Surfacing Behavior of Juvenile Loggerhead Sea Turtles (*Caretta caretta*) in North Carolina

By

B. Wren Patton

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Abstract approved:

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Selina Heppell

Sea turtles are endangered species that can be censused with aerial surveys, but the number of turtles in an area must be extrapolated to include animals that are submerged. Twenty-one satellite tags were attached to juvenile loggerhead sea turtles (*Caretta caretta*) in North Carolina. I analyzed surfacing and dive behavior recorded by the tags to determine whether time of day, time of year, location or wave height were important factors for development of more accurate population estimates in aerial surveys. I also analyzed differences in percent time at the surface based on a tag's salt water switch and its depth gauge. I found significantly greater surfacing during the day during April-June for two turtles and greater surfacing during the night during October-December for four turtles. Turtles in offshore habitats surfaced more often than those in inshore and nearshore habitats. Only one turtle that experienced wave heights greater than 2.5m showed a negative correlation between surfacing and wave height. The depth gauge consistently recorded an order of magnitude greater percent time near the surface than the salt water switch, and overall trends in behavior were different, suggesting the salt water switch is inadequate for recording surfacing events for aerial survey extrapolations.

Key Words: Loggerhead sea turtle, *Caretta caretta*, surfacing behavior, satellite telemetry, salt water switch, depth gauge, wave height, time at depth

Corresponding e-mail address: B.Wren.Patton@msn.com

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APPROVED:

Mentor, representing Fisheries & Wildlife

Committee Member, representing Zoology

Committee Member, representing the National Oceanic and Atmospheric Administration

Chair, Biology Program

Chair, Department of Fisheries & Wildlife

Director, International Degree

Dean, University Honors College

I understand that my project will become part of the permanent collection of Oregon State University, University Honors College. My signature below authorizes release of my project to any reader upon request.

B. Wren Patton, Author

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Introduction

Project Initiative

As a NOAA Hollings Scholar Intern, I worked with the NMFS Beaufort Laboratory, North Carolina, on a study concerning surfacing intervals of juvenile loggerhead sea turtles. While there, I participated in the tagging, tracking, and data analysis of satellite-tagged loggerhead sea turtles. I was a co-author on the original publication, "Surfacing behavior of loggerhead (*Caretta caretta*) sea turtles in estuarine and coastal waters of North Carolina", a NOAA Technical memorandum (Braun-McNeill et al 2010). I was given permission to continue working with the data for this undergraduate thesis.

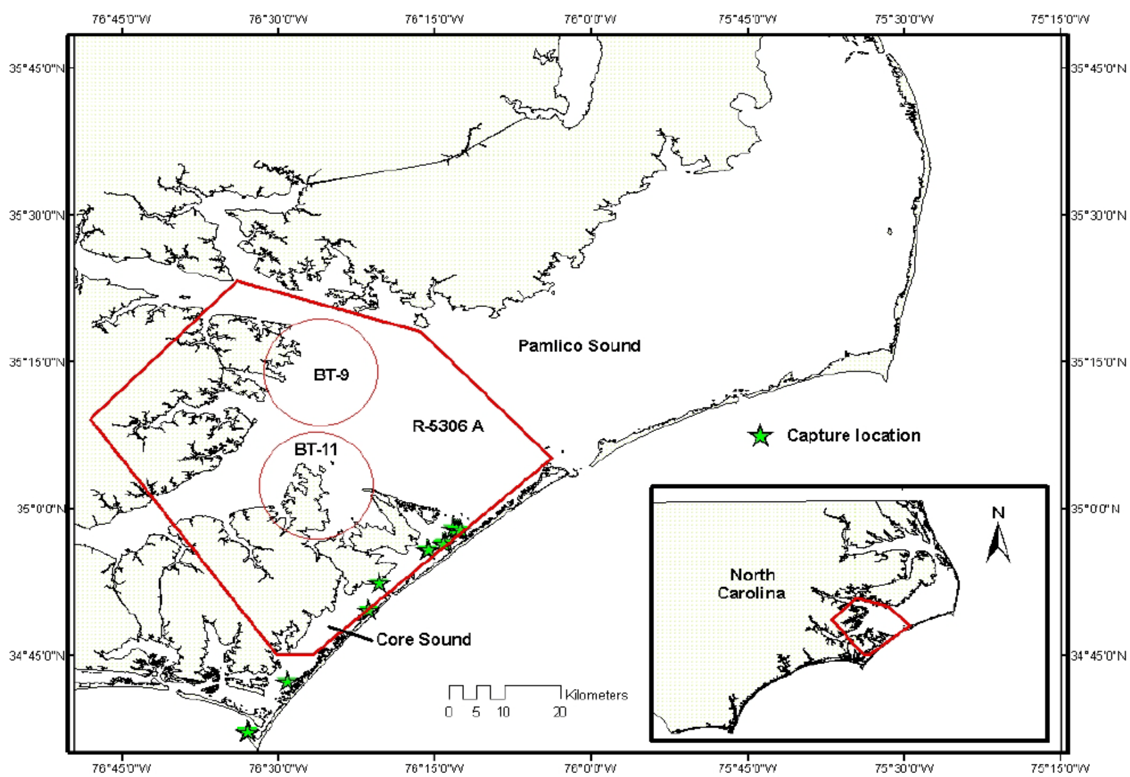

Figure 1. Locations of sea turtle capture in Core and Pamlico Sounds, N.C., USA. Green stars indicate capture locations, red lines show perimeter of restricted airspace R5306A, while red circles depict bombing targets BT-9 and BT-11. Image reproduced from NOAA Technical Memorandum NMFS-SEFSC-605 (Braun-McNeill et al 2010).

The initial study was instigated in response to the U.S. Navy's request for population estimates of sea turtles. Loggerhead, green (*Chelonia mydas*) and Kemp's ridly (*Lepidochelys kempii*) utilize the waters of North Carolina as both developmental and foraging habitat (Avens et al 2003). The U.S. Navy conducts training exercises at two bombing ranges (BT-9 and BT-11) that include habitat commonly used by sea turtles. Because sea turtle species are protected under the Endangered Species Act, the National Marine Fisheries Service (NMFS) was contracted to estimate the number and distribution of turtles in the two areas. Accurate population size and seasonal distribution estimates are required for Section 7 consultation, part of the ESA that requires federal agencies and the military to determine risks associated with permitted activities (http://www.nmfs.noaa.gov/pr/laws/esa/).

Aerial abundance surveys were conducted from July 2004 to April 2006 to count turtles in and around the bombing ranges (Goodman et al. 2007). However, the proportion of turtles below the surface (and therefore undetectable from the air) is unknown for North Carolina's juvenile loggerheads. Surfacing behavior of sea turtles has been studied in Virginia and Georgia, and behavior has been shown to vary by both season and region (Epperly et al 1995b; Mansfield 2006). To determine surfacing behavior for North Carolina turtles, 20 loggerheads were equipped with satellite tags. Turtles were found to spend 0.1 to 12.5% of their time on the surface of the water based on a salt water switch which records time spent directly at the surface (Braun-McNeill et al 2010). Because it was reasoned that turtles near, but not directly at, the surface of the water would be visible in an aerial survey up to depths of one meter during normal turbidity and cloud conditions, percent time spent within one meter of the surface was also examined. Near surface was found to be 23% at minimum. These percentages were utilized to produce the correction factor for the aerial surveys in order to account for unseen turtles. Corrected densities ranged from 0.01 to 2.2 turtles/km^2 in the sounds and from 0.2 to 25.6

turtles/km^2 in the coastal region. Corrected abundance estimates ranged from 16 to 4,997 turtles in the sounds and from 44 to 3,552 turtles in the coastal region (Braun-McNeill et al 2010).

Because there are many intrinsic and extrinsic factors influencing a turtle's behavior, it is important to identify which factors can bias efforts to extrapolate aerial survey counts in different areas. In our original report, we focused on differences in surface time for turtles in estuarine versus nearshore waters, as depth has been shown to play a major role in feeding and diving patterns (Bjorndal 1997; Pritchard 1997). Based on my literature review, I hypothesized that other factors could also be important, such as time of day and season. A large body of research has shown that loggerheads and other marine turtle species show significantly different surfacing behavior by time of day (Parrion 1958; Schwartz and Jensen 1991; Revelles et all 2007), season (Schwartz and Jensen 1991; Nelson 1996; Dellinger and Freitas 2000; Godley et al 2003; Hatase et al 2006; Mansfield 2006; Revelles et al 2007), and location (Mansfield 2006; Cardona et al 2005; Dellinger and Freitas 2000; Howell 2010). I was interested in determining whether it was possible to isolate the most important drivers of the variation in surfacing behavior. If, for example, time of day was a major determinant of variation in surfacing behavior, a more accurate population estimate from an aerial survey might be obtained if the correction factor did not include night surfacing behaviors, as aerial surveys are never conducted in the dark. A more accurate knowledge of differences in day versus night behavior can also be useful to understand and predict potential for interactions with boats and fishing gear. The first goal of my study was to examine the dive patterns of the tagged turtles in relation to these factors, in addition to a more in-depth analysis of differences based on location. I consequently examined surfacing behavior based on the salt water switch and the depth gauge independently over time of year, time of day, habitat type (inshore, nearshore, and offshore) and individual turtle.

Both the saltwater switch and depth gauge on a satellite tag have inherent unreliabilities that may prevent accurate indication of time spent on or near the surface (Braun-McNeill et al 2010). McClellan and Read (2007) noted that the salt water switch may not be triggered with each surfacing event if the turtle raises only its head to breath, leaving the salt water switch below the water. The salt water switch may also be prevented from triggering due to high wave, wind, or rainy conditions. On the other hand, relying on the depth gauge requires the assumption that observers on aerial surveys will consistently be able to see to one meter depth, an assumption that may prove faulty in anything but ideal environmental conditions, as turbidity, sediment load, wind, sun, cloud, mist or rain can all influence visibility into the water column. Additionally, waves moving above a stationary turtle may cause the depth gauge to register changes in depth that are not reflective of the turtle's movement. Despite these drawbacks, the salt water switch and depth gauge were the primary methods of determining surfacing behavior by marine animals found in my literature review (Dellinger and Freitas 2000; Godley et al 2003).

My project's second goal, therefore, was to determine whether there is a significant difference between trends in surfacing behavior based on the salt water switch and time spent within the first meter of the water column based on the depth gauge. While percent time spent within 0-1m will naturally be greater than percent time spent directly at the surface, if the two methods' trends show a consistent pattern, it can be assumed that each is a relatively reliable proxy for surfacing behavior that may be seen from an aerial survey. If this is the case, it would support the use of the salt water switch data as the primary indicator of surfacing behavior, since it is available at a greater resolution (hourly) than is the depth gauge data. With the salt water switch, a correction factor can be produced to approximate near-surface visibility by multiplying the salt water switch surfacing time by an appropriate factor.

Additionally, I was interested in whether surfacing behavior was correlated with wave height or barometric pressure, as Minamikawa et al. (2000) noted that loggerhead turtles fitted with satellite tags in Japan dove to avoid high wave height, but little research has been done to confirm this since that time. I included barometric pressure as a proxy for weather events, with the hypothesis that if turtles dove to avoid high wave events, lower surfacing intervals may also be associated with drops in barometric pressure, indicating the presence of a cold front and a change in weather.

Null Hypotheses:

- There is no significant difference among times of year, times of day, or locations for the salt water switch or the depth gauge.
- General trends in surfacing behavior based on the salt water switch and depth gauge are comparable.
- There is no significant relationship between percent time spent within one meter of the surface and wave height or barometric pressure.

Literature Review

Loggerhead sea turtles, *Caretta caretta,* are a primarily carnivorous species of marine turtle and are listed as threatened under the Endangered Species Act of 1973. The species has a circumglobal distribution in temperate, subtropical, and tropical waters (Dodd 1988; Bjorndal 1997; Pritchard 1997). After hatching on sandy beaches, the young turtles head to pelagic habitats, feeding primarily on jelly organisms and portunid crabs until they grow large enough to dive to and feed on benthic organisms (Bjorndal 1997; Musick and Limpus 1997). This generally occurs when the turtles have reached a straight carapace length (SCL) of approximately 40-60cm (Bolten 2003), which is currently thought to be 7-10 years of age in the North Atlantic (Bjornda1997). Most juveniles then undertake a transoceanic migration to recruit to neritic habitats where they forage on mollusks and crustaceans (Bowen et al 2004). While the turtles migrate seasonally to avoid cold temperatures, some homing behavior has been shown in juveniles, and a proportion of turtles in feeding grounds have been shown to be significantly related to nearby nesting populations (Bowen et al 2004; Avens et al 2003). Once sexual maturity is reached at around 90 cm and 35 years of age, the adult turtles embark on periodic migrations every two to three years between neritic feeding habitats and nesting rookeries (Dodd 1988; Bolten 2003; Hatase 2007).

Loggerhead turtles frequently spend over 90% of their time underwater, and have therefore been dubbed ‘surfacers’ as opposed to ‘divers’ (Renaud and Carpenter 1994; Hochscheid et al 2010). Animals considered ‘surfacers’ include elephant seals and Weddell seals as well as all species of marine turtles, all of which spend most of their time underwater and surface only briefly, primarily to breathe (Hochscheid et al 2010). Because the vast majority of their time is spent below the surface, most research into sea turtle behavior has been directed at their dive profiles and subsurface behavior rather than surfacing behavior. Nonetheless, a number of studies have specifically addressed surfacing behavior of loggerhead sea turtles, often to aid extrapolation of aerial survey population size estimates, and it is possible to extrapolate a general idea of time at surface from descriptions of dive behavior. The following is a review of research in sea turtle dive and surfacing behavior in approximately chronological order.

The earliest studies of loggerhead turtle surfacing behavior were primarily observations of captive turtles within aquariums. Layne (1952) indicated loggerheads at the South Boston aquarium surfaced every 2.1 minutes while actively swimming, and every 12.7 minutes while resting. Parrish (1958) noted that loggerheads at Marineland surfaced more during the day than during the night, surfacing every 35-45 minutes at night but every 30 seconds to 10 minutes while swimming and every 10.56 minutes while resting during the day.

Early field investigations of marine turtle surfacing behavior were mainly conducted by direct visual observation of green turtles. These studies showed that green turtles generally stay submerged when near shore except when they need to breathe (Bjorndal 1980; Ogden et al 1983; Tenney et al 1974). While Bjorndal was primarily concerned with grazing behavior, Ogden et al (1983) visually surveyed regularly utilized inshore feeding habitat in addition to acoustically tracking three turtles from the 25th of April to the 8th of May. From the visual observations, turtles were found to be generally inactive at night and mid-day. Surfacing behavior was most evident on sunny days during late to mid-morning (1000 – 1100 hours) and in the mid-afternoon (1500 – 1600 hours). There were also “distinctive” periods of low surfacing activity during the middle of the day and in the early morning and late afternoon (Ogden et al., 1983).

Lutz and Bentley (1985), in a study of two captive green turtles in outdoor tanks, found that only one to three seconds were spent at the surface breathing, typically with only a single exhalation and rapid inhalation, while the rest of the time was spent underwater. Swartz and

Jensen (1991) conducted a similar study of both green and loggerhead captive-reared turtles held in outdoor tanks from May through November. One adult male, one adult female, and six juvenile loggerheads, along with one subadult green turtle, were observed in fifteen 24-hour periods. Rain, wind, cloud cover, and phase of moon all had no significant effect on the behavior of the turtles. Subadult male and female loggerheads behaved similarly; however, the adult male loggerhead occasionally exhibited 'basking' behavior at the surface, and generally stayed within the water column or at the surface while the females rested or swam along the bottom until surfacing to breathe. The female green turtle was generally more active than the female loggerheads swimming throughout the water column (Schwartz and Jensen 1991).

Significantly greater breathing rates occurred during spring (May to June) for all of the turtles in this captive study. Lowest breathing rates occurred during September, with an increase in breathing rates again in the latter part of fall. The adult male and female loggerheads and subadult female green turtle breathed more often during day than night over all seasons. Generally the turtles took at least one breath per hour; however, they could go extended periods without breathing. The longest interval between breaths was 10 hours for the adult male loggerheads, 20 hours for the adult female loggerheads, and 12 hours for the juvenile loggerheads. All turtles also periodically displayed "charging", when turtles took rapid successive breaths at the surface, behavior that was not associated with any particular time of day or season (Schwartz and Jensen 1991).

The earliest tracking attempt of loggerheads was conducted by Carr (1962), who attached helium balloons with monofilament line to the carapaces of six adult females. This allowed them to be geographically tracked for less than one day. Satellite tracking was shown to be a viable method for loggerhead turtles in 1982 with a study by Stoneburner, who successfully tracked eight loggerheads off the coast of Georgia, but did not record any dive or surfacing behavior.

It was not until Renaud and Carpenter (1994) that more specific dive behavior of loggerhead turtles was successfully produced via satellite telemetry. They outfitted four loggerhead sea turtles captured in the Gulf of Mexico with Argos linked satellite tags. The turtles were then released back into inshore Gulf of Mexico waters. Renaud and Carpenter found that over any given season, 90% to 95% of the turtles' time was spent under the water and that there were definite seasonal patterns in the number and duration of submergences by day and night, although they did not track surfacing time specifically. Much longer submergences were found during night than during day for all seasons, suggesting that with longer submergences, less time was spent at the surface during night than day. Summer showed the shortest submergence times, while winter showed the longest submergence times, suggesting that more time was potentially spent at the surface during summer, while less time was spent at the surface during winter (Renaud and Carpenter 1994).

Nelson (1996) observed subadult loggerhead sea turtles spent a greater percentage of their time (19.0%) on the surface in the spring compared to other times of the year in St. Mary's entrance channel in Georgia.

Four loggerhead females were satellite tagged by Papi et al (1997) and displaced down the coast of Mozambique before the turtles had the opportunity to lay eggs. They were then tracked over the course of their return journey to the nesting site. The turtles showed significantly shorter dive duration at night than during the day, unlike most other trends seen, as well as shorter dives during migration than when at feeding grounds.

Dellinger and Freitas (2000) conducted the first study of pelagic sea turtle diving behavior by satellite telemetry. Pelagic juvenile loggerheads were captured at Madiera Island, Portugal. Five juvenile loggerheads were tagged with satellite-linked time-depth recorders and released in April-May, and five were tagged and released in September. Turtles spent most of their time within 0-1m of the surface, with on average 35% of a six-hour period spent in that depth bin. There was a secondary peak at 10-25m depth, with turtles spending on average 20% of a six-hour period in that depth bin, Figure 2. While there was no significant difference between spring and fall released turtles, turtles spent on average more time at the surface during spring than fall. It is important to note that the depth categories do not sum to 100%, as each bar is a percent of six hours spent within each depth averaged over several months, and the depth bins increase in size with depth.

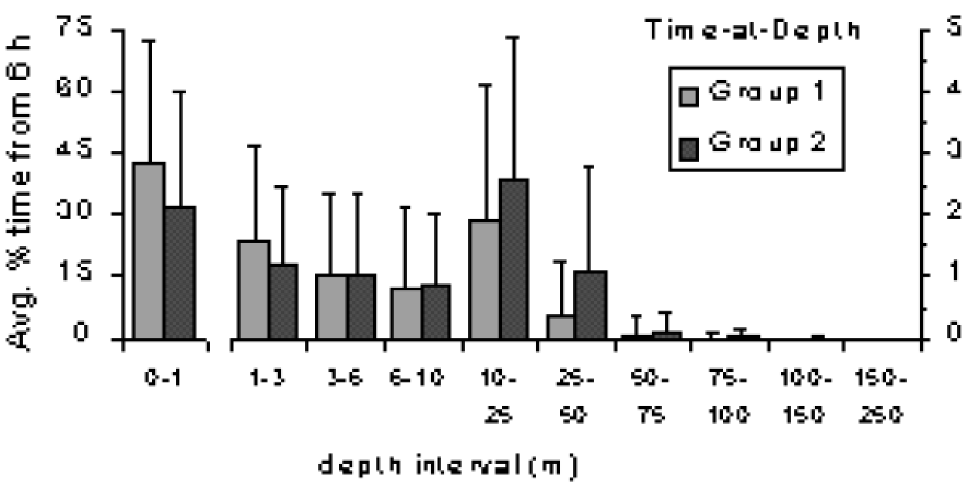

Figure 2. Percent of 6 hours spent at depth for Group 1 (spring released) and Group 2 (fall released) juvenile loggerhead sea turtles off the west coast of Africa. Averaged over nearshore and offshore locations. Reproduced from Dellinger and Freitas (2000).

Another study utilizing time-depth recorders was conducted by Houghton et al (2002). Two loggerhead turtles were tagged with archival storage tags while nesting on Alagadi Beach, Cyprus in June and July. The tags were retrieved after the internesting interval. The vast majority of time for both turtles was recorded at depths shallower than 20m. Both turtles spent a large amount of time resting on the sea bed, but spent more time at or near the surface as nesting dates approached (Houghton et al 2002). Godley et al (2003) also tagged and tracked two female loggerhead turtles following nesting at Alagadi Beach in June and July. Both turtles showed longer dives at night and early morning in inshore waters, with shorter dives during the day (with periods of longest dives being 0200 – 0800 hours for one and 2200 – 0400 for the other), but only one turtle showed diel differences in dive behavior during periods of travel. This turtle also showed longer dives at night and early morning with the period of longest dives during 2200 – 0400 hours. Both turtles showed longer dives in the fall and winter than earlier in the year (Godley 2003).

Radio and sonic telemetry was used by Southwood et al (2003) in a study on the dive behavior of juvenile green turtles in Australia conducted in December (Australia's summer) and August (Australia's winter). The turtles spent significantly more time within the first meter of the surface during winter than during summer, spending almost twice as much time at depths less than one meter during the winter than during the summer. There was also more time spent at the surface during the day than during the night, and deeper dives were conducted during the day than during the night (Southwood et al 2003). A similar study by Hazel et al (2009) of 19 immature and adult green turtles in Australian inshore waters showed shorter and shallower dives during the day than during the night. Longer dives were associated with decreasing seasonal temperatures. There were small peaks of time spent within one meter of the surface at both dawn and dusk over all seasons, compared to the middle of the day or night (Hazel 2009).

In a study similar to that conducted as the impetus for this study (Braun-McNeill et al 2010), immature loggerhead turtles were both satellite tagged and surveyed aerially in the Belearic Archipelago in the western Mediterranean (Cardona et al 2005). Five juvenile loggerheads were caught by divers in April while basking over the continental shelf. Average SCL was 41.36cm. Once released, all five turtles avoided the continental shelf and remained pelagic throughout the duration of the time they were tracked (48 to 159 days). The turtles spent on average 35.1 ± 19.7% of the time at the surface, with no significant difference over time of day during the course of the study (spring and summer). The smallest turtle (SCL of 37.1cm) spent significantly more time at the surface (67%) than all other turtles. Gomez de Segura et al (2003) also conducted aerial surveys in the Spanish Mediterranean. However, as surfacing behavior was not available for loggerhead turtles in that area at that time, no correction was made for turtles below the surface.

Hatase et al (2006) showed two female loggerheads tagged in Japan had longer dive durations with seasonal decrease in water temperature, while Hochscheid et al (2005) found a tagged loggerhead in the South Tyrrhenian Sea venture only infrequently to the surface, at times only appearing once during daylight hours. Hawksbill turtles equipped with time-depth recorders were also found to have longer dives during the winter while in foraging grounds (Storch et al 2005).

Mansfield (2006), in an effort to estimate population abundance of sea turtles in Virginia, conducted aerial surveys as well as satellite and radio telemetry to determine surfacing behavior. She found that mean percent time spent at the surface varied seasonally, peaking in spring when surface time ranged from 9.9% to 30.0% with significant differences among individuals.

A study in the Algerian Basin (western Mediterranean) of ten juvenile loggerheads showed no effect of seasonality on time spent at the surface at night; however, time spent at the surface during daylight hours showed greatest surfacing behavior in spring (Revelles et al 2007). Additionally, the turtles spent longer at the surface during the day than during the night.

A study investigating extended surfacing behavior of ten immature loggerhead turtles in the Mediterranean by Hochscheid et al (2010) by satellite tagging showed no discernable pattern of extended surfacing behavior by season or time of day. An extended surfacing time was considered any time the salt water switch was dry for more than ten minutes. Less than two percent of total time over all the turtles was spent in an extended surfacing event; however, almost all events occurred when turtles had either conducted dives longer than their aerobic limit or when they had recently dove through a strong thermocline into cold water temperatures (Hochscheid et al 2010).

Seventeen pelagic juvenile loggerhead turtles incidentally captured in the long-line fishery were satellite tagged in the North Pacific Ocean (Howell et al 2010). Eighty percent of time was spent within the top five meters of depth, and over 90% of time was spent within the top ten meters of depth over all turtles. Deeper, longer dives were made in the first quarter of the year, and longer dives were made during the night than during the day. Interestingly, however, turtles spent more time within the 0-15m depth range at night than during the day (Howell et al 2010).

A study by Minamikawa (2000) indicated that loggerhead turtles dive to avoid rough conditions at the surface, however, no other studies have been found showing similar correlations.

Overall, loggerheads and other marine turtles have been found to surface more during the day than during the night (Parrish 1958; Ogden et al 1983; Swartz and Jensen 1991; Eckert 1986; Southwood 2003; Hazel et al 2009; and Revelles et al 2007). Similarly, longer dives at night (from which it is a reasonable extrapolation to assume shorter surfacing intervals) are common among both loggerhead and other species of marine turtles (Renaud and Carpenter 1994; Godley et al 2003; Hazel 2009; Howell 2010) with the exception of turtles observed along the coast of southern Africa, which showed the opposite trend (Papi et al 1997). Two studies indicated that peaks in surfacing behavior appeared in green turtles during the earlier and latter part of the day, with lulls in surfacing both in the middle portion of the day and night (Hazel 2009 and Ogden 1983). Pelagic juveniles have been found to spend more time at the surface than their nearshore counterparts, with both Cardona et al (2005) and Dellinger and Freitas (2000) finding that approximately 35% of time was spent at the surface. Howell (2010) similarly found pelagic juveniles to spend the majority of their time near the surface of the water. Seasonal trends show longer dives during the winter for loggerhead and other marine turtles (Godley et al 2003; Hatase et al 2006; Storch et al 2005; Mansfield 2006; Revelles et al 2007) with more surfacing during the spring (Schwartz and Jensen 1991; Nelson 1996; Dellinger and Freitas 2000). Elucidating surfacing behavior is very important for the purpose of producing accurate population estimates, as a correction factor of 5% on a count of 100 turtles will produce an estimate of 2000 turtles, while a 35% correction will produce a population estimate of only 286 turtles.

Methods

Eight Argos-linked Wildlife Computer SPOT5 satellite tags and 13 Wildlife Computer SPLASH satellite tags (Redmond, Washington, USA) were attached to loggerhead sea turtles incidentally caught in pound nets in Core and Pamlico Sounds by the NMFS, NOAA Beaufort Laboratory. One of these turtles was tagged with both a SPOT5 and SPLASH satellite tag, resulting in a total of twenty tagged turtles. See Figure 1 for capture locations; see Table 1 for release date and transmission length for each turtle. Turtles were captured as part of an ongoing in-water sampling effort during the summers of 2007 and 2008. Pound nets are a form of passive fishing gear composed of a lead (a long straight net) connecting with a series of staked nets forming an enclosure with a narrow opening (Figure 3). Nets are open to the surface of the water, therefore allowing turtles to breath and making mortalities uncommon (Epperly et al., 2007).

Figure 3. A pound net in Pamlico Sound. Photo by B. Wren Patton.

Table 1. Release date, length of transmission, and tag type of each turtle.

Turtle ID	Date Released	Length of Transmission	Tag Type
42599	5/7/2008	98	SPLASH
42600	5/5/2008	57	SPLASH
42601	5/19/2008	45	SPLASH
42602	5/28/2008	40	SPLASH
42603	5/28/2008	26	SPLASH
42604	5/19/2008	164	SPLASH
42605	5/14/2008	169	SPLASH
42664	6/4/2008	47	SPLASH
43635	6/13/2008	133	SPLASH
43638	6/2/2008	224	SPLASH
43639	6/2/2008	64	SPLASH
43697	5/14/2008	69	SPLASH
43699	5/5/2008	216	SPLASH
75425	7/24/2007	276	SPOT5
75426	7/31/2007	31	SPOT5
75427	8/7/2007	208	SPOT5
76454	8/24/2007	245	SPOT5
76455	10/9/2007	185	SPOT5
76456	10/11/2007	192	SPOT5
76457	10/11/2007	187	SPOT5
76458	11/1/2007	0	SPOT5

Turtles were brought to shore for tag attachment. Straight-Line Carapace Length (SCL), a measurement from the midpoint of the nuchal scute (the large, scale-like plate at the foremost point of the shell and just behind the turtles head) to the farthest posterior tip of the carapace, was taken for each turtle. Turtles were also weighed and flipper tagged with Inconel Style 681 tags (National 3 Band and Tag Company, Newport, Kentucky, USA). These tags were attached to the trailing edge of each back flipper. A 125 kHz unencrypted Passive Integrated Transponder (PIT) tag (Destron-Fearing Corp., South St. Paul, Minnesota, USA) was also subcutaneously injected into muscle of the left front flipper.

To apply the satellite tags, all epibiota were removed from the first and second vertebral and costal scutes on the turtles' back, which were then lightly scrubbed with sandpaper to provide a better surface for adherence. The area was rinsed with fresh water and dried with acetone. The tags were attached to this area with a high-strength, low-temperature epoxy adhesive (Power Fast™, Powers Fasteners, Brewster, New York, USA; Mitchell 1998) (Figure 4). SPOT5 tags were additionally secured with fiberglass cloth and resin according to the procedure set out in Balazs et al (1996). When the adhesive was set, turtles were returned as close to the site of capture as possible (Figure 5). All tags weighed less than 1% of total body weight of the turtle.

Figure 4. Attachment of satellite tag to turtle carapace with epoxy adhesive. Photo by Lisa R. Goshe.

Figure 5. Location of satellite tag attachment. Photo by M. April Goodman.

Both SPOT5 and SPASH tags were equipped with a salt water switch. The amount of time each hour in a 24-hour day that the switch was dry was recorded as an indicator of the minimum percent time each turtle spent at surface. Both were also equipped with a temperature sensor, and time spent within temperature bins was recorded. Temperature bins were <8, 10, 12, 14, 16, 18, 20, 22, 24, 26, 30 and >30 degrees Celsius. SPLASH tags had an additional depth gauge based on a pressure sensor which recorded time spent in a four-hour period within depth bins of 0-1, 1-2, 2-3, 3-5, 5-10, 15-30, 30-50, 50-75, 75-100, 100-125, 125-150, 150-200 and >200 meters. Counts of the number of times a turtle entered or left both depth and temperature bins were also recorded by both tags. To facilitate data transmission from tag to satellite, all data were compressed into eight bits. Therefore, time at temperature and time at depth were transformed to a percent of total for analysis, and no absolute time at depth or dive profile data are available.

Tags were programmed to transmit data whenever a turtle surfaced to breath via ultra-high frequency (UHF) messages to NOAA's Polar Orbiting Environmental Satellites (POES). Data were transmitted daily over a 10-hour period beginning around dawn and ending around dusk. Night data were stored to be transmitted the next day. These messages were received by Argos equipment, then transmitted to an Argos processing center from which the data were sent via e-mail to a specified address. Tag locations were calculated at the Argos processing center utilizing the Doppler effect on transmission frequency (Argos User's Manual 2008).

Data were archived and filtered with the Satellite Tracking and Analysis Tool (STAT) (Coyne and Godley 2005). Turtles were filtered based on accuracy of location to codes 1, 2, or 3 (Argos accuracy codes are shown in Table 2), likely swimming speeds (<6 km/hr), distance between locations (<75km for relatively stationary, and <100km for migrating turtles), and locations over water. Data without location information were not included in this analysis because location is central to the hypotheses. Additionally, one turtle that was determined to have died was excluded, as was data for one turtle recorded while caught in a pound net (a fisherman reported the incident and returned the tag). After these data were eliminated, 376 total days of hourly percent time at surface based on the salt water switch remained, and 931 four-hour periods of time at depth data remained. These remaining data were converted from Greenwich Mean Time in which they were recorded to Eastern Standard Time in order for time of day to be more biologically relevant.

Table 2. Argos location accuracy codes and estimated accuracy (ARGOS User's Manual 2008). Table reproduced from NOAA Technical Memorandum NMFS-SEFSC-605 (Braun-McNeill et al 2010).

Class Code	Number of messages received per satellite pass	Accuracy
3	4 messages or more	<250m
2	4 messages or more	250m – 500m
1	4 messages or more	500m – 1500m
0	4 messages or more	>1500m
A	3 messages	No accuracy estimation
B	2 messages	No accuracy estimation

I examined surfacing behavior based on the salt water switch as well as percent time at depth data for differences among habitats (inshore, nearshore, and offshore), time of year (by quarter: Quarter 1—January to March, Quarter 2 – April to June, Quarter 3 – July to September, Quarter 4 – October to December) and times of day, as well as for differences among individual turtles. Epperly et al (1995) showed that objects below but still near to the surface of the water are usually visible during aerial surveys, therefore this study assumed that turtles within one meter of the surface would be visible to aerial surveys as well.

I assumed that size of turtle did not have a significant impact on surfacing behavior, in part because the sample size was too small for further division and because no differentiation in size was made during the aerial surveys for which this study was completed.

I compared the trends seen percent time at the surface based on the salt water switch with the percent time spent within the first meter of wave, based on the depth gauge, but only for turtles that simultaneously recorded both time at depth from the depth gauge and percent time at surface based on the salt water switch. Additionally, I compared depth gauge data with wave height and barometric pressure. Wave height and barometric pressure data were obtained from NOAA Weather Buoys, the locations for which are indicated in Figure 6. Wave height and barometric pressure data were recorded hourly by the buoys. I correlated percent time spent within 0-1m with data from the closest weather buoy to the position of each turtle at any one time.

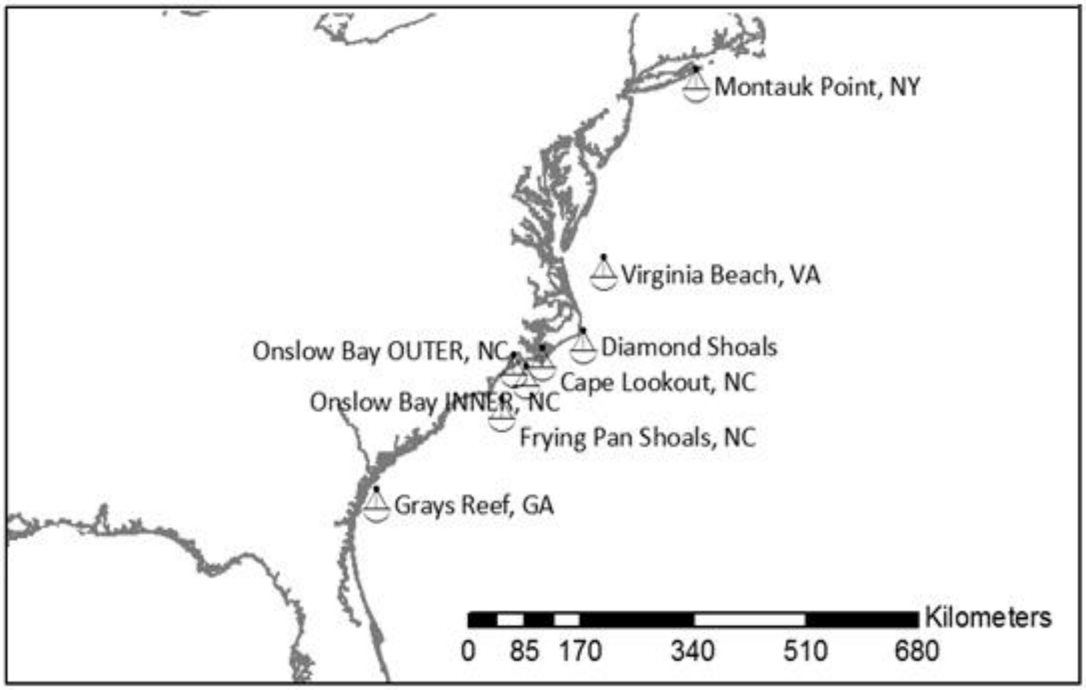

Figure 6. Locations of NOAA weather buoys used to determine wave height and barometric pressure.

I defined inshore, nearshore, and offshore habitats as being within the barrier islands, external to the barrier islands to depths of 20m, and external to the barrier islands in depths greater than 20m respectively. This is in contrast to the use of the COLREGS Demarcation Line, which was used in Braun-McNeill et all (2010). I produced these definitions because, in the case of inshore, within the barrier islands offshore ocean conditions are muted by the presence of the islands, and therefore provides significantly different habitat conditions than external to the islands. This corresponds essentially with the COLREGS Demarcation Line. Nearshore was defined as being external to the barrier islands but within 20m depth. A 20m depth cut off was justified because in waters less than twenty meters deep, river runoff on the east coast produces stratified bands of nearshore water that result in unique density-driven circulation patterns (Kjerfve and Sneed 1983). Additionally, there is precedent in using 20m depth as the cutoff for nearshore environments by the National Park Service, the National Marine Fisheries Service, and the EPA (NMFS 2006; Warren et al 2010). I defined offshore as any depths external to the barrier islands deeper than 20m but still within the edge of the continental shelf. No category external to the edge of the continental shelf was included, as no turtles in this study ventured this far away from shore.

I retrieved Atlantic coastal bathymetry from the NOAA National Geophysical Data Center Geophysical Data System (GEODAS), imported it into ArcGIS 9 and projected to UTM 18N. I also imported all turtle data to ArcGIS and projected from Geographic WGS84 to UTM 18N. I then sorted turtles by habitat and exported back to Microsoft Excel©. Prior to analysis, data were arcsine transformed to satisfy normality requirements for statistical analysis (Zar 1999).

There were unique difficulties in the statistical analysis of this data set. There were unequal sample sizes for all categories, including time of day, season, and location due to the variation inherent in each turtle's path and behavior, and because each turtle remained operational for a different amount of time. Additionally, within the overall data set, the behavior of each individual turtle was autocorrelated because the surfacing behavior of any one hour may be dependent on the hour before. Further, the likelihood of the turtle being in any one location is dependent on where the turtle had been recently. As a result, the entire data set is composed of a series of autocorrelated groups. Past research has shown time of day, season, location, and individual turtle to all be significant confounding variables. Enough variation was present within these data that it was, for the most part, not possible to average over any one of these factors. However, once the available data were grouped by all of these factors, very small sample sizes were inevitable. Finally, a very large portion of the data set was excluded for lacking GPS locations. Because it is impossible to tell why the tag may not have been able to determine location, there may be an undeterminable pattern to the missing data. For example, particularly short surfacing events may result in the loss of position location, potentially skewing the results for any circumstance resulting in shorter surfacing intervals. Because the mechanism or reason the location data were not recorded is unknown, it is intrinsically impossible to make any kind of adjustment to account for the missing data.

Given these difficulties, a traditional statistical analysis was eschewed, as too many inherent assumptions of the various potential statistical methods were violated. The best statistical approach to a data set with these issues is a complex multilevel modeling system, treating each turtle as a basic factor and treating data as space and time sampling for each individual turtle. Additionally, determining which statistical test was most appropriate would only be determined after completing significant modeling to establish the most important factors (Savin, personal communication). Unfortunately, modeling was beyond the scope of this project. In lieu of complex modeling, another qualitative assessment was completed. Where possible, data were reduced to a 'yes or no' summary for each turtle, and a one-sample randomization test (also known as a "sign test") (Manly 1997) was used to compare the fraction of turtles displaying the behavior to a null of 0.5. This was used to compare day versus night behaviors. Additionally, a sign test was also used to determine the likelihood that greater surfacing in offshore and quarter 1 was due to chance alone.

As time at depth was recorded in four-hour periods while percent time at surface was recorded hourly, I averaged percent time at surface data over corresponding four-hour periods to facilitate comparison. I also averaged hourly wave height and barometric pressure over four-hour periods to compare to the depth gauge as well. Where appropriate, I produced 95% confidence intervals for averaged surfacing behavior for season, time of day, location, and individual turtle. Where I averaged over more than one turtle, I used the number of turtles as the n-value (over individual observations) to produce 95% confidence intervals. Where I was only averaging over a single turtle, I used the number of observations as n to produce 95% confidence intervals.

I conducted a correlation analysis to determine whether there was a relationship between time spent in the first meter of water and wave heights, as well as for near-surface time and barometric pressure as a proxy for weather phenomenon.

Results

General Information

Turtle straight-line carapace length (SCL) ranged from 54.2cm to 95.8cm, with a mean of 70.1cm ± a standard deviation of 10.9cm. SPOT5 tags transmitted for a range of 0 to 276 days, while SPLASH tags transmitted for a range of 26 to 224 days. When data without location information were excluded, there were a total of 1207 observations over 19 turtles for analysis. Eleven turtles recorded both time at depth and salt water switch data, two recorded only time at depth but no salt water switch data, and the remainder recorded salt water switch but no time at depth data.

Of all turtles, only five made major migratory movements, making a total of ten significant migrations while the rest displayed more localized movement patterns. Of these ten migrations, no particular time of year was favored, with three movements occurring during both quarters 1 and 2, and two movements occurring during quarters 3 and 4. No tag recording time at depth survived through the winter, so no percent time at depth data are available for quarter 1. An example of a turtle displaying more localized movement patterns is shown in Figure 7, while Figure 8 shows an example of a turtle showing migratory behavior. Maps of each individual turtle's movements can be seen in Braun-McNeill et al (2010) in addition to summary statistics for each turtle.

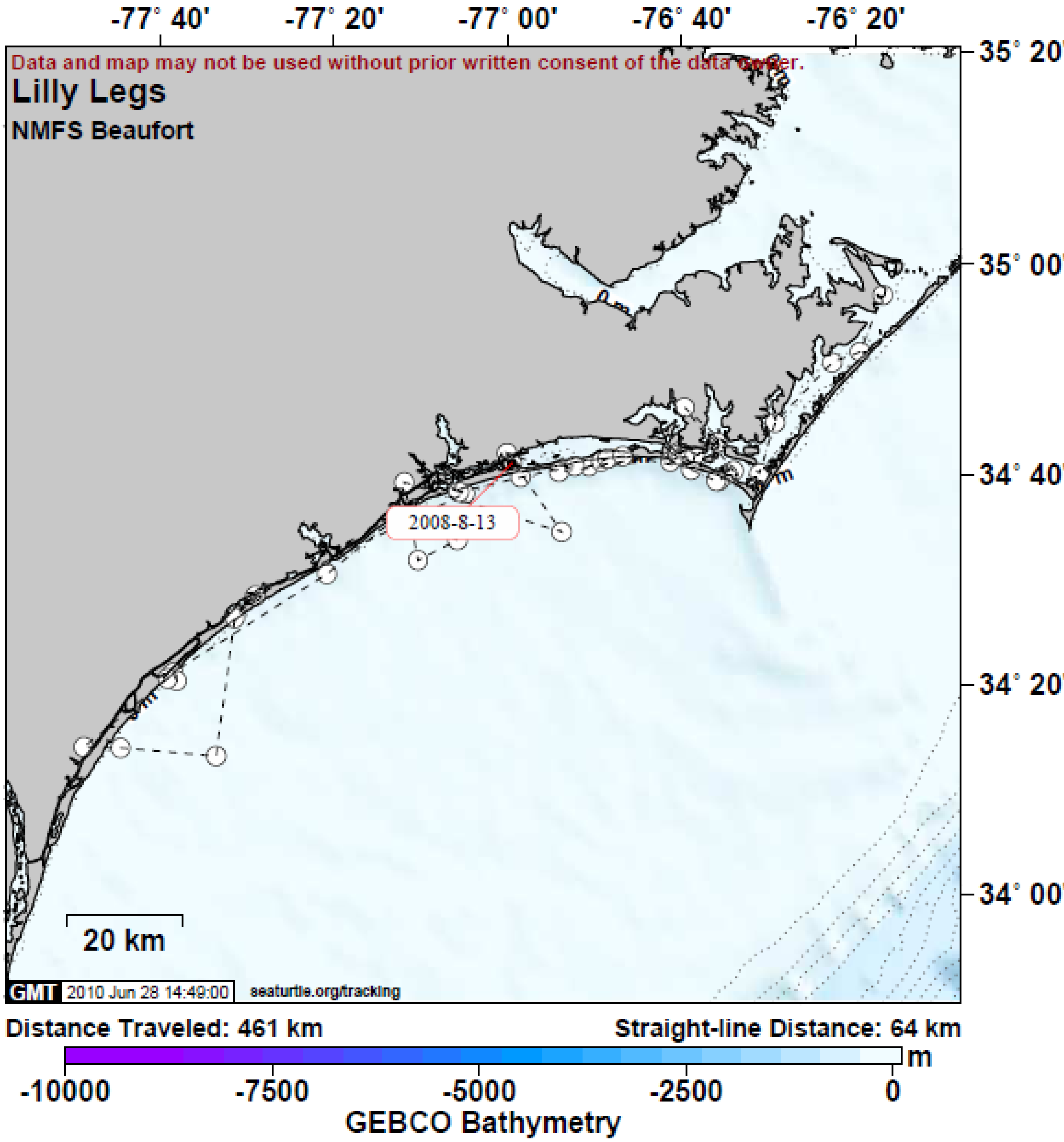

Figure 7. Path of Turtle 42599.Turtle release date was May 7, 2008; tag transmitted for 98 days. Turtle 42599 remained primarily in nearshore North Carolina waters.

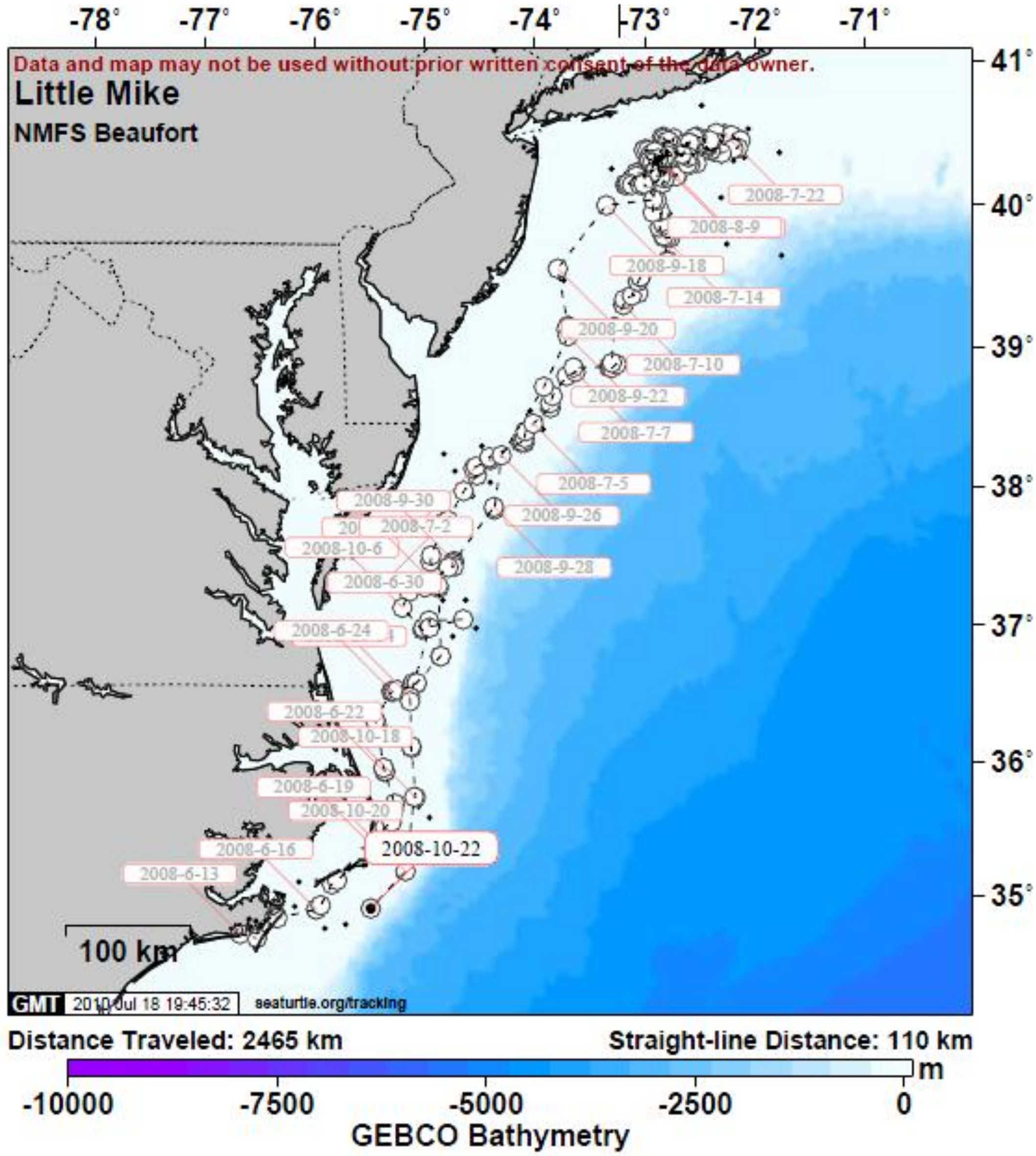

Figure 8. Path of Turtle 43635.Turtle release date was June 13, 2008; tag transmitted for 133 days. Turtle 43635 traveled from the Core Sound area to New York in primarily offshore waters before returning to Pamlico Sound.

Depth Gauge

Of the 13 turtles outfitted with a tag recording time at depth data, three were recorded in all three habitats (inshore, nearshore, and offshore) while eight were recorded in at least two habitats. Of the remaining five turtles that only recorded in one habitat, three were exclusively inshore and two were exclusively nearshore. There were no turtles exclusive to offshore.

Table 3. Percent time spent within one meter of the surface by individual turtle, quarter, and location. Number of observations and 95% confidence intervals for each turtle can be found in Table A-1 in Appendix I. No turtles with a depth gauge were observed during quarter 1.

	Quarter 2			Quarter 3			Quarter 4		
Turtle	In-shore	Near-shore	Off-shore	In-shore	Near-shore	Off-shore	In-shore	Near-shore	Off-shore
42599	17.9	17.9	-	-	-	-	-	-	-
42600	28.3	31.6	38.4	-	-	-	-	-	-
42601	-	7.9	-	-	-	-	-	-	-
42602	21.2	-	-	9.9	-	-	-	-	-
42603	44.5	-	-	-	-	-	-	-	-
42604	11.1	20.6	-	-	16.9	24.3	-	-	47.7
42605	9.5	2.9	-	16.6	-	-	-	-	-
42664	18.8	-	-	8.5	-	-	-	-	-
43635	44.0	32.5	51.8	-	-	66.0	-	-	36.4
43638	13.1	-	-	-	-	-	-	-	11.9
43639	-	-	-	-	6.0	5.5	-	-	-
43697	10.2	-	-	58.4	26.5	-	-	-	-
43699	66.8	52.6	-	5.5	-	-	-	-	-

Only one turtle (turtle 43635) recorded a single location (offshore) in all three quarters for which time at depth data were available. In that case, quarter 3 showed the greatest percent time spent within one meter of the surface followed by quarter 2 then quarter 4 (Table 3). One other turtle recorded time at depth for three quarters, turtle 42604. For that turtle, quarter 4 showed greatest time within 0-1m offshore over quarter 3, and quarter 2 showed greater percent time within 0-1m than quarter 3 while nearshore. Of the two turtles for which all three locations were recorded during a single season (42600 and 43635) both showed greatest percent time within 0-1m while offshore. Three of four turtles for which offshore behavior was recorded with at least one other location within a single season showed greater percent time in offshore. Four of seven turtles for which both inshore and nearshore data were available within a single season showed greater percent time spent within 0-1m while inshore, while one turtle was equal between habitats. However, the probability of getting 3/4 or 4/6 turtles showing these behaviors cannot be said to be significantly different from random chance (P-value 0.6250 and 0.6875 respectively).

When broken down by time of day (Figure 9) and averaged over location, percent of each four-hour period spent at 0-1m showed no major differences by time of day or by quarter. While quarters 3 and 4 generally alternated for greatest surfacing behavior, both were consistently greater than quarter 2 but too little data were recorded over all seasons to determine significance. Quarter 4 showed the greatest variability. This is because quarter 4 is represented by only three turtles in the 15:00 bin, and by only two turtles for all other time bins, with a maximum of six observations over any time of day. A summary of turtles present in other quarters can be seen in Tables A-2 through A-5 in Appendix I.

When considering all depths, not just surfacing behavior, behavior averaged over all turtles and times of year showed greatest percent time in a four-hour period was spent in the 2-3m depth bin while inshore (27.7 ±3.7%), followed by 1-2m (25.5± 2.8%), and 0-1m (18.7 ± 3.0%). Percent time at depth dropped off considerably for depth bins deeper than 3m. In nearshore waters, greatest percent time was recorded in 0-1m and 5-10m (20.7 ± 3.6% and 20.6 ± 7.7% respectively). 1-2m was next greatest, at 11.8 ± 2.5%. However, it is important to note that only the first three bins are of consistent size (1m) and therefore objectively comparable, as size of the bins increase with depth thereafter. While offshore, percent time was greatest in the 0-1m depth bin at 59.3 ± 5.2%, with the next closest bin, 1-2m, at 5.5 ± 1.3%.

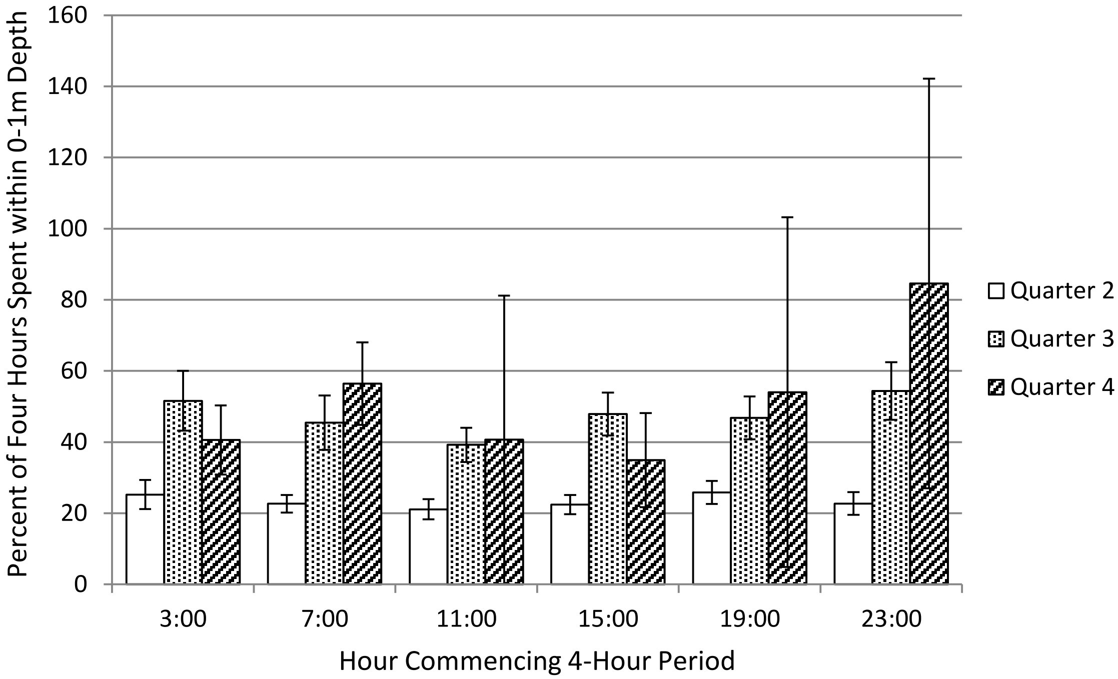

Figure 9. Percent of four hours spent within 0-1m depth by time of day and quarter. Quarter 2 is April – June; Quarter 3 is July – September; Quarter 4 is October – December. Error bars are 95% confidence intervals produced using the number of turtles for n. Number of turtles range from 9 to 12 in quarter 2, 6 to 8 in quarter 3, and 3 to 6 in quarter 4. Number of turtles and number of observations for each quarter and time of day is located in Table A-2, while individuals recorded in each quarter and time of day can be found in Tables A-3 through A-5 in Appendix I.

Similar patterns were seen when analyzed by time of year (Figure 10), with no major differences apparent by quarter. When split by individual turtle as well, two primary patterns appear. In quarter 2, four of six turtles show behavior similar to the pattern described, greatest percent time spent around 3-5m depth with little to no presence in any deeper depth bins. Four of six turtles do not provide enough data to say significantly that the pattern was not due to random chance, however (p-value 0.688). The other two turtles showed greatest percent time spent in 0-1m, rapidly dropping off through the 1-2m and 2-3m depth bins. Both of these turtles (42600 and 43699) spent a large amount of time in inshore waters bordering on nearshore, however, which may explain some of the differences. One turtle (42599) recorded a small amount of time within the 15-30m depth bin, unusual for inshore habitat as those depths border the deeper side of nearshore habitats. However, inshore locations are not defined by depth, but rather by the perimeter of barrier islands, so it is possible to reach those depths in inshore habitat.

Again in quarter 3, two primary patterns appear amongst the ten turtles when analyzed individually. Seven of the ten showed the pattern of greatest time spent in the 2-3 or 3-5m depth bins, with decreasing time spent in each bin as it approaches the surface. The other three showed greatest percent time in the 0-1m depth bins. Including quarter 2 turtles, 11 of 16 turtles spent more time around 3-5m depths, which is worthy of note, although still not significant (p-value 0.210).

Three turtles were represented in the nearshore dive profiles in quarter 2. Of these three, two had similar profiles of relatively constant percent time in each depth bin out to 15-30m depth. One (turtle 42599) averaged around 15% time in each depth bin out to 15m depth before dropping off in the 15-30m depth bin, while the other (turtle 42600) averaged approximately 8% across each depth bin out to the 10-15m depth bin before dropping off. Turtle 42600 did show slightly greater percent time within 0-1m than all others at 32 ± 8.66%. The third turtle had dramatically different behavior, with consistently very low percent time within each depth bin (approximately 3.5% across all depth bins including 0-1m) until the 5-10m bin. There percent time shot up to 82 ± 8.27%. This turtle is driving the secondary peak in percent time at depth seen in Figure 10 in nearshore. Five turtles are represented in nearshore during quarter 3. Of these, three showed slightly greater percent time in the 5-10m depth range, with two showing the pattern seen offshore with greatest percent time spent in the 0-1m depth bin and fairly low percent time spread consistently over the subsequent depth bins out to the 15-30m depth bin.

Only one turtle is represented in offshore habitats during quarter 2 (turtle 42600). It showed much greater percent time in the 0-1m depth bin (38 ±12.6%) with low but consistent percent time spread out across the depth bins to a maximum of the 30-50m depth bin. In quarter 3, three turtles are represented offshore. One of these three (turtle 43635) shows the same pattern seen in turtle 42600, with much greater surfacing in the 0-1m depth bin (64.7 ± 0.057%). The other two show greater percent time in the 15-30m depth bin – a deeper peak similar to that shown frequently in nearshore habitats. Quarter 4 was similarly represented by three turtles offshore. Turtle 43635 showed the same pattern of much greater time in the 0-1m bin (55.9 ± 0.43%). Both of the remaining two showed greater surfacing both in the 0-1m depth bin and around the 30-50m depth bin, combining both patterns seen offshore in the other two quarters.

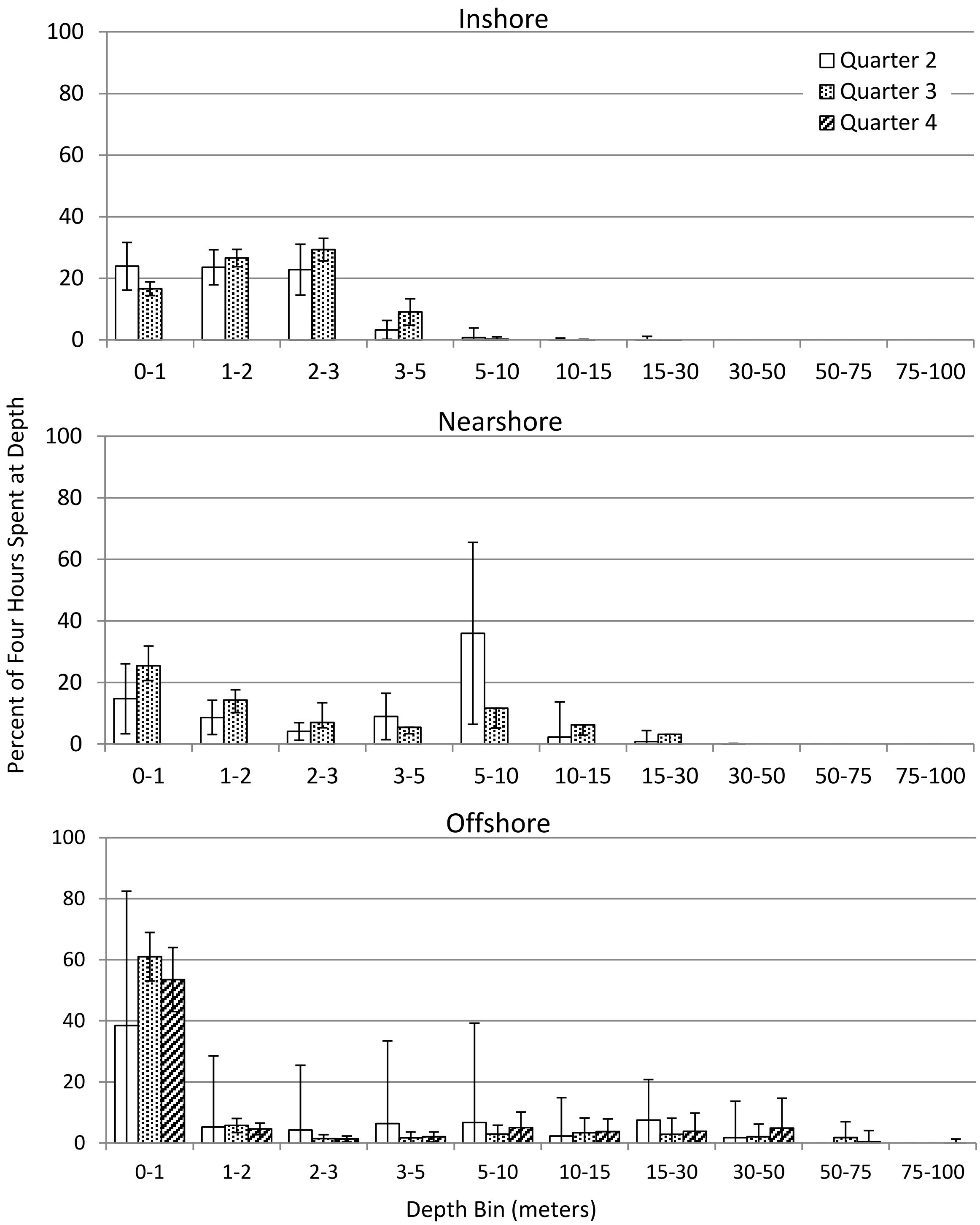

Figure 10. Percent of four hours spent within specified depth bins by time of year and location, averaged over all turtles. 95% confidence intervals were produced using the number of turtles for n. Number of turtles range from 7 to 9 in inshore habitats, 3 to 6 in nearshore habitats, and from 1 to 3 in offshore habitats. Turtles representing each quarter and location can be seen in Table A-6 in Appendix I. No data were available for inshore and nearshore habitats in quarter 4. No presence in depths greater than 100m was recorded. Quarter 2 is April – June; Quarter 3 is July – September; Quarter 4 is October – December.

Salt Water Switch

Percent time spent at the surface based on the salt water switch by hour was much lower and more variable in inshore and nearshore locations compared to offshore locations, with frequent 24-hour periods where no surfacing behavior was recorded at all. Average percent time at the surface for inshore and nearshore locations can be seen in Table 4.

Table 4. Average inshore and nearshore percent time spent at surface each hour based on the salt water switch by quarter over all turtles. 95% Confidence intervals are based on number of turtles represented. No turtles were recorded inshore during quarter four.

	Inshore		Nearshore	
	Percent of Hour At Surface	95% Confidence Interval	Percent of Hour At Surface	95% Confidence Interval
Quarter 1	0.0018	0.061	0.18	1.36
Quarter 2	0.029	0.15	0	0
Quarter 3	0.049	0.61	2.02	5.80
Quarter 4	N/A	N/A	1.69	23.18

While graphically it appears that quarter 2 conclusively shows greater surfacing behavior offshore, this is not necessarily the case (Figure 11). This quarter includes only two turtles, and none of the turtles that were present in three of four quarters were represented in quarter 2.

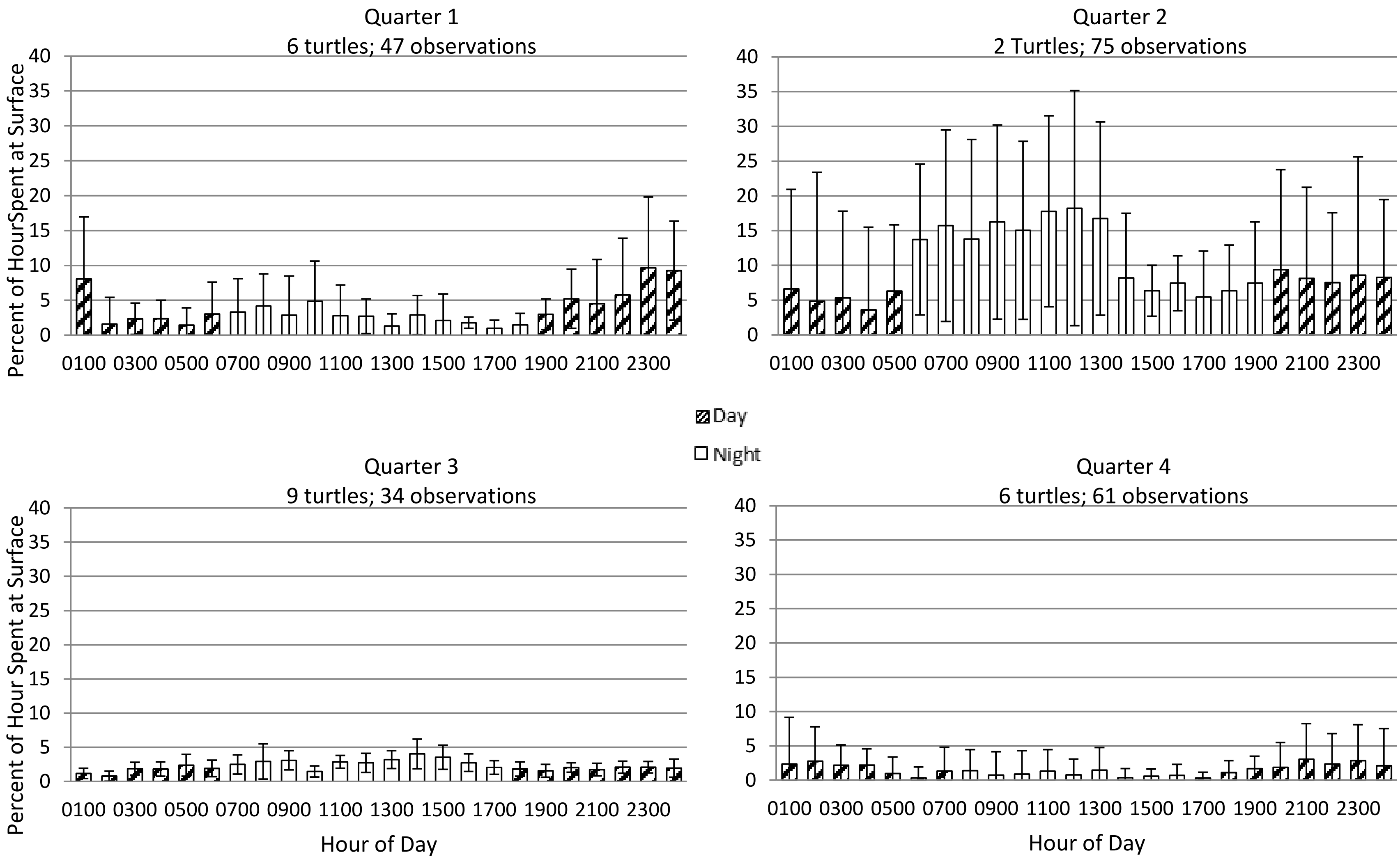

Figure 11. Percent of each hour in a 24-hour period spent at surface, offshore, based on the salt water switch. Error bars indicate 95% error with n being the number of turtles sampled within each quarter. Number of turtles and observations can be found above each graph. Turtles represented in each graph can be seen in Table A-7 in Appendix I. Quarter 1 is January – March; Quarter 2 is April – June; Quarter 3 is July – September; Quarter 4 is October – December.

Table 5. Average percent of one hour spent at the surface based on the salt water switch by individual turtle and time of year, for offshore locations only. Number of observations and 95% confidence intervals for each turtle and quarter provided in Table A-8 in Appendix I.

Turtle	Quarter 1	Quarter 2	Quarter 3	Quarter 4	Quarter of Greatest Surfacing
42600	5.5	-	-	-	N/A
42604	-	7.1	11.8	-	Quarter 3
43635	-	9.8	8.0	-	Quarter 2
43638	-	-	1.7	-	N/A
75425	3.55	-	0.2	2.4	Quarter 1
75427	-	-	-	0.97	N/A
76454	3.35	-	0.60	2.68	Quarter 1
76455	6.8	-	1.5	1.1	Quarter 1
76456	0.928	-	0.61	0.52	Quarter 1
43635	3.98	-	0.58	1.1	Quarter 1

Of turtles for which behavior was recorded in quarters 1, 3, and 4, five of five turtles had greatest surfacing behavior over all locations during quarter 1. While five out of five (100%) compared to a null of 0.5 is still too few to be deemed not due to random chance (p-value 0.0625), that all five turtles showed this pattern is noteworthy. The next-greatest surfacing behavior was split fairly evenly between quarter 3 and quarter 4 (two turtles for which quarter 3 showed the next greatest surfacing behavior, and three turtles for quarter 4). Two turtles were recorded in quarters 2 and 3. Of these turtles, one had greater surfacing behavior during quarter 2, and one in quarter 3. However, only one day's worth of observations were recorded in quarter 3 for the turtle showing greater average surfacing in that quarter, and therefore nothing conclusive can be drawn about whether or not these turtles showed greater surfacing during quarter 2, despite the suggestive nature of the graph in Figure 11.

Table 6. Average percent of one hour spent at the surface based on the salt water switch by individual turtle and location, averaged over all times of year. Number of observations and 95% confidence intervals for each turtle and location can be seen in Table A-9 in Appendix I.

Turtle ID	Inshore	Nearshore	Offshore	Location of Greatest Surfacing
42599	7.9×10^{-03}	2.2×10^{-03}	-	Inshore
42600	0	8.8×10^{-03}	5.47	Offshore
42602	0.20	-	-	N/A
42603	0.062	-	-	N/A
42604	5.6×10^{-03}	0	7.48	Offshore
42605	7.3×10^{-05}	7.4×10^{-03}	-	Nearshore
42664	6.9×10^{-04}	-	-	N/A
43635	8.8×10^{-03}	0	9.55	Offshore
43638	0.015	-	1.72	Offshore
43699	0.016	-	-	N/A
75425	-	7.65	2.48	Nearshore
75427	-	1.69	0.97	Nearshore
76454	-	0.51	2.49	Offshore
76455	0.22	2.11	2.13	Offshore
76456	-	1.05	0.66	Nearshore
76457	0.062	-	1.70	Offshore

Of the ten turtles for which offshore locations were recorded, seven showed greatest surfacing behavior offshore, although the pattern still cannot be said to be significantly different from random chance (p-value 0.348). The other three turtles had greatest surfacing behavior while nearshore. Two turtles were only recorded in nearshore and inshore locations, of which one showed greater percent time at surface inshore while the other had greatest surface time in nearshore. Supporting tables with counts of observations and 95% confidence intervals can be found in Appendix I, under the heading Salt Water Switch.

Table 7. Ratio of entries for which greater surfacing was seen during the day to total number of entries recorded (not including entries for which there was zero surfacing behavior recorded) by turtle, quarter, and location. **indicates significantly more surfacing during the day than during the night. *indicates significantly greater surfacing during the night than during the day.

	Quarter 1			Quarter 2			Quarter 3			Quarter 4		
Turtle	Inshore	Nearshore	Offshore	Inshore	Nearshore	Offshore	Inshore	Nearshore	Offshore	Inshore	Nearshore	Offshore
42599	0/1	1/1	-	-	-	-	-	-	-	-	-	-
42600	0/0	0/1	3/3	0/0	-	-	-	-	-	-	-	-
42602	-	-	-	-	** 16/21	-	-	-	-	-	-	-
42603	-	-	-	-	5/5	-	-	-	-	-	-	-
42604	2/2	-	-	0/1	0/0	** 8/9	-	-	1/1	-	-	-
42605	0/0	1/2	-	1/1	-	-	1/1	-	-	-	-	-
42664	-	-	-	3/3	-	-	-	-	-	-	-	-
43635	-	-	-	0/1	0/0	** 57/66	-	-	6/10	-	-	-
43638	-	-	-	5/5	-	-	-	-	0/1	-	-	-
43697	0/0	-	-	1/1	-	-	-	-	-	-	-	-
43699	0/0	-	-	0/1	-	-	-	-	-	-	-	-
75425	-	-	2/5	-	-	-	-	½	1/1	-	-	5/16
75427	-	-	-	-	-	-	-	-	-	-	1/7	* 1/9
76454	-	-	5/18	-	-	-	-	2/4	2/6	-	-	* 0/6
76455	-	-	3/5	-	-	-	0/1	0/3	0/1	-	-	* 0/14
76456	-	1/3	2/8	-	-	-	-	0/1	1/6	-	-	* 0/12
76457	-	-	2/8	-	-	-	8/13	-	4/8	-	-	0/4

Turtle 42602 was the only turtle to show significant diel differences in surfacing time in nearshore habitat, with more time spent at the surface during the day than during the night (p-value 0.027) during quarter 2. Both turtles 42604 and 43635 had significantly greater surfacing time during the day than during the night while offshore in quarter 2 (p-values 0.039 and 1.18×10^{-9} respectively). During quarter 4 there were four turtles (75427, 76454, 76455, and 76456) that had significantly lower surfacing time while offshore during the day than during the night, the opposite trend as seen in quarter 2 (p-values 0.040, 0.031, 1.22×10^{-4}, and 4.88×10^{-4} respectively). In total, only seven of 17 turtles showed any significant diel differences in surfacing behavior based on the salt water switch, too few to state conclusively that these results were not a result of chance alone (p-value 0.6291).

Depth Gauge and Salt Water Switch Comparison

Only turtles with both a salt water switch and depth gauge simultaneously recording were included in the comparison of depth gauge to salt water switch trends. It is immediately apparent from Figure 12 that, ignoring the approximate order of magnitude difference between the salt water switch and depth gauge, the overall trends were very different over both time of day and location. In quarter 2, the depth gauge showed greatest percent time offshore followed by inshore and , while the salt water switch showed greatest percent time at surface followed by nearshore, then inshore, although surfacing behavior for inshore was practically zero. Quarter 3 showed the greatest percent time within 0-1m offshore according to the depth gauge followed by nearshore and inshore, while the salt water switch showed practically no surfacing behavior again in inshore and nearshore locations, although both salt water switch and depth gauge showed greatest surfacing offshore.

Hourly trends also showed differences. While inshore locations showed greater surfacing during the early part of the day using the salt water switch data, no such trend was apparent for the depth gauge (Figure 12). In nearshore locations, the depth gauge showed a peak in surfacing in the 1100 – 1400 depth bin, a trend invisible in the salt water switch data. Finally, while both salt water switch and depth gauge showed greater surfacing offshore overall, the increase in surfacing in the earlier part of the day and dip at 1500 – 1800 was again invisible in the depth gauge data.

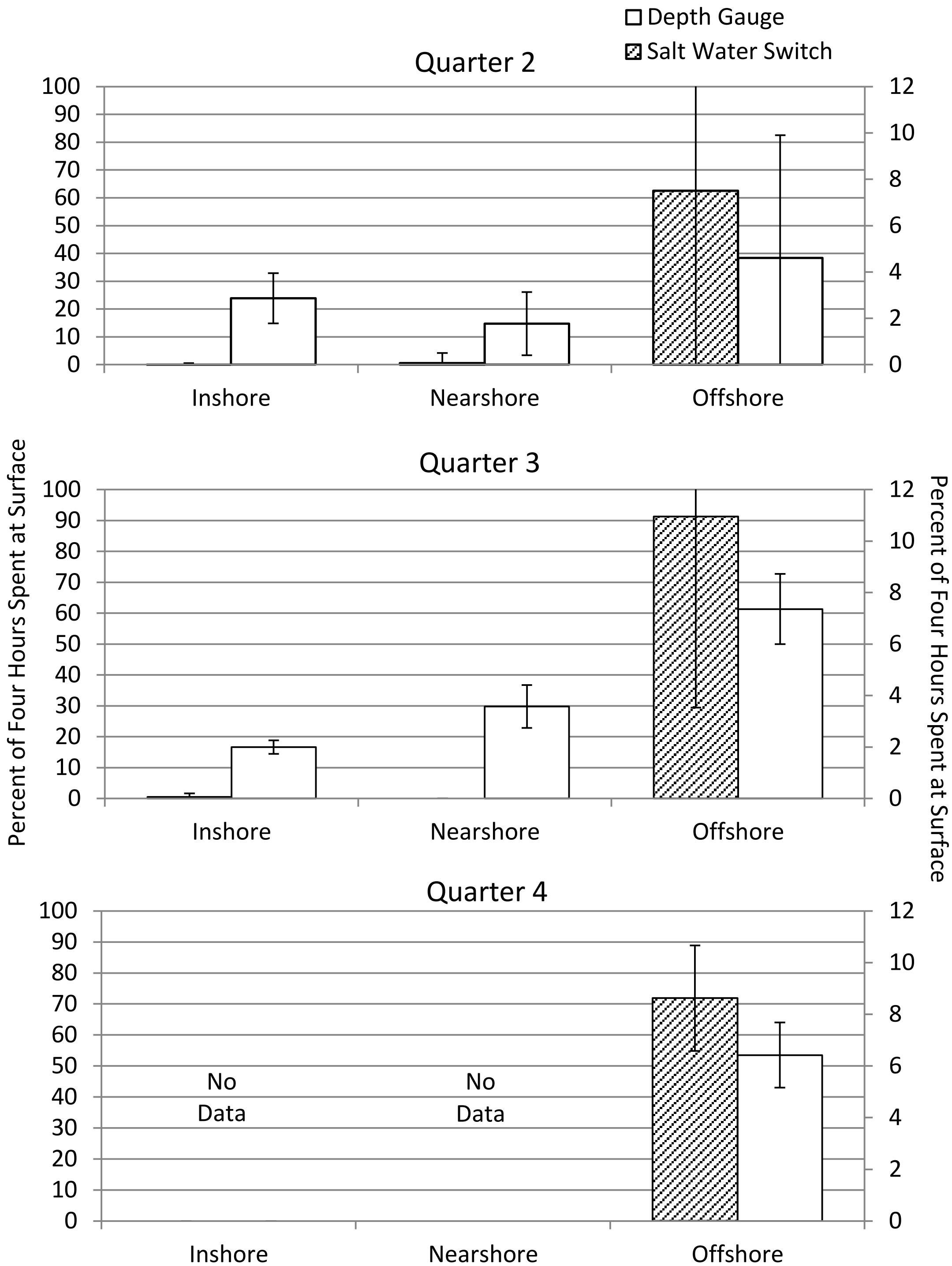

Figure 12. Percent Time at Surface based on the salt water switch (right-hand axis) and depth gauge (left-hand axis) respectively, by location and time of year. Only turtles for which depth gauge and salt water switch data were simultaneously recorded were included. Quarter 2 is April – June; Quarter 3 is July – September; Quarter 4 is October – December. Error bars are 95% confidence intervals with n being the number of turtles. N ranges from 6 to 10 inshore over both gauges, 2 to 3 nearshore for the salt water switch and 4 to 7 for the depth gauge, and 1 to 3 offshore for both gauges. Turtles represented in each graph are located in Table A-10 in Appendix I.

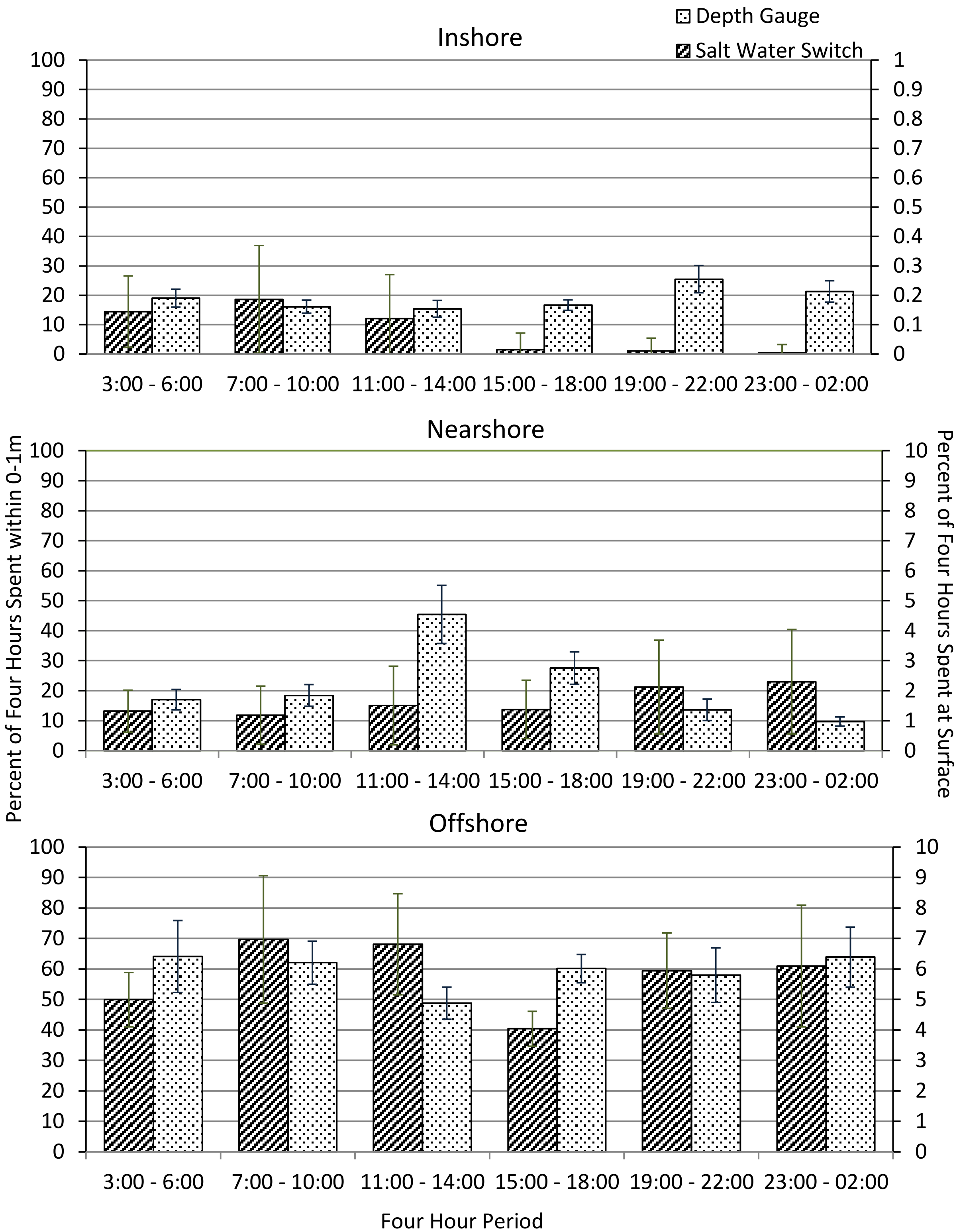

Figure 13. Percent of four-hour period spent within 0-1m and spent at the surface, based on the depth gauge (left axis) and salt water switch (right axis) respectively. Numbers of turtles range from 9 to 13 for inshore, 6 to 12 for nearshore, and 3 for the depth gauge and 10 for the salt water switch offshore. Number of turtles represented by each hour can be seen in Table A-11, Appendix I. Only turtles simultaneously recording with both a depth gauge and salt water switch were included.

Surfacing Behavior, Wave Height, and Barometric Pressure

A correlation analysis of wave-height with percent time spent within 0-1m based on the depth gauge over all turtles showed no significant correlation between wave-height and surfacing behavior, Figure 14 (p-value 0.14). When each turtle was regressed individually, no significant correlations were found for all turtles except turtle 43635 (Figure 15). A regression of barometric pressure with percent time spent within 0-1m over all turtles also showed no significant correlation (p-value 0.06). As with wave-height, when regressed individually by turtle no significant correlation between surfacing behavior and barometric pressure were found, with the exception of turtle 43635 (Figure 16). However, no significant correlation was found between barometric pressure and wave-height over the same period (p-value 0.71).

Turtle 43635 was the only turtle to experience wave-heights greater than 2.5m, reaching a maximum of 4.66m, Figure 14. This turtle showed a negative correlation between wave-height and surfacing behavior (p-value 5.58×10^{-12}). This trend can be seen more explicitly in Figure 17 where wave height and surfacing behavior are graphed together. When short- term variation is smoothed by means of a rolling average, it is clear that generally when wave height increases time at the surface decreases.

There is a slight but significant correlation between barometric pressure and percent time at surface for turtle 43635 (p-value 0.030) (Figure 16 and Figure 18). As with wave height, turtle 43635 is the only turtle to show a significant correlation between barometric pressure and surfacing behavior, and is the only turtle to experience wave heights greater than 2.5m. The correlation is not as strong as seen with wave-height, and it is unlikely that this result is anything but the product of chance.

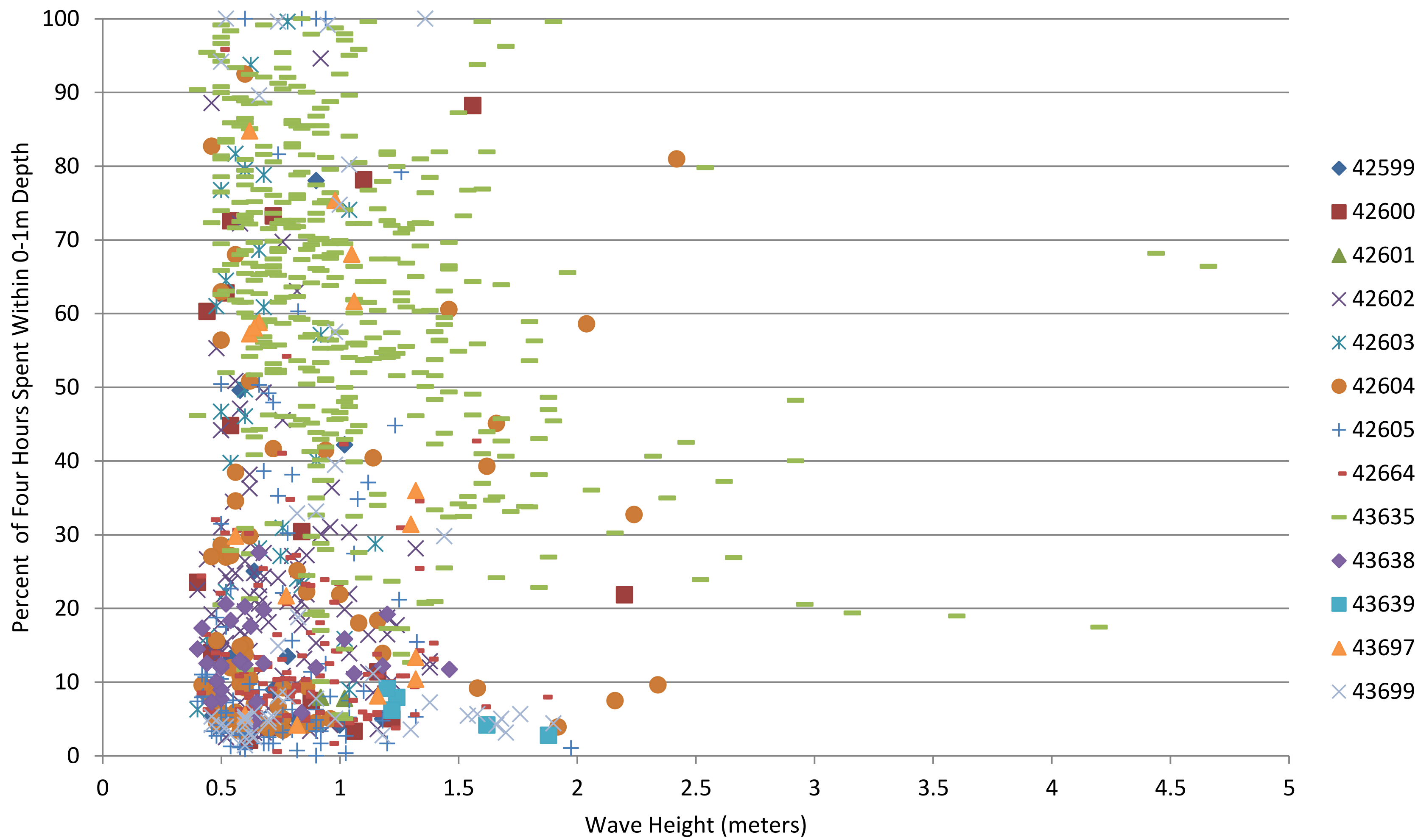

Figure 14. Percent time in four hours spent within 0-1m of surface by local wave height for each individual turtle. Equation for linear trend line over all turtles: y = 3.1199x + 35.667; R^2 = 0.0024. Wave height is determined from nearest NOAA Weather Buoy to each turtle's location.

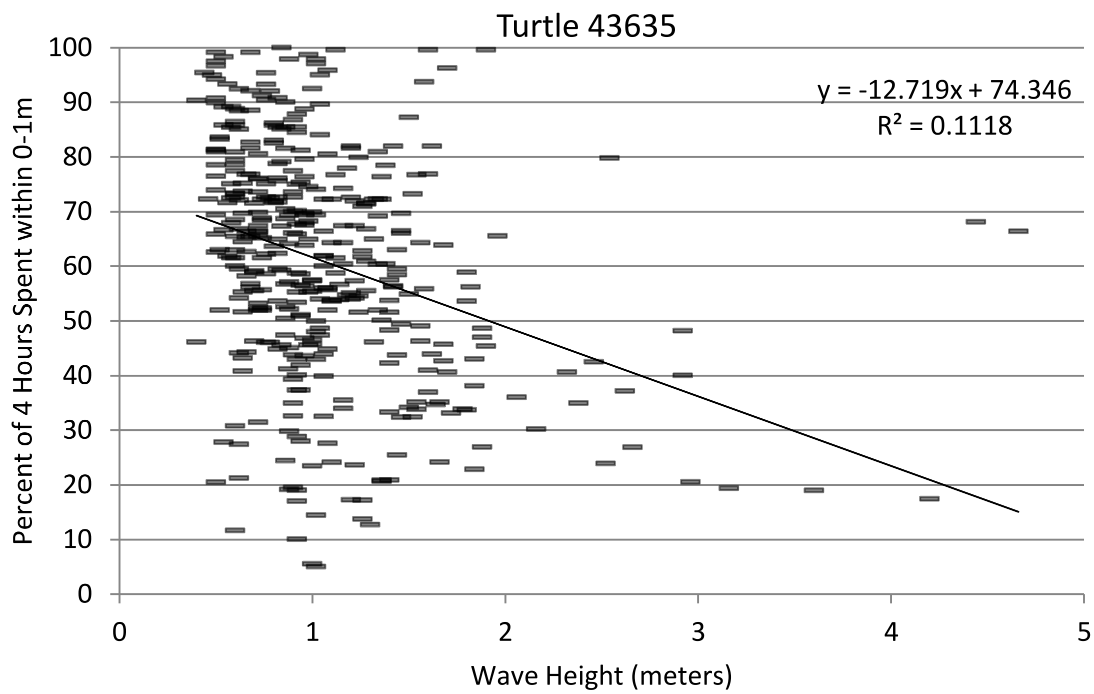

Figure 15. Wave-height versus percent time spent within 0-1m based on the depth gauge for turtle 43635. Wave height is determined by the nearest NOAA Weather Buoy to the turtle's location.

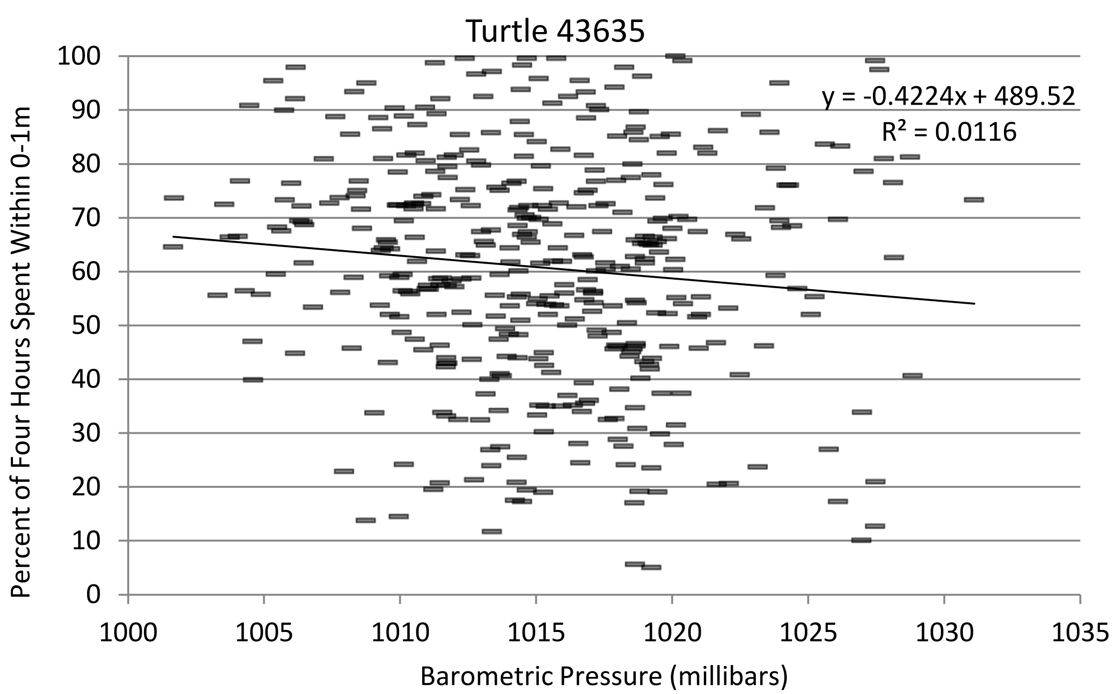

Figure 16. Barometric pressure (millibars) versus percent time spent within 0-1m for turtle 43635. Pressure is determined by the nearest NOAA Weather Buoy to the turtle's location.

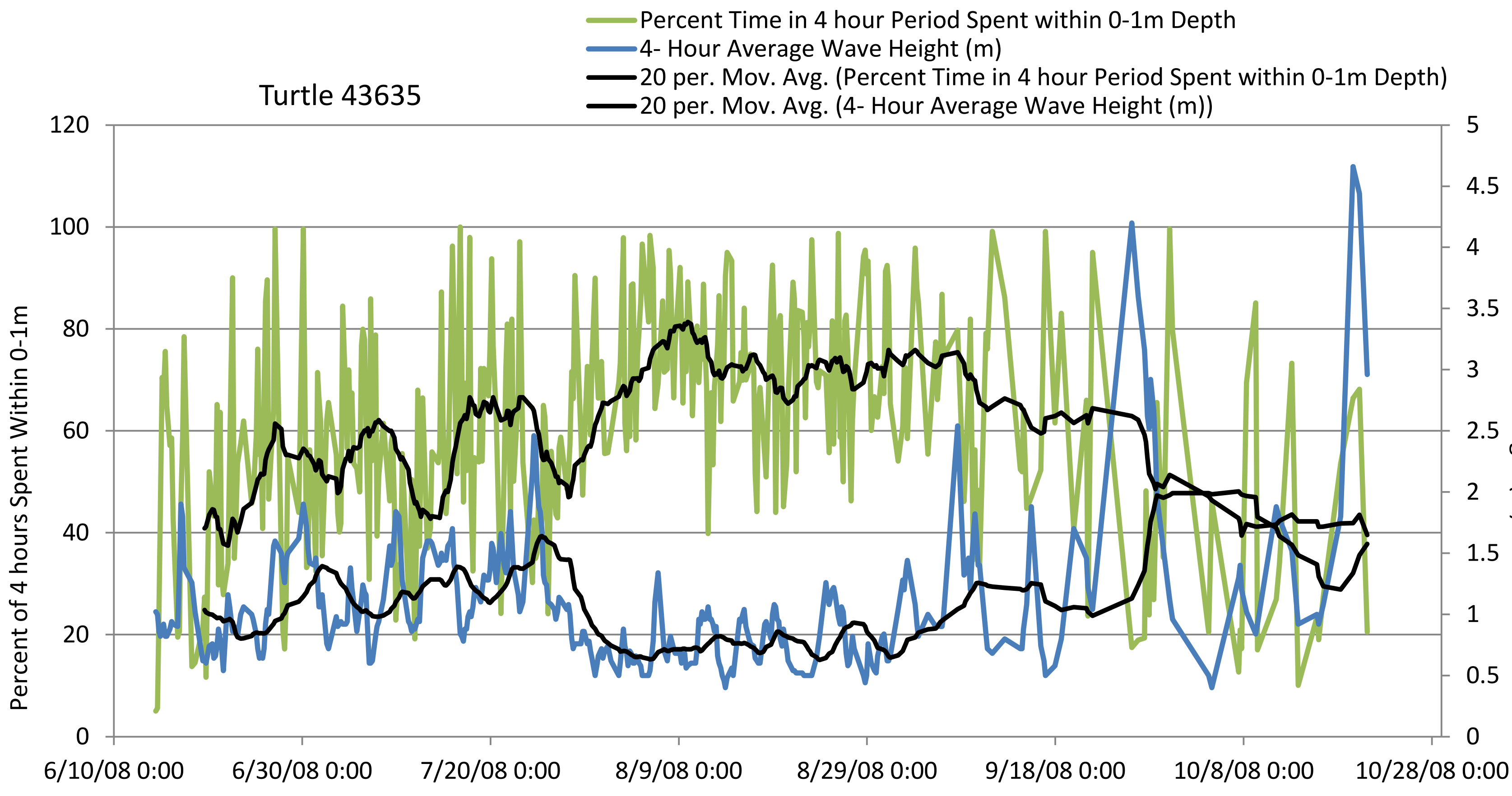

Figure 17. Percent of four hours turtle 43635 spent at the surface graphed with wave height. The left axis is percent of four hours spent within 0-1m, while the right axis is wave height (m).Black lines are 20 per. moving averages to clarify trends. Time period graphed extended over 4 months, from 6/10/2008 to 10/28/2008. Wave height is determined from nearest NOAA weather buoy to turtle's location.

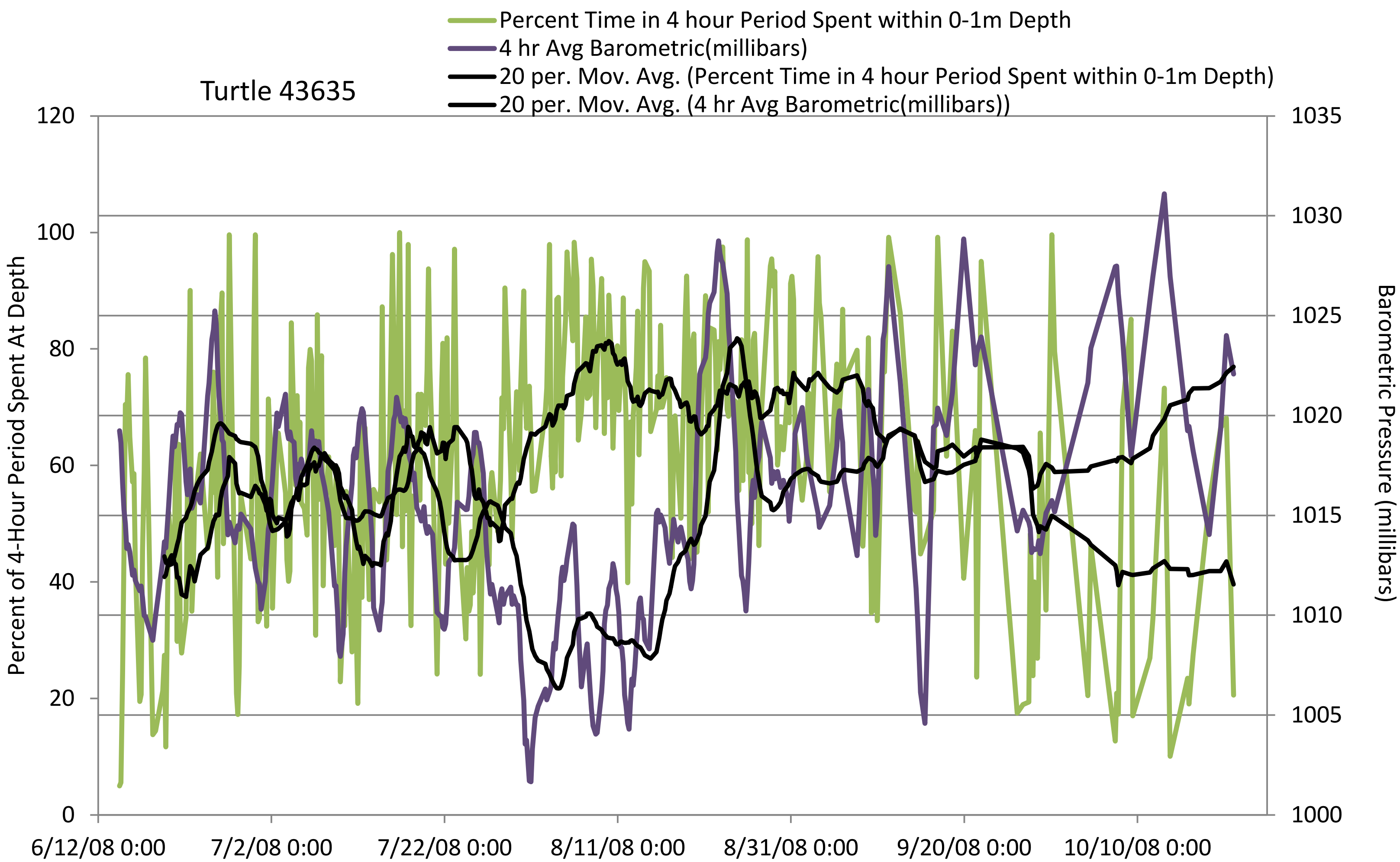

Figure 18. Percent of four hours spent at the surface through time for turtle 43635 barometric pressure through time. The left axis is percent of four hours spent within 0-1m, while the right axis is barometric pressure (millibars). Barometric pressure was determined by the nearest NOAA Weather Buoy to the turtle's location. Black lines are 20 per. moving averages to clarify trends. Time period graphed extended over 4 months, from 6/10/2008 to 10/28/2008. Wave height is determined from nearest NOAA weather buoy to turtle's location.

Discussion

Summary and Conclusions

Very different patterns were found in percent time spent at depth by inshore, nearshore, and offshore locations. Broad trends showed approximately equal surfacing across depth bins 0-1m, 1-2 and 2-3 in nearshore environments and greater percent time in the 0-1m bin with a lower secondary peak in and around the 5-10m bin for nearshore habitats. Finally, a much greater percent time in the 0-1m bin in offshore environments with consistently very low percent time spread across all depth bins out to 30-50m (Figure 10). It is important to note, however, that because depth bins are only equal for the first three and depth bins increase in size with depth thereafter that greater percent times recorded in deeper depths may be simply due to the fact that a broader range is being included. When size of the bin is accounted for, the general trend over all locations, turtles, and seasons is of decreasing time spent in each bin for any depths greater than 10m.

Dellinger and Freitas (2000) found turtles spent more time at the surface in waters less than one meter deep, with a strong secondary peak in and around 10-25m depths (Figure 2), a pattern that appears to be a combination of the nearshore and offshore patterns I observed in this study, as the depth bins were grouped relatively similarly for both studies. Their percent time at depth data were over 6-hour periods and averaged over all locations. Observing the turtle tracks it is apparent that the turtles spent their time primarily in nearshore and offshore habitats off the northwest coast of Africa, suggesting that similar behavior is represented in both studies. The high levels of presence in the 2-3m depth bin inshore may indicate sleeping or feeding on the bottom, as a vast area of inshore habitat does not exceed five meters deep.

Nearshore habitats show a peak in 5-10m depth bin, depths within the nearshore habitat are primarily composed of depths less than 10m, again suggesting utilization of the ocean floor.

Both the salt water switch and the depth gauge documented greater time at the surface in offshore habitats than nearshore or inshore habitats, a trend consistent with results recorded by Cordona et al (2005) and Howell (2010). Both Cordona et al (2005) and Dellinger and Freitas (2000) reported that approximately 35% of time was spent at the surface while offshore. This is much greater than the greatest surfacing behavior recorded by the salt water switch which showed slightly less than 20% of time spent at the surface at the very maximum levels reached (Figure 11). However, percent time spent within 0-1m averaged over all locations came much closer to the 35% time reported, with 15% time spent at the surface at the minimum in nearshore habitats and 61% of the time spent within 0-1m at maximum in offshore habitats (Figure 10). The greater percent time at surface spent while offshore for both salt water switch and depth gauge data over all quarters may be due to utilization of the sea floor feeding and sleeping purposes while turtles are in nearshore and inshore habitats. Alternately, turtles may spend more time travelling while in offshore habitats, and may therefore need to spend more time at the surface to satisfy oxygen requirements.

No major differences in diel dive patterns were found in the time at depth data (Figure 9). However, because the percent time at depth was automatically averaged over four hour periods, some precision of the data were lost, potentially erasing some patterns of behavior that may have been originally present. There were statistically significant differences in diel surfacing patterns in the salt water switch data for certain turtles, however, with significantly greater surfacing during the day recorded during nearshore habitat in quarter 2 for one turtle, and in offshore habitat for two turtles (Table 6). This is consistent with patterns shown in previous research (Parrish 1958; Ogden et al 1983; Swartz and Jensen 1991; Eckert 1986;

Southwood 2003; Hazel et al 2009 and Revelles et al 2007). There was also significantly more surfacing during the night than during the day for four turtles offshore in quarter 4 (Table 6). This trend is not as common in the literature, though Papi et al (1997) did show shorter dive duration during the night than during the day for migrating internesting loggerheads, suggesting greater surfacing behavior during the night than during the day.

Not enough data were available across all times of year and locations to conclusively state that one time of year over another showed greater surfacing behavior based on the depth gauge, however, quarters 3 and 4 were greater than quarter 2 overall (Figure 9). This is not consistent with previous studies, which have shown that spring has significantly greater surfacing than any other season (Schwartz and Jensen 1991; Nelson 1996; Dellinger and Freitas 2000). However, the salt water switch data did show greater absolute surfacing behavior in Quarter 2 which does correlate with the behavior described in these studies, but as only two turtles made up the sample it was again impossible to state that it was significantly greater than any other time of year. Based on the salt water switch, lowest surfacing was recorded in quarter 4 overall, which does correlate with lowest surfacing during the winter described in several studies (Godley et al 2003; Hatase et al 2006; Storch et al 2005; Mansfield 2006; Revelles et al 2007); however, again not enough data were available to indicate significance. Differential surfacing behavior by quarter in general may be a product of different seasons being associated with different primary behaviors, such as feeding, basking or migratory behaviors. It is not clear from this study whether any of these activities dominated within certain quarters, as, in the case of migratory patterns, only ten significant movements were made among five turtles, while the rest displayed more localized movement patterns. Of these ten movements, no particular season was favored, with three movements occurring during both quarters 1 and 2, and two movements occurring during quarters 3 and 4. If these patterns should exist, however, they do not explain the disparity in patterns observed in the salt water switch versus the depth gauge.

When salt water switch and depth gauge data were directly compared, approximately an order of magnitude of difference was found in surfacing behavior overall between the two surfacing methods (Figure 12). Additionally, overall trends in surfacing behavior over location by the salt water switch and depth gauge were very different by location and by quarter. While both showed greatest surfacing behavior offshore compared to inshore and nearshore habitats, offshore surfacing was relatively much greater for the salt water switch compared to inshore and nearshore surfacing behavior than offshore according to the depth gauge. Additionally, nearshore habitats consistently showed lowest surfacing behavior overall based on the salt water switch; but according to the depth gauge, in quarter 2 nearshore habitats showed greater surfacing than inshore habitats, while the reverse was true during quarter 1 (Figure 12).

These disparities may be due to an inherent unreliability of the salt water switch. The switch is dependent on becoming completely clear of salt water to register a surfacing event, and completely inundated again to register submergence. As the switch is located on the carapace of the turtle, it may not be triggered by a breathing turtle if the turtle lifts only its head clear of the water during a breathing event (McClellan and Read 2007). Therefore, turtles may not be consistently triggering the salt water switch during surfacing. Rain, high wind or wave action may also compromise the ability of the salt water switch to register surfacing behavior, as it may not clear completely enough to register a “dry” event if water is falling, waves are washing into it, or wind is causing spray to fall on it. Alternatively, the differential day versus night surfacing behavior by the salt water switch may be explained by turtles surfacing with a different profile depending on their primary activity for a particular time of day. The greater levels of surfacing behavior at night during quarter 4 compared to during the day may indicate that the turtles' profiles are more parallel to the water during night than during the day. Potentially, during the night when turtles spend more time sleeping, they may rise to the surface more slowly and therefore more equally across the body than during the day, when they may make more directed movement toward the surface, resulting in a more angled profile with a correspondingly lower likelihood of triggering the salt water switch. More research is necessary to determine whether this may be the case.

The depth gauge has its own inherent unreliability however. It is impossible to determine based on a pressure sensor whether a turtle is shown as travelling between two depth categories because of intentional movement, or whether the turtle is staying in one place while waves pass overhead and it is the passing of peaks and troughs of the wave that is causing the differential pressure readings, an area for which further research would be very useful.

While percent time spent within 0-1m showed no significant correlation with wave-height over all turtles, there was a significant correlation for turtle 43635. This turtle was the only to experience wave heights greater than 2.5m, suggesting wave height has no impact on surfacing behavior within 'normal' wave height conditions, but that during higher wave height events turtles may avoid the surface to avoid unnecessary jostling or turbulence at the surface. More research with a greater range of wave-heights is necessary to determine if this is the case. Similarly, barometric pressure, investigated as a proxy for weather events, showed no significant correlation to percent time spent within 0-1m of the surface, with the same exception of turtle 43635. Although both wave height and barometric pressure showed a significant correlation to surfacing behavior, there was no significant correlation between wave height and barometric pressure during the same period. As wave height is frequently caused by weather events from a great distance, it is reasonable that local barometric pressure would not necessarily correlate with local wave height, and it is likely that the significant correlation found is due to chance.

Recommendations for Future Research

While any method aimed at determining surfacing behavior inevitably has its weaknesses, strictly for the purposes of producing a correction factor for aerial surveys, utilizing the time at depth gauge for percent time within 0-1m may provide the most accurate approximation within the constraints of the current system. This is because it includes time spent near the surface when the turtle may still be visible from an aerial survey, but not register as being at the surface. If, as the data suggest, turtles show different patterns of time spent within 0-1m than directly at the surface as recorded by the salt water switch, simply applying a correction factor to the salt water switch surfacing behavior to include time spent near the surface may not provide an accurate summary of actual time spent within the visible range of aerial surveys.

Alternatively, using a time-depth archive-style tag may produce a much more accurate, greater resolution picture of surfacing behavior that could allow for more direct measurements than the binned approach used by the SPLASH and SPOT5 satellite tags. Of course, archive-style tags have their own difficulties particularly as the tag needs to be manually retrieved from the turtle again. This is why most archive style tags have been utilized on nesting females known to return to certain beaches for nesting, as opposed to juveniles that may not reappear consistently in a single location for many years.

Satellite tags collecting time at depth and surfacing information may still be able to produce a better picture of surfacing behavior if those are the sole data being collected, and/or are given the greatest upload priority. Satellite tags are restricted by the speed at which they can upload information to orbiting satellites, and data-flow can be interrupted if a turtle dives in the middle of a transmission. In such cases, prioritizing the order in which data are uploaded can ensure that the most critical data are received even if the transmission is incomplete.

Adding capacity for the tags to store data longer term and 'opportunistically' uploading data as turtles are on the surface and satellites are available could also go a long way to ensuring more complete data.

With regards to producing correction factors for aerial surveys, it appears that location is the most important source of variation in surfacing behavior, and therefore producing separate correction factors according to habitat type is particularly critical. Beyond this, producing a correction factor specific to the time of year in which the surveys are being conducted would also help mitigate some of the variability. Finally, utilizing only daytime surfacing behavior in producing a correction factor may also mitigate some variability, as no aerial surveys are ever conducted during the night. This would prevent the possibility of any different night-time surfacing patterns influencing the correction factor produced for strictly daylight use.

Fisheries & Wildlife Management Outreach Product

I produced an educational brochure targeted toward a general audience of recreational boaters off the south Atlantic coast, who may not have had significant prior knowledge of sea turtles or their behavior. The goal was to provide basic education about how to help minimize the impact of boating on sea turtles and create an awareness of their presence in the area.

A copy of the brochure can be found in Appendix II.

International Issues in Sea Turtle Conservation

Loggerhead sea turtles, *Caretta caretta,* are circumglobally distributed in temperate, subtropical and tropical waters (Dodd 1988; Bjorndal 1997; Pritchard 1997; Hatase 2007), Figure 19. Despite once being highly abundant across the world's oceans, they, along with the six other species of marine turtles are now recognized to be under serious threat. All species of sea turtles are listed as endangered under the *International Union for Conservation of Nature* (IUCN) Red List of Threatened Species (Gillespie 2006), and have been listed in Appendix I of both the Convention of Migratory Species and the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) in 1985 and 1981 respectively (Gillespie 2006; Bolten 2009) making international trade illegal.

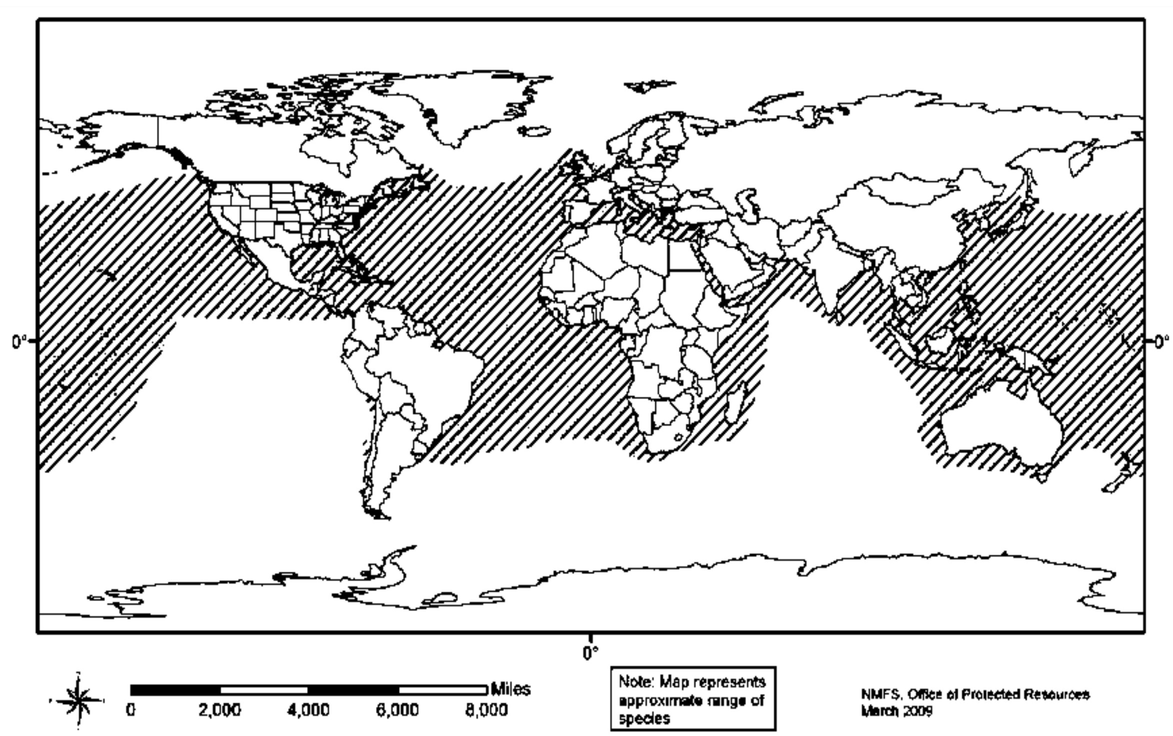

Figure 19. Range of the Loggerhead sea turtle. Map produced by the NMFS Office of Protected Resources, March 2009.

Marine turtles are also protected under the Convention on Migratory Species (Gillespie 2006). Loggerheads are listed under the Endangered Species Act (ESA) as threatened, and the other species are listed as variously threatened or endangered (Bolten 2009). Internationally, Loggerheads are listed as endangered under Australia's Environment Protection and Biodiversity Protection Act 1999 (Dept. of Sustainability, Environment, Water, Population and Communities 2010). However, the particular life history of sea turtles makes for unique difficulties in any conservation attempt. For sea turtle conservation to be successful, both an overarching international approach is necessary to contend with the turtles' disregard of human political boundaries, and a local community-derived approach is necessary for the success and longevity of the conservation attempt within the framework of our own social and economic system.

Loggerhead sea turtles are late maturing, long lived animals. Sexual maturity is reached around 35 years of age and turtles are estimated to live up to 67 years in the wild (Ernst 2009). Female turtles nest once every two to three years on sandy beaches, leaving the eggs to incubate for several months before the hatchling turtles make their way out to sea (Bolten 2009; Ernst 2009). The juvenile turtles will remain pelagic, feeding on plankton and primarily drifting passively with oceanic currents until they recruit to nearshore coastal habitat (Bjorndal 1997; Musick & Limpus 1997; Bolten 2003). However, even after the juvenile turtles have recruited to coastal habitat, they may still return periodically to pelagic habitat for years before reaching sexual maturity (Hatase et al 2007; Schofield et al 2010). Once maturity is reached, the turtles make periodic migrations between nesting and foraging habitat that can frequently involve a trans-oceanic crossing (Southwood & Avens 2009; Godley et al 2010). For example, 57% of Loggerheads foraging in the Mediterranean were found to have hatched in the United States (Bowen 1994).

In a hatchling's first foray from nesting ground to open ocean, the turtle will cross no fewer than four different legal boundaries under international law. The incubating eggs and newly hatched young crawling to the first break of waves are within the terrestrial territory of the sovereign State it has been deposited upon. That State possesses sovereign rights over the turtle as a resource. As the hatchling begins swimming out from the beach, it enters the territorial sea of the State, over which the State again has absolute sovereignty to regulate its resources so long as it does not cause harm to other States. As the turtle swims farther out to sea, it will enter the Exclusive Economic Zone (EEZ). While some conservation responsibilities are required by the Law of the Sea Convention, again the State has sovereign right to dispose of its resources here as it will. Once the hatchling has reached its open ocean habitat, it will have reached the high seas. The State nor any other entity has sovereign right to the turtle as a resource, and as a result, every state has the right to exploit the resources (Wold 2002) – a classic 'tragedy of the commons' (Dutton and Squires 2008). Over the course of its life, a single turtle may pass through any number of states' sovereign waters and the high seas.

For this reason, an international approach is fundamentally necessary for conservation efforts to be successful. The first country to recognize the need for sea turtle conservation was Mexico in 1927 (Namnum 2002), but it was not until 1968 that the need for sea turtle protection was recognized internationally with an IUCN resolution on the International Protection of the Environment (Gillespie 2006). There is still no one overarching international treaty specifically for the protection of sea turtles, nor is there any central authority that can organize and enforce their conservation (Gillespie 2006; Wold 2002; Dutton and Squires 2008). The basic legal framework for the protection of marine turtles is present in the 1992 Convention on Biological Diversity, which states that while each state has sovereign rights to exploit, conserve and/or manage its natural resources (as stated in the Law of the Sea Convention), such exploitation must avoid any damage to the environment or resources of any other states or regions beyond national jurisdiction. Additionally, specific exceptions are placed on highly migratory species as a ‘shared resource’ requiring states sharing the migratory species to cooperate through ‘appropriate international organizations’ for the purposes of conservation and the promotion of optimum utilization among states (Gillespie 2006; Wold 2002). However, while the rules provide a framework for sea turtle protection, they do not require it. Additionally, it has been argued that the rules do not apply to sea turtles (Wold 2002). It is also interesting to note that the United States is not among the 192 states that have ratified the Convention on Biological Diversity (Snape 2010). While sea turtles are protected internationally under CITES, it only specifies protection against international trade, only one of a plethora of issues threatening sea turtles worldwide (Wold 2002).

Where international rulings are lacking, more comprehensive approaches have been put forth in regional agreements. The Convention on the Conservation of Migratory Species of Wild Animals (CMS) has listed all seven species of sea turtles as requiring international cooperation for their conservation, and six have been listed as endangered. Through CMS, nations on the west coast of Africa have produced a Memoranda of Understanding to protect turtles, as did another group of nations in the Indian Ocean and South East Asia. Nations in the Caribbean have been required to take stringent conservation measures on the intentional capture and killing of turtles (though not required to protect nesting beaches) by the Protocol Concerning Specially Protected Areas and Wildlife, while nearby the Cooperative Agreement for the Conservation of Sea Turtles of the Caribbean Coast of Costa Rica, Nicaragua and Panama was established. Most of the rest of the western hemisphere is covered by the Inter-American Convention for the Protection and Conservation of Sea Turtles (the first treaty exclusively focused on sea turtles), which disallows the intentional capture, killing, and trade in sea turtles and requires the use of Turtle Excluder Devices (TEDs) allowing the escape of turtles from shrimp nets (Wold 2002; Gillespie 2006). The Pacific generally comprises a gap in international sea turtle protection, an issue particularly dangerous as Japan and the Pacific Islands hold some of the most important breeding and migration areas in the world (Gillespie 2006; Dutton and Squires 2008). For these treaties to successfully conserve sea turtles, however, they must address the three biggest threats to sea turtle survival: fisheries bycatch; habitat degradation; and international and/or domestic trade and consumption (Gillespie 2006; Wold 2002). These issues will be addressed in turn.

Bycatch

Bycatch is the portion of a commercial fishing catch that is composed of unintentionally caught, unwanted animals. The rise of the shrimping industry has coincided with the dramatic population reduction of marine turtle species as a result of unintentional bycatch (Gillespie 2006; Wold 2002; Joyner and Tyler 2000; Wallace et al 2008). Some estimates suggest that for every one kilogram of shrimp, five kilograms of other unintentionally captured organisms are also taken, with sea turtles making up a significant portion of these. In the 1990's, bycatch of turtles in shrimp trawlers was indicated to be the largest anthropogenic source of turtle mortality, with 70-80% of dead turtle strandings on beaches attributed to interactions with the fishery (Crowder et al 1995; Joyner and Tyler 2000; Pritchard 1997). The issue of bycatch has been highly emphasized in the CMS, which referred to it as a "matter of urgency" (Gillespie 2006).

To mitigate this issue, Turtle Excluder Devices (TEDs) were developed, a mechanism by which turtles could safely escape shrimp nets without the loss of shrimp, Figure 20. TEDs, when correctly installed, have been shown to reduce turtle mortality from 44% to 97% of pre-TED installation levels (Crowder et al 1995; Weber et al 1995). In 1992 the United States made the installation of TEDs mandatory for all shrimp trawlers (Crouse 1993), and shortly thereafter passed federal legislation banning the import of any shrimp caught without the use of TEDs. This, however, set in motion three separate cases in the World Trade Organization (WTO), ruling that one country cannot unilaterally set the environmental standards of another, forcing the U.S. to release its embargo (Joyner and Tyler 2000; Gillespie 2006). This ruling is consistent with a similar case involving a U.S. embargo on tuna caught by dolphin-unsafe means. There again the embargo was struck down, ruling that a product cannot be differentiated on the basis of how it was made (Joyner and Tayler 2000).

Figure 20. A Loggerhead sea turtle escaping from a Turtle Excluder Device (TED). Photo courtesy of NOAA.

Shrimping vessels are not the only to incur sea turtle bycatch. Sea turtles are also consistently caught in longline, gillnet, pound net, set-net, trawl, and purse seine nets throughout their range by fishing fleets of all origins (Gillman et al 2010; Donoso and Dutton 2010; Lewiston et al 2004). Evidence increasingly indicates that artisanal, small scale fisheries are becoming the biggest threat to sea turtle survival. Studies have shown this to be the case in the greater Caribbean region, Chile, Mexico and Baja California, Peru, and Japan (Lee Lum 2006; Peckham et al 2007 and 2008; Alfaro-Shigueto et al 2007; Ishihara 2007; Gilman et al 2010). While this is a pervasive problem, the best solution is unlikely to be overarching legislation. Rather, because each fishery – across geographic location, culture, and target fish – will have different gear design, material, and method, the best method to reduce turtle bycatch will be correspondingly different (Gilman 2010). Only by working with the local community can the most effective measures for any given situation be ascertained and effectively put in place.

What seems the most obvious method of reducing fishery bycatch – the closure of offending fisheries – may not actually be the most effective technique, ignoring the protest of the fishery itself. Technological advances in satellite tracking has provided huge insight into the migratory behavior of sea turtles for the purposes of conservation, as without an understanding of where these turtles go over the course of their life history, it is impossible to implement protection measures for either the turtles or their habitat (Godley et al 2002; Zbinden 2007; Avens 2003). Unfortunately, more often than not satellite studies are showing an extraordinarily broad range and variable pattern of sea turtle paths (Hays et al., 2006; Godley et al 2010; Zbinden 2007), with one study showing turtles with a foraging home range anywhere from $10km^2$ to $1000km^2$ (Schofield et al 2010), making the method of area closures as a primary strategy less effectual than might be hoped. For example, in the Algerian Basin, juvenile Loggerheads experience one of the largest bycatch rates in the world (Witzell and Cramer 1995; Caminas et al. 2006). Even though the locations of high turtle use have been clearly identified, the area fully encompassed primary fishing grounds, and turtle presence is year-round, regional or seasonal closures are ineffectual unless the entirety of the Algerian basin were closed to fishing completely. As this is an impossible feat, the remaining practical possibilities include reducing overall fishing efforts where possible and modifying fishing gear appropriately to make turtles less likely to be caught (Revelles et al 2007; Schofield 2010).

Habitat Degradation

Habitat degradation is another pressing issue for sea turtle conservation. Coastal areas are arguably the most valuable areas to both sea turtles and human economy. Sea turtles rely on these coastal zones for feeding, migration, mating and resting, and rely on the shores themselves for nesting. At the same time, coasts are a centerpiece in the human enterprises of tourism, fishing, trade, and transport, to name a few (Bjorndal 1997; Revelles 2007; Gillespie 2006; Hazel 2009; Hays et al., 2003; Parra et al., 2006; Schofield et al., 2007). Coastal development is a threat for several reasons. Not only can it result in the degradation or complete eradication of the sandy beach habitat required for nesting, but the lights from nearby developments can disorient turtles, causing hatchlings as well as nesting females to follow the lights instead of approach the ocean (Mann 1976; Longcore and Rich 2004).

In many regions there is a constant battle between the pull to protect pristine areas for threatened and endangered species, and exploitation of the area for the development of tourism and financial gain. For example, Xcacel beach in Mexico's Caribbean was at one point said to host the most genetically diverse population of sea turtles in the world, but despite an ecological ordinance passed in 1994 by the Mexican government making the area a marine sanctuary, the land was sold to hotel developers (Hardman 2003). While international outcry forced the project to a standstill for over a decade, the fate of the beach is still not certain. The necessity for coastal protection of sea turtle habitat and individuals is recognized, however, in the Management Plan for the Indian Ocean and South-East Asian Region, the before mentioned Agreement for the Caribbean Coast of Costa Rica, Nicaragua and Panama and the Memorandum of Understanding for the Atlantic Coast of Africa (Gillespie 2006; Wold 2002). Pelagically, marine debris and pollution are factors in the decline of sea turtles. Both Loggerhead and Leatherback turtles ingest plastic bags which can look similar to jellyfish, and the accumulation of plastic in the stomach can lead to choking or starvation. Additionally, turtles can become entangled in monofilament fishing line or discarded fishing nets (National Research Council 1990). Organochlorine compounds and heavy metals have also been found in the tissues of several species of turtles in the U.S., Ascension Island, and France (Keller et al 2004; National Research Council 1990), which have been shown to impact Loggerhead immunoresponse (Keller et al 2006). While it is extraordinarily difficult to pinpoint and regulate the input of pollutants or marine debris, numerous treaties have been developed in the attempt to prevent and regulate the influx of waste at the international level, such as the International Conventions for the Prevention of Pollution from Ships (MARPOL) (Gillespie 2006; Nollkaemper 1994; Sheavly and Register 2007).

Arguably one of the most pressing issues within the realm of sea turtle habitat degradation is the impact of rising sea levels associated with climate change. Significant loss to nesting habitat has been projected for beaches in the Caribbean (32% loss with a 0.5m increase in sea level), South Carolina, USA (51.4% loss of a particular nesting beach with a 0.53m increase in sea level), and Hawaii (up to 35% loss with a 0.48m rise), with relatively similar impacts on nesting beaches predicted around the world, depending on beach inclinations (Fish et al 2005; Daniels et al 1993; Baker et al 2006). The issue of climate change is such a broad and contentious subject of national and international debate that no attempt will be made to address it in this paper. Suffice it to say that no substantial international agreement has been signed to date that effectively addresses the issue or commits to significant steps toward its mitigation (Wemaere 2010).

International and Domestic Trade and Consumption

Finally, the third major threat to sea turtle conservation is the domestic and international trade of sea turtles – both legal and illegal. There has been a huge historic and ongoing market for sea turtle products and remains, particularly in Asia where the demand for Hawksbill shell is particularly high. Over 30,000 Hawksbill shells per year were being imported to Japan from over fifteen different countries in the 1990's, with Fiji and the Solomon Islands being the largest suppliers (Gillespie 2006). It is not just the shells that are in demand nor is the market restricted to Asia, as sea turtle heads have been sold as home décor in Uruguay (Lopez 2001) and there is a history of brisk trade in sea turtles between the United States and Mexico (Steiner 1994). International economic disparities are primarily at the heart of this issue, as whether or not the local human population is concerned about marine turtles, the incentive for a poor and struggling populace to exchange their turtles for a large commission to a developed country with high demand for sea turtle products is simply too strong. While some nations such as Fiji are actively trying to curb their exports by domestic efforts, others make no attempt to stem the flow of illegal endangered species products (Gillespie 2006). The best method to stem the flow may therefore be by addressing the demand side of the equation, as without the drive of high demand producing extraordinary prices, the supply will dwindle of its own accord.

Sea turtles may be taken legally by indigenous peoples where the traditions and relationships are long-standing according to most international treaties (Gillespie 2006). For example, the indigenous peoples of the South Pacific Islands have long utilized sea turtles as a primary source of protein (Allen 2007), and as a result, may take both eggs and adults. Some treaties put stronger limits on this take than others, including the Indian Ocean and South-East Asian Region Agreement that only allows for indigenous take on the condition that the harvests are sustainable and do not contradict the management regime in effect. A number of treaties, including the Pacific Regional Marine Turtle Conservation Programme, operates under the assumption that subsistence take will not have a significant impact on the survival of the species, an assumption that may not be founded in fact depending on the number of people utilizing subsistence take, and status of the marine turtle population from which they are taking (Gillespie 2006). Some indigenous groups, such as the Yolngu of Northern Australia, are taking it upon themselves to develop a management strategy for sea turtles combining both western knowledge and indigenous practices with the aim of conserving both the species and their culture (Kennet et al 2004).

Conservation Efforts

Each of the three broad threats facing sea turtles (fisheries bycatch, habitat degradation, and human trade and consumption) is a complex, trans-boundary issue in and of itself. While ideally a single overreaching international policy would specifically address the unique problems of sea turtles, the various initiatives currently present do address most aspects of sea turtle conservation in most parts of the world (Dutton and Squires 2008; Wold 2002; Gillespie 2006). What is holding back these measures is the issue of enforcement. A state may make agreements or regulations with the best intentions for sea turtle conservation possible, but if that nation becomes politically unstable or does not have the resources to enforce the measures agreed upon, the signatures do not help sea turtle populations on their own (Gillespie 2006). This is a problem in countries including, but not limited to Mexico, Indonesia, Malaysia, Sri Lanka and the Maldives (Koch et al 2006; Suriyani 2009; Hilterman and Goverse 2005; Chan 2006; Fisher 1995). This issue can be somewhat mitigated by the involvement of local communities in producing and enforcing conservation regulations, as communities with a concrete investment in the welfare of their endangered species population are more likely to self-regulate take and consumption (Lejano and Ingram 2007).

In international law, the sovereign right to exploit resources within international waters or inside a state's territory is fundamentally assured, despite basic restrictions for the protection of species against extinction. While CITES prohibits international trade in the endangered animals, there are no international legal requirements for the protection of an endangered species' habitat. That protection must be voluntarily offered by individual states (Wold 2002). Unfortunately, the distribution of costs and benefits of marine turtle protection is frequently very unequal. The benefits, in particular, 'existence-value' are appreciated primarily by high-income developed countries, or high income groups within developing countries. The costs, including lost income, livelihood, and sustenance directly from utilization of the turtles, in addition to the foregone incomes from resources related to turtles, such as shrimp or fish, primarily fall to lower income communities in developing nations (Dutton and Squires 2008). Additionally, should conservation efforts be successful, all entities benefit – whether or not they were involved in the sacrifices required to make it happen. This produces a 'free rider' difficulty, as the incentives are lower to participate if the desired effect can be (at least theoretically) achieved without full participation (Dutton and Squires 2008; Campbell 2007).

It is therefore of utmost importance for any conservation effort to be instigated with the full knowledge and willing participation and input from the local community upon which the effort will depend (Dutton and Squires 2008; Campbell 2007; Gillespie 2006). A case example can be found in the Turtle Islands, a group of small islands in Philippines. Since the 1950's turtle eggs had been collected for sale on the black-market to Taiwan and other parts of Asia. Early in the 1980's a small group of conservationists from the Philippine government arrived seeking to foster a program that would allow both the continued revenue of sea turtle egg take and introduce a sustainable management program that would allow the population to regrow. Members of the community integral to the egg harvest were integrated as wardens, while residents were still allowed a small but equal allowance of eggs. At the end of the decade, egg conservation rose from less than 50% prior to the 1980's to an estimated 80%. However, in 2001 the Philippine congress passed the Wildlife Resources Conservation and Protection Act, which strictly prohibited any and all egg harvest. The response from the Turtle Islands Municipal Council was to refuse compliance and establish autonomy of the community. It was determined the egg revenue was too important for livelihoods to be stricken off completely. Almost immediately subsequent to the national ruling turtle egg conservation efforts were terminated, and consumption returned to pre-1980 levels in less than a year (Lejano and Ingram 2007).

This example underlines the message that a conservation program must be tailored to and supported by the local community to be successful. Giving local groups the opportunity to take ownership of their resources in a committed and sustainable way can smooth the divisions produced by a state mandate to 'cease and desist', ultimately producing a stronger, more enduring, and therefore more successful conservation program. Recognizing this, a recent study in Greece was conducted to evaluate whether a course in sea turtle conservation for elementary school students resulted in either an increase in knowledge or attitudes of the students, with the conclusion that with more knowledge students' understanding and concern for sea turtle conservation became stronger and more defensible (Dimopoulos et al 2008).

Sea turtle conservation requires both a 'top down' and 'bottom up' approach to be successful. Due to the highly migratory nature of the turtles, any management effort will be unsuccessful if enacted solely by one concerned group or nation. On the other hand, without full local input, knowledge, and participation, mandated conservation regulations are generally doomed to failure in nations without an already large conservationist base or resources for strict enforcement. Combining these disparate strategies into a community -rooted approach with international cooperation and oversight is the best hope for sea turtle conservation worldwide.

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Appendix I

Tables included in this Appendix

are presented under the same heading

as their respective discussions in the main text.

Depth Gauge

Table A-1. Count of observations and 95% confidence intervals for percent time spent within 0-1m based on the depth gauge by individual turtle in Figure 9 in the main text.

	Quarter 2						Quarter 3						Quarter 4					
	Inshore		Nearshore		Offshore		Inshore		Nearshore		Offshore		Inshore		Nearshore		Offshore	
Turtle	#	95% Conf	#	95% Conf	#	95% Conf	#	95% Conf	#	95% Conf	#	95% Conf	#	95% Conf	#	95% Conf	#	95% Conf
42599	4	16.81	8	2.20	-	-	-	-	-	-	-	-	-	-	-	-	-	-
42600	6	8.52	7	8.66	4	12.61	-	-	-	-	-	-	-	-	-	-	-	-
42601	-	-	2	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-
42602	93	0.19	-	-	-	-	2	4.94	-	-	-	-	-	-	-	-	-	-
42603	31	1.29	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
42604	20	1.45	6	5.23	-	-	-	-	4	2.29	31	0.80	-	-	-	-	3	1.27
42605	57	0.28	8	0.23	-	-	25	1.14	-	-	-	-	-	-	-	-	-	-
42664	59	0.24	-	-	-	-	56	0.05	-	-	-	-	-	-	-	-	-	-
43635	9	4.92	8	3.43	44	0.53	-	-	-	-	324	0.06	-	-	-	-	19	1.37
43638	26	13.13	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	0.01
43639	-	-	-	-	-	-	-	-	3	0.21	2	1.86	-	-	-	-	-	-
43697	4	1.58	-	-	-	-	8	2.01	4	7.81	-	-	-	-	-	-	-	-
43699	4	16.37	5	4.54	-	-	34	0.08	-	-	-	-	-	-	-	-	-	-

Table A-2. n and number of entries for 95% confidence intervals seen in Figure 9, for time at depth spent within 0-1m according to the depth gauge, by quarter and time of day.

	Quarter 2		Quarter 3		Quarter 4	
Start of 4Hr Period	Number of Turtles	Number of Entries	Number of Turtles	Number of Entries	Number of Turtles	Number of Entries
3:00	10	69	7	75	3	5
7:00	12	68	6	79	2	6
11:00	10	70	8	94	2	5
15:00	10	67	7	84	2	4
19:00	11	68	8	87	2	6
23:00	9	63	6	77	2	3

Table A-3. Turtles represented in Figure 9 during quarter 2 by time of day. X indicates the turtle was recorded during the four-hour period indicated.

Turtle	3:00	7:00	11:00	15:00	19:00	23:00
42599	X	X	X	-	X	X
42600	X	X	X	X	X	X
42601	-	X	-	-	X	-
42602	X	X	X	X	X	X
42603	X	X	X	X	X	X
42604	X	X	X	X	X	X
42605	X	X	X	X	X	X
42664	X	X	X	X	X	X
43635	X	X	X	X	X	X
43638	X	X	X	X	X	X
43697	-	X	-	X	-	-
43699	X	X	X	X	X	X

Table A-4. Turtles represented in Figure 9 during quarter 3 by time of day. X indicates the turtle was recorded during the four-hour period indicated.

Turtle	3:00	7:00	11:00	15:00	19:00	23:00
42602	-	-	X	-	X	-
42604	X	X	X	X	X	X
42605	X	X	X	X	X	X
42664	X	X	X	X	X	X
43635	X	X	X	X	X	X
43639	X	-	X	X	X	-
43697	X	X	X	X	X	X
43699	X	X	X	X	X	X

Table A-5. Turtles represented in Figure 9 during quarter 4 by time of day. X indicates the turtle was recorded during the four-hour period indicated.

Unique Turtles	3:00	7:00	11:00	15:00	19:00	23:00
42604	X	X	-	-	-	-
43635	X	X	X	X	X	X
43638	X	-	-	X	-	-
42605	-	-	X	-	-	-
43699	-	-	-	-	X	X

Table A-6. Turtles represented in Figure 10 by time of year and location. 2, 3, and 4 indicate quarters 2, 3 and 4 respectively.

Turtle	Inshore	Nearshore	Offshore
42599	2	2	-
42600	2, 3	2	2
42601	-	3	-
42602	2, 3	-	-
42603	3	-	-
42604	2, 3	3	3, 4
42605	2, 3	2	-
42664	3	-	-
43635	3	3	3, 4
43638	-	-	-
43638	-	-	4
43639	-	3	3
43697	2, 3	3	-
43699	2, 3	3	-

Salt Water Switch

Table A-7. Turtles represented in Figure 11. Quarters in which each turtle was present in offshore locations. X indicates the turtle was recorded during the quarter indicated.

Turtle ID	Quarter 1	Quarter 2	Quarter 3	Quarter 4
42600	X	-	-	-
42604	-	X	X	-
43635	-	X	X	-
43638	-	-	X	-
75425	X	-	X	X
75427	-	-	-	X
76454	X	-	X	X
76455	X	-	X	X
76456	X	-	X	X
76457	X	-	X	X

Table A-8. Count of entries and 95% confidence intervals for mean percent time of one hour spent at the surface offshore indicated in Table 5 of the main text.

Turtle	Quarter 1		Quarter 2		Quarter 3		Quarter 4	
	Count	95% Conf. Interval	Count	95% Conf. Interval	Count	95% Conf. Interval	Count	95% Conf. Interval
42600	72	0.97	-	-	-	-	-	-
42604	-	-	216	0.16	24	0.82	-	-
43635	-	-	1584	0.016	240	0.044	-	-
43638	-	-	-	-	24	0.21	-	-
75425	120	0.24	-	-	24	0.14	0.16	0.092
75427	-	-	-	-	-	-	216	0.05
76454	432	0.054	-	-	144	0.038	144	0.17
76455	216	0.19	-	-	24	0.21	336	0.05
76456	192	0.033	-	-	144	0.036	288	0.019
43635	192	0.13	-	-	192	0.024	96	0.11

Table A-9. Count of observations and 95% confidence intervals for average percent time at surface by location and turtle seen in Table 6 in the main text.

Turtle ID	Inshore Count	Inshore 95% Conf. Interval	Nearshore Count	Nearshore 95% Conf. Interval	Offshore Count	Offshore 95% Conf. Interval
42599	24	0.03	48	9.2×10^{-03}	-	-
42600	96	0	24	0.034	72	0.97
42602	576	5.5×10^{-03}	-	-	-	-
42603	192	0.014	-	-	-	-
42604	120	5.3×10^{-03}	48	0	240	0.14
42605	528	1.2×10^{-03}	48	0.030	-	-
42664	600	3.8×10^{-04}	-	-	-	-
43635	24	0.034	24	0	1824	0.013
43638	168	5.9×10^{-03}	-	-	24	0.21
43699	312	4.8×10^{-03}	-	-	-	-
75425	-	-	48	1.03	528	0.062
75427	-	-	168	0.15	216	0.051
76454	-	-	96	0.06	720	0.028
76455	24	0.140027	72	0.42	480	0.049
76456	-	-	96	0.09	624	9.1×10^{-03}
76457	456	4.5×10^{-03}	-	-	480	0.032

Depth Gauge and Salt Water Switch Comparison

Table A-10. Turtles represented in Figure 12 by time of year and location. 2, 3, and 4 indicate quarters 2, 3 and 4 respectively. Only turtles for which both a salt water switch and depth gauge were simultaneously recording were included.

	INSHORE		NEARSHORE		OFFSHORE	
Turtle	Salt Water Switch	Depth Gauge	Salt Water Switch	Depth Gauge	Salt Water Switch	Depth Gauge
42599	2	2	2	2	-	-
42600	2, 3	2 ,3	2	2	2	2
42602	3	2, 3	-	2	-	-
42603	3	3	-	-	-	-
42604	2, 3	2, 3	3	2, 3	3, 4	3, 4
42605	2, 3	2, 3	2	2	-	-
42664	3	3	-	-	-	-
43635	3	3	3	3	3, 4	3, 4
43638	3	3	-	-	4	4
43697	2, 3	2, 3	-	2, 3	-	-
43699	2, 3	2, 3	-	2, 3	-	-

Table A-11. Number of turtles and number of observations represented in Figure 13, a comparison of salt water switch to depth gauge by hour.

Start of 4Hr Period	Inshore				Nearshore				Offshore			
	Salt Water Switch		Depth Gauge		Salt Water Switch		Depth Gauge		Salt Water Switch		Depth Gauge	
	Turtles	Obser-vations	Turtles	Obser-vations	Turtles	Obser-vations	Turtles	Obser-vations	Turtles	Obser-vations	Turtles	Obser-vations
3:00	13	130	10	72	10	28	7	9	10	217	3	68
7:00	13	130	10	75	10	28	6	10	10	217	3	68
11:00	13	130	9	86	10	28	6	7	10	217	3	76
15:00	13	130	10	71	10	28	7	11	10	217	5	73
19:00	13	130	13	161	10	28	7	12	10	217	3	77
23:00	13	130	11	70	10	28	5	6	10	217	3	67

Appendix II