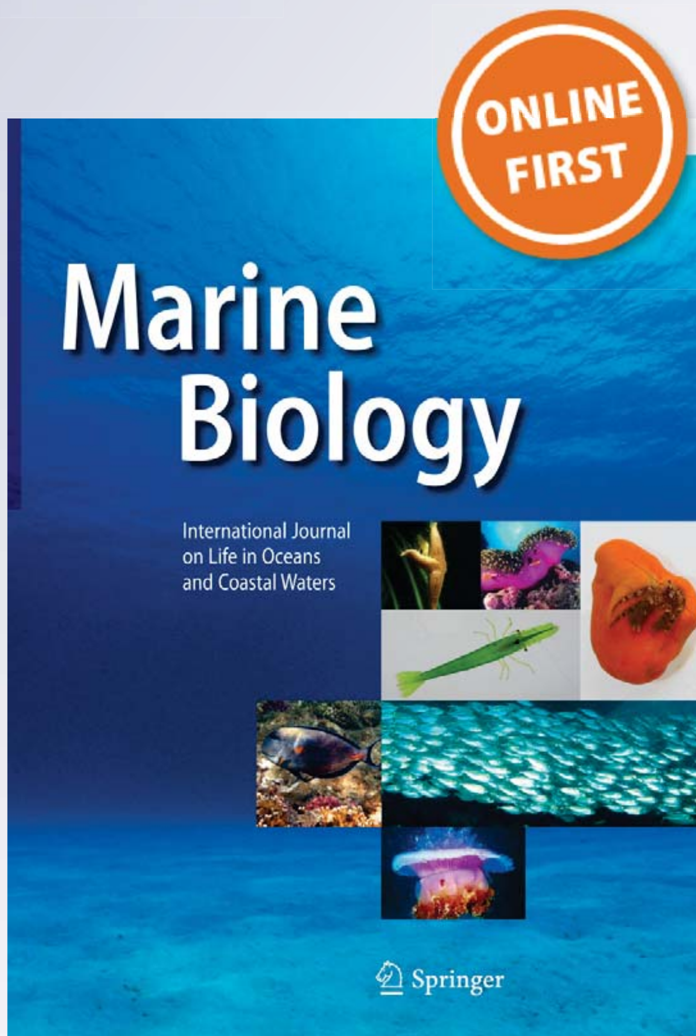
*Movement patterns of juvenile sand tigers (*Carcharias taurus*) along the east coast of the USA*

**Jeff Kneebone, John Chisholm & Gregory Skomal**

**Marine Biology**
International Journal on Life in Oceans and Coastal Waters

ISSN 0025-3162

Mar Biol
DOI 10.1007/s00227-014-2407-9




Springer

Mar Biol
DOI 10.1007/s00227-014-2407-9

ORIGINAL PAPER

# Movement patterns of juvenile sand tigers (*Carcharias taurus*) along the east coast of the USA

**Jeff Kneebone · John Chisholm · Gregory Skomal**

Received: 1 November 2013 / Accepted: 5 February 2014


**Abstract** To date, movement patterns of juvenile sand tigers (*Carcharias taurus*) along the east coast of the USA have been loosely defined. Given the magnitude of the purported decline in the sand tiger population in the western North Atlantic (WNA), characterization of the species' movement patterns throughout this broad area is essential for the effective management and recovery of this population. Using passive acoustic telemetry, pop-up satellite archival transmitting tags, and conventional fishery-dependent tag/recapture data, seasonal movements of juvenile sand tigers (ages 0–2 years; <125 cm fork length) were monitored between Maine and Florida along the US east coast from 2007 to 2013. Collectively, tag data indicated that juvenile sand tigers undergo extensive seasonal coastal migrations moving between summer (June–October) habitat (Maine to Delaware Bay) and winter (December–April) habitat (Cape Hatteras to central Florida) during the spring (April–June) and fall/early winter (October–December). Juvenile sand tigers occurred in a wide range of temperatures (9.8–26.9 °C) throughout the year, but spent the majority of their time in water from 12 to 20 °C. Given the extensive movements and continuous utilization of relatively shallow (<80 m) nearshore waters exhibited by these relatively small individuals throughout their first years of life, it is imperative that precautions be taken to limit negative effects of anthropogenic interactions on this species (i.e., fisheries bycatch, coastal degradation) in an effort to rebuild and sustain the WNA population.

Communicated by J. Houghton.

**Electronic supplementary material** The online version of this article (doi:10.1007/s00227-014-2407-9) contains supplementary material, which is available to authorized users.

J. Kneebone (✉)
School for Marine Science and Technology, University of Massachusetts Dartmouth, 200 Mill Road Suite 325, Fairhaven, MA 02719, USA
e-mail: jeff.kneebone@gmail.com

J. Chisholm · G. Skomal
Massachusetts Marine Fisheries, 1213 Purchase St., New Bedford, MA 02740, USA

## Introduction

The sand tiger (*Carcharias taurus*; Rafinesque 1810) is a large coastal shark that occurs along the east coast of the USA from the Gulf of Maine south to the Gulf of Mexico in the western North Atlantic (WNA) Ocean (Bigelow and Schroeder 1953; Gilmore et al. 1983; Compagno 1984; Gilmore 1993). Throughout this range, there is some evidence that the sand tiger population has declined as much as 80–90 % since the mid-1970s (Musick et al. 1993; Castro et al. 1999; Musick et al. 2000). Such declines and concerns over the species' low productivity (Gilmore 1993; Goldman 2002) have prompted the National Marine Fisheries Service (NMFS) and Atlantic States Marine Fisheries Commission (ASMFC) to prohibit the possession of this species in all US federal waters and in state waters from Maine to Texas (NMFS 1999; ASMFC 2008). However, despite their wide range, purported population decline, and general interest to fishery managers, limited ecological data exist for this species throughout this geographic area.

At present, the large-scale horizontal movement patterns of sand tigers along the US east coast are loosely defined. Several studies have utilized presence/absence trends in recreational, commercial, and fisheries survey catch data to describe annual seasonal migrations of individuals from southern (e.g., North Carolina to Florida) to northern (e.g.,

Published online: 27 February 2014

southern New England, Cape Cod, Gulf of Maine) latitudes in the spring (April–June) and a return to southern locations in the fall (October–November) (Bigelow and Schroeder 1953; Gilmore et al. 1983; Gilmore 1993). Published tagging data for this species in the WNA are limited to a single conventional tagging study by Kohler et al. (1998), which corroborated general north/south movements, primarily between North Carolina and Delaware Bay. However, relatively few recapture events existed at the time of publication ($n = 31$), and no recapture information was available near the northern extent of the species' range (e.g., Gulf of Maine). Furthermore, the available data do not adequately describe movement patterns for all life stages, particularly juveniles.

Although broad regions of juvenile sand tiger essential fish habitat (EFH) have been identified in the current NMFS shark fishery management plan (NMFS 2009), the extent to which individuals utilize these areas remains largely unknown. For example, the effectiveness of current time–area closures to fishing (NMFS 2006; ASMFC 2008) at reducing sand tiger bycatch is unknown because seasonal habitat use in these areas has yet to be fully examined over the life history of this species. Furthermore, given the importance of juvenile survivorship to sand tiger population growth rates (Cortés 2002; Goldman 2002), identification of habitat that may serve as juvenile EFH is critical for effective management of the species. The objectives of this study were to utilize pop-up satellite archival transmitting (PSAT) tags, passive acoustic telemetry, and conventional fishery-dependent tag/recapture analyses to examine the horizontal and vertical movements and seasonal habitat use of juvenile sand tigers tagged in New England coastal waters (i.e., Rhode Island north to Maine).

## Materials and methods

### Shark capture and tagging

During the months of June–September, 2006–2011, 145 juvenile sand tigers (<125 cm FL, age 0–2; Goldman et al. 2006) were captured and tagged within Plymouth, Kingston, Duxbury (PKD) Bay, MA, off Harwich, MA, and off Point Judith, RI (Fig. 1). Within PKD Bay, sharks were captured using conventional rod and reel tackle, circle hooks, and chunks of menhaden (*Brevoortia tyrannus*) for bait (see Kneebone et al. 2013 for details). Sharks were captured off Harwich and Point Judith in fixed commercial fish traps. Once landed, each shark was removed from the water, the hook was removed (if appropriate and possible without harming the shark), and tonic immobility was induced by restraining the shark ventral side up (Watsky and Gruber 1990) in a V-shaped table lined with pre-wetted neoprene. All sharks captured throughout the study period were tagged externally with conventional NMFS 'M-type' shark tags (Kohler and Turner 2001). Prior to release, fork length (FL; cm) and sex were recorded for each shark. All sharks were captured, handled, and released in accordance with Massachusetts Division of Marine Fisheries regulations.

### *Passive acoustic telemetry*

A subset of captured sharks ($n = 78$) were tagged internally with individually coded acoustic transmitters (2008, 2009: model V16-4L, nominal delay = 30–90 s, life = 2,779 days; 2010: models V16-4L, V16T-4L, nominal delay = 45–135 s, life = 3,650 days; 2011: model V16T-4L, nominal delay = 45–135 s, life = 3,280 days, model V9AP-2L, nominal delay = 60–180 s, life = 123 days, and model V9AP-2H, nominal delay = 60–180 s, life = 81 days; Vemco Division, AMIRIX Systems Inc., Halifax, NS) in PKD Bay, MA ($n = 73$), and Point Judith, RI ($n = 5$). Model V16T transmitters were equipped with temperature sensors with a measurement range of −5 to 35 °C. All transmitters were implanted in the body cavity through a small (2–3 cm) abdominal incision on the ventral side of the shark along the midline, anterior to the pelvic fins. Following insertion of the transmitter, the incision was closed with 3–4 interrupted sutures (2-0 PDS II, Ethicon Inc., NJ). All surgical procedures were completed within 5–10 min, and sharks were held in the water at the side of the vessel for release immediately following tagging.

Movements of acoustically tagged sand tigers along the east coast of the USA (from Cape Ann, MA, to Cape Canaveral, FL) were monitored through collaboration with the Atlantic Cooperative Telemetry (ACT) Network (www.theactnetwork.com), a network of researchers from several institutions/agencies that maintain arrays of Vemco acoustic receivers in numerous locations along the coast. Functionally, this network operates by encouraging researchers to upload transmitter detection information to an online database that is shared among all members of the network. In the event that any user obtains detection data from a transmitter that is not their own, a query of the ACT database enables the detector to determine the identity of the transmitter (i.e., species and initial tagging location) and obtain contact information for the tagger. Detection data obtained from this network can be used to examine large-scale movement patterns of individuals (or groups of individuals) over extended periods (i.e., months–years). Movement of tagged sharks back into PKD Bay in years following tagging was monitored through annual deployment of a fixed receiver array from May to October, 2010–2011 (see Kneebone et al. 2012 for details).

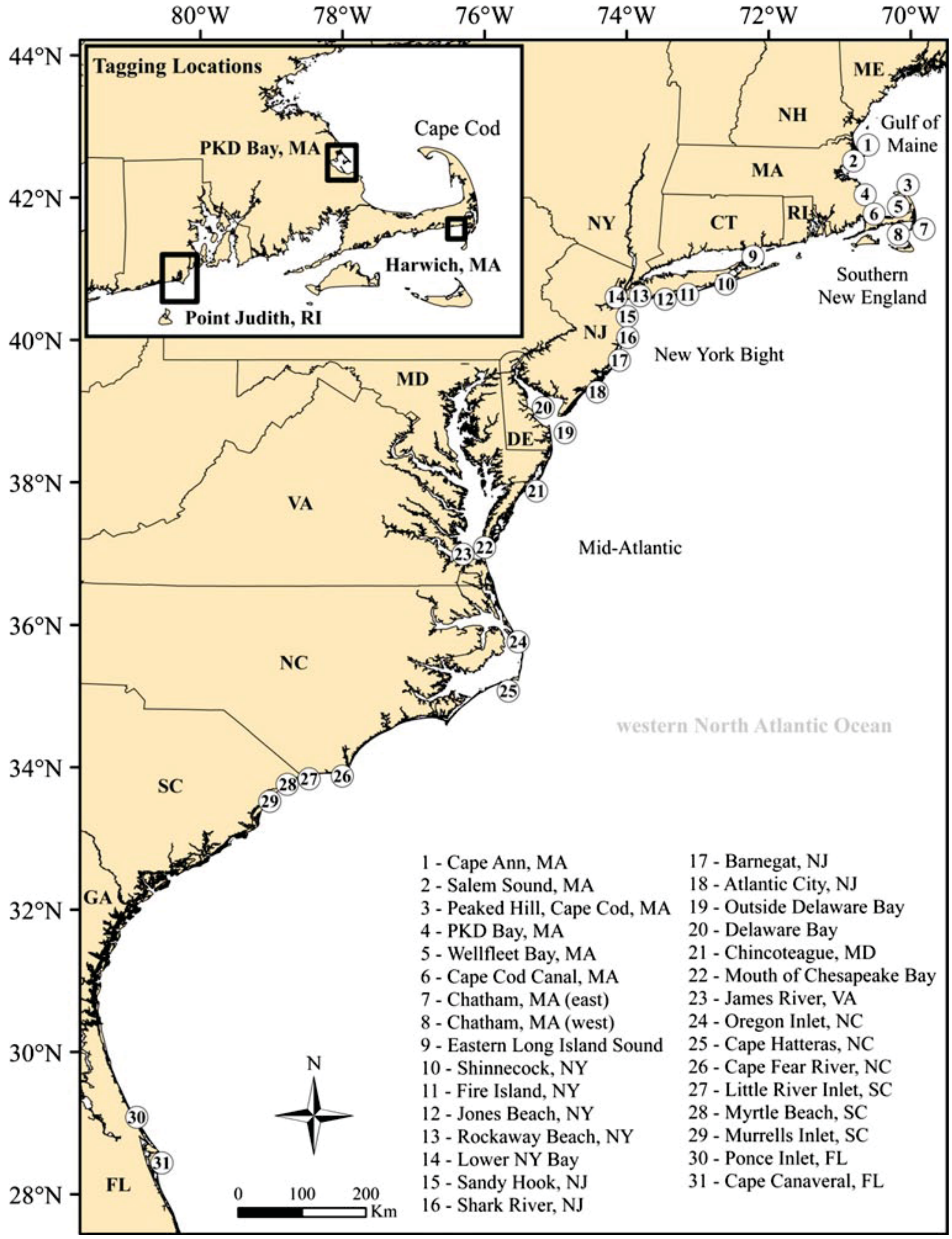



**Fig. 1** Location of acoustic receivers deployed as part of the Atlantic Cooperative Telemetry Network on which acoustically tagged juvenile sand tigers were detected. *CT* Connecticut, *DE* Delaware, *GA* Georgia, *FL* Florida, *MA* Massachusetts, *MD* Maryland, *ME* Maine, *NC* North Carolina, *NH* New Hampshire, *NJ* New Jersey, *NY* New York, *RI* Rhode Island, *SC* South Carolina, *VA* Virginia, *PKD* Plymouth, Kingston, Duxbury

*PSAT tags*

To gain further insight into the large-scale movement patterns and habitat use of juvenile sand tigers, 15 specimens were tagged externally with PSAT tags (models Mk-10, miniPAT; Wildlife Computers, Redmond, WA, USA) in PKD Bay, MA ($n = 10$), off Harwich, MA ($n = 3$), and off Point Judith, RI ($n = 2$) (Table 1). All tags were attached to a ~10 cm stainless steel tether connected to a medical-grade plastic dart, which was inserted in the dorsal musculature near the base of the first dorsal fin. Tags deployed in 2011 were also covered with a thin layer of anti-fouling paint and tested to ensure they were positively buoyant with the tether and dart attached. At tagging, a small incision was made at the base of the dorsal fin and the dart inserted deep into the muscle tissue. Incisions were closed with 3–4 interrupted sutures (2-0 PDS II, Ethicon Inc., NJ) for all tags deployed in 2010 and 2011. All tags were programmed for deployments of 6–12 months (Table 1) and set to archive depth and temperature data at 30 s intervals; data were grouped into 12 user-defined bins and summarized every 24 h. Since tagging occurred in summer during the sharks' seasonal occurrence in New England coastal waters, pop-up dates were programmed so as to capture individual habitat use during the winter and spring. All tags were also

**Table 1** Tagging information for 15 juvenile sand tigers fitted with pop-up satellite archival transmitting (PSAT) tags

| Shark | Sex | FL (cm) | Tag type | Tagging | | Pop-up | | | Days | Comment |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Date | Location | Scheduled date | Actual date | Location | | |
| ST0601 | M | 109 | Mk-10 | 7/5/2006 | Harwich, MA | 7/1/2007 | – | | | DNR[d] |
| ST0602 | F | 96.5 | Mk-10 | 7/10/2006 | Harwich, MA | 7/1/2007 | – | | | DNR[d] |
| ST0701 | M | 104 | Mk-10 | 6/27/2007 | Harwich, MA | 1/1/2008 | – | | | DNR[d] |
| ST0702 | F | 95.5 | Mk-10 | 9/30/2007 | PKD Bay, MA | 12/1/2007 | 11/29/2007[ab] | Duck, NC | 60 | PR; ND[d] |
| ST0703 | F | 94 | Mk-10 | 9/30/2007 | PKD Bay, MA | 1/1/2008 | – | | | DNR[d] |
| ST0947 | M | 104 | Mk-10 | 8/26/2009 | PKD Bay, MA | 1/15/2010 | 10/21/2009 | S of Block Island, RI | 56 | PR |
| ST0956 | F | 101 | Mk-10 | 9/22/2009 | PKD Bay, MA | 1/15/2010 | 9/27/2009 | PKD Bay, MA | 5 | PR |
| ST1019 | M | 92 | miniPAT | 6/21/2010 | Point Judith, RI | 1/1/2011 | 1/1/2011[b] | Frying Pan Shoal, NC | 194 | ND |
| ST1020 | F | 102 | miniPAT | 6/21/2010 | Point Judith, RI | 1/1/2011 | – | | | DNR |
| ST1052 | F | 101 | miniPAT | 8/30/2010 | PKD Bay, MA | 6/1/2011 | 6/1/2011[c] | New York Bight | 275 | FD |
| ST1054 | M | 97 | miniPAT | 8/31/2010 | PKD Bay, MA | 6/1/2011 | – | | | DNR |
| ST1057 | M | 97 | miniPAT | 9/17/2010 | PKD Bay, MA | 3/15/2011 | 10/22/2010 | SW of Martha's Vineyard | 35 | PR |
| ST1032 | F | 101 | miniPAT | 9/8/2011 | PKD Bay, MA | 4/15/2012 | – | | | DNR |
| ST1101 | M | 95 | miniPAT | 9/14/2011 | PKD Bay, MA | 4/15/2012 | – | | | DNR |
| ST1122 | M | 97 | miniPAT | 9/15/2011 | PKD Bay, MA | 4/15/2012 | – | | | DNR |

*FL* fork length, *DNR* did not report, *PR* premature release, *ND* no data were able to retrieved from tag, *FD* full deployment, *MA* Massachusetts, *NC* North Carolina, *RI* Rhode Island, *PKD* Plymouth, Kingston, Duxbury

[a] Tag found with tether washed up on a beach in Duck, NC, short of scheduled pop-up date. No data could be retrieved

[b] Pop-up location was available and incorporated as a conventional recapture location; tag failed to log data

[c] Tag popped-up on 6/1/2011 but did not transmit Argos messages until 7/23/2011

[d] Tag manufacturer indicated that tags had software problem that may have impaired functionality

programmed with a premature release mechanism that enabled the release of tags from any fish that may have suffered post-release mortality; tags were programmed to release if tagged fish remained at a constant depth (±1 m) for a period of 5–10 days.

## Data analysis

### *Passive acoustic telemetry*

Detection data from acoustic transmitters were obtained from the ACT Network between October 2009 and May 2013 and compiled into a database of individual detection events. A detection event was defined as any period during which a tagged shark was detected by any acoustic receiver(s) deployed within a discrete area during a given month. Since detection data were often available from multiple receivers deployed within a broad area (e.g., Delaware Bay), receivers were grouped into 31 discrete areas (Fig. 1). To elucidate temporal trends in horizontal movements, all detection events observed for each individual were pooled and the timing, duration, and location of detection events examined. Temperature sensor detection data obtained from transmitters equipped with temperature sensors (i.e., model V16T) were pooled by month over all areas and plotted to examine trends.

### *PSAT tags*

Daily light-level data retrieved from each tag were modeled using a light-based state-space model in the 'trackit' package (Nielsen and Sibert 2007) in the R statistical environment (R Core Development Team 2009). Initial daily geolocation estimates were refined with bathymetric correction that adjusted each estimate to an area within its confidence interval that was consistent with the maximum daily depth as measured by the tag. All bathymetric corrections were performed through modification of code within the 'analyzepsat' package (Galuardi 2010) in R. Sand tigers are well known to be benthic, spending the majority of time at or near the bottom (Bigelow and Schroeder 1953; Bass et al. 1975; Compagno 1984; Cliff 1989; Smale 2002); thus, this correction provided a more robust estimate of daily position.

Binned depth and temperature data from each tag were analyzed to determine the proportion of time at depth and temperature. Daily minimum, maximum, and average water temperature data as well as daily minimum and maximum

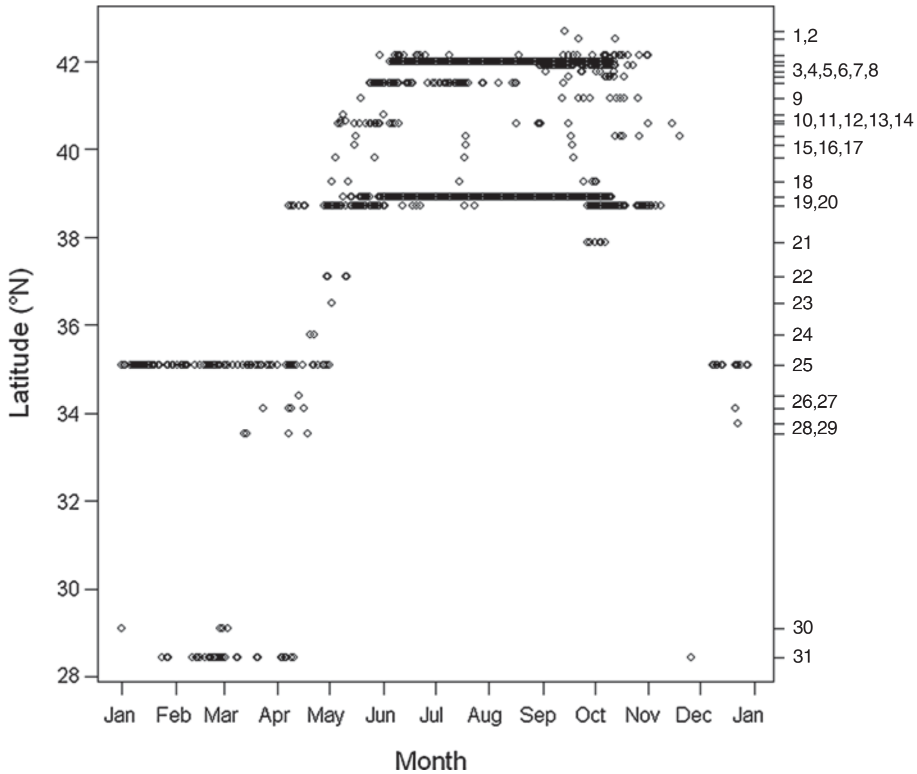



**Fig. 2** Locations of all acoustic detections obtained from receivers deployed as part of the Atlantic Cooperative Telemetry Network during all months of the year. Individual detection locations are numbered (*right y*-axis) according to Fig. 1

depth data were also plotted to elucidate monthly (i.e., seasonal) trends.

*Conventional tags*

Fishery-dependent recapture data were obtained from sharks tagged as part of this study as well as from the NMFS Cooperative Shark Tagging Program (Narragansett, RI). This program generously contributed tagging and recapture information accrued since 1993 (i.e., since the publication of Kohler et al. 1998) for juvenile sand tigers that were ≤125 cm FL at the time of recapture. All tag and recapture data were plotted to examine horizontal movement patterns over time.

## Results

### Tagging

One hundred and forty-five juvenile sand tigers (80 male and 65 female), ranging in size from 68 to 120 cm FL (mean ± SD = 92 ± 8 cm), were captured during this study and tagged with NMFS conventional shark tags. The 78 sharks tagged with acoustic transmitters (43 male, 35 female) ranged in size from 78 to 108 cm FL (mean ± SD = 91 ± 7 cm) and the 15 PSAT-tagged individuals (8 male, 7 female; Table 1) from 92 to 109 cm FL (mean ± SD = 99 ± 5 cm).

### Passive acoustic telemetry

Over the course of the study, 60 of the 78 (77 %) acoustically tagged sand tigers were detected by acoustic receivers deployed along the US east coast as part of the ACT Network. A total of 227,687 detections were logged from all months of the year from 31 coastal areas spanning Cape Ann, MA, south to Cape Canaveral, FL (Fig. 1; Supplementary Table 1) including 181,454 detections from eight individuals that returned to PKD Bay for up to 2 years following tagging (46,233 detections occurred outside PKD Bay). Individual sharks were detected by ACT Network receivers during 1–25 detection events (mean ± SD = 7 ± 6 events); extensive movement data were available for 21 sharks that were monitored for ≥10 detection events.

Juvenile sand tigers underwent extensive seasonal migrations in the spring and fall between summer and winter habitat (Fig. 2; Supplementary Table 1). From June to September, sharks were detected at numerous locations throughout a broad region from Delaware Bay north to Cape Ann, MA, being observed most often within PKD Bay, around Cape Cod (Chatham and Wellfleet Bay, MA), and within Delaware Bay. During the fall (October to November), individuals were detected over a vast expanse from PKD Bay to Cape Canaveral, FL, as they moved southward along the coast. Throughout the winter months (December–March), individuals were detected from Cape Hatteras, NC, south to Cape Canaveral, FL;

some individuals were observed to spend extended periods of time within each of these regions. During spring (April–May), sharks exhibited northward movement along the coast, being detected from Murrells Inlet, SC, north to Cape Cod, MA.

PSAT tags

A high degree of failure (80 %) was observed for all PSATs deployed throughout the study period (Table 1). Broad-scale horizontal movement data were available from only three tags (20 %): one reported after its scheduled pop-up date (ST1052) and two popped-up prematurely (ST0947, ST1057). Pop-up locations were also available for two tags in which a memory failure precluded the retrieval of any data logged throughout its deployment period (ST0702; ST1019). These tags were treated as conventional fishery-dependent recaptures and subsequently included in that analysis.

*Horizontal movements*

In general, PSAT-tagged sharks exhibited relatively extensive seasonal movement patterns. Two juvenile male sharks (ST0947: 97 cm; ST1057: 104 cm) were tagged within PKD Bay, MA, during late August and mid-September 2010 and tracked for 56 and 35 days, respectively, before their tags popped-up prematurely (Table 1; Fig. 3). Bathymetric correction of light-based geolocation estimates for shark ST0947 was problematic in the vicinity of Cape Cod and Nantucket Shoals (areas off the Massachusetts coast with complex bathymetry) and yielded an erratic horizontal movement track. Consequently, the uncorrected (i.e., light-based) track was utilized to describe horizontal movements in this shark. Following tagging, each shark remained within PKD Bay for several days (ST0947: 14 days; ST1057: 4 days) as temperature and depth records were consistent with those observed in PKD Bay during this period (Kneebone et al. 2012). Upon moving out of the embayment, sharks swam at depths of 0–80 m in water 9.8–20.6 °C as they travelled eastward around Cape Cod, MA, and southwestward along the shelf in southern New England from September to October (Fig. 4). On or about October 21, 2010, one of these sharks (ST1057) appeared to have died; the tag was on the bottom (32 m) for 3 days immediately prior to release. The cause of the premature release from the other shark (ST0947) was unknown; no anomalous data were observed immediately prior to the tag's release.

An extensive horizontal track was available for a single 101-cm female shark tagged in PKD Bay, MA, on August 30, 2010 (ST1052; Fig. 5). Examination of depth data revealed that this tag released from the animal as scheduled (June 1, 2011), but remained on or near the surface without transmitting any ARGOS messages until June 8. It then subsequently sank and remained at depth (48 m) until July 7 before re-surfacing. The first ARGOS transmissions were received on July 23. As a result of this anomalous activity, an accurate pop-up location (on June 1) was unavailable. For modeling purposes, the most probable track of this shark was created without a known pop-up location, which was subsequently estimated based on the light-based geolocation corresponding to the initial pop-up date (June 1).

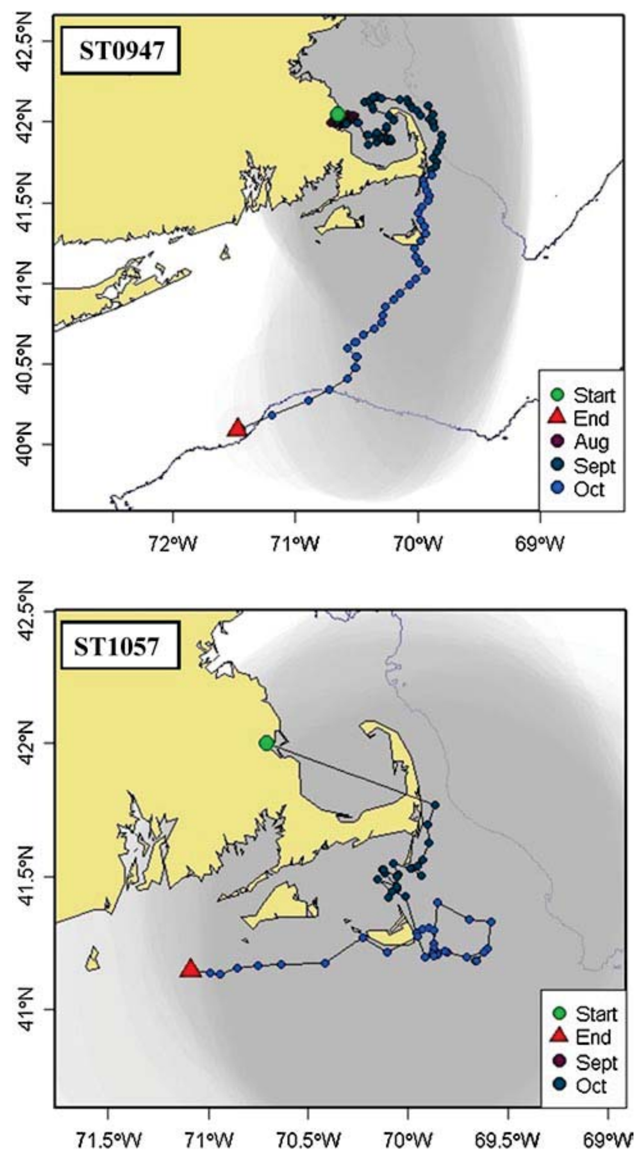



**Fig. 3** Movements of juvenile sand tigers tagged with pop-up satellite archival transmitting tags. Both tags reported premature of their scheduled release date and represent 56 day (ST0947) and 35 day (ST1057) tracks. *Colored circles* represent light-based geolocation estimates (ST0947) corrected for local bathymetry (ST1057). *Gray ellipses* represent light-based geolocation error

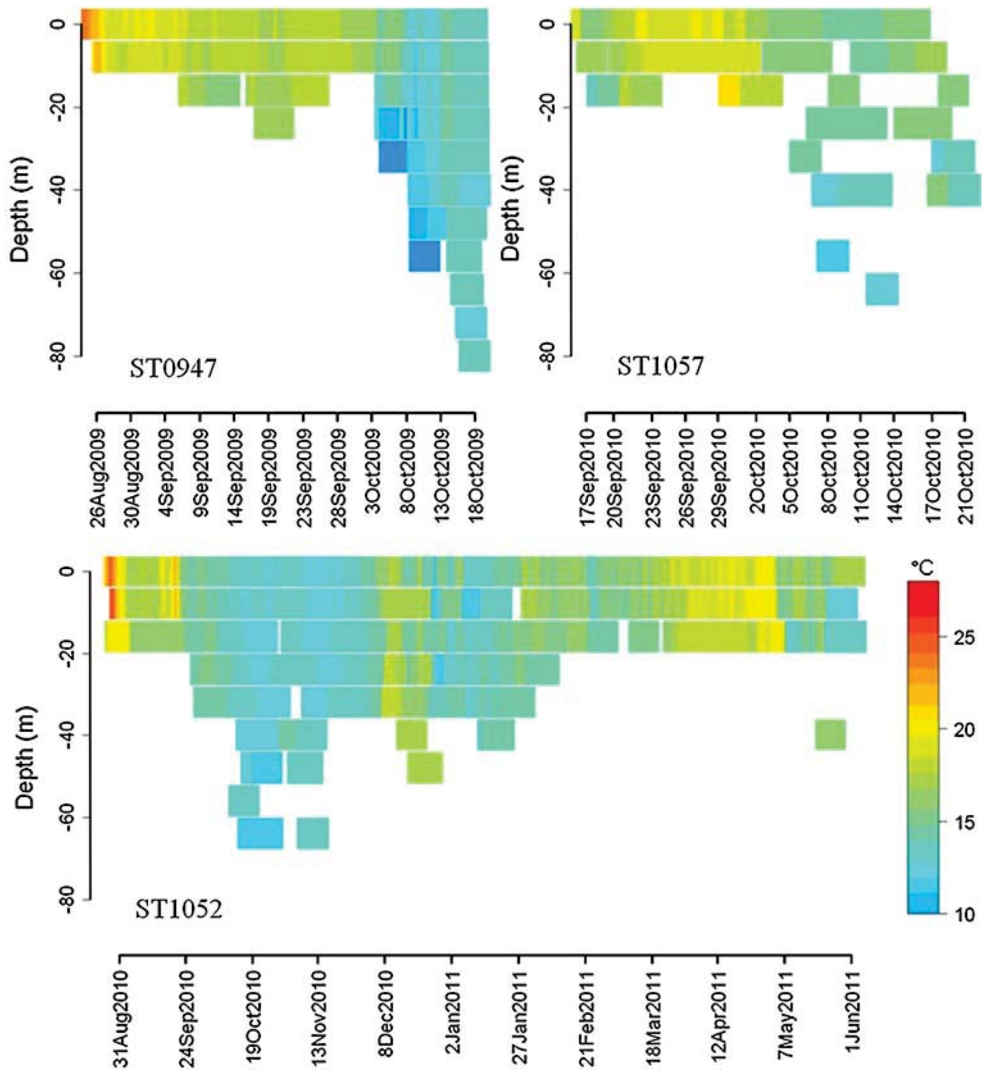



**Fig. 4** Depth and temperature-at-depth distribution for the three juvenile sand tigers tagged with pop-up satellite archival transmitting tags

Following tagging, this shark remained within PKD Bay until September 12; temperature and depth records were consistent with those observed in PKD Bay during this period (Kneebone et al., 2012). From this date through early November, the shark moved eastward around Cape Cod, MA, and then southward within coastal waters off southern New England and the New York Bight/mid-Atlantic in depths of 0–80 m and temperatures of 11.0–16.8 °C (Figs. 4, 5). Southward movement continued during December and early January when the shark travelled from Cape Hatteras, NC, to central Florida at depths of 0–48 m and temperatures of 10.8–22.2 °C. From mid-January to early March, the shark overwintered in coastal waters (0–16 m; 12.6–18.6 °C) from Cape Canaveral south to Stuart, FL. Northward movement up the coast commenced during March and was observed until the tag popped-up and reported in the vicinity of the New York Bight on June 1. During that period, the shark swam in depths of 0–40 m and temperatures of 11.0–22.0 °C. Collectively, the track spanned 275 days during which the shark travelled approximately 5,925 km (21.5 km day$^{-1}$).

*Vertical movements and depth preferences*

Due to the high number of PSAT failures and the brevity of existing tracks, limited information was available on vertical movements. In general, juvenile sand tigers were observed from 0 to 80 m, on average spending 83 and 98 % of their time in waters <20 and <35 m, respectively (Fig. 6). Limited data precluded a thorough analysis of depth preferences over time (i.e., months); however, data from the single extensive (275 day) track indicated that the shark was present in deeper waters from October to February (Fig. 4). All three sharks moved vertically to the surface (<1 m) during the majority (ST1052: 81 %; ST0947: 91 %; ST1057: 98 %) of the days each was tracked.

Conventional tags

Fishery-dependent recapture information was available for a total of 16 juvenile sand tigers tagged with NMFS conventional shark tags (Table 2), ten of which were tagged as part of this study (including two PSAT-tagged sharks that experienced tag failure; Table 1). Time at liberty ranged from 27 to 735 days (mean ± SD = 278 ± 216 days). An illogical capture date was reported for one individual, thereby precluding the calculation of time at liberty. Recapture locations ranged from Scarborough, ME, south to Cape Point, NC (Fig. 7), with all but one recapture occurring from July to November.

Temperature preferences

Temperature data obtained from 13 sharks tagged with acoustic transmitters equipped with temperature sensors (V16T) and 3 PSAT-tagged individuals indicated that juvenile sand tigers occupied water temperatures ranging from 9.8 to 26.9 °C throughout all months of the year (Fig. 8). The three PSAT-tagged sharks were most commonly observed in waters ranging from 12 to 20 °C, spending 91 % (ST1052), 93 % (ST0947), and 99 % (ST1057) of their time within this range (Fig. 6). These sharks also experienced relatively wide daily temperature ranges (i.e., minimum to maximum daily temperatures) of 0.2–8.8 °C (mean ± SD = 2.1 ± 1.6). Monthly water temperatures experienced by PSAT- and acoustically tagged individuals varied throughout the year, with distinct seasonal trends (Fig. 8). In general, sharks experienced lower temperatures (on average) from November to May, with the greatest monthly temperature ranges observed during the summer months.

## Discussion

Despite their relatively small size and young age, juvenile sand tigers undergo extensive (up to ~2,500 km) seasonal migrations along the US east coast from Maine to as far south as central Florida. In general, two distinct migratory periods (northward: April–June; southward: October–December) were apparent throughout a calendar year, when sharks moved along the coastline (in <80 m of water) between summer and winter habitat (Fig. 9). Clearly, these data indicate that juvenile sand tigers occur over a broad geographic range along the US east coast and experience a wide array of habitats and environmental conditions (e.g., temperature). Furthermore, the occurrence of a large number of individuals within New England coastal waters of the Gulf of Maine during the summer months warrants the extension and characterization of NMFS juvenile EFH throughout this region.

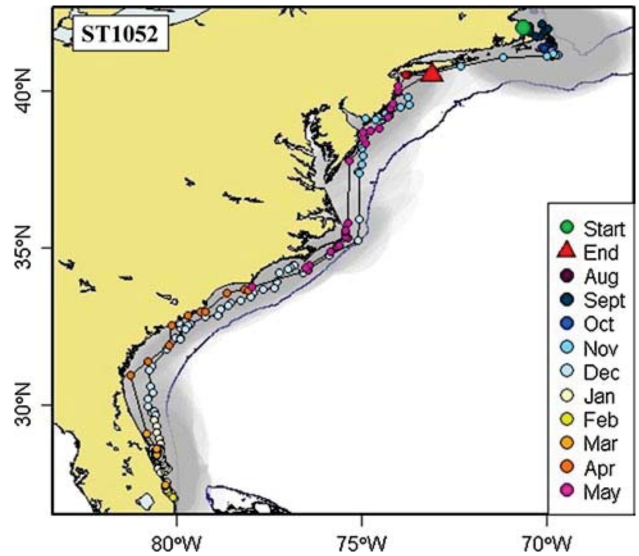



**Fig. 5** Movement of a 101-cm female juvenile sand tiger tagged with pop-up satellite archival transmitting tag during a 275 day track. *Colored circles* represent light-based geolocation estimates corrected for local bathymetry. *Gray ellipses* represent light-based geolocation error

After parturition off the southeastern USA during February and March (Gilmore et al. 1983; Gilmore 1993), young of the year (YOY; defined as those individuals <95 cm FL; Goldman et al. 2006) sand tigers migrate northward through the coastal waters of the mid-Atlantic and southern New England during the first few months of life. Though no direct tagging data were available to document this movement, observations of numerous YOY sharks off Point Judith, RI, within PKD Bay, MA, and various regions along southern New England during late spring to early summer (J. Kneebone, unpublished observations; Skomal 2007; Kneebone et al. 2012) support this assertion. From June to October, YOY sharks were observed from Great Bay, NJ, north to Scarborough Beach, ME, while larger, presumably older, juveniles (>95 cm FL; ages 1 and 2; Goldman et al. 2006) were observed from Delaware Bay north to Cape Ann, MA; published capture records indicate that juvenile sharks also occur further north in the Gulf of Maine (Bigelow and Schroeder 1953). Collectively, the available data suggest that juvenile sand tiger EFH may be distributed continuously from Delaware Bay north to southern Maine, though further research on specific areas of high abundance/importance (i.e., nursery habitat) is warranted.

Acoustic detection data and information from the single full PSAT track suggest that juvenile sand tigers occupy coastal waters from Cape Hatteras, NC, south to central Florida during the winter months. Throughout this broad range, tagged individuals were observed most frequently in the vicinity of Cape Hatteras, NC, and Cape Canaveral,

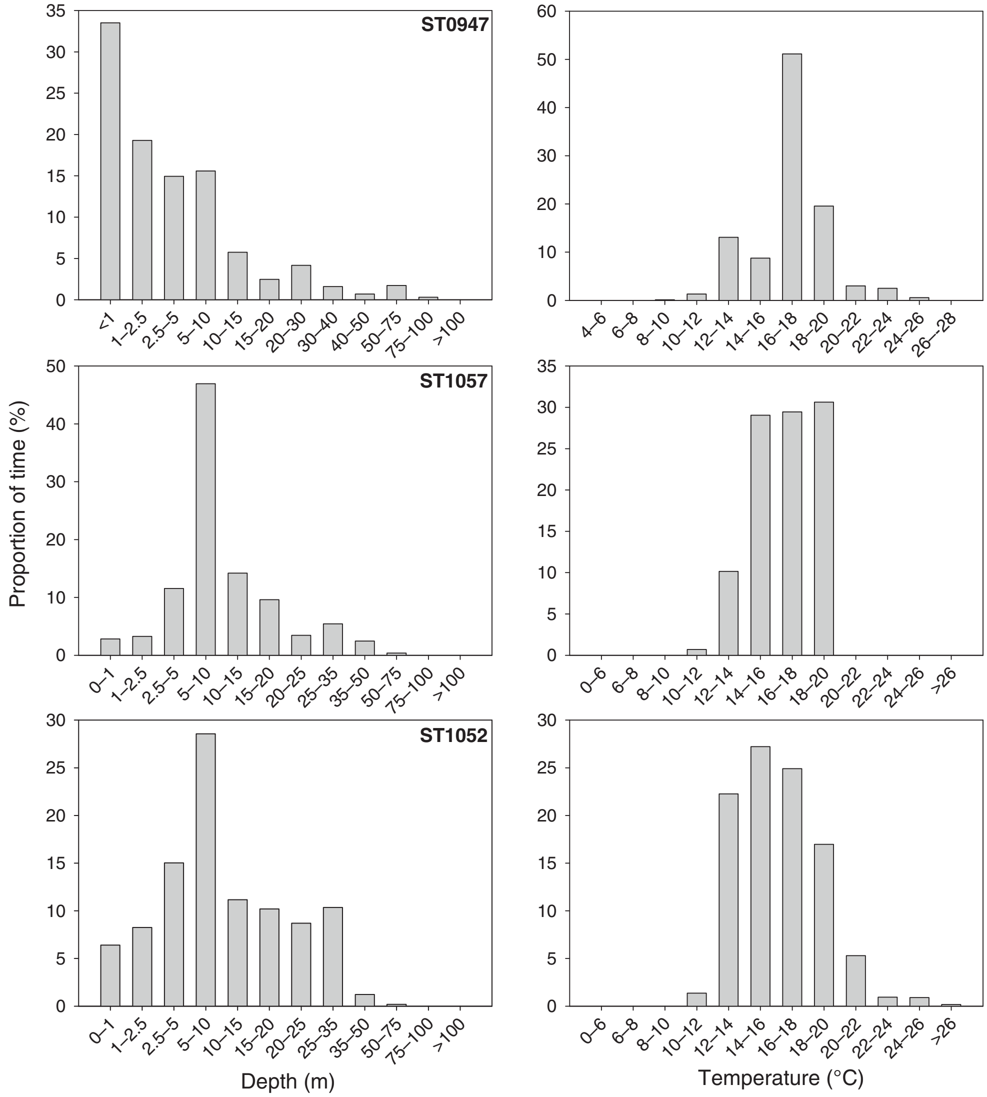



**Fig. 6** Proportion of total time spent at depth (*left*) and temperature (*right*) for three sharks tagged with pop-up satellite archival transmitting tags. Data from two sharks (ST0947, ST1057) represent brief tracks (56 and 35 days, respectively), while data from ST1052 are representative of a 275 day period

FL—two areas that seemingly support a seasonal abundance of sharks and, therefore, may contain nursery habitat. For example, of the 64 acoustically tagged sharks whose transmitters were still active during at least one winter following tagging, 13 (20 %) were detected intermittently within a small receiver array off Cape Hatteras, NC, during the months of December–April, indicating some degree of residency in this area. Six other individuals (9 %), as well as a single PSAT-tagged individual, were also observed during the same months within a broad area off central Florida. In addition, 27 individuals (43 %) were detected briefly on receivers off Cape Hatteras, NC, either during the fall or spring, presumably during their migration to/from overwintering grounds south of the area. However, despite the annual observation of sharks within these two areas, 15 individuals (23 %) were not detected on any receiver during the winter months, indicating that they utilized winter habitat elsewhere along the coast that was devoid of receiver coverage during the study period. Clearly, future research is required to identify, characterize, and describe specific areas/habitats that may serve as winter nursery habitat throughout this broad range.

The seasonal migratory behavior of juvenile sand tigers observed in this study generally corroborates that previously described by Gilmore (1993). Interestingly, however, Gilmore (1993) did not imply that juvenile sand tigers occupy seasonal nursery habitat north of Cape Cod. Clearly, the available data indicate that juvenile sand tigers do indeed currently utilize summer nursery habitat throughout Gulf of Maine coastal waters, despite not being historically

**Table 2** Conventional fishery-dependent tag and recapture data obtained from the National Marine Fisheries Service Cooperative Shark Tagging Program from 1998 to 2012

| Sex | FL (cm) | Tagging | | Recapture | | Days at liberty |
|---|---|---|---|---|---|---|
| | | Date | Location | Date | Location | |
| F | 94 | 10/15/2004 | S of Shinnecock Inlet, NY | 3/10/2006 | Cape Point, NC | 511 |
| F | *120* | 7/12/2005 | Great Bay, NJ | 7/1/2006 | Holgate Beach, NJ | 354 |
| F | *91* | 7/11/2007 | Great Bay, NJ | 11/15/2007 | Pamlico Sound, NC | 127 |
| F | 91 | 9/30/2007 | PKD Bay, MA | 6/21/2008 | West Dennis Beach, MA | 265 |
| F | *87* | 7/8/2008 | W of Little Egg Inlet, NJ | 7/22/2009 | W of Little Egg Inlet, NJ | 379 |
| F | 88.5 | 7/17/2009 | PKD Bay, MA | 7/1/2010 | Newport, RI | 349 |
| M | 86.5 | 7/17/2009 | PKD Bay, MA | 11/28/2009 | Rudee Inlet, VA | 134 |
| F | 91 | 8/3/2009 | PKD Bay, MA | 8/17/2011 | Point Judith, RI | 379 |
| M | 95 | 9/20/2009 | PKD Bay, MA | 9/25/2011 | SE of Point Judith, RI | 735 |
| M | 97 | 6/7/2010 | Point Judith, RI | 8/29/2010 | Harwich, MA | 83 |
| M | 89 | 6/7/2010 | Point Judith, RI | 7/4/2010 | Scarborough, ME | 27 |
| F | *125* | 7/6/2010 | Great South Bay, NY | 8/9/2010 | Great South Bay, NY | 34 |
| M | 99 | 7/12/2010 | PKD Bay, MA | 11/15/2011 | E of Block Island, RI | 491 |
| F | *125* | 6/5/2011 | Indian River Inlet, DE | 7/5/2011 | Point Judith, RI | 30 |
| M | 84 | 7/7/2011 | PKD Bay, MA | [a] | S of Martha's Vineyard, MA | [a] |
| M | 108 | 7/17/2011 | PKD Bay, MA | 9/12/2012 | Corolla, NC | 423 |

Estimated lengths at tagging are indicated in italics

*FL* fork length, *DE* Delaware, *NJ* New Jersey, *NY* New York, *NC* North Carolina, *MA* Massachusetts, *ME* Maine, *RI* Rhode Island, *VA* Virginia, *PKD* Plymouth, Kingston, Duxbury

[a] Erroneous recapture information

encountered within this region in high abundance (Bigelow and Schroeder 1953; Kneebone et al. 2012). The investigation of factors driving the apparent increased seasonal abundance of this species north of Cape Cod was beyond the scope of this study, although it is possible that greater numbers of juvenile sharks are moving further north as a result of environmental (i.e., water temperature) or density-dependent factors (i.e., population recovery and re-colonization of historical habitat). Regardless, the extensive use of habitat within the Gulf of Maine suggests that this region supports juvenile sand tiger EFH that should be described in future NMFS juvenile EFH documents.

Acoustic and conventional tagging data suggest that juvenile sand tigers migrate north to New England waters up until about age two (~125 cm FL; Goldman et al. 2006). Of the 17 acoustically tagged sharks that returned to this region in years following tagging, 12 were putatively age-0 (YOY) and five putatively age-1 (95–110 cm; Goldman et al. 2006) at tagging. Furthermore, of the 12 YOY sharks that returned in the year following tagging, three were also observed the following year (i.e., were present in New England for three consecutive years). Interestingly, other acoustically tagged individuals that were either YOY or age—1 at tagging in New England spent extended periods within Delaware Bay during the summer months in the year(s) following tagging. When coupled with the lack of observations of sharks >125 cm FL (i.e., >age—2) in New England (current study; Skomal 2007; Kneebone et al. 2012), these data suggest that an ontogenetic shift in migratory behavior likely occurs around age 1–2 years, in which individuals cease to migrate north into Cape Cod/Gulf of Maine waters and remain in more southern waters (e.g., RI south to Delaware Bay).

Seasonal movement patterns observed in this study were also consistent with those described for juvenile sand tigers in the southwest (SW) Atlantic and South Africa. Lucifora et al. (2002) provided some evidence of seasonal north–south migrations of juvenile sand tigers off Argentina in the SW Atlantic, while Dicken et al. (2007) suggested that juvenile sand tigers undergo annual cyclical north–south movements to and from summer nursery habitat off the coast of South Africa. Furthermore, Dicken et al. (2007) reported fishery-dependent recaptures in close proximity to release locations for up to 3 years post-release and suggested that juvenile sharks may exhibit natal nursery homing. Indeed, the return of several sharks to seasonal nursery habitat in PKD Bay, MA, for up to 2 years following tagging in the current study suggests that juvenile sand tigers do exhibit some degree of inter-annual fidelity to nursery areas in the WNA, thereby affirming the importance of this habitat as EFH. Such behavior has also been documented in juvenile sandbar

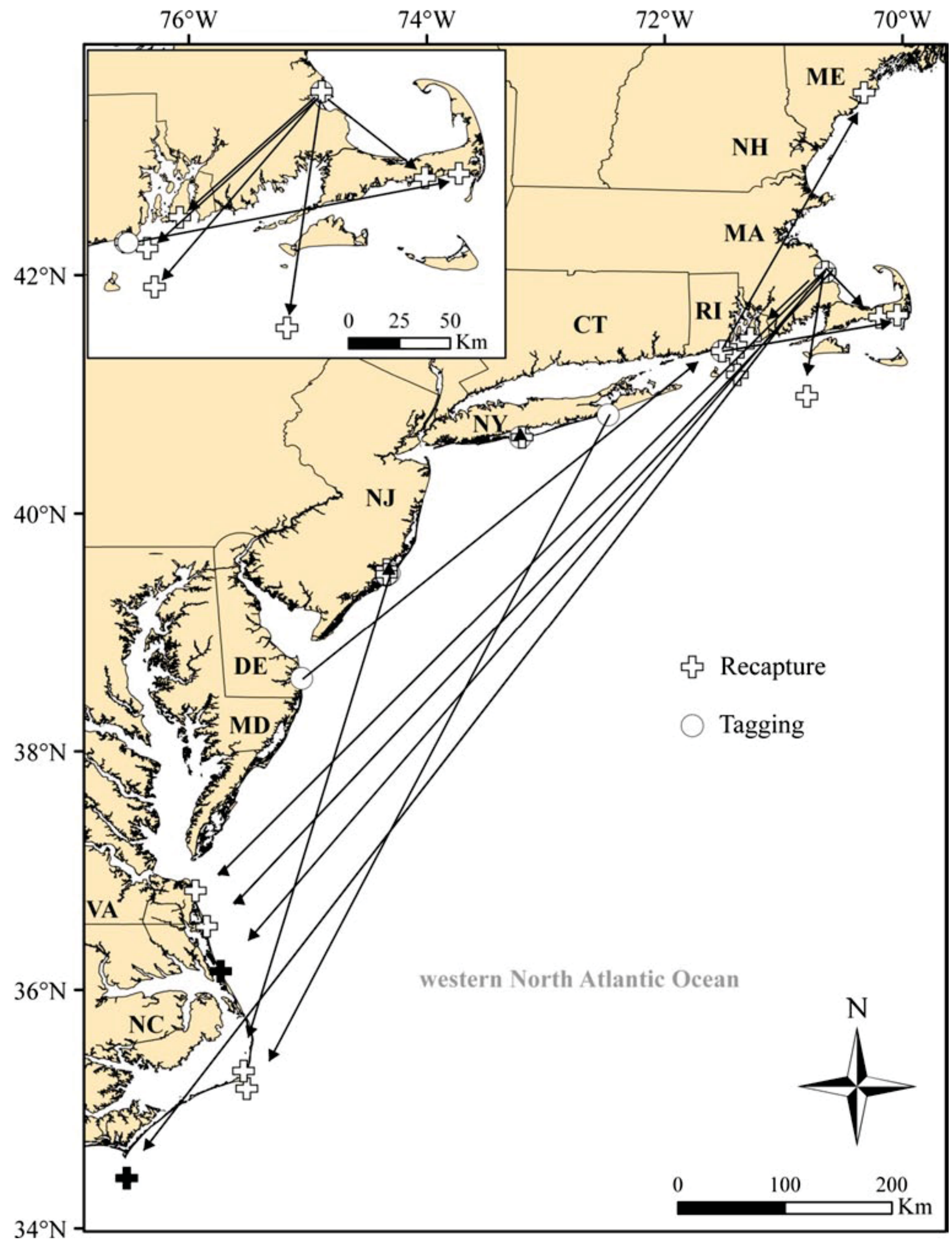



**Fig. 7** Locations of conventional fishery-dependent tag and recapture events. Pop-up locations from two failed pop-up satellite archival transmitting tag deployments (*solid black cross*) are also presented. *Arrows* positioned near the recapture location designate the direction of movement. *CT* Connecticut, *DE* Delaware, *MA* Massachusetts, *MD* Maryland, *ME* Maine, *NC* North Carolina, *NH* New Hampshire, *NJ* New Jersey, *NY* New York, *RI* Rhode Island, *VA* Virginia

sharks, *Carcharhinus plumbeus* (Merson and Pratt 2001), and blacktip sharks, *Carcharhinus limbatus* (Hueter et al. 2005).

The overall magnitude of the seasonal migration exhibited by juvenile sand tigers off the east coast of the USA is greater than that previously described for juvenile conspecifics in other geographic regions. Data from the single extensive PSAT track suggest that a 101-cm female shark travelled from PKD Bay, MA, south to central Florida from early October to early January, covering a distance of ~2,250 km in roughly 100 days. Similarly, acoustic detection data documented extensive movements of four YOY sharks (78–89 cm FL) from PKD Bay, MA, south to Cape Canaveral, FL in 116–172 days. Furthermore, the return of two of these individuals to PKD Bay and/or Chatham, MA, in years following tagging confirmed movements in excess of 5,000 km over a 247–262 day period during the first year of life. Interestingly, other individuals were observed to migrate shorter distances between summer habitat ranging from Delaware Bay north to New England and overwintering habitat in the vicinity of Cape Hatteras, NC—unidirectional distances of 500–1,250 km. Previous studies on immature sand tigers (<150 cm FL) have suggested that young individuals migrate shorter distances

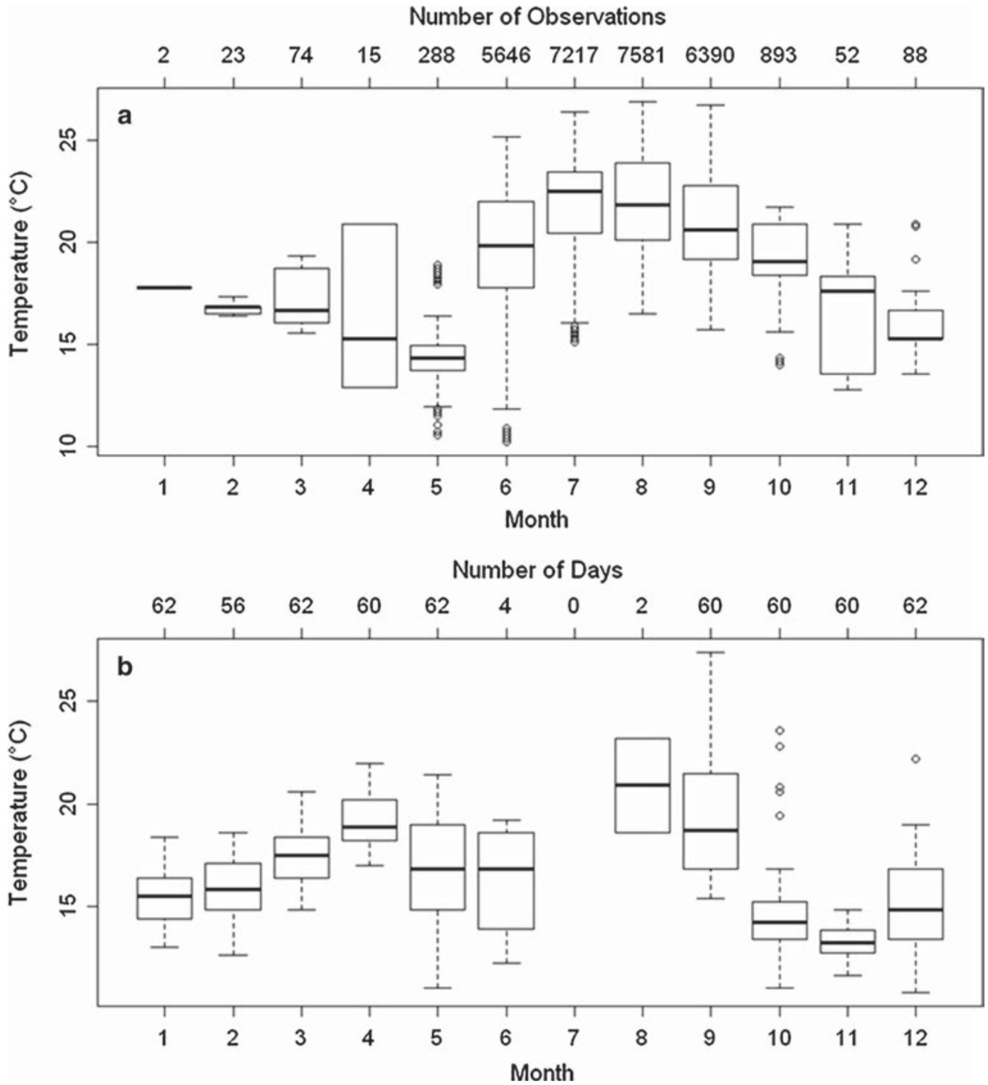


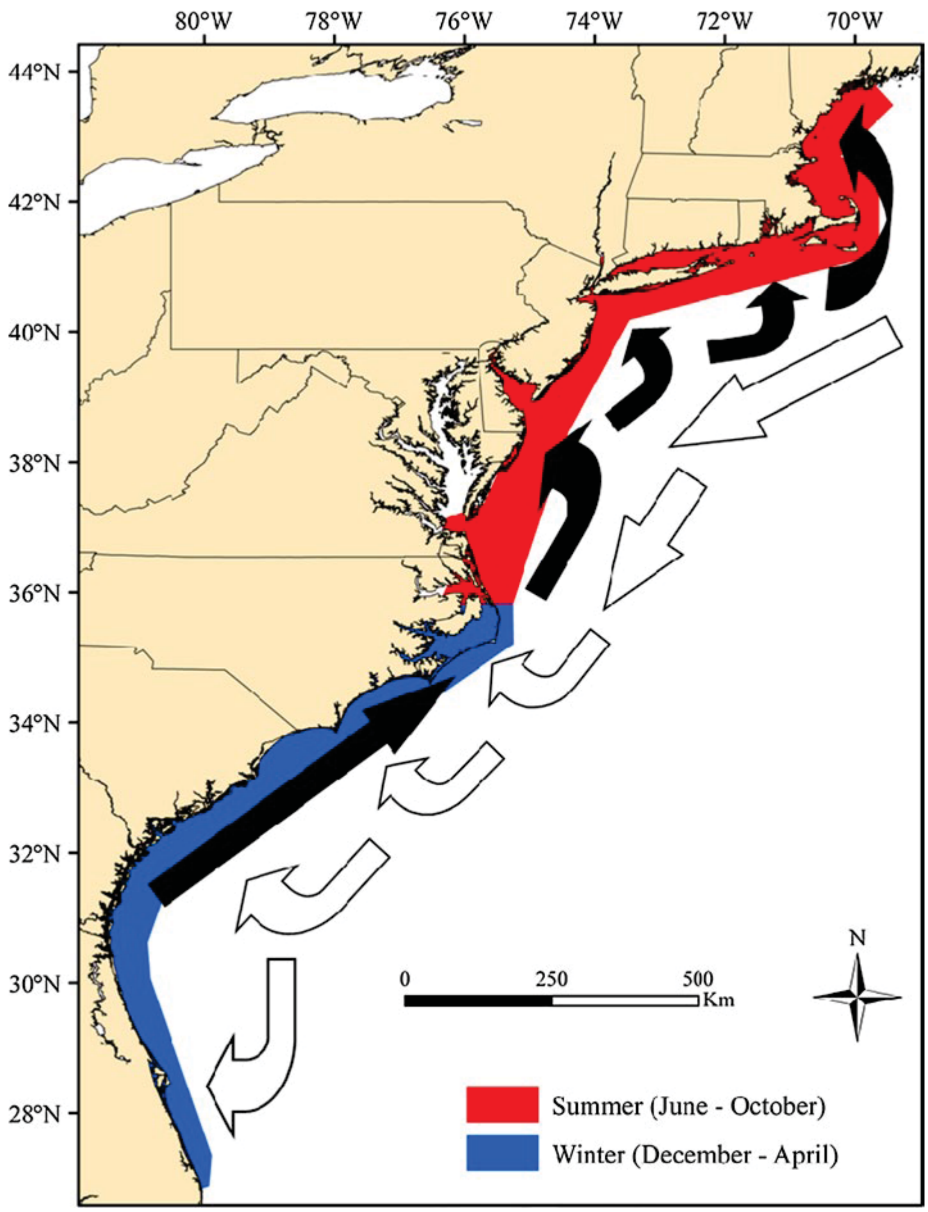

**Fig. 8** Monthly boxplots of temperature data collected from **a** 13 acoustic transmitters equipped with temperature sensors (V16T) and **b** three pop-up satellite archival transmitting tags. *Solid black lines* within each box represent the median monthly temperature

than mature individuals, traveling unidirectional distances of 100–400 km (Otway and Ellis 2011) and 653 km (Bansemer and Bennett 2011) off eastern Australia, and up to 268 km off South Africa (Dicken et al. 2007). In contrast, considering the lack of mature sand tigers in New England waters (Bigelow and Schroeder 1953; Skomal 2007; Kneebone et al. 2012) and their documented movement patterns (e.g., Gilmore 1993; Kohler et al. 1998), it appears as though juvenile sand tigers may exhibit more extensive annual movements off the east coast of the USA than larger, mature individuals.

Depth data obtained in this study suggest that juvenile sand tigers follow coastal bathymetric contours throughout their extensive coastal migration. Though limited to a few individuals, PSAT-tagged sharks spent a large percentage of time in relatively shallow water <35 m (98 %) and rarely ventured into water >50 m. In addition, the detection of numerous acoustically tagged individuals on receivers deployed in close proximity to shore (i.e., on coastal navigational aids or near piers and jetties) suggests that migration may occur, in part, in very shallow water (i.e., <10 m) along the shoreline. These depth preferences are consistent with those reported for larger sand tigers off eastern Australia (152–251 cm FL; Otway and Ellis 2011) and South Africa (203–308 cm FL; Smale et al. 2012). While those two studies reported greater maximum depths (232 m in Australia and 108 m in South Africa), both suggested that sand tigers spent the majority of their time in waters <40 m. In addition, both studies suggested that forays into deeper waters (i.e., >50 m) were linked with migratory movement, a finding consistent with the vertical movements observed for juvenile sand tigers in this study during their north/south migration (Fig. 4).

The frequent observation of PSAT-tagged juvenile sand tigers at the surface (i.e., <1 m) lends further support to the occurrence of 'gulping' behavior in this species. Originally described by Bass and Ballard (1972) as a form of buoyancy control, this behavior involves movement to the

**Fig. 9** Proposed seasonal migration undertaken by juvenile sand tigers along the east coast of the USA. Spring (April–June; *black arrows*) and fall (October–December; *white arrows*) migrations are evident between broad summer and winter habitat




surface to swallow air, which is retained in the stomach to achieve neutral buoyancy at depth. Recently, Smale et al. (2012) reported that these gulping events occur relatively frequently, sometimes multiple times within a given day. In this study, PSAT-tagged individuals were found to spend a small fraction (i.e., <1 %) of their daily time at the surface, yet they ventured to the surface in >80 % of the days during which they were tracked. Although such behavior may also be associated with surface feeding, the relatively brief amount of time at the surface, particularly on days when individuals spent the majority of their time at depths >35 m, suggests an alternative motive, such as gulping.

Temperature preferences exhibited by juvenile sand tigers in this study were very similar to those reported for sub-adult and adult sand tigers throughout their range. Off the east coast of the USA, juvenile sand tigers experienced temperatures ranging from 9.8 to 26.9 °C, spending the majority of their time (91–99 %) between 10 and 20 °C. Similarly, larger conspecifics inhabited water from 9.8 to 22.4 °C off South Africa (Smale et al. 2012) and 14–26 °C off eastern Australia, spending 96 % of their time between 17 and 24 °C in the latter region (Otway and Ellis 2011). As noted by Smale et al. (2012), these relatively large temperature ranges are due, in part, to vertical excursions to cooler water at depth, but also are reflective of seasonal temperature fluctuations. For example, in this study, the lowest absolute water temperature recorded by a PSAT-tagged sand tiger (9.8 °C) was in October at a depth of 56 m, one of the deepest depths observed. In addition, average monthly water temperatures experienced by juvenile sand tigers followed a typical seasonal pattern with higher temperatures during the summer months (June–September). Interestingly, the range of temperatures experienced by sand tigers within a given month was markedly higher during the summer months, potentially a result of the greater seasonal stratification of the water column at northern latitudes during the summer (Skomal et al. 2009). Nevertheless, juvenile sand tigers may inhabit a more narrow temperature range during their seasonal migration and within their overwintering habitat.

The high PSAT tag failure rate experienced in this study was troubling and hindered the documentation of juvenile sand tiger habitat use throughout their coastal migration. Of the 15 tags deployed, only six transmitted Argos messages (40 %), two on their scheduled date (13 %) and four prematurely (27 %). In addition, three tags suffered memory failures (20 %) that precluded the retrieval of data logged during the deployment period. Several factors may influence PSAT failure including tag malfunction (Hays et al. 2007), aerial damage (Hays et al. 2007), scavenging by predators (Kerstetter et al. 2004), and bio-fouling (Wilson et al. 2006; Hays et al. 2007). Of these, bio-fouling, possibly of the satellite transmission switch (Hays et al. 2007), was likely the factor that contributed to the high failure rate observed in this study. Bio-fouling of external conventional tags is well documented to be problematic for sand tigers (Otway and Burke 2004; Dicken et al. 2011) and was thought to contribute to PSAT failure in sand tigers tagged off eastern Australia (Otway and Ellis 2011). In this study, though no direct evidence for bio-fouling of PSATs was observed, several conventionally tagged sharks recaptured >1 year after tagging were observed to have significant fouling of their external conventional tags (J. Kneebone, personal observation). In addition, weak and intermittent Argos transmissions received from multiple PSAT tags immediately following their scheduled pop-up date suggest that these tags may have experienced reduced buoyancy upon detachment from the animal. Taken together, these observations/findings along with the propensity for juvenile sand tigers to inhabit shallow, light-intense waters where bio-fouling is more prevalent, suggest that, aside from tag memory malfunction, bio-fouling was likely the greatest factor influencing the high PSAT tag failure rate observed in this study.

The synergy of information from PSAT, passive acoustic, and conventional tagging analyses enabled a relatively detailed documentation of juvenile sand tiger shark seasonal migration and habitat use along the US east coast. Despite minimal PSAT success, the recent expansion in the number of coastal acoustic receiver arrays deployed along the US east coast within the ACT Network enabled the tracking of a large number of individuals over vast distances and prolonged time periods. Overall, given the extensive movements and continual utilization of nearshore (<80 m) waters exhibited by these relatively small (<125 cm FL), young (age 0–2) individuals during their first years of life, it is imperative that precautions be taken to limit negative anthropogenic impacts on this species (i.e., fisheries bycatch, coastal degradation) in an effort to rebuild and sustain the WNA population.

**Acknowledgments** The authors gratefully acknowledge Dave Lindamood for enabling the initial documentation of sharks in PKD Bay, Donald Beers, and the Duxbury Harbormaster's Office for providing dockage during sampling, Andy Danylchuk for providing acoustic tags, receivers, and creative input, and Ben Galuardi for his help with PSAT geolocation analyses. Thanks also to Nancy Kohler, Pat Turner, Lisa Natanson, and Ruth Briggs of the NMFS Apex Predators Program/Cooperative Shark Tagging Program for providing fishery-dependent tag and recapture data. This study would not have been possible without the volunteer members of the ACT Network who provided detection data including: Dewayne Fox and Lori Brown (Delaware State University); Jennifer Cudney and Andrea Dell'Apa (East Carolina University); Keith Dunton (Stony Brook University); Eric Reyier (IHA Environmental Services); Matt Bolus (University of Massachusetts Amherst); Bill Hoffman (Massachusetts Division of Marine Fisheries); Tom Savoy (Connecticut Department of Energy and Environmental Protection); Elizabeth Miller (South Carolina Department of Natural Resources); Matthew Balazik (Virginia Commonwealth University); Michael Loeffler (North Carolina Department of Environment and Natural Resources); and Carter Watterson (US Navy). This research was funded by awards from the NOAA Proactive Conservation Program, the Sea World Conservation Society, and the Massachusetts Environmental Trust as well as support from the Federal Aid in Sportfish Restoration Act. This is Massachusetts Division of Marine Fisheries Contribution No. 47.

## References

ASMFC (Atlantic States Marine Fisheries Commission) (2008) Interstate fishery management plan for Atlantic coastal sharks. ASMFC, Washington, DC, p 172

Bansemer CS, Bennett MB (2011) Sex- and maturity-based differences in movements and migration patterns of grey nurse sharks, *Carcharias taurus*, along the eastern coast of Australia. Mar Freshw Res 62:596–606

Bass AJ, Ballard JA (1972) Buoyancy control in the shark *Odontaspis taurus* (Rafinesque). Copeia 3:594–595

Bass AJ, D'Aubrey JD, Kistnasamy N (1975) Sharks of the east coast of southern Africa. IV. The families Odontaspididae, Scapanorhynchidae, Isuridae, Cetorhinidae, Alopiidae, Orectolobidae and Rhiniodontidae. Invest Rep Oceanogr Res Inst S Afr 39:102

Bigelow HB, Schroeder WC (1953) Fishes of the Gulf of Maine. Fish Bull 53:74

Castro J, Woodley CM, Brudeck R (1999) A preliminary evaluation of the status of shark species. FAO fisheries technical paper no. 380, FAO, Rome, p 72

Cliff G (1989) The breeding migration of the sand tiger shark, *Carcharias taurus*, in Southern African waters. In: Presented at the 5th annual meeting of the American Elasmobranch Society, San Francisco State University, San Francisco, CA, USA (abstract), p 76

Compagno LJV (1984) FAO Species catalog, vol 4, part 1 and 2: sharks of the world: an annotated and illustrated catalogue of shark species known to date. FAO fisheries synopsis 125. FAO, Rome

Cortés E (2002) Incorporating uncertainty into demographic modeling: application to shark populations and their conservation. Conserv Biol 16:1048–1062

Dicken ML, Booth AJ, Smale MJ, Cliff G (2007) Spatial and seasonal distribution patterns of juvenile and adult raggedtooth sharks (*Carcharias taurus*) tagged off the east coast of South Africa. Mar Freshw Res 58:127–134

Dicken ML, Nance SP, Smale MJ (2011) Sessile biofouling on tags from recaptured raggedtooth sharks (*Carcharias taurus*) and their effects on tagging studies. Mar Freshw Res 62:359–364

Galuardi B (2010) Analyzepsat. R package version 3.0. http://code.google.com/p/analyzepsat/

Gilmore RG (1993) Reproductive biology of lamnoid sharks. Environ Biol Fish 38:95–114

Gilmore RG, Dodrill JW, Linley PA (1983) Embryonic development of the sand tiger shark *Odontaspis taurus* (Rafinesque). Fish Bull 81:201–225

Goldman KJ (2002) Aspects of age, growth, demographics and thermal biology of two lamniform shark species. Dissertation, Virginia Institute of Marine Science, Virginia

Goldman KJ, Branstetter S, Musick JA (2006) A re-examination of the age and growth of sand tiger sharks, *Carcharias taurus*, in the western North Atlantic: the importance of ageing protocols and use of multiple back-calculation techniques. Environ Biol Fish 77:241–252

Hays GC, Bradshaw CJA, James MC, Lovell P, Sims DW (2007) Why do Argos satellite tags deployed on marine animals stop transmitting? J Exp Mar Biol Ecol 349:52–60

Hueter RE, Heupel MR, Heist EJ, Keeney DB (2005) Evidence of philopatry in sharks and implications for the management of shark fisheries. J Northwest Atl Fish Sci 35:239–247

Kerstetter DW, Polovina JJ, Graves JE (2004) Evidence of shark predation and scavenging on fishes equipped with pop-up satellite archival tags. Fish Bull 102:750–756

Kneebone J, Chisholm J, Skomal GB (2012) Seasonal residency, habitat use, and site fidelity of juvenile sand tigers *Carcharias taurus* in a Massachusetts estuary. Mar Ecol Prog Ser 471:165–185

Kneebone J, Chisholm J, Bernal D, Skomal GB (2013) The physiological effects of capture stress, recovery, and post-release survivorship of juvenile sand tigers (*Carcharias taurus*) caught on rod and reel. Fish Res 147:103–114

Kohler NE, Turner PA (2001) Shark tagging: a review of conventional methods and studies. Environ Biol Fish 60:191–223

Kohler NE, Casey JG, Turner PA (1998) NMFS cooperative tagging program, 1962–1993: an atlas of shark tag and recapture data. Mar Fish Rev 60:1–87

Lucifora LO, Menni RC, Escalante AH (2002) Reproductive ecology and abundance of the sand tiger shark, *Carcharias taurus*, from the southwestern Atlantic. ICES J Mar Sci 59:553–561

Merson RR, Pratt HL (2001) Distribution, movements and growth of young sandbar sharks, *Carcharhinus plumbeus*, in the nursery grounds of Delaware Bay. Environ Biol Fish 61:13–24

Musick JA, Branstetter S, Colvocoresses JA (1993) Trends in shark abundance from 1974 to 1991 for the Chesapeake Bight region of the U.S. mid-Atlantic coast. NOAA technical report NMFS 115

Musick JA, Harbin MM, Berkeley SA, Burgess GH, Eklund AM, Findley L, Gilmore RG, Golden JT, Ha DS, Huntsman GR, McGovern JC, Parker SJ, Poss SG, Sala E, Schmidt TW, Sedberry GR, Weeks H, Wright SG (2000) Marine, estuarine, and diadromous fish stocks at risk of extinction in North America. Fisheries 25:6–30

Nielsen A, Sibert JR (2007) State-space model for light-based tracking of marine animals. Can J Fish Aquat Sci 64:1055–1068

NMFS (2006) Final consolidated Atlantic highly migratory species fishery management plan. DOC/NOAA/NMFS HMS Management Division, Silver Spring

NMFS (2009) Amendment 1 to the consolidated Atlantic highly migratory species fishery management plan: essential fish habitat. Final EFH Map for neonate/YOY sand tiger shark (*Carcharias taurus*). NOAA, National Marine Fisheries Service, Highly Migratory Species Management Division, Silver Spring, MD

NMFS (National Marine Fisheries Service) (1999) Final fishery management plan for Atlantic tunas, swordfish, and sharks. DOC/NOAA/NMFS HMS Management Division, Silver Spring

Otway NM, Burke AL (2004) Mark-recapture population estimate and movements of grey nurse sharks. EA project no. 30786/87, NSW Fisheries final report series no. 63

Otway NM, Ellis MT (2011) Pop-up archival satellite tagging of *Carcharias taurus*: movements and depth/temperature-related use of south-eastern Australian waters. Mar Freshw Res 62:607–620

R Development Core Team (2009) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. ISBN: 3-900051-07-0. http://www.R-project.org/

Skomal GB (2007) Shark nursery areas in the coastal waters of Massachusetts. In: McCandless CT, Kohler NE, Pratt HL Jr (eds) Shark nursery grounds of the Gulf of Mexico and east coast waters of the United States, vol 50. American Fisheries Society symposium, pp 17–33

Skomal GB, Zeeman SI, Chisholm JH, Summers EL, Walsh HJ, McMahon KW, Thorrold SR (2009) Transequatorial Migrations by basking sharks in the western Atlantic Ocean. Curr Biol 19:1–4

Smale MJ (2002) Occurrence of *Carcharias taurus* in nursery areas of the Eastern and Western Cape, South Africa. Mar Freshw Res 53:551–556

Smale MJ, Booth AJ, Farquhar MR, Meÿer MR, Rochat L (2012) Migration and habitat use of formerly captive and wild raggedtooth sharks (*Carcharias taurus*) on the southeast coast of South Africa. Mar Biol Res 8:115–128

Watsky M, Gruber SH (1990) Induction and duration of tonic immobility in the lemon shark *Negaprion brevirostris*. J Fish Physiol Biochem 8:207–210

Wilson SG, Polovina JJ, Stewart BS, Meekan MG (2006) Movements of whale sharks (*Rhincodon typus*) tagged at Ningaloo Reef, Western Australia. Mar Biol 148:1157–1166