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Migratory Patterns and Habitat Use of the Sand Tiger Shark (*Carcharias taurus*) in the Western North Atlantic Ocean

By

Shara Marie Teter

Submitted to the Faculty of Nova Southeastern University Oceanographic Center in partial fulfillment of the requirements for the degree of Master of Science with a specialty in:

Marine Biology and Coastal Zone Management

Nova Southeastern University

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Abstract

Large population declines for sand tiger sharks (*Carcharias taurus*) in parts of its global range are well documented, resulting in a strong need for biologically informed conservation and management measures. Although sand tigers in the western North Atlantic have been listed as a Species of Concern by the US government since 1997, details of their seasonal migratory movements and especially vertical habitat use patterns along the US East Coast are limited. Understanding these movement patterns is vital to reducing fishery-related mortality of these sharks and informing other management efforts aimed at recovery of their stocks in the US Atlantic. Although survey and fishery-dependent data have revealed a general picture of the seasonal distribution patterns of sand tiger sharks, details of the areas specifically used by these sharks and their movements between such areas remain unclear. Additionally, information on vertical habitat use such as preferred depth and temperature, as well as variability observed among sexes, size classes and geographic locations would provide insight into the fine-scale distribution of sand tigers to aid better management practices. Here, I report on the horizontal and vertical movements of sand tiger sharks along the US East Coast determined through use of pop-up archival transmitter (PAT) tags and supplemental acoustic telemetry. PAT tags were deployed on 14 sand tiger sharks in Delaware Bay in late summer 2008. Sufficient archived depth and temperature data were obtained from 11 sharks (eight male, three female), and sufficient light data allowed construction of long-term horizontal tracks for 10 sharks (seven male, three female) using a Kalman filter state-space model. Duration of tag deployment per animal ranged from 64-154 days ($\bar{x}$ =121.6). All seven male sharks left Delaware Bay in late summer/early autumn and
migrated south along the US East Coast reaching waters off North Carolina, where they remained until transmitter detachment during the winter months. In contrast, all three females moved out of Delaware Bay into deeper, offshore waters east of the bay near the continental slope. During southern migration of males, average depth utilized was positively correlated to shark size. The smallest males spent on average over 90% of their time in waters <40 m, whereas intermediate and large sized males spent only 54 and 38% of their time at depths <40 m, respectively. Female sharks spent an average of 46% of their time in waters <40 m after leaving Delaware Bay. All sharks remained within a relatively narrow temperature range, spending at least 95% of their time in waters 17-23°C, with little difference between size classes or sexes. Horizontal movements of male migrating sand tigers also revealed several areas of concentrated activity along their southern migratory routes. Migratory patterns of sand tiger sharks along the US East Coast appear most similar to patterns displayed by this species along the coast of South America. Further delineation of western North Atlantic continental shelf and slope core areas of sand tiger shark activity, especially for females, will inform efforts to reduce interactions with commercial fisheries and measures to avoid habitat degradation - management aspects that will aid in reducing mortality and enhance rebuilding of sand tiger stocks along the US East Coast.

**Keywords:** *Carcharias taurus*, sand tiger sharks, satellite telemetry, essential habitat, vertical movements
Introduction

The ability of animals to move is central to their individual success, as well as to sustainability of their populations. Both long-distance and fine geographic-scale movements are related to an animal’s capability to find mates, acquire prey, and access favorable habitats, and are integral components contributing to the evolutionary fitness of the animal. Revealing the patterns of these movements is a key component of understanding a species’ behavior, population dynamics, and life history (Rubenstein and Hobson 2004). On a broader scale, movement patterns of individuals can reflect a wide range of interactions with other species within its ecosystem, and may therefore be indicative of the role of the animal in ecosystem processes (Holyoak et al. 2008; Nathan et al. 2008). For species that are vulnerable to overexploitation or warrant interest in sustainably managing their populations, understanding movements and habitat use is fundamental for application of effective management plans and successful conservation (Rubenstein and Hobson 2004).

Despite strong interest in movement patterns of highly mobile marine species, information on this topic remains disjointed for many species, and until recently tools for examining such questions were limited. This lack of knowledge is understandable given the vastness and inaccessibility of the marine environment, and the challenges associated with tracking the movements of highly mobile marine organisms for extended periods of time (Weng et al. 2008). For decades, the major methods used to examine movements of sharks were basic tag and recapture approaches. Although studies employing such conventional tag and recapture methods have revealed much about the general
movements, distribution, mortality, and stock structure of a variety of species (Kohler et al. 1998, Aires-da-Silva et al. 2009, Kohler and Turner 2009), information on the route taken between tagging and recapture locations remained unknown. Advances in acoustic telemetry, and more recently in satellite telemetry technology, now provide the ability to investigate details of individual fish movements over long distances and extended time periods, and have been useful in the study of movement patterns and habitat use of several shark species (e.g., Bonfil et al. 2005, Heupel et al. 2006; Weng et al. 2004, 2008; Nasby-Lucas et al. 2009; Abascal et al. 2011; Howey-Jordan et al. 2013).

The sand tiger shark (*Carcharias taurus*) is a large lamniform shark occurring in much of the world’s temperate and sub-tropical waters with the exception of the central and eastern Pacific Ocean (Compagno et al. 2005). This species is largely coastal in habitat and often associated with rocky reefs, caves, gullies, shipwrecks, and near shore sandy bottom habitats (Pollard et al. 1996, Otway et al. 2003, Barker et al. 2011). A combination of slow growth, late maturation, and exceptionally low fecundity (two young reported annually (Gilmore 1993, Gordon 1993) or biennially (Cliff 1989, Branstetter and Musick 1994)) makes the sand tiger extremely vulnerable to over-exploitation (Branstetter and Musick 1994, Goldman et al. 2006). Dramatic declines in abundance have been documented in areas where the sand tiger’s largest populations once existed, with targeted commercial, spearfishing, and bang stick fishing activities depleting populations off the east coast of Australia and in the western South Atlantic (Pollard et al. 1996, Otway et al. 2004, Chiaramonte et al. 2007). In US waters, where this species ranges from the Gulf of Maine to Florida and into parts of northern Gulf of Mexico (Castro 2011), population declines have also been reported in the Chesapeake
Bight Region of the U.S. Mid-Atlantic Coast (Musick et al. 1993, Ha 2006). Given these factors, sand tiger sharks are listed as globally “Vulnerable” on the IUCN Red List (Pollard and Smith 2009), and as critically endangered along the east coast of Australia (Pollard et al. 2003) and western South Atlantic (Chiaramonte et al. 2007). In the U.S., this species is designated a Species of Concern, has been prohibited from fishery landings since 1997, and is managed under the US National Marine Fisheries Services Consolidated HMS Fishery Management Plan (http://www.nmfs.noaa.gov/pr/pdfs/species/sandtigershark_detailed.pdf. Accessed August 10, 2013).

The magnitude of sand tiger population declines in US Atlantic waters remains uncertain. Musick et al. (1993) and Ha (2006) estimated declines as high as 75% to 99.8%, respectively, from historical levels in the Chesapeake Bay and adjacent coastal waters. In contrast, Carlson et al. (2009) estimated population declines of only 0.2% - 6.2% based on analysis of different databases and time scales. Despite this uncertainty in the status of sand tiger shark stocks along the US East Coast, Carlson et al. (2009), recognizing the extreme vulnerability of sand tigers to overfishing, recommended its continued listing as a Species of Concern and inclusion in the shark prohibited species management group.

Given declines in abundance that have occurred in other locations where the sand tiger has been subject to even modest exploitation, precautionary approaches for conservation and management of this species are warranted throughout its distribution. Mortalities persist in areas where protection measures have been implemented, with sand tigers being caught and killed in non-target longline, handline, rod and reel, gillnet
fisheries, as well as in beach meshing programs and as accidental recreational catch (Goldman 2002, Smale 2002, Dicken et al. 2006). Due to the low reproductive output and low rebound potential of sand tigers, even this modest rate of fishing mortality undoubtedly hinders recovery of stocks and may even lead to population declines (Smith et al. 1998).

The need for better information on sand tiger shark migrations and habitat use throughout its range has prompted several studies, including those utilizing modern telemetry technologies (Bansemer and Bennett 2011, Otway and Ellis 2011, Kneebone et al. 2012). Movements of sand tiger sharks have been examined along the continental coasts of eastern North and South America, South Africa, and eastern Australia, together forming a body of evidence demonstrating that these sharks engage in relatively large scale north-south seasonal migrations. These studies indicate that seasonal movements are influenced by reproductive cycle, and differ between sex, age class, reproductive status and geographic location (Gilmore 1993, Lucifora et al. 2002, Bansemer and Bennett 2011). Although the seasonal movements of sand tigers along the coasts of Australia and South Africa have been fairly well documented (Bass et al. 1975, Smale 2002, Otway et al. 2003; Dicken et al. 2006b, 2007; Bansemer and Bennett 2011, Otway and Ellis 2011), information for sand tigers along the US East Coast remains fragmentary (Gilmore et al. 1983, Gilmore 1993, Kohler et al. 1998). In this region, winter-spring mating appears to occur in nearshore waters off eastern Florida (late February-April) and North and South Carolina (late April-early June) (Gilmore et al. 1983, Gilmore 1993, Castro 2011). In the summer, juveniles and mature male sand tigers are thought to move north of North Carolina, while mature females presumably remain south of Cape Hatteras.
Capture of females with near-term embryos, and females that have recently given birth during November-April in waters off Florida, suggest parturition occurs at these locations in winter-spring (Gilmore 1993). Newborn sharks seemingly also move north in late spring-early summer, with a number of bays and estuaries as far north as Massachusetts serving as summer nurseries dominated by juveniles (Gilmore 1993, Kneebone et al. 2012).

Location of discrete nurseries and details of seasonal movements and areas of concentrated activity by different demographic groups of sand tigers in other regions along the US East Coast remain unclear. Identification of nurseries and core areas of activity for mature sharks would provide managers at both the state and federal level with information on spatial and temporal habitat requirements for sand tiger sharks (Kneebone et al. 2012). Such information would be useful for improved understanding of interactions among sand tiger sharks and human activities, and assessment of management measures currently in place directed towards enhanced survival of the sharks, or protection of their essential habitat. Additionally, elucidating movement of sand tigers in relation to existing US longline shark fishery time/area closures (e.g., the Mid-Atlantic Shark Area (MASA)), designed to reduce juvenile mortality of other fishery prohibited shark species would determine the effectiveness of these closures for reducing sand tiger shark mortality from fishery bycatch.

The objectives of my study were to: 1) examine seasonal migration of sand tiger sharks along the US East Coast and compare findings with conspecific patterns observed in other parts of the world, 2) quantify habitat use of sand tigers during their seasonal migrations, including comparing habitat use between shark size classes and sexes, and 3)
infer the potential protection and vulnerability of sand tigers within areas of concentrated habitat use along the US East Coast.

**Methods and Materials**

*Shark Tagging*

In late summer 2008, 13 pop-up archival transmitter (PAT) tags were deployed on 14 sand tiger sharks caught in Delaware Bay, with one tag being recovered and redeployed on a different shark, and considered as a new tag thereafter, for a total of 14 tags. Two models of tags, PTT-100 and X-tags (Microwave Telemetry, Inc., Columbia, MD), were deployed on 11 male and three female sharks. Sharks were caught using longlines (366 m, 0.64 cm braided nylon) with 25 baited circle hooks placed every 12 meters (McCandless *et al.* 2007), and the lines soaked for approximately two hours. Smaller sharks were brought on board the fishing vessel to be tagged, measured, and sexed, while larger sharks were kept in the water alongside the boat. PAT tags were attached using an umbrella dart connected to the transmitter with 20 cm of 400 kg test monofilament encased in surgical tubing, with the dart inserted into the dorsal musculature lateral to the first dorsal fin (Domeier *et al.* 2005). Tags were labeled with contact information in the event of recovery, and programmed to detach after periods ranging from 123-184 days. All sharks carrying PAT tags were also tagged with acoustic transmitters (VEMCO Ltd., Halifax, Nova Scotia, v16) for detection by an array of acoustic receivers located within Delaware Bay, and for possible detection by receivers deployed by other researchers outside Delaware Bay along the US East Coast. Acoustic transmitters, coated with
biologically inert silicone elastomer (Dow Corning Silastic®) to minimize rejection rate
(Johnny Moore (Delaware State University) pers. comm.), were surgically inserted into
the shark’s body cavity through a 2.5 cm long incision and the wound closed with several
stitches of a degradable suture material (PDS Maxon – Polyglyconate 1).

Data Analysis

The PAT tag archived temperature, depth and light-based geolocation data were
downloaded via the Argos satellite system when the tags detached from the sharks and
floated to the sea surface. Daily latitude and longitude positions were generated onboard
the tags by built-in proprietary software (Microwave Telemetry, Inc.) from daily light
level data collected by each tag. Because using light data alone may result in errors in
geolocation estimates, a Kalman filter state-space model (kftrack package) in the R
statistical environment (R Development Core Team; The R Project) was used to refine
these estimates and create the most probable horizontal track for each shark (Sibert et al.
2003). For tracks that did not obtain proper model convergence when all parameters
were set to be optimized, the mean rate of displacement in the x and y direction (u and v
parameters) were fixed at their initial value (refer to kftrack help documentation and
Sibert et al. 2003).

Shark detections on acoustic receivers (VEMCO, VR2 model) located inside and
immediately outside Delaware Bay were used to estimate the departure time of PAT
tagged sharks from the bay. Acoustic detections were also used in concert with the PAT
tag derived geolocation estimates to increase the accuracy of the most probable track by
using the location and date of the last acoustic detection as the starting point for
constructing the most probable migratory track. Acoustic receivers in the array have a detection range of approximately 1000 m (D. Fox pers. comm.), and hence a detection on a receiver places a shark within a small area at a known date and time. Once a Kalman filtered, most probable track was estimated, a bathymetry correction tool (R environment) which utilized the maximum daily depth recorded by the PAT tag was used to further refine (Galuardi et al. 2010) the light-based geolocation track (with the exception of Shark 2 whose shallow maximum depth combined with short track duration and limited displacement hindered use of the bathymetry correction tool).

Final geolocations from the most probable tracks of all sharks were used to create 25%, 50%, 75%, and 95% kernel utilization distributions (KUDs) in ArcGIS (v9.2; Hawth’s Tools) to examine activity space for each month. The 50% KUDs are referred to as “core areas” in this study, and were used as the basis for examining the vulnerability of sand tigers to fishing effort. Fishing effort estimates (number of US pelagic longline fishery hooks set) were obtained from Guillermo Diaz (NOAA HMS, pers. comm.). The 50% KUDs were also used to examine spatial and temporal overlap with the boundaries of the MASA. Although core areas could not be directly compared to fishing effort in the US bottom longline fishery due to confidentiality requirements, the shark bottom longline observer program (Hale et al. 2010) and bycatch data along the U.S. East Coast from the NOAA National Bycatch Report (NMFS 2011) were also taken into consideration when examining vulnerability.

PAT tags archived temperature (±0.17° C) and pressure (±5.4 m) at 15 minute intervals. Temporal depth and temperature profiles (see Appendices), and histograms (10 m; 1°C bins) were used to examine vertical habitat use of individual sharks.
Kolmogorov–Smirnov (K-S) tests were used to determine if significant differences in depth and temperature utilization existed among individual sharks. Relationships between size of shark (total length) and depth, temperature, displacement rate, and date of departure were examined using linear regression.

Detections of additional sand tiger sharks (i.e. sharks lacking PAT tags) tagged in Delaware Bay with acoustic transmitters (n = 167; deployed 2008-2011) on receivers located in various places along the US East Coast provided further information on timing of seasonal movements of sand tigers, and were used for comparison with movements of PAT tagged sharks.

**Results**

*Tag Performance*

Thirteen of the 14 PAT tags deployed reported, with 11 tags providing usable data (Table 1), including data from eight males (168–232 cm total length – TL (hereafter all lengths refer to TL), and three females (197–228 cm). Eight of the 11 tags used in the analysis (73%) remained attached either for the entire programmed time, or in the case of two tags, to within three days of the programmed release date (Table 1). The remaining three tags released after 64, 76 and 125 days resulting in overall tag deployments ranging from 64–154 days (\( \bar{x} = 121.6 \) days). Light data collected by transmitters were sufficient for the construction of horizontal migratory tracks for 10 individuals (seven male; three female) (Fig. 1-10). The two tags that reported, but did not provide usable data, detached prematurely after only 12 and 14 days, respectively. There were not sufficient light data
to create a horizontal track for either shark; furthermore, because there were no corresponding acoustic detections for these two sharks, they were not used in my analysis. Data from Shark 9 (Table 1) were used only in depth and temperature analyses, because the light data provided so few daily geolocation estimates it did not allow for the construction of a reliable horizontal track.

Because of the possibility that sand tigers would spend extended periods of time near the bottom, the constant depth feature of the PAT tags was disabled to avoid premature pop-off of transmitters. This prevented determination of an exact pop-off location for two transmitters (Sharks 2 and 3) because of a long lag time between transmitter detachment and first transmission; however, it was possible to create a most probable track for both of these sharks.

**Seasonal Migrations**

Because of the uncertainty associated with determining geolocations generated from popup satellite transmitter light data, it was not possible to determine exact dates of departure of sharks from Delaware Bay. However, a combination of archived depth and acoustic detections provided clear indications of departure date of an individual from the bay. Sharks carrying PAT tags were last detected acoustically in Delaware Bay between August 29 and October 19, and the majority were also detected on receivers outside the bay a short time later. All three females and four of the eight males were last detected in the bay during the period October 6-19. The timing of departure from the bay for 64% of the sharks carrying PAT tags, as well as departure during the first two weeks of October across multiple years of numerous sharks tagged with acoustic transmitters only (D. Fox,
pers. comm.), indicated that a high proportion of sand tiger sharks depart their summer residence in Delaware Bay during the first three weeks of October.

After leaving Delaware Bay, all seven males for whom horizontal tracks were constructed, immediately began moving south; they generally remained on the continental shelf and all eventually reached waters off North Carolina (Fig. 4-10). At several locations on the continental shelf, most of the males slowed their southward progress spending 2-4 weeks within relatively small areas before continuing their migration south. The males arrived in waters south of Cape Hatteras at different times, as early as September and as late as December. The majority of males remained in neritic waters close to the edge of the continental shelf south of Cape Hatteras until detachment of their PAT tags between December-February.

In contrast to the males, all three female sharks moved eastward after leaving Delaware Bay, exhibiting little or no southward movement, to deeper offshore waters near the continental slope east of New Jersey (Fig. 1-3). Track duration for females ranged from 76–151 days, with the two longer tracks showing movements farther eastward, and slightly north, remaining relatively close to the edge of the continental shelf. Although only three females were tracked, their movements were generally similar both temporally and spatially.

Kernel utilization density analysis illustrated patterns of departure from Delaware Bay and progressive eastward (for females) and southward (for males) movements from late summer to winter (Fig. 11-16). In late August/September sharks utilized waters inside Delaware Bay, and continental shelf waters south of the bay (Fig. 11). October was a transitional month with most of the sharks exiting the bay and beginning to move
south or east, although two males (Sharks 4 and 6) had already reached waters off Cape Hatteras (Fig. 12). By November, all tagged sharks were absent from Delaware Bay, with female activity concentrated several hundred km east of the bay, whereas males heavily utilized locations off the southern border of Virginia and south of Cape Hatteras (Fig. 13). In December males and females continued to move in different directions with males in waters off North Carolina and the two remaining females several hundred km east of New Jersey near the edge of continental shelf (Fig. 14). In January, the four remaining males concentrated their movements near Cape Hatteras, and the single female still carrying a PAT tag remained at the edge of the continental shelf east of New Jersey (Fig. 15). By February PAT tags had detached from all but two sharks, both males and both in waters south of Cape Hatteras (Fig. 16).

Displacement was calculated as the straight-line distance from tagging location to pop-off location and ranged from 203-688 km, with an average displacement of 509.4 (±134.4) km, yielding an average displacement rate of 3.98 (±0.87) km/d for all sharks combined. Displacement rate during migration (defined as starting from time and location of last Delaware Bay acoustic detection to time and location of PAT pop-off) ranged from 4.9–7.8 km/d (̅x = 6.2 km/d) for females and 4.2 - 5.8 km/day (̅x = 5.1 km/d) for males, with an overall average of 5.4 (±1.05) km/d for sexes combined. Linear regression and correlation analysis showed no significant relationship between size and migratory displacement rate (p > 0.05), or between size and date of departure (p >0.1) for either sex.
**Vertical Habitat Use**

Depths utilized by the two largest male sand tiger sharks differed significantly (K-S test; $p \leq .05$) from all other sharks during migrations, but not in Delaware Bay. While in Delaware Bay (average depth ~10 m [maximum depth ~45m]; 90% of the bay < 18 m (Zheng *et al.* 1993)), 68% of PAT tag depth records for both males and females were less than 11 m. All depths recorded were less than 33 m for females and less than 38 m for males.

As sharks departed the bay depth records for both sexes increased beyond the shallow depths recorded within the bay, particularly for males. Average depths occupied by individual male sand tiger sharks during southern migration ranged from 18–73 m, with a significant positive relationship between average depth and size of male shark (Fig. 17 [$r^2=0.82$, $p < .01$]). Male sand tiger sharks showed no significant difference in depth utilization between day and night ($p >0.1$).

Based on visual comparison, dive profiles of males during their southern migrations followed three major patterns corresponding to size of shark (Fig. 18). For the three smallest males ($\leq 202$ cm) over 90% of depths occupied were <40 m and with the exception of one individual (Shark 6) on one day, no depths greater than 60 m were recorded. The average deepest dive recorded for the three smallest males was $77.0 \pm 25.4$ m. Three males in the middle size class (213–222 cm) occupied somewhat deeper depths, with slightly over 50% of their time spent in water <40 m and over 95% of their depths recorded at depths of <60 m. Average deepest dive recorded for the three males in the middle size class was $95.0 \pm 15.6$ m. For the two largest males (228–232 cm) only 38% of depths recorded were less than 40 m and approximately 45% of depth records
were at depths of greater than 80 m. Average deepest dive for the two largest males was 180.0 ± 8.0 m, including the deepest depth recorded (188 m) of any shark tracked, observed for the largest shark tracked in the study (232 cm). Results of a K-S test comparing depths of sharks tracked at least 120 days indicated that the two largest male sharks occupied significantly greater depths than all other sharks, including females ($p \leq .05$).

Average depth of females during migration ranged from 11.1-47.1 m, with maximum recorded depths averaging 77.0 ± 16.4 m. Females occupied deeper waters as they moved east, increasing from an average depth of 12.4 m during the first 30 days of migration ($n = 3$) to just over 50 m for the last 30 days tags were attached ($n = 2$). There was also no significant difference in depth utilization between day and night for females ($p >0.1$), indicating that sand tiger sharks did not migrate vertically through the water column.

Despite temporal changes in depth and differences in depth among male size classes, as well as differences in horizontal movements between sexes, water temperature occupied by sand tiger sharks did not vary greatly. Water temperatures occupied by all sand tiger sharks ranged from 13-26°C, with an average of greater than 95% of temperature records falling between 17-23°C, and over 85% within the narrower four degree range of 18-22°C (Fig. 19). Average water temperature experienced by sharks in Delaware Bay was 22.2°C (±1.58) for females, and 19.3°C (±1.3) for males, with approximately 90% of values falling between 19–23°C for both sexes (Fig. 19). At the time sharks left the bay, temperatures archived by PAT tags ranged from 18.9–20.1°C for females, and between18.3–23.6°C for males. During migration, average temperature
recorded was 20.1°C (±1.66) for females and 20.9°C (±1.59) for males. There was no significant difference in water temperature occupied between sexes or among size classes (K-S test, \( p > 0.1 \)), and there was no significant difference in water temperature occupied between day and night for male or female sand tiger sharks.

**Protection/Vulnerability of Sand Tiger Sharks**

To examine potential interaction between sand tiger sharks and the US pelagic longline fishery, I compared core area of activity of PAT tagged sand tiger sharks (male and female combined) with the number of hooks set by vessels monitored as part of the US pelagic fishery within the geographic confines of the core area. For purposes of this analyses I used the 50% KUDs for all sharks combined during each month as a proxy for core areas of activity of sharks. I compared US pelagic longline hooks set within core areas to hooks set outside core areas for each month. Hooks set outside core areas were within the US EEZ and limited by the latitudinal boundaries from the most northern and southern PAT tag geolocations. This provided an indication of the scale of fishing within core areas in relation to overall effort of the pelagic longline fishery within the distributional range of sand tiger sharks tracked in my study (Guillermo Diaz, NOAA HMS pers. comm.). There were no hooks set within sand tiger core areas in September, and only about 12,000 hooks set in core areas in October, compared to over 340,000 outside core areas. Nearly 120,000 hooks were set in core areas in November through December, compared to approximately 90,000 hooks set outside core areas during that time frame. There were no hooks set within core areas in January or February.
Though confidentiality requirements did not allow assessment of fishing effort (number of hooks set) in core areas by the US shark bottom longline fishery, summary data available from the US National Bycatch Report (NMFS 2011) and the shark bottom longline observer program (Hale et al. 2010) documented the occurrence of sand tiger sharks as bycatch in South East US fisheries. Estimates of 309 sand tiger sharks and 14,924 kg as bycatch in 2005 in the southeast region, which includes areas off North Carolina, together with reports by fishery observers that small numbers of sand tigers are captured in the shark bottom longline fishery (with 4-6% observer coverage), further illustrate that sand tigers are subject to fishing pressure in US waters.

Of 477 total geolocations from the 10 horizontal tracks that were created, only 51 (10.7%) fell within the spatial boundaries of the MASA; most geolocations occurred outside the MASA to the north and east of the area boundary (Fig. 20). Though the majority of sand tiger shark core areas fell outside the MASA, its boundaries encompassed more core area during the months of November and December (Figs. 13-14), when the area is open to fishing, than it did during the closure months January and February (Figs. 15-16). Additionally, although PAT tags had detached by February, tags on four male sharks provided 49 geolocation estimates during the time period in which the MASA is closed to bottom longlining (January 1-July 31 each year); only six of these locations fell within the MASA boundary during that time (Fig. 20).

**Migration Patterns Inferred from Acoustic Detections**

Acoustic data from receivers inside Delaware Bay revealed that the majority of PAT/acoustic tagged sand tiger sharks returned to Delaware Bay in subsequent years.
Nine of the eleven sharks (82%) tagged in 2008, returned to Delaware Bay in the summer of 2009 (June and July), including all three females and six males; all nine sharks were last detected in the bay in the autumn of 2009 (end of September through the first two weeks of October). Notably, the same six males and two of the females (73%) were again detected in Delaware Bay in the summer 2010 (June and July), with the last detections that year occurring from the end of July to mid-October.

Sharks that had been tagged in Delaware Bay with only acoustic tags (n = 167; deployed 2008-2011) were detected on acoustic receiver arrays distant from the bay. Immature and mature sharks of each sex were detected on receivers located off Cape Hatteras, NC, as well as near Myrtle Beach and Charleston, SC. Immature males (n=4) were detected in late December and mid-January, as well as in mid-May. Mature males (n=8) were detected in mid to late December, late March, and early to mid-May. Immature females (n=3) were detected in late December, early April, and early May, and mature females (n=2) were detected mid to late December and in mid-April. Additionally, three sharks were detected near Cape Canaveral, FL; an immature female in July, a mature male in January, and an immature male that was detected in two consecutive winters near Cape Canaveral, with corresponding summer detections in Delaware Bay.

**Discussion**

Popup satellite transmitters used in this study performed well in terms of deployment duration, and this methodology was an effective means of obtaining data on migrations...
and habitat use of sand tiger sharks that has been difficult to obtain by other means. PAT tags detached prior to programmed date from all three females compared with only one of the eight males that reported. Although these are low sample sizes for drawing robust inferences on gender tag retention, it is notable that Otway and Ellis (2011) also reported lower PAT tag retention for females. These observations raise the possibility that females may exhibit behaviors responsible for a higher frequency of premature PAT tag detachment compared with males.

*Seasonal Horizontal Migration Patterns*

The results of my study support the general patterns of seasonal movements proposed for sand tiger sharks along the US East Coast by previous research, although with several modifications. Sand tigers arrive in Delaware Bay in late May to mid-June (D. Fox, pers. obs.), presumably traveling primarily from locations to the south where they overwinter. The sharks spend the summer months in the bay, although they may leave for short periods of time (D. Fox, unpubl.). Towards the end of the summer sharks begin exiting the bay, with most departing by late October. Male sharks tracked with PAT tags in this study all moved south along the eastern seaboard, eventually arriving in waters off North Carolina. Movements of these males are in agreement with previously postulated (based on fishery catch and reproduction timing data) north-south seasonal movements of sand tigers along the US East Coast (Bigelow and Schroeder 1948, Gilmore 1993). My PAT tag data suggest that migrating males move south along pathways close to the continental shelf edge, outside state management jurisdiction waters.

Based on data from additional sand tiger sharks tagged with acoustic transmitters, movement south along the US East Coast at the end of summer/early fall is common,
although this is inferred from patchy detections on acoustic receivers at several locations, rather than a series of continuous locations as were obtained with PAT tags. Mature and immature sand tigers of both sexes tagged with acoustic transmitters were detected off North Carolina and Florida in winter months, suggesting that north-south seasonal migration is exhibited by most demographic segments of the population. One exception appears to be pregnant females, which may not move north in the summer based on the absence of pregnant females captured in Delaware Bay in summer months (D. Fox, unpubl.) and in agreement with Gilmore (1993) who described the summer northward movement of mature males and juveniles, but not pregnant females.

Since most demographic segments of the sand tiger shark population move south in colder months (my study; Gilmore 1993), my finding of eastward, offshore movements by females tagged with PAT tags was surprising, although not unprecedented. Bigelow and Schroeder (1948) suggested a half century ago that some sand tiger sharks may migrate offshore instead of immediately migrating north or south, and Gilmore (1993) hypothesized that males might move offshore in summer, but neither reference was specific to females. With the caveat of only a small sample size of PAT/acoustic tracked females (n=3) in my study, my findings combined with the suggestions of Bigelow and Schroeder (1948) and Gilmore (1993) raise interesting questions about the a variety of directional migratory patterns that may be exhibited by sand tigers.

While males may undergo seasonal latitudinal migrations, movement of females appears to be more complex. Gilmore (1993) provided evidence that mating and gestation take place in the same location for mature females in waters off North Carolina and Florida, and that pregnant females remain in these southern locations rather than
migrating north during summer. The females tracked in my study were 197 cm, 217 cm, and 228 cm. Based on size of maturity for females at 220-230 cm (Gilmore et al. 1983), these sharks, as a whole, might represent a specific demographic segment of females that are nearly mature, or recently mature, but have yet to reproduce. If this is the case, segregation from other segments of the population (namely mature males), could be a mechanism to delay mating and pregnancy until the sharks reach a larger size. Spatial and temporal segregation of male and female sharks of several species is well documented (Klimley 1987, Mucientes et al. 2009), but such behavior for sand tigers remains unclear. Although speculative, it is possible that these eastward migrating females are moving towards the warmer waters of the Gulf Stream and eddies with elevated productivity (Bowman and Iverson 1978, Owen 1981, Le Févre 1986). Movement to such habitats may provide this female sand tiger demographic segment with a suitable temperature environment and higher prey availability, while avoiding the physical stresses of mating attempts that would be encountered during a southern migration. I recognize, however, that this hypothesis needs testing as the PAT tags remained on the three eastward migrating females only through January, and it is possible that the sharks moved south after detachment of the transmitters.

Migratory patterns of sand tiger sharks differ among geographic locations around the world, making species-wide generalizations difficult. The migration to higher latitude summer habitats by all US East Coast sand tiger population segments, except pregnant females, and mating in over-wintering, warmer water areas off North Carolina and Florida (Gilmore 1993), has some parallels to movements described for sand tiger sharks along the eastern seaboard of South America. Lucifora et al. (2002) described the
presence of juvenile and mature sharks of both sexes in Anegada Bay, Argentina in late spring through autumn, but also noted the absence of pregnant females from these areas. Mating is thought to occur at these higher latitude locations, followed by migration of all demographic segments to lower latitudes and warmer waters off Brazil in autumn-winter (Lucifora et al. 2002). The following spring-summer sharks again migrate south along the coast of South America to heavily utilized regions such as Anegada Bay, with the exception of pregnant females which remain in warmer waters off Brazil during spring-autumn (Lucifora et al. 2002). Differential movement of pregnant and non-gravid females results in fewer mature females arriving in Anegada Bay in summer. The observed sex ratio of 2:1 for mature males to mature females in Anegada Bay is consistent with a two year reproductive cycle, where approximately 50% of the mature females are pregnant and remain in waters off Brazil during gestation (Lucifora et al. 2002). Movements of mature males in colder months is uncertain since low numbers have been captured in both Argentinian waters to the south and in waters off Brazil to the north, possibly indicating movement of mature males offshore to continental shelf waters.

There are a number of differences in movements of sand tiger sharks in South Africa and eastern Australia compared to movements along the east coasts of North and South America. In South Africa and Australia pregnant females undergo predictable and consistent migrations and exhibit three distinct locations specifically for mating, for gestation and for parturition (Bass et al. 1975; Dicken et al. 2006b, 2007; Bansemer and Bennett 2011). After mating, pregnant females move north to spend early months of gestation in warmer waters. In winter months, near-term pregnant females move south to cooler waters where they give birth in the late winter/spring (Smale 2002, Dicken et al.
This poleward movement to cooler waters for parturition contrasts with equatorial movements to warmer water for parturition off South America and movement patterns off the US East Coast, where pregnant females apparently do not migrate, or at most undergo very short migrations (Gilmore 1993, Lucifora et al. 2002). The well synchronized and consistent movements of adults in conjunction with reproductive characteristics observed, infer a two year reproductive cycle for sand tiger sharks in South Africa (Dicken et al. 2007), similar to that suggested for sand tiger sharks along the east coast of South America by Lucifora et al. (2002) and along the US East Coast by Goldman et al. (2006).

Juvenile sand tigers in South Africa and eastern Australia exhibit much more limited movements and do not appear to undergo synchronized migrations (Dicken et al. 2006b, Bansemer and Bennett 2011) compared with juveniles along North and South American coasts. There is speculation that juveniles in South Africa continuously occupy geographically distinct nurseries during the first 4-5 years of life (Smale 2002, Dicken et al. 2006b, 2007). In contrast, juveniles along the US East Coast appear to undergo long distance seasonal migrations and may even travel greater distances than adults in the course of their seasonal migrations. For example, summer nursery areas used by juvenile sand tigers are located at the northernmost extent of their distribution off Massachusetts (Kneebone et al. 2012), and juveniles tagged with acoustic transmitters in Delaware Bay were detected in winter months on receivers as far south as Cape Canaveral, FL.

Vertical Habitat Use During Migrations
PAT tagged sand tiger sharks underwent seasonal shifts in habitat occupied, moving from shallow-water estuarine summer habitat within Delaware Bay to deeper, offshore continental shelf waters during migration and occupancy of winter habitat. Sharks tracked in my study occupied a range of depths during migration, but the majority of records were at depths of <80 m. These depths are in general agreement with previous reports for sand tiger sharks, and for the most part are similar to findings for sharks tracked with PAT tags in previous studies. Smale et al. (2012) found that PAT tagged sand tiger sharks in South Africa spent a high proportion of their time at depths of <60 m, with occasional movements to deeper continental shelf waters. Otway and Ellis (2011) reported that for sand tigers tracked with PAT tags off eastern Australia, 94% of depth values recorded for males and 97% for females were < 80 m. In my study nearly 100% of depth records were <80 m other than for the two largest males tracked, which used substantially deeper water with 45% of values at depths greater than 80 m. There are a number of reports of sand tigers at depths of 40-60 m both in shallow, inshore waters as well as offshore deep water (Boschung and Couch 1962, Bass et al. 1975, Moore and Farmer III 1981, Russel 1993), and there are additional references of sand tigers most frequently inhabiting depths of < 30 m (Bigelow and Schroeder 1948, Bass and Ballard 1972, Smale 2005). Although while in Delaware Bay sharks usually occupy depths of < 30 m, during migration along the US East Coast they routinely occupy greater depths. Otway and Ellis (2011) found that sand tigers off the Australian east coast also moved into deeper waters while migrating, but occupied shallower water while on their summer and winter grounds. Several male sharks tracked in my study moved into shallower water in late December/early January, which may reflect a similar shift to inshore,
shallower water at the completion of migration. Gilmore (1993) theorized that mature female sand tigers may occupy greater depths than other demographics. The three females tracked in my study remained in relatively shallow water at depths similar to males of the same size; however, the females were immature or recently mature, and depth behavior of larger mature females remains unclear.

Differences observed in horizontal movements and vertical habitat utilization among sexes and size classes of sand tiger sharks in my study illustrate that these demographic segments likely occupy different habitats. This movement and habitat use variability likely differentially influences susceptibility of the different demographic segments to capture and mortality in commercial (shark bottom longline, pelagic longline, and gillnet fisheries) and recreational fisheries using different gear types, thus impacting conservation and management efforts for this shark.

All three females and half the males that I tracked left Delaware Bay within a two week period between October 6-19, consistent with departures observed for a much larger number of sharks carrying acoustic transmitters (D. Fox, unpubl.). Interestingly, although a few temperatures recorded by PAT tags fell just below 18°C while sharks were in the bay, the minimum temperature recorded by PAT tags at the time each shark was last acoustically detected was 18°C, which corresponds well temporally with surface water temperatures recorded by Delaware Bay NOAA buoys (the temperature fell below 18°C for the first time on Oct 19, 2008 [NOAA, NDBC - Station BRND1])¹. Temperature may therefore be the putative cue for sand tiger departure from the bay.

¹ http://www.ndbc.noaa.gov/station_page.php?station=brnd1
It is interesting to note that variation in temperatures occupied by sharks was much narrower than variation in depths occupied. Sharks remained mostly within the same narrow range of temperatures within Delaware Bay and during migration, with minimal differences displayed among size classes and sexes. Sharks in my study spent approximately 88% of their time between 18-22°C; similar to values of 96% of time at temperatures of 17-24°C reported for sharks tracked with PAT tags off eastern Australia (Otway and Ellis 2011). Smale et al. (2012), on the other hand, reported cooler mean ambient temperature records (15.3-18.4°C) from sand tiger sharks tracked with PAT tags off South Africa.

Vulnerability to Fisheries

The modest number of sharks tracked using satellite tags in my study, combined with the limited spatial accuracy obtained with PAT tags (see confidence intervals around each estimated track), requires caution in extrapolating these results to sand tiger shark movements on a broad scale. However, several inferences can be made from my findings. Movement of females to the east (rather than south) of Delaware Bay and as far as 600-700 km offshore near the continental slope opens the possibility that there may be an area utilized by nearly or just mature female sand tigers in winter at this northern location. The extent to which this area may be used by such females and the reproductive status of these females is uncertain. However, my results suggest that the existence of a previously unrecognized, northern overwintering area for sand tigers warrants investigation.
Horizontal tracks of all the male sand tigers generated from the PAT tag data were similar, although depth data revealed differences in vertical habitat use among size classes. Limits to the accuracy of PAT tag geolocations precluded determination of whether juvenile male sharks were moving in waters closer to shore during migration or remaining higher in the water column farther offshore. Occupation of different depths by different size classes could result in higher probability of capture of a particular size class in fisheries operating at a specific range of depths (Cortés et al. 2010).

During their southerly migrations, male sharks exhibited varying periods of time when they showed little net southward movement. This behavior is reflected in the areas of high use during migration, illustrated by the KUD analysis (Fig. 11-16). These distinct areas used by multiple sharks during their southerly migrations represent additional habitat frequented by sand tigers, and represent locations that may be important for successful migration between summer and winter habitats. Migration punctuated by regular stops at “resting areas” was also observed for sand tiger sharks tracked with PAT tags off the east coast of Australia (Otway and Ellis (2011), suggesting that this behavior may be typical of migrating sand tiger sharks in general. Sand tigers may be more vulnerable to capture in fisheries in such high utilization areas that presumably have structural or productivity characteristics that cause cessation of southern migration and limited movements within a restricted area for several weeks. More detailed studies of these locations would further refine understanding of critical habitat of sand tigers, allowing additional evaluation of vulnerability to fisheries and enabling enactment of additional management measures such as area closures or minimizing habitat degradation, if warranted.
The MASA was established to reduce capture of dusky and sandbar sharks in an effort to enhance recovery of their populations, but with temporal and spatial modifications has potential for reducing fishing mortality of sand tiger sharks also. The pathway and timing of migration of sand tigers revealed in my study indicate the probability of a higher rate of interactions with pelagic fishing gear in November and December, when the largest amount of hooks are set in the 50% KUD core areas. The MASA is also open to bottom longline fishing during this time. Heavy utilization by sand tigers of locations within and in close proximity to the MASA raises the possibility of the MASA providing protection for this species. Based on results of my study, however, it appears that sand tiger sharks may typically arrive in the MASA prior to January 1, the date at which closure to fishing begins. Additionally, although PAT tags have an error associated with their light-derived geolocations, five out of seven male sharks had geolocations that fell within the MASA in December (prior to area closure), and there were numerous geolocations just outside the eastern boundary of the MASA (Fig. 20). These findings suggest that modifying the timing of the existing MASA area closure to begin in December as well as extension of the eastern boundary of the MASA would likely provide protection to sand tigers through reduced bycatch and mortality in fisheries that operate in these locations. For example, Burgess and Morgan (2003) stated that during 1994-2003 a total of 355 sand tiger sharks (2.3% of the shark catch) were caught in the bottom longline fishery that operated in the area where the MASA was later established.

Although landing of sand tigers is prohibited in US waters, their capture in a variety of commercial and recreational fisheries on the US East Coast undoubtedly results in at
least some mortality even if sharks are released alive. As pointed out in past reviews, given the low reproductive output and low intrinsic rate of increase for sand tigers, even minimal mortality can hinder recovery of stocks (Goldman et al. 2006, Carlson et al. 2009). The feeding habits and tendency of sand tigers to swallow hooks and become gut hooked, resulting in damage of internal organs, exacerbates the problem of post-release fishing mortality. This circumstance creates a challenge for even well intentioned fishers who release sand tigers when they occur as bycatch (Dicken et al. 2006a, Lucifora et al. 2009).

Given the high probability of at least some fishing mortality of sand tigers caught in fisheries, an understanding of the scale of interactions between humans and sand tiger sharks is imperative for assessment of threats to recovery efforts and for modifications in management policy aimed at enhanced recovery of stocks. An integral part of this process is identification of areas heavily utilized by sand tiger sharks on a seasonal basis and delineation of pathways traveled between distant locations. My study has provided information on timing of migration, location of migratory routes for different demographic segments, and has quantified habitat use during migrations. Studies on movement patterns, habitat use and fine-scale use of inshore and nursery areas (Kneebone et al. 2012, D. Fox unpubl.) will continue to refine our understanding of the ecology of sand tiger sharks and to contribute further towards effective management of the western North Atlantic sand tiger shark population.
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<th>Tagging Date</th>
<th>Pop-off Date</th>
<th>Programmed Duration (days)</th>
<th>Actual Track Duration (days)</th>
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Figure 1. Horizontal track of female Shark 1. Black circles represent tagging location, and color coded tracks begin with the date and location of the last acoustic detection in Delaware Bay. Triangles mark tag pop-off. Gray shading indicates the 95% confidence interval around the estimated track.
Figure 2. Horizontal track of female Shark 2. Black circles represent tagging location, and color coded tracks begin with the date and location of the last acoustic detection in Delaware Bay. Triangles mark tag pop-off. Gray shading indicates the 95% confidence interval around the estimated track.
Figure 3. Horizontal track of female Shark 3. Black circles represent tagging location, and color coded tracks begin with the date and location of the last acoustic detection in Delaware Bay. Triangles mark tag pop-off. Gray shading indicates the 95% confidence interval around the estimated track.
Figure 4. Horizontal track of male Shark 4. Black circles represent tagging location, and color coded tracks begin with the date and location of the last acoustic detection in Delaware Bay. Triangles mark tag pop-off. Gray shading indicates the 95% confidence interval around the estimated track.
**Figure 5.** Horizontal track of male Shark 5. Black circles represent tagging location, and color coded tracks begin with the date and location of the last acoustic detection in Delaware Bay. Triangles mark tag pop-off. Gray shading indicates the 95% confidence interval around the estimated track.
Figure 6. Horizontal track of male Shark 6. Black circles represent tagging location, and color coded tracks begin with the date and location of the last acoustic detection in Delaware Bay. Triangles mark tag pop-off. Gray shading indicates the 95% confidence interval around the estimated track.
Figure 7. Horizontal track of male Shark 7. Black circles represent tagging location, and color coded tracks begin with the date and location of the last acoustic detection in Delaware Bay. Triangles mark tag pop-off. Gray shading indicates the 95% confidence interval around the estimated track.
Figure 8. Horizontal track of male Shark 8. Black circles represent tagging location, and color coded tracks begin with the date and location of the last acoustic detection in Delaware Bay. Triangles mark tag pop-off. Gray shading indicates the 95% confidence interval around the estimated track.
Figure 9. Horizontal track of male Shark 10. Black circles represent tagging location, and color coded tracks begin with the date and location of the last acoustic detection in Delaware Bay. Triangles mark tag pop-off. Gray shading indicates the 95% confidence interval around the estimated track.
Figure 10. Horizontal track of male Shark 11. Black circles represent tagging location, and color coded tracks begin with the date and location of the last acoustic detection in Delaware Bay. Triangles mark tag pop-off. Gray shading indicates the 95% confidence interval around the estimated track.
Figure 11. Kernel Utilization Distribution of *C. taurus* in August-September. Colored areas represent 25% (brown), 50% (red), 75% (orange), and 95% (yellow) of total distribution. The Mid-Atlantic Shark Area (closed status begins January 1) is shaded and outlined in white.
Figure 12. Kernel Utilization Distribution of *C. taurus* in October. Colored areas represent 25% (brown), 50% (red), 75% (orange), and 95% (yellow) of total distribution. The Mid-Atlantic Shark Area (closed status begins January 1) is shaded and outlined in white.
Figure 13. Kernel Utilization Distribution of *C. taurus* in November. Colored areas represent 25% (brown), 50% (red), 75% (orange), and 95% (yellow) of total distribution. The Mid-Atlantic Shark Area (closed status begins January 1) is shaded and outlined in white.
Figure 14. Kernel Utilization Distribution of *C. taurus* in December. Colored areas represent 25% (brown), 50% (red), 75% (orange), and 95% (yellow) of total distribution. The Mid-Atlantic Shark Area (closed status begins January 1) is shaded and outlined in white.
Figure 15. Kernel Utilization Distribution of *C. taurus* in January. Colored areas represent 25% (brown), 50% (red), 75% (orange), and 95% (yellow) of total distribution. The Mid-Atlantic Shark Area (closed status begins January 1) is shaded and outlined in white.
Figure 16. Kernel Utilization Distribution of *C. taurus* in February. Colored areas represent 25% (brown), 50% (red), 75% (orange), and 95% (yellow) of total distribution. The Mid-Atlantic Shark Area (closed status begins January 1) is shaded and outlined in white.
Figure 17. Linear regression of average depth during migration versus total length for male *C. taurus* with tracks > 120 days ($R^2 = 0.8186$, $P < .01$). Blocks represent individual sharks.
Figure 18. Depth profiles of three male *C. taurus*. Circles represent date of last acoustic detection in Delaware Bay. The green line represents Shark 5 (186 cm TL); brown line represents Shark 7 (213 cm TL); blue line represents Shark 11 (232 cm TL).
Figure 19. Average temperature range of *C. taurus* while in Delaware Bay and during migration. White bars represent migratory temperatures; grey bars represent Delaware Bay temperatures. (Migration temperatures include all sharks (n = 11), and Delaware Bay temperatures include sharks that remained in the bay > 7 days after tagging (n = 8))
Figure 20. Mid-Atlantic Shark Area (MASA) Closure. Green circles represent geolocations that were inside the MASA boundaries during the closure period. All other circles represent geolocations outside the MASA, or inside the boundaries but not during the closed period.
Appendix A – Depth Profiles

Appendix A-1. Depth profile for Shark 1.
Appendix B – Temperature Profiles

Appendix B-1. Temperature profile for Shark 1.
Appendix B-2. Temperature profile for Shark 2.
Appendix B-3. Temperature profile for Shark 3.
Appendix B-5. Temperature profile for Shark 5.
Appendix B-8. Temperature profile for Shark 8.
Appendix B-10. Temperature profile for Shark 10.
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