten turtles returned to the open ocean (Figure 17b), where they remained for up to 262 days. Loggerheads cannot feed on benthic organisms in this habitat because water depths exceed their dive capabilities (Lutcavage & Lutz 1997). One turtle, after spending 210 days in the oceanic realm,
returned to coastal waters for 102 days before migrating back to the open ocean for 30 days, after which its transmissions ceased.

The mean SCL of neritic turtles was 62.6 cm (SD 4.9, range 57.5 – 75.8); that of oceanic turtles was 64.0 cm SCL (SD 7.3, range 52.9 – 74.2). Their sizes were not significantly different ($F_{1,21} = 0.32, P = 0.58$).

**Discussion**

My results show that loggerheads do not undergo a discrete ontogenetic niche shift and add to speculation (Bolten 2003) and a growing body of evidence (Witzell 2002; Hatase et al. 2006; Hawkes et al. 2006) that the life history of sea turtles is considerably more complex than previously understood. Tracking individuals in the wild has provided considerable insight into movement behaviors, but individual variation may not always be recognized as significant. For example, in two decades of satellite telemetry studies, a few loggerheads were tracked into the Gulf Stream for short periods of time (Byles 1988, Keinath 1993, Morreale & Standora 1998), but these results were, for the most part, discounted as anomalous. Morreale and Standora (2005) later suggested that some juvenile loggerheads migrate seasonally between coastal habitats and warmer offshore waters. My study demonstrates clearly that the oceanic environment remains an important habitat for loggerheads even after they venture into neritic foraging grounds, sometimes for several years. Indeed, large juveniles such as those in my study
are routinely observed as by-catch in pelagic longline fisheries in oceanic waters (Watson et al. 2005).

The factors responsible for this observed variation in life history strategies are not yet clear. Size did not explain the difference in migratory destination in this study, however potential explanatory factors such as age, sex, condition, or nesting beach origin are possible (Chapter 4). I can infer, however, from other research that these differences are unlikely to explain the variation I observed. Juvenile loggerheads captured in North Carolina are a mixed-stock aggregation (Bowen et al. 2005), although most are from Western Atlantic rookeries (Bass et al. 2004), and are female biased (2:1) (Braun-McNeill et al. 2007).

Using skeletochronology and stable isotopes, Snover (2002) suggested that loggerheads settled into the neritic environment at 49 cm SCL. She found increased growth rates and a trophic shift following settlement that was consistent with a transition from pelagic to benthic habitat and prey, but reported that growth rates in the neritic habitat were slower than predicted (Snover 2002, Snover et al. 2007). The behavioral complexities I describe in terms of life history strategy may not be evident in such studies because of the observed variation in growth or diet. In particular, I conclude that ontogenetic shifts exhibited by loggerhead turtles appear to be facultative and reversible, rather than fixed.
The intra-population variation I observed may have significant consequences for both the description of sea turtle life histories and for the conservation of these protected species. Sea turtle by-catch in fisheries that occur within the Exclusive Economic Zones of nations can be mitigated (e.g., the use of Turtle-Excluder Devices in US trawl fisheries), but when loggerheads spend protracted periods in the ocean, they are at risk from largely unregulated international fisheries (e.g., pelagic longlines for swordfish and tuna). My study suggests that as many as one-third of the demographically critical large juvenile loggerheads (Crowder et al. 1994) may remain vulnerable to fisheries by-catch in the open ocean much longer than previously understood.
Chapter 4: Discovering juvenile loggerhead foraging dichotomies using stable isotopes and telemetry
**Introduction**

Loggerhead sea turtles (*Caretta caretta*) are long-lived and highly migratory marine reptiles that undergo profound ontogenetic changes in habitat and diet throughout their lives (Carr 1987, Musick & Limpus 1997). After hatching, small juvenile loggerheads spend more than a decade in the epipelagia amongst floating *Sargassum* and feeding opportunistically on nektonic organisms (Carr 1987, Bjorndal et al. 2000, Snover 2002, Bolten 2003). These turtles then return to neritic waters as large juveniles and adopt a demersal foraging strategy (Carr 1987, Musick & Limpus 1997, Hopkins-Murphy et al. 2003). During this developmental period, the turtles undergo morphometric and physiological changes that are consistent with changes in their foraging ecology (Kamezaki & Matsui 1997, Hochscheid et al. 2007). The optimal timing of this shift in habitat and diet has profound consequences for an individual’s survivorship, stage duration, and time to maturity (Snover 2008).

Until recently, it was believed that juvenile loggerhead turtles experienced a permanent and irreversible niche shift, driven by a trade-off between growth and predation risk (Werner and Gilliam 1984). Recent studies have demonstrated that this ontogenetic pattern can be highly variable, as the oceanic-to-neritic shift is facultative for sea turtle species, life stages, and populations around the world (Witzell 2002, Hatase et al. 2002, 2006, Hawkes et al. 2006, Mansfield 2006, Casale et al. 2008), including foraging juveniles in the North Atlantic (Chapter 3). Although behavioral polymorphisms have
been reported, at the present time we do not understand the ecological factors driving this plasticity in movement patterns of sea turtles. It is likely that a complicated array of both physical and biological factors, operating at a variety of scales, influence which path a particular individual may follow (Mueller & Fagan 2008). Identification of driving factors affecting marine turtles’ movement patterns would provide important insights for guiding conservation efforts through stock assessments, jeopardy analyses, and management actions (Chapter 3, NMFS & US FWS 2008, Wallace et al. 2008).

The purpose of the present study was to examine this behavioral plasticity and determine if the different migratory strategies observed in wild populations can be explained by the biology of these animals. To do so I returned to the juvenile loggerhead sea turtles that I first followed via satellite telemetry in 2002 in North Carolina, USA (Chapter 3). These turtles exhibited two clear migratory patterns: one overwintering in neritic coastal waters (as expected from the original life history model) and the other returning to the pelagic realm. I briefly review the potential drivers of this variability below.

Food is one obvious and important potential motivator. Foraging histories provide natural indicators of habitat use, particularly between spatially and trophically distinct marine environments such as neritic/benthic and oceanic/pelagic communities. Due to differences in prey abundance and quality according to habitat, variation in foraging areas used by individuals of the same population can affect important life
history traits such as growth rates, thereby influencing population dynamics.

Loggerheads are opportunistic carnivores (Dodd 1988). In the neritic habitat these
turtles consume a wide range of benthic invertebrates such as crabs, mollusks, and
shrimp, as well as occasional marine plants (reviewed in Bjorndal 1997). In addition to
natural diet items, loggerheads also opportunistically consume fishery discards (Dodd
1988, Seney & Musick 2007). In contrast to the knowledge of loggerhead diets in the
neritic habitats, little information exists on the diet of Atlantic loggerheads in the open
ocean, particularly for sub-adult and adult turtles. Small juveniles feed in the epipelagia
on gelatinous organisms (i.e., jellyfish, hydroids, salps), pelagic snails and barnacles, and
Sargassum and its associated fauna (reviewed in Bjorndal 1997). Turtles in transition
between habitats may consume both benthic and pelagic fauna, although this has never
been demonstrated. Information also is lacking on variability in diet across seasons.

In addition to foraging history, philopatry (both proximate and ultimate) could
also explain variation in movement behaviors. Juvenile loggerheads may exhibit
homing behavior to particular foraging grounds after completing their seasonal
migrations (Lutcavage & Musick 1985, Avens et al. 2003). It is possible that individual
turtles may venture inshore to sample the neritic environment, but return to the open
ocean for up to a number of years (Chapter 3, Bolten 2003, Casale et al. 2008).
Alternatively, animals could inhabit different neritic foraging grounds in different years.
Mixed stock analyses of mitochondrial DNA (mtDNA) haplotype frequency have suggested that juveniles home to their natal rookery, although not as precisely as adults (Bowen et al. 2004). Source populations for North Carolina’s foraging aggregation are derived primarily from western Atlantic rookeries (northeast Florida to North Carolina, south Florida, northwest Florida, Dry Tortugas, Mexico and Brazil) but also include a small proportion of individuals from Mediterranean nesting beaches (Greece and Turkey) as well (Bass et al. 2004). An individual’s natal beach identity is currently unavailable, but examination of haplotype frequencies may provide insight into which sub-populations contribute to a select group of turtles (e.g., Haas et al. 2008).

Sex is another attribute that could explain variation in turtle movement. For example, it is possible that males and females use different habitats when not breeding. The sex ratio of the North Carolina juvenile foraging aggregation is female biased (2:1); similar to other juvenile populations in the southeastern US (Braun-McNeill et al. 2007).

In this study I combine information I collected on stable isotope ratios of $\delta^{15}$N and $\delta^{13}$C, capture and re-migration histories, genetic haplotype frequencies, body size, and sex ratios to examine variation in the migratory destinations of loggerhead sea turtles in the North Atlantic, as monitored by satellite telemetry.
Methods

Data collection

Based on previous satellite tracking (Chapter 3), I classified the movements of 35 juvenile loggerhead sea turtles captured in North Carolina estuaries and categorized their destinations as neritic, oceanic, or unknown. Turtles were classified as ‘oceanic’ if their migratory movements took them past the continental shelf, as defined by the 200 m isobath (n=10), ‘neritic’ if they remained on the shelf (n=18), or ‘unknown’ if their tracks were too short (i.e., < 1 mo.) to determine a destination (n=7) (Figure 18, Chapter 3). I previously described the movements of 30 of these animals tagged in 2002 and 2003 (Chapter 3).

![Figure 18: Map of migratory destinations of satellite tracked sea turtles tagged between 2002 – 2004 modified from Chapter 3. Green ellipse is for neritic turtles, blue dashed ellipse is for oceanic turtles.]

Here I include an additional five turtles tagged in 2004 (Figure 19). I began tracking most turtles in the autumn (September – November), although five were tagged
during the summer (May – June). From each turtle I: collected a 5 cc blood sample from the dorsal cervical sinus for sex determination (Braun-McNeill et al. 2007) and stable isotope analysis (SIA) (Wallace et al. in press); collected a 3 mm skin biopsy from a rear flipper for genetic analysis (Bass et al. 2004); and checked for tags and marked new turtles with flipper and PIT tags (Epperly et al. 2007). I measured standard straight and curved carapace lengths (SCL and CCL) (Epperly et al. 2007), photographed the turtle, and then prepared the carapace for satellite transmitter attachment (Chapter 3).

Figure 19: Map of study area. Stars indicate capture locations of sea turtles. Colored boxes are locations where potential prey samples were collected; neritic (green) and oceanic (blue). Red dashed line denotes position of the Gulf Stream when prey samples were collected (August – September 2007). Shading is bathymetry showing the continental shelf and break.
Between July and September 2007, I collected potential neritic prey items within North Carolina estuaries and potential oceanic prey items from the Gulf Stream off of North Carolina (Figure 19) for SIA. The neritic prey samples were obtained by hand, crab pot, or pound net and included muscle tissue from blue crabs, Callinectes sapidus (n=4); lightning and knobbed whelks, Busycon contrarium (n=6) and B. carica (n=4) respectively; spider crabs, Libinia emarginata (n=11), horseshoe crabs, Limulus polyphemus (n=10); and homogenized whole-body tissue from cannonball jellyfish, Stomolophus meleagris (n=5). Oceanic prey samples were obtained with a dip-net and included homogenized tissues of four species of jellyfish – moon jellies, Aurelia aurita (n=5); mauve stingers, Pelagica noctiluca (n=8); sea nettles, Chrysaora quinquecirrha (n=6); and lion’s mane jelly, Cyanea capillata (n=1) – as well as Sargassum spp. (n=10) and associated fauna. I separated invertebrates and fish from Sargassum plants for SIA. Because of their small body size, I pooled samples of whole crustaceans taken from different Sargassum patches to obtain a large enough sample. These included Sargassum crabs, Portunis sayi (n=10) and shrimp, Latreutes fucorum and Leander teruicornis (n=8). Individual small juvenile fishes were also sampled; filefish, Monocanthus hispidus (n=10) and yellow jack, Carangoides bartholomaei (n=5).

**Stable isotope approach**

Analysis of stable isotope ratios in various tissues has been successful in describing foraging dichotomies within individuals (Snover 2002, Reich et al. 2007),
within (Hatase et al. 2002, 2006, Caut et al. 2008) and between life stages (Arthur et al. 2008), between populations (Wallace et al. 2006b) and between species (Godley et al. 1998) of wild marine turtles. Stable isotope ratios of nitrogen ($^{15}$N:$^{14}$N, typically referred to as $\delta^{15}$N) and carbon ($^{13}$C:$^{12}$C, typically referred to as $\delta^{13}$C) are often used as indicators of trophic level and feeding location of consumers, respectively (DeNiro & Epstein 1978, 1981, Minagawa & Wada 1984, Peterson & Fry 1987, Hobson 1999). Isotopic signatures of diet items are integrated into consumer tissues in a relatively predictable manner during anabolism (DeNiro & Epstein 1978, 1981, Peterson & Fry 1987), such that lighter isotopes tend to be excreted while heavier isotopes are enriched from prey to predator with a degree of tissue specific fractionation (Peterson & Fry 1987). Across taxa, nitrogen is enriched through the food chain to a much greater degree than carbon; nitrogen typically ranging from 3 – 4 ‰ and carbon ranging from 0 – 1 ‰ per trophic level (DeNiro & Epstein 1978, 1981, Tieszen et al. 1983, Minagawa & Wada 1984, Hobson 1999). The reflection of a consumer’s diet depends largely on a given tissue’s metabolic turnover rate (Tieszen et al. 1983, Hesslein et al. 1993), and therefore tissues must be judiciously selected in the context of the question at hand (Hobson 1999). For example, rapidly processed reptilian tissues such as blood plasma represent information on recent feeding (i.e., weeks - months), whereas bone collagen which turns over slowly may represent a lifetime of integration (Godley et al. 1998, Seminoff et al. 2007, Reich et al. 2008).
Sample processing

Genetic samples were stored in DMSO and later analyzed for mitochondrial DNA (mtDNA) haplotype frequencies at the NMFS Southwest Fisheries Science Center, Molecular Ecology Laboratory as described in Haas et al. (2008). This analysis employed the haplotype nomenclature of marine turtle mtDNA sequences shared through the Archie Carr Center for Sea Turtle Research (http://accstr.ufl.edu/ccmtdna.html). Blood samples were separated into plasma and red blood cell (rbc) components by centrifuge and stored in a freezer at -80°C for later analysis. Half of the plasma sample was used in serum testosterone radioimmunoassay (RIA) for sex determination at Grice Marine Laboratory, College of Charleston in Charleston, South Carolina; see Braun-McNeill et al. (2007) for details on this procedure. I used the other half of the plasma and the rbc sample for SIA. In ectothermic vertebrates such as turtles, plasma reflects a short term diet history (i.e., weeks – 4 mos) and rbcs represent a foraging history integrated over a longer period (i.e., 2 – 7 or more mos) (Seminoff et al. 2007, Reich et al. 2008). Turtles were primarily collected in the autumn, so plasma samples likely reflect the summertime and autumn foraging in the estuaries and rbc samples would be more representative of the entire previous year, including overwintering periods.

I dried all turtle and prey samples at 60°C for 48-72 hr (except for oceanic jellies which were dried for up to 3 weeks) and then ground them into powder. I microspooned 0.5 – 2.5 mg subsamples into sterilized tin capsules for analysis by mass
spectrometry at the Duke University Environmental Stable Isotope Laboratory (DEVIL), in Durham, North Carolina (see Wallace et al. (in press) for analytical details). Lipids were not extracted, so I applied a post hoc lipid correction factor to my carbon isotope ratios (δ¹³C) (Post et al. 2007). Similar to Revelles et al. (2007) and Wallace et al. (in press), I accounted for isotopic discrimination between turtles and potential prey using discrimination factors (Δdt) measured in similarly sized juvenile green turtles’ tissues; blood plasma (Δdt δ¹³C: -0.12 ± 0.03 ‰, Δdt δ¹⁵N: 2.92 ± 0.03 ‰) and rbc (Δdt δ¹³C: -1.11 ± 0.05 ‰, Δdt δ¹⁵N: 0.22 ± 0.03 ‰) (Seminoff et al. 2006).

Data analysis

I conducted conventional and bootstrapped logistic regression analyses to explore whether the variation in migratory destination (neritic versus oceanic) was influenced by factors such as diet (i.e., δ¹³C, δ¹⁵N), capture status (i.e., first time, or recapture), subsequent remigration, haplotype, sex, and body size. Unfortunately, there was sufficient variation to evaluate only four of these parameters with logistic regression (δ¹³C, δ¹⁵N, remigration, body size). Separate models were run for blood plasma and rbc isotope signatures.

I used Akaike’s Information Criterion (AIC) to guide optimum parameter selection with conventional modeling and p-values with bootstrap modeling. Sample sizes differed among parameters because of missing data for some variables; therefore AICs could only be compared directly between models with equal sample size (i.e., δ¹³C
= \delta^{15}N and remigration = size). I had small sample sizes and because certain variables (i.e., remigration) were highly skewed, I ran bootstrap models in order to provide more robust parameter estimation (given probable violations of maximum likelihood estimation-based logistic regression assumptions). Parameter estimation was determined by randomly re-sampling the data with replacement over 10,000 iterations to approximate the sampling distribution. Regression analyses were performed in R using the BRGLM package (Bias Reduced Generalized Linear Model; Kosmidis & Firth 2008) with a binomial family and logit link function; the BRGLM function penalizes the maximum likelihood estimate for cases of perfect separation in the data (i.e., when there is perfect correspondence between the binary response variable and a categorical predictor). I also used univariate t-tests to explore variation in habitat destinations and tissue type.

Isotope mixing models are useful tools for inferring diet composition through the estimation of the proportional contribution of sources (potential prey items) within a mixture (consumer tissue) (Phillips & Gregg 2001, 2003, Phillips et al. 2005). Linear mixture models such as those implemented in ISOSOURCE (Phillips & Gregg 2003), iteratively combine potential source (i.e., prey) isotope values which result in all possible solutions for the observed mixture (i.e., consumer) value. However, ISOSOURCE is limited with respect to the number of sources which can be evaluated at one time, does not allow for explicit handling of variation in the data (i.e., assesses means only), and
requires that mixture sub-groups must be run separately. To account for the many potential neritic and oceanic prey items in my study, the wide variability in isotope ratios for individual sources and uncertainty in discrimination factors, and my desire to run all turtle groups (neritic, oceanic, and unknown) simultaneously for a more robust estimate of my data (Parnell et al. 2008, Jackson et al. 2009), I used a Bayesian isotopic mixing model available as an open source R package, SIAR (Stable Isotope Analysis in R; Parnell et al. 2008). The SIAR model is fit via Markov Chain Monte Carlo (MCMC) methods producing simulations of plausible values of dietary proportions of sources consistent with the data using a Dirichlet prior distribution (Parnell et al. 2008, Jackson et al. 2009). I ran the SIAR MCMC with 500,000 iterations discarding the first 50,000 samples and then thinning by 21 (i.e., \((\text{number of groups} \times (\text{number of sources} + \text{number of isotopes}))\) or \(((3) \times (5 + 7))\)) to reduce sample autocorrelation. The resulting probability density function distributions of the feasible foraging solutions produced by SIAR allow direct identification of the most probable solution (i.e., the median value) (Parnell et al. 2008, Jackson et al. 2009). Upper and lower credibility intervals describe the range of feasible contribution of a particular diet item.

Prior to running SIAR, I grouped ecologically similar prey which turtles might consume, although not all groups were statistically similar for both \(\delta^{13}C\) and \(\delta^{15}N\) (e.g., oceanic jellyfish spp., *Sargassum* and associated organisms) (Phillips et al. 2005). My analyses therefore included three turtle (i.e., mixture) groups (neritic, oceanic,
unknown), three neritic prey groups (crabs, whelks, cannonball jellyfish), and two oceanic prey groups (jellies and fish, \textit{Sargassum} and its commensal crabs and shrimp). I ran separate mixing models for plasma and rbc.

\textbf{Results}

\textbf{Turtle behavior and biology}

My sample of loggerhead sea turtles ranged in size from 52.9 – 82.2 cm SCL (mean ± 1 standard deviation (SD) 63.1 ± 7.7 cm). Five of the 35 turtles had been previously captured and marked prior to satellite tracking; 3 of these were neritic animals and 2 were unknowns. Remigration into the estuaries following tagging was determined either from satellite tracks or re-capture records (NMFS Southeast Fisheries Science Center (SEFSC), Beaufort, NC Lab unpublished data). Fourteen loggerheads remigrated in subsequent years; all were neritic animals.

Two of the turtles were male (1 oceanic and 1 neritic), 24 were female (7 oceanic, 11 neritic, and 6 unknown) and gender was not determined for 9 turtles (2 oceanic, 6 neritic, and 1 unknown) (NMFS SEFSC, Beaufort, NC Lab unpublished data). Genetic analysis of 26 loggerheads revealed 6 unique haplotypes (CC-A1, CC-A2, CC-A3, CC-A10, CC-A13, CC-A14) (Table 5) (NMFS SEFSC, Beaufort, NC Lab unpublished data). Of these, haplotype CC-A13 had not been identified on any nesting beach in the published literature, but had been documented in longline by-catch from the Northeast Atlantic Distant (NED) region (LaCasella et al. 2007) and termed “Azores foraging” in
Table 5: mtDNA haplotypes of loggerhead nesting populations in the Atlantic and Mediterranean as described in Bass et al. (2004), Bowen et al. (2004), Encalada et al. (1998), Bolten et al. (1998), and http://accstr.ufl.edu/ccmtdna.html including haplotypes found in our groups of neritic, oceanic, and unknown juvenile turtles from the North Carolina estuarine foraging aggregation. NED stands for NMFS Northeast Distant statistical zone.

<table>
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<tr>
<th>Rookery Size</th>
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<td>SFL</td>
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<td>NED</td>
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<td>Unknown</td>
<td>-</td>
</tr>
</tbody>
</table>
Bass et al. (2004). Most turtles (22) were either CC-A1 or CC-A2 haplotypes which are both common to several western Atlantic rookeries (Table 5). Rare haplotypes occurred only in 4 neritic turtles (Table 5).

**Stable isotopes**

I obtained stable isotope signatures from plasma samples from 28 turtles and rbc samples from 24 turtles (Table 6); blood samples were unavailable for 7 turtles. The trophic range of all loggerheads varied 5.2 ‰ and 5.2 ‰ for plasma and rbc δ^{15}N, (Figure 20 a and c), and varied 4.5 ‰ and 3.1 ‰ for plasma and rbc δ^{13}C, respectively (Figure 20 b and d). Among all turtles, differences between plasma and rbc isotope ratios were statistically different ($t_{33} = 10.4$, $p < 0.001$). Neritic turtles had significantly higher δ^{15}N values in both plasma ($t_{15} = 2.1$, $p = 0.02$) and rbcs ($t_{13} = 2.3$, $p = 0.02$) than oceanic turtles, but did not differ in δ^{13}C in either tissue (plasma $t_{15} = 0.7$, $p = 0.26$, rbc $t_{15} = 1.4$, $p = 0.10$). Plasma and rbc isotope ratios from unknown turtles were not statistically different from either neritic (δ^{15}N plasma $t_{8} = 0.5$, $p = 0.30$, rbc $t_{5} = 0.1$, $p = 0.45$; δ^{13}C plasma $t_{8} = 0.4$, $p = 0.35$, rbc $t_{5} = -0.3$, $p = 0.39$) or oceanic turtles (δ^{15}N plasma $t_{10} = 1.1$, $p = 0.16$, rbc $t_{5} = -1.0$, $p = 0.19$; δ^{13}C plasma $t_{10} = -0.1$, $p = 0.46$, rbc $t_{5} = 0.9$, $p = 0.2$).

Mean (± 1 SD) isotopic signature and elemental values for loggerhead turtles and potential prey are presented in Table 6. Standard deviations of carbon isotope ratios varied more than nitrogen ratios for most prey items (Table 6, Figure 21). Although there were no significant differences in δ^{13}C values between neritic and oceanic prey...
Table 6: Stable isotope signatures and elemental compositions of loggerhead sea turtles and potential prey items. Values are means (± 1 standard deviation). Sample size is denoted by n.

<table>
<thead>
<tr>
<th>Common Name</th>
<th>%N</th>
<th>%C</th>
<th>C:N</th>
<th>∂15N</th>
<th>∂13C</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Mixtures</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>loggerheads</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>plasma (n=28)</td>
<td>11.86 (0.85)</td>
<td>41.23 (1.99)</td>
<td>3.49 (0.20)</td>
<td>11.88 (1.48)</td>
<td>-17.57 (1.25)</td>
</tr>
<tr>
<td>rbc (n=24)</td>
<td>13.77 (1.01)</td>
<td>45.03 (3.31)</td>
<td>3.27 (0.02)</td>
<td>8.98 (1.41)</td>
<td>-17.48 (0.67)</td>
</tr>
<tr>
<td>neritic loggerheads</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>plasma (n=14)</td>
<td>11.90 (0.90)</td>
<td>41.11 (2.40)</td>
<td>3.46 (0.19)</td>
<td>12.33 (1.35)</td>
<td>-17.41 (1.26)</td>
</tr>
<tr>
<td>rbc (n=13)</td>
<td>13.71 (1.24)</td>
<td>44.82 (3.97)</td>
<td>3.27 (0.02)</td>
<td>9.30 (1.23)</td>
<td>-17.43 (0.61)</td>
</tr>
<tr>
<td>oceanic loggerheads</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>plasma (n=8)</td>
<td>11.90 (1.00)</td>
<td>41.47 (1.71)</td>
<td>3.50 (0.26)</td>
<td>11.04 (1.37)</td>
<td>-17.76 (1.20)</td>
</tr>
<tr>
<td>rbc (n=6)</td>
<td>14.18 (0.47)</td>
<td>46.59 (1.89)</td>
<td>3.28 (0.02)</td>
<td>8.14 (0.93)</td>
<td>-17.74 (0.37)</td>
</tr>
<tr>
<td>unknown loggerheads</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>plasma (n=6)</td>
<td>11.72 (0.62)</td>
<td>41.21 (2.42)</td>
<td>3.52 (0.12)</td>
<td>11.92 (1.66)</td>
<td>-17.69 (1.48)</td>
</tr>
<tr>
<td>rbc (n=5)</td>
<td>13.41 (0.78)</td>
<td>43.68 (2.41)</td>
<td>3.26 (0.02)</td>
<td>9.16 (2.20)</td>
<td>-17.27 (1.08)</td>
</tr>
<tr>
<td><strong>Neritic Sources</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>blue crab (n=4)</td>
<td>12.00 (1.36)</td>
<td>38.61 (2.70)</td>
<td>3.23 (0.15)</td>
<td>9.28 (0.38)</td>
<td>-16.26 (1.65)</td>
</tr>
<tr>
<td>horseshoe crab (n=10)</td>
<td>12.30 (0.89)</td>
<td>43.35 (2.31)</td>
<td>3.53 (0.10)</td>
<td>11.62 (0.46)</td>
<td>-16.97 (1.31)</td>
</tr>
<tr>
<td>spider crab (n=11)</td>
<td>12.77 (0.88)</td>
<td>41.68 (2.81)</td>
<td>3.27 (0.19)</td>
<td>10.65 (0.48)</td>
<td>-17.92 (1.33)</td>
</tr>
<tr>
<td>crabs (n=25)</td>
<td>12.46 (0.97)</td>
<td>41.86 (2.98)</td>
<td>3.37 (0.20)</td>
<td>10.82 (0.93)</td>
<td>-17.27 (1.46)</td>
</tr>
<tr>
<td>whelks (n=10)</td>
<td>13.09 (0.67)</td>
<td>44.76 (1.47)</td>
<td>3.42 (0.16)</td>
<td>9.41 (0.57)</td>
<td>-17.01 (0.70)</td>
</tr>
<tr>
<td>cannonball jellyfish (n=5)</td>
<td>5.86 (1.53)</td>
<td>26.18 (7.64)</td>
<td>4.44 (0.17)</td>
<td>7.92 (0.22)</td>
<td>-18.85 (0.08)</td>
</tr>
<tr>
<td><strong>Oceanic Sources</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>moon jellyfish (n=5)</td>
<td>0.97 (0.40)</td>
<td>4.03 (1.77)</td>
<td>4.08 (0.27)</td>
<td>8.52 (0.55)</td>
<td>-19.50 (0.58)</td>
</tr>
<tr>
<td>mauve stinger jellyfish (n=8)</td>
<td>3.43 (1.34)</td>
<td>14.76 (6.18)</td>
<td>4.17 (0.53)</td>
<td>4.61 (0.68)</td>
<td>-17.95 (0.51)</td>
</tr>
<tr>
<td>sea nettle jellyfish (n=6)</td>
<td>0.88 (0.20)</td>
<td>2.99 (0.66)</td>
<td>3.39 (0.24)</td>
<td>5.19 (0.25)</td>
<td>-17.20 (0.68)</td>
</tr>
<tr>
<td>lion’s mane jellyfish (n=1)</td>
<td>1.20 (0.00)</td>
<td>4.75 (0.00)</td>
<td>3.96 (0.00)</td>
<td>5.29 (0.00)</td>
<td>-17.46 (0.00)</td>
</tr>
<tr>
<td>filefish (n=10)</td>
<td>9.57 (0.93)</td>
<td>38.61 (2.59)</td>
<td>4.07 (0.44)</td>
<td>5.92 (1.02)</td>
<td>-18.60 (0.74)</td>
</tr>
<tr>
<td>yellow jack (n=5)</td>
<td>8.89 (0.35)</td>
<td>33.05 (1.62)</td>
<td>3.72 (0.09)</td>
<td>5.41 (0.28)</td>
<td>-17.84 (0.23)</td>
</tr>
<tr>
<td>jellies &amp; fish (n=35)</td>
<td>5.11 (3.92)</td>
<td>20.35 (15.46)</td>
<td>3.92 (0.46)</td>
<td>5.78 (1.39)</td>
<td>-18.20 (0.91)</td>
</tr>
<tr>
<td>Sargassum plant (n=10)</td>
<td>1.86 (0.68)</td>
<td>33.15 (4.01)</td>
<td>21.67 (13.42)</td>
<td>1.54 (1.62)</td>
<td>-16.09 (0.91)</td>
</tr>
<tr>
<td>Sargassum crab (n=10)</td>
<td>5.96 (1.30)</td>
<td>29.62 (3.79)</td>
<td>5.07 (0.67)</td>
<td>5.09 (1.13)</td>
<td>-15.55 (1.44)</td>
</tr>
<tr>
<td>Sargassum shrimp (n=8)</td>
<td>8.34 (0.57)</td>
<td>36.28 (2.06)</td>
<td>4.36 (0.30)</td>
<td>4.07 (0.65)</td>
<td>-16.66 (0.53)</td>
</tr>
<tr>
<td>Sargassum + (n=28)</td>
<td>5.18 (2.84)</td>
<td>32.78 (4.32)</td>
<td>10.80 (11.33)</td>
<td>3.53 (1.96)</td>
<td>-16.06 (1.11)</td>
</tr>
</tbody>
</table>
Figure 20: The isotopic range of loggerheads from plasma (A and B) and red blood cells (C and D). $\delta^{15}$N isotope ratios are in panels A and C and $\delta^{13}$C ratios are in panels B and D.
Figure 21: Bivariate plots of isotopic signatures of loggerhead sea turtles and potential prey. Points are means and error bars are ±1 standard deviation. Color scheme uses green for neritic turtles, yellow for unknown turtles, and blue for oceanic turtles. Boxes show segregation of neritic (green) and oceanic (blue) prey groups.
items ($t_{89} = -0.7$, $p = 0.25$), $\delta^{15}N$ values of neritic prey were significantly elevated relative to oceanic prey ($t_{100} = 16.4$, $p << 0.0001$) (Figure 21).

**Multivariate modeling**

The parameters that provided the best model fit for predicting turtle habitat destinations were remigration and $\delta^{15}N$ for both the conventional and bootstrapped logistic regression analyses and for both tissues (i.e., plasma and rbc; habitat $\sim \delta^{15}N +$ remigration). AIC values of one –, two –, three –, and four – parameter models are presented in Table 7.

**Table 7: AIC values for BRGLM logistic regression models.**

<table>
<thead>
<tr>
<th>Model</th>
<th>AIC plasma</th>
<th>AIC rbc</th>
</tr>
</thead>
<tbody>
<tr>
<td>habitat $\sim \delta^{15}N$</td>
<td>28.649</td>
<td>23.407</td>
</tr>
<tr>
<td>habitat $\sim \delta^{13}C$</td>
<td>32.374</td>
<td>26.270</td>
</tr>
<tr>
<td>habitat $\sim$ size</td>
<td>40.470</td>
<td>40.470</td>
</tr>
<tr>
<td>habitat $\sim$ remigration</td>
<td>21.715</td>
<td>21.715</td>
</tr>
<tr>
<td>habitat $\sim \delta^{15}N + \delta^{13}C$</td>
<td>27.573</td>
<td>25.486</td>
</tr>
<tr>
<td>habitat $\sim \delta^{15}N +$ size</td>
<td>30.407</td>
<td>24.662</td>
</tr>
<tr>
<td>habitat $\sim \delta^{15}N +$ remigration</td>
<td>13.769</td>
<td>13.517</td>
</tr>
<tr>
<td>habitat $\sim \delta^{13}C +$ size</td>
<td>34.356</td>
<td>28.319</td>
</tr>
<tr>
<td>habitat $\sim \delta^{13}C +$ remigration</td>
<td>19.979</td>
<td>14.876</td>
</tr>
<tr>
<td>habitat $\sim$ size + remigration</td>
<td>23.720</td>
<td>23.720</td>
</tr>
<tr>
<td>habitat $\sim \delta^{15}N + \delta^{13}C +$ size</td>
<td>28.534</td>
<td>26.785</td>
</tr>
<tr>
<td>habitat $\sim \delta^{15}N + \delta^{13}C +$ remigration</td>
<td>12.801</td>
<td>15.594</td>
</tr>
<tr>
<td>habitat $\sim \delta^{13}C +$ size + remigration</td>
<td>21.491</td>
<td>17.270</td>
</tr>
<tr>
<td>habitat $\sim$ size + remigration</td>
<td>16.127</td>
<td>15.760</td>
</tr>
<tr>
<td>habitat $\sim \delta^{15}N + \delta^{13}C +$ size + remigration</td>
<td>19.467</td>
<td>19.292</td>
</tr>
</tbody>
</table>

Remigration was significant in both regression methods (plasma $p_{\text{BRGLM}} = 0.022$, $p_{\text{bootstrapBRGLM}} = 0.0001$, rbc $p_{\text{BRGLM}} = 0.020$, $p_{\text{bootstrapBRGLM}} = 0.0001$), while $\delta^{15}N$ was only
significant bootstrapped analysis of plasma (plasma $p_{BRGLM} = 0.097$, $p_{bootstrapBRGLM} = 0.019$, rbc $p_{BRGLM} = 0.199$, $p_{bootstrapBRGLM} = 0.097$) (Table 8). However, because of the perfect separation in remigration data (i.e., only neritic animals remigrated), the regression models may have artificially deflated the significance of the $\delta^{15}$N variable. The standard errors of the bootstrapping results were similar to the conventional BRGLM (Table 8) indicating that my model results were robust.

Table 8: Logistic regression results of the best-fit model predicting turtle habitat destinations. * indicates statistically significant variables.

a. Penalized maximum likelihood results

<table>
<thead>
<tr>
<th>Coefficients</th>
<th>Estimate</th>
<th>Standard Error</th>
<th>Z-value</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>plasma</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>intercept</td>
<td>15.670</td>
<td>9.187</td>
<td>1.706</td>
<td></td>
</tr>
<tr>
<td>$\delta^{15}$N</td>
<td>-1.219</td>
<td>0.733</td>
<td>-1.662</td>
<td>0.097</td>
</tr>
<tr>
<td>remigration</td>
<td>-5.153</td>
<td>2.249</td>
<td>-2.292</td>
<td>0.022*</td>
</tr>
</tbody>
</table>

b. Bootstrap results

<table>
<thead>
<tr>
<th>Coefficients</th>
<th>Mean</th>
<th>Standard Error</th>
<th>2.5 % LCL</th>
<th>97.5 % UCL</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>plasma</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>intercept</td>
<td>18.204</td>
<td>10.084</td>
<td>3.174</td>
<td>45.832</td>
<td></td>
</tr>
<tr>
<td>$\delta^{15}$N</td>
<td>-1.423</td>
<td>0.838</td>
<td>-3.694</td>
<td>-0.057</td>
<td>0.019*</td>
</tr>
<tr>
<td>remigration</td>
<td>-5.505</td>
<td>1.699</td>
<td>-10.138</td>
<td>-3.435</td>
<td>0.0001*</td>
</tr>
</tbody>
</table>

rbc

<table>
<thead>
<tr>
<th>Coefficients</th>
<th>Mean</th>
<th>Standard Error</th>
<th>2.5 % LCL</th>
<th>97.5 % UCL</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>intercept</td>
<td>10.123</td>
<td>8.327</td>
<td>-0.257</td>
<td>28.321</td>
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</tr>
<tr>
<td>$\delta^{15}$N</td>
<td>-1.029</td>
<td>1.002</td>
<td>-3.266</td>
<td>0.291</td>
<td>0.097</td>
</tr>
<tr>
<td>remigration</td>
<td>-4.272</td>
<td>1.019</td>
<td>-6.102</td>
<td>-2.589</td>
<td>0.0001*</td>
</tr>
</tbody>
</table>
**Turtle trophic niche**

Bivariate plots (Figure 22) of isotopic signature demonstrate the mixing space of potential prey groups, in which proximity to the source indicates the greatest contribution to the diet (Phillips & Gregg 2001). Isotopic signatures of neritic turtles were nearest to the neritic crabs and whelks for plasma (*i.e.*, recent foraging), while those of oceanic turtles were more removed from these prey items and centered in the mixing polygon towards jellyfish (Figure 22a). The isotope signatures of the unknown turtles were intermediate to the oceanic and neritic turtles for plasma samples. All turtles fell within the perimeter of prey values (Figure 22a).

The case for the rbcs (*i.e.*, protracted foraging) was slightly different. In these cases all turtles were shifted to the right side of the mixing space and were unbounded by prey (Figure 22b), but they still remained in the mixing polygon because my model encompasses the entire range of data, not just the mean values. Neritic and unknown turtles were found higher along the $\delta^{15}$N axis and nearest to whelks. Oceanic turtles were lower in both $\delta^{15}$N and $\delta^{13}$C and toward the *Sargassum* community (Figure 22b). In both the plasma and rbc samples (*i.e.*, between summer foraging and overwintering seasons), there was a clear distinction between neritic and oceanic turtle groups in the direction expected based on their habitat assignment derived from satellite tracking (Figure 23). Thus, the combined telemetry and stable isotope data indicate that oceanic turtles exploited pelagic prey items to a greater degree than neritic turtles and neritic
Figure 22: Results of SIAR Bayesian mixing model showing the trophic mixing space shaped by potential neritic and oceanic prey. Values indicate the most likely proportional contribution of each diet item where green stands for neritic turtles, yellow for unknown turtles, and blue for oceanic turtles. A. Results from blood plasma samples (recent foraging history). B. Results for red blood cell samples (protracted foraging history).
turtles were feeding on benthic prey to a greater degree than oceanic turtles. The isotope signatures of the unknown turtles were intermediate to the oceanic and neritic turtles for rbc samples.

Figure 23: Mean (± 1 standard deviation) $\delta^{15}$N values of plasma (summer; squares) and red blood cells (winter; circles) for turtle groups demonstrating clear seasonal shifts in foraging behavior consistent with movement polymorphisms documented by satellite tracking.

The potential foraging solutions produced by the SIAR mixing model for my plasma samples demonstrate that benthic crabs made up the largest contribution to the summer and autumn diets of neritic turtles (median, 95th% CI; 41%, 16 – 70%), followed by whelks (29%, 0.3 – 53%) (Table 9a, Figure 24a). The median values of the probability density functions are the most likely level of contribution to the diet, but solutions could fall anywhere within the credibility intervals (CI) (Parnell et al. 2008, Jackson et al. 2009).
Table 9: Bayesian mixing model results of median and 95th% credibility intervals of proportional prey contributions to loggerhead diets.

a. neritic loggerheads

<table>
<thead>
<tr>
<th>Prey Type</th>
<th>Median</th>
<th>2.5 % LCI</th>
<th>97.5 % UCI</th>
</tr>
</thead>
<tbody>
<tr>
<td>plasma</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>crabs</td>
<td>0.41</td>
<td>0.16</td>
<td>0.70</td>
</tr>
<tr>
<td>whelks</td>
<td>0.29</td>
<td>0.003</td>
<td>0.53</td>
</tr>
<tr>
<td>cannonball jellyfish</td>
<td>0.12</td>
<td>0</td>
<td>0.33</td>
</tr>
<tr>
<td>jellies &amp; fish</td>
<td>0.08</td>
<td>0</td>
<td>0.23</td>
</tr>
<tr>
<td>Sargassum +</td>
<td>0.06</td>
<td>0</td>
<td>0.16</td>
</tr>
<tr>
<td>rbc</td>
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<td></td>
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</tr>
<tr>
<td>crabs</td>
<td>0.11</td>
<td>0</td>
<td>0.25</td>
</tr>
<tr>
<td>whelks</td>
<td>0.14</td>
<td>0</td>
<td>0.31</td>
</tr>
<tr>
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<td>0.16</td>
<td>0</td>
<td>0.34</td>
</tr>
<tr>
<td>jellies &amp; fish</td>
<td>0.25</td>
<td>0.01</td>
<td>0.43</td>
</tr>
<tr>
<td>Sargassum +</td>
<td>0.33</td>
<td>0.20</td>
<td>0.33</td>
</tr>
</tbody>
</table>

b. oceanic loggerheads

<table>
<thead>
<tr>
<th>Prey Type</th>
<th>Median</th>
<th>2.5 % LCI</th>
<th>97.5 % UCI</th>
</tr>
</thead>
<tbody>
<tr>
<td>plasma</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>crabs</td>
<td>0.24</td>
<td>0.02</td>
<td>0.43</td>
</tr>
<tr>
<td>whelks</td>
<td>0.22</td>
<td>0.001</td>
<td>0.40</td>
</tr>
<tr>
<td>cannonball jellyfish</td>
<td>0.21</td>
<td>0.003</td>
<td>0.40</td>
</tr>
<tr>
<td>jellies &amp; fish</td>
<td>0.19</td>
<td>0</td>
<td>0.37</td>
</tr>
<tr>
<td>Sargassum +</td>
<td>0.13</td>
<td>0</td>
<td>0.28</td>
</tr>
<tr>
<td>rbc</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>crabs</td>
<td>0.05</td>
<td>0</td>
<td>0.20</td>
</tr>
<tr>
<td>whelks</td>
<td>0.08</td>
<td>0</td>
<td>0.26</td>
</tr>
<tr>
<td>cannonball jellyfish</td>
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</table>
c. unknown loggerheads

<table>
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<tr>
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<th>97.5 % UCI</th>
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<td>0.04</td>
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Cannonball jellyfish were consistently represented in only the oceanic turtles in my study, although it is likely that the other turtles occasionally consume them (Table 9, Figure 24). My mixing model results suggested that crabs and whelk were also a consistent part of the diet for loggerheads with unknown migratory destinations but to a lesser degree than for neritic loggerheads (Table 9a, c, Figure 24). Model solutions for plasma samples always represented benthic prey items as a greater part of the diet for neritic turtles than for oceanic turtles (Figure 22a). Results from the SIAR mixing model for rbc samples consistently included the Sargassum community and oceanic jellies and fish for all three groups of turtles while at the same time the proportion of neritic crabs and whelks sharply declined from plasma samples (Table 9, Figure 24). Median values per prey type were relatively even among turtle groups (Figure 22).
Figure 24: Results of SIAR Bayesian mixing model showing 95th, 75th, and 50th% credibility intervals of feasible prey contributions to neritic, oceanic, and unknown turtle diets. The series of plots in A. are from plasma samples and B. are from red blood cell samples.
Discussion

Variation in habitat use and feeding strategies among individual animals from the same population can be manifested in variation in expression of life history traits, such as survivorship, growth rates, fecundity, and thus can differentially influence population dynamics. In this study I was able to differentiate turtles exhibiting two divergent migratory strategies (Chapter 3) on the basis of diet composition determined by stable isotope ratios and remigration histories. Specifically, I demonstrated that turtles that use open-ocean habitats have lower stable nitrogen isotope ratios than do turtles that remain within neritic areas, indicating dietary dichotomy among juvenile loggerheads from the same population. Although stable isotope signatures reflected dietary histories of loggerheads prior to determination of spatial habitat use via satellite telemetry, the agreement between the dietary compositions and migration patterns between the two groups of turtles suggest that these feeding and habitat use strategies were persistent characteristics in the turtles sampled. Thus I conclude that a clear dichotomy exists whereby at least two different groups of turtles exhibit significant variation in foraging behaviors (e.g., oceanic versus neritic), with other turtles (e.g., unknowns) not showing a clear preference for either extreme. These behavioral polymorphisms could be driving inter-individual variation in somatic growth rates (Braun-McNeill et al. 2008) and survivorship (Sasso et al. 2007) observed in this population. Long-term mark-recapture studies, combined with supporting information from other sources, such as satellite telemetry, stable isotope analyses, and genetic
analyses can elucidate complex life cycle and life history patterns for enhanced conservation management approaches.

In addition to the dichotomy in feeding strategy that I identified between oceanic and neritic turtles, I also found evidence of seasonal dietary shifts within the two groups. Because of the different time periods that rbcs (i.e., long-term) and blood plasma (i.e., short-term) integrate loggerhead dietary histories, I was able to identify a shift in $\delta^{15}$N signatures that corresponded to an offshore-inshore seasonal movement in both groups of turtles. Benthic invertebrates dominated the putative summer and autumn diets of the turtles, but cannonball jellyfish were only consistently present in the oceanic turtles’ diet, demonstrating their selection of pelagic prey. However, when looking at a more extended temporal window of foraging, as I did through the use of rbcs, I found that all groups of turtles fed on pelagic prey items (Table 9). Seminoff et al. (2007) cautioned against seasonal inference from SIA; however, I believe my results are showing seasonal changes in foraging behavior (Figure 23). Juvenile and loggerhead adult loggerheads routinely overwinter off North Carolina near the warm waters of the Gulf Stream (Keinath 1993, Epperly et al. 1995a, c, Mansfield 2006, Hawkes et al. 2007, Chapter 3) giving them access to oceanic fauna aggregated in frontal eddies. If overwintering sites are as consistent as summer foraging areas, which is likely, then from my satellite tracks I can infer that these loggerheads were feeding opportunistically in the epipelagia at the edge of the Gulf Stream during the previous winter and spring.
Unknown turtles were intermediate and likely contain both neritic and oceanic animals (Figure 23).

The fact that I was able to identify this behavioral polymorphism in rapidly assimilated blood plasma during a metabolically active period of the year suggests that, despite their size, the oceanic turtles may not yet have been successful benthic foragers. Four of the 10 oceanic turtles were caught multiple times within their tagging season, indicating that they were consistently sampling the neritic environment, although they chose not to stay there. On the other hand, turtles that demonstrated the classical case of neritic settlement exhibited higher nitrogen isotope values and site fidelity within and between seasons. For these neritic animals at least, North Carolina estuaries provided a reliable and productive developmental foraging habitat.

Benthic crustaceans are found on the continental shelf throughout the year, although their abundance and distribution varies seasonally (Stehlik et al. 1991, Viscido et al. 1997). Demersal crabs are generally in low abundance in the winter in the Mid-Atlantic Bight, but shrimp can be abundant (Viscido et al. 1997). Brachyurans such as the rock crab (*Cancer irroratus*) migrate across the shelf into nearshore waters during the winter while lady crabs (*Ovalipes ocellatus*) remain in shallower areas throughout the year and likely burrow in the winter (Stehlik et al. 1991). I did not sample benthic invertebrates on the continental shelf so I am unable to directly compare isotopic signatures with estuarine samples, but my values were similar to epibenthic invertebrates from the Newfoundland and Labrador shelf regions (Sherwood & Rose
The decline in the contribution of neritic, benthic prey items between plasma and rbc samples, indicates that they were rarely consumed outside of the summer and autumn foraging season.

Some authors have suggested that sea turtles hibernate or become dormant in the winter based on signature dive profiles (Ogren & McVea 1995, Hochscheid et al. 2005, Hawkes et al. 2007) and therefore might not feed during this period. However, Hochscheid et al. (2007) noted that overwintering behavior is temperature dependent and that loggerheads maintain some movement and potentially feed during the winter. Turtles inhabiting the warm waters along the Gulf Stream would be metabolically active and therefore likely continue to feed at some level. When resources are in short supply and animals undergo starvation, $\delta^{15}N$ values increase as animals catabolize their own tissue proteins (Perga & Gerdeaux 2005), although this potential has not been evaluated in reptiles. The lower $\delta^{15}N$ values in the rbcs suggest instead that turtles switched to feeding on oceanic prey items.

Neritic prey items nearly disappeared from the diet in rbc samples of oceanic turtles which had significantly lower $\delta^{15}N$ than neritic turtles. This implies that the turtles I categorized as oceanic post-tagging were likely feeding in the open ocean prior to their arrival in North Carolina estuaries. *Sargassum* often occurs in dense mats and provides a host of associated fauna (Coston-Clements et al. 1991), likely accounting for a third of their diet based on my mixing model. In particular, mauve stingers have been described as an important part of oceanic loggerhead diets (Bolten & Balazs 1995).
found that pelagic jellies and juvenile fishes probably made up a third of the diet of oceanic loggerheads in this study. Gross energy densities of jellyfish are about three times lower than marine alga and eight times lower than fish (Doyle et al. 2007), but can sustain marine turtles (Lutcavage & Lutz 1996, Wallace et al. 2006a). Nutrient content is higher in gonadal and arm tissue than bell tissue (Doyle et al. 2007), but turtles probably consume smaller jellyfish whole. Isotopic signatures of moon jellies were more similar to cannonball jellyfish in my samples, which were again consistent diet items only for oceanic turtles. Both of these jellyfish are commonly found in continental shelf waters (Calder 1982, Lucas 2001). Interestingly, cannonball jellyfish frequently maintain an association with spider crabs, carrying a post-larval sized crab in their bell (Gutsell 1928), but I have no information on whether they may be consumed together or whether the crab escapes. Spider crabs were only a limited component of immature loggerhead diets reported in Wallace et al. (in press).

Smith et al. (1996) demonstrated a distinct freshwater to marine gradient in $\delta^{13}$C values in diets of three sub-species of harbor seals (*Phoca vitulina*). I was surprised to find no difference in $\delta^{13}$C for either turtle or prey samples. It may be that the spatial gradient in $\delta^{13}$C is not as distinct within the marine environment as it is between freshwater and marine environments. Along the North Carolina coast, the Gulf Stream is a fluid barrier between the continental shelf waters and the Sargasso Sea; however, it also exchanges water between these two provinces by entrainment and meanders at various times of the year (Pietrafesa et al. 1985, Gross 1987, Olson 2001). My oceanic
prey samples were similar in $\delta^{15}$N and only slightly more enriched in $\delta^{13}$C compared to those reported in the Mediterranean Sea (Revelles et al. 2007) and the western Pacific Ocean (Hatase et al. 2002). $\delta^{13}$C was highly variable in prey samples resulting in shifting turtle isotope signatures outside of the center of the mixing space for rbc samples in this study and the skin tissue of Revelles et al. (2007), but not for my plasma samples. Such decoupling of carbon and nitrogen incorporation rates has been reported in other isotope studies, but is not well understood (Seminoff et al. 2007, Reich et al. 2007, Arthur et al. 2008). Despite these complexities, I was able to demonstrate a clear difference in the trophic level of feeding.

In addition to diet selectivity, my groups of neritic and oceanic turtles were distinguished by their later patterns of remigration into estuarine waters. In the six years since I began satellite tracking these turtles, none of the oceanic turtles have returned to North Carolina estuaries (based on satellite tracks and re-capture data). On the other hand, approximately 80% of the neritic turtles remigrated in the following year (Chapter 3) showing a characteristic pattern of strong site fidelity to their capture location (Avens et al. 2003). Some turtles visit other nearby neritic foraging grounds (my unpublished data) for reasons yet not understood, but these animals do not move routinely between the oceanic and neritic habitats.

I did not find variation in life history strategy to be related to body size (Chapter 3). Size morphs have been found in adult female loggerheads where smaller females migrate to pelagic feeding habitats and larger females remain in the neritic habitat.
(Hatase et al. 2002, Hawkes et al. 2006), but not in green turtles (Hatase et al. 2006). Within the North Carolina loggerhead population, Braun-McNeill et al. (2008) found a large variability in size at recruitment and in growth rates which resulted in an elongated neritic stage duration of 16 – 23 years for turtles between 50 – 80 cm SCL (Braun-McNeill et al. 2008). Their longest re-capture record of juvenile loggerheads from North Carolina is 7 years, where turtles range in size from 45.1 – 86.5 cm SCL (Braun-McNeill et al. 2008). Habitat choice may contribute to much of the observed variation in growth rates via resource availability and energy expenditure (Hatase et al. 2004, Hatase & Tsukamoto 2008, Braun-McNeill et al. 2008, Wallace et al. in press). I could not assess growth rates in oceanic turtles in my study because they have not yet been recaptured.

Ultimately I was not able to rule out a potential role of sex and haplotype in the observed life history variability, but it seems clear that neither of these factors are strong explanatory candidates. In my study, large juvenile female turtles seemed equally likely to return to the open ocean as they were to remain within coastal waters. When beach specific primers are developed, I could explore the potential for a role of inherited behavior, although it has been argued that plasticity is favored in populations migrating through spatially variable environments (Kingsolver et al. 2002). Loggerhead turtles are probably using more proximate environmental cues and experiences to make decisions on habitat selection; the ultimate basis for such decisions is often difficult to characterize in highly migratory large vertebrates.
The combination of satellite telemetry and the collection of biological data allowed me to explain some of this life history variability in juvenile loggerhead sea turtles captured in North Carolina. A natural extension of this work would be to develop stable isotope markers that could directly identify behavioral phenotypes. Moreover a bioenergetic assessment of variation in dietary composition would provide insight into variability in growth rates and improve stage duration estimation through simulations similar to those in Snover (2008).
Synthesis

The study of movement ecology is coming into an age of its own (Holden 2006). Because we cannot directly observe the lives of marine mega-fauna, biotelemetry allows us to track wild animals remotely across vast expanses of ocean for up to several years at a time. This approach offers the potential to address research questions pertaining to ecology, behavior, life history, and conservation (Cooke 2004). The goals of my dissertation were to employ satellite telemetry to collect empirical data on the movements and habitat use of juvenile loggerhead (Caretta caretta), green (Chelonia mydas), and Kemp’s ridley (Lepidochelys kempii) sea turtles and to use these data to describe aspects of their ecology and conservation. I identified the patterns of habitat use and individual variation in these patterns. I was able to test directly the concept of discrete ontogenetic shifts in habitat and diet of juvenile loggerhead turtles and to evaluate current conservation measures designed for the recovery of their populations. My work has improved our understanding of sea turtle habitats in North Carolina estuaries and identified the areas where these turtles migrate and overwinter. This research also lays the groundwork for future studies that will explore how variation in habitat use and feeding strategies can be manifested in variation in life history traits that affect fitness directly, such as survivorship, growth rates, stage durations, and fecundity.

I began by tracking individual turtles in North Carolina estuaries to examine how their patterns of habitat use in space and time overlapped with a large-mesh gill net.
fishery for flounder that had a history of sea turtle by-catch. I used these near real-time data to evaluate state and federal management measures established to reduce by-catch levels. I found species-specific habitat preferences that contributed to their risk of encountering fishing gear and was able to predict areas of high by-catch from patterns of overlap between sea turtle habitat use and flounder fishing effort. My research supported a controversial federal management decision to close the autumn deepwater gill net fishing area in Pamlico Sound to mitigate the by-catch of loggerhead and Kemp’s ridley turtles.

I also found that this current suite of conservation measures did not reduce the by-catch of green turtles, because they restricted fishing effort to shallow water seagrass habitat that is preferred by these turtles. I was able to identify several behaviors that put green turtles at risk to incidental capture in large-mesh gill nets during the summertime. Green turtles used very small foraging areas and both turtles and fishers preferred seagrass edges near structures (i.e., shore, shoals, and marsh islands). Gill nets set over a tidal cycle in an established foraging site are highly likely to encounter green turtles. Furthermore, I established that turtles interacted with multiple gears within a season which could result in detrimental physiological effects even if the turtle is released alive from each encounter with fishing gear.

One of the most notable and serendipitous aspects of my research occurred after the turtles left North Carolina estuaries in the autumn. I described the variability in
loggerhead site fidelity and migratory destinations. I found that juvenile loggerheads
do not all migrate south for the winter; many overwinter off North Carolina near the
dge of the Gulf Stream and return to their site of capture the following year.
Remarkably, however, about one third of the turtles returned to the open ocean for up to
several years. This led me to conclude that the long held notion of a discrete ontogenetic
habitat shift between the oceanic and neritic habitat was incorrect for juvenile
loggerheads (and possibly greens). These results have profound consequences for both
the description of sea turtle life histories and for their conservation as they remain
vulnerable to largely unregulated fisheries in the high seas for longer periods than
previously appreciated.

I pursued the potential ecological drivers of this variability in movement
behavior and investigated whether these behaviors were persistent over time. I
discovered that migratory destination was not likely to be related to genetic stock
structure, sex, or size of the turtles. Through the use of stable isotope analysis, however,
I found that variation in these movement behaviors was related to foraging selectivity.
The dietary histories of these turtles were consistent with the movement behaviors I
observed through satellite telemetry. The isotopic signatures of loggerheads that
remained in neritic waters were similar to potential benthic prey items I sampled from
the estuary, in contrast to the turtles that returned to the oceanic realm, whose
signatures were similar to pelagic prey I sampled in the Gulf Stream. I was able to also
find a seasonal signal by using multiple tissues of differing fractionation rates. It appears that oceanic turtles feed epipelagically in the open ocean prior to their arrival in North Carolina estuaries while neritic turtles were likely feeding on pelagic prey associated with the Gulf Stream in the months before capture. These data were consistent with my telemetry findings which suggested a persistence of individual behaviors over time. This part of my research may be useful for understanding variation in growth rates and determining stage durations upon which conservation measures are guided.

Despite decades of local and international conservation efforts, many sea turtle populations are still threatened by the collateral damage of anthropogenic activities. In North Carolina, juvenile turtles encounter a variety of fisheries while foraging during the summer and autumn months and on their overwintering grounds during the winter and spring months. We now know that many of these turtles are also at continued risk of incidental capture in high seas fisheries throughout the year. Elucidation of species-specific habitat preferences and behaviors has enhanced our understanding of these encounters. These types of data have been used in the past to improve exploitation of a resource (Parrish 1999), but here I have presented them explicitly in the context of design or improvement of conservation measures (Parrish 2005). I have provided a specific case study for inshore gill net fisheries. A further extension of these data would be to explore the potential of dynamic marine reserves (Hooker & Gerber 2004).
Although some aspects of my research did not come to fruition within my dissertation, I hope to continue to explore them in the future. Specifically, as improvements in quantitative approaches for analyzing animal movement data in dynamic contexts are developed (Schick et al. 2008), I hope to determine important environmental factors influencing the habitat selection of sea turtles in both neritic and oceanic waters. I would like to delve further into the study of oceanic features such as major boundary currents, fronts, and eddies as oceanic habitats for marine turtles and other fauna and determine whether these individuals are actively seeking out regions within the North Atlantic gyre, or whether they are passively drifting in surface currents. It is my hope that as we continue to uncover aspects of the ecology of marine organisms, that this information will be embraced and applied to the conservation of our oceans.
Appendix A

Comparison of location accuracy estimates reported by Service Argos, Inc. (LC = location class) and pre-deployment transmitter evaluation measured as deviation from true location following Hays et al. (2001) \( (\sigma_x = 1 \text{ standard deviation of location error in longitude}, \sigma_y = 1 \text{ standard deviation of location error in latitude}) \). Deviation is the mean \((\pm 1 \text{ standard deviation})\) distance from the true location.

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<th>Messages Received</th>
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<th>( \sigma_y ) (km)</th>
<th>Deviation (km)</th>
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Appendix B

Results of the Williamson Spatial Overlap Index (SOI), sea turtle by-catch, and sea turtle strandings for each PSGNRA by fishery week. ♦ denotes Hurricane Isabel.

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Biography

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Doctor of Philosophy, Environment (May 2009)
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Publications


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Student Travel Awards to attend and present at the International Symposium on Sea Turtle Biology and Conservation (2004 (San Jose, Costa Rica), 2005 (Savannah, GA), 2006 (Crete, Greece), 2007 (Myrtle Beach, SC)) and the Biologging II Conference in St. Andrew’s, Scotland (2005)


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