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Overwinter habitat use of young-of-the-year white sharks (*Carcharodon carcharias*) off the eastern United States

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Abstract—Despite recent increases in the number of studies that have focused on the movements and habitat use of juvenile and adult white sharks (*Carcharodon carcharias*) in the Northwest Atlantic Ocean off the eastern United States, there is comparatively little information on the movements of young-of-the-year (YOY) white sharks, particularly in the overwinter season. Simultaneous satellite and acoustic tagging were conducted on YOY white sharks in 2016 and 2017, and data from their first overwinter period (December through April) were analyzed. Tracks of 9 white sharks offer a preliminary characterization of overwinter habitat use. During 2 winter periods over consecutive years, YOY white sharks occupied continental shelf waters (bottom depths: <100 m) off the coasts of North and South Carolina with mean sea-surface temperatures of 14.9–21.2°C, mean sea-surface heights of −0.5–0.2 m, and mean chlorophyll-*a* concentrations of 0.4–2.8 mg/m^3. Their overwinter habitat extended over 950 km south of the current essential fish habitat established for YOY white sharks; however, it did overlap with a seasonal closure area that restricts bottom longline fishing. These results provide preliminary evidence for the existence of an overwinter nursery area for YOY white sharks in U.S. waters of the Atlantic Ocean.

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Effective conservation and management of highly migratory marine species relies on adequate characterization of focal habitat areas that often vary across seasons (Federal Register, 2017; Kohler and Turner, 2019). The designation of essential fish habitat (EFH) for every fish stock federally managed under the Magnuson-Stevens Fishery Conservation and Management Act (Magnuson-Stevens . . . 2020) provides a platform for managers to analyze and mitigate the effects on those habitats from fisheries, coastal development, and offshore energy activities (Federal Register, 2017). However, fundamental data on distribution and habitat association are lacking for many highly migratory species. This lack of information is particularly true for the young-of-the-year (YOY) and juvenile life stages of many shark species found in U.S. waters of the Atlantic Ocean, given that most habitat use studies have focused on nursery areas used in summer, when species are abundant in nearshore or inshore areas that can be easily sampled (Heupel et al., 2007; McCandless et al., 2007). There has been considerably less research on overwinter habitats of juvenile sharks, owing to the logistical difficulties of field sampling during winter months in northern latitudes.

Research into the seasonal movements and habitat of YOY white sharks (*Carcharodon carcharias*) in the Northwest Atlantic Ocean has only recently advanced, facilitated by multiple electronic tagging and tracking studies (Curtis et al., 2018; Shaw et al., 2021). Although Casey and Pratt (1985) were the first to report the occurrence of YOY and juvenile white sharks in the New York Bight, Curtis et al. (2018)

confirmed that this region functions as a summer nursery area, using satellite and acoustic telemetry. During this season, YOY white sharks typically occupy waters off the south shore of Long Island, New York, in depths <40 m, sea-surface temperatures (SST) of 18–22°C, and chlorophyll-*a* (Chl-*a*) concentrations >2 mg/m^3 (Shaw et al., 2021). Despite this improved understanding of the summertime habitat use of YOY white sharks, information on overwinter habitat use has been limited to data for only a few individuals tracked to coastal waters of North and South Carolina from December 2016 through April 2017 (Curtis et al., 2018). Larger juvenile and adult white sharks (>2.5 m in total length [TL]) typically overwinter over a broad area encompassing the east and west coasts of Florida and occasionally offshore pelagic waters (Adams et al., 1994; Curtis et al., 2014; Skomal et al., 2017), but it is not known if YOY white sharks occupy similar areas during this season.

In U.S. waters of the Atlantic Ocean, the white shark is a prohibited species under National Marine Fisheries Service (NMFS) Atlantic Highly Migratory Species fishery regulations. The NMFS also designates EFH for YOY, juvenile, and adult white sharks to help minimize adverse effects on habitats important to each of these life stages, with the current EFH for YOY white sharks covering a broad portion of the continental shelf waters from Cape Cod, Massachusetts, to southern New Jersey (Federal Register, 2017). Although not specifically designed to protect white sharks, several fishery time-area closures in the U.S. waters of the Atlantic Ocean afford protections to coastal and pelagic shark populations (NMFS[1]). Relative abundance of white sharks in the Northwest Atlantic Ocean appears to be increasing in response to these fisheries management measures; however, the population remains data poor and biologically vulnerable, and there is uncertainty in regional population dynamics (Curtis et al., 2014; Skomal et al., 2017).

The purposes of this study were to provide the first characterization of overwinter distribution and habitat use of YOY white sharks and to assess the degree to which existing spatial fisheries management measures align with that distribution. The results of this work enhance the growing body of information on the spatial ecology of white sharks in the Northwest Atlantic Ocean off the eastern United States (Curtis et al., 2014; Skomal et al., 2017; Curtis et al., 2018; Shaw et al., 2021) and provide data necessary for making practical recommendations that may improve fisheries management.

Materials and methods

Young-of-the-year white sharks were tagged during August in 2016 and 2017 by using methods described by Curtis et al. (2018) and Shaw et al. (2021). Briefly, recreational rod-and-reel shark fishing techniques were used to catch sharks offshore of Montauk, New York. Upon capture, each shark was guided to a boatlift platform on the MV *OCEARCH* and raised out of the water for tagging and sample collection, while a raw seawater hose was placed in its mouth to irrigate its gills. A satellite-linked smart position or temperature transmitter (SPOT-258A[2], Wildlife Computers Inc., Redmond, WA; 3-year tag life) and an acoustic transmitter (Vemco V16-6H, Innovasea Systems Inc., Boston, MA; 10-year tag life) were attached to each shark. Smart position or temperature tags were attached to the first dorsal fin, permitting tag transmission to Argos satellites whenever the fin broke the sea surface. Acoustic transmitters were surgically implanted into each shark's coelomic cavity through a small incision that was sutured closed. Handling and tagging of all sharks was done in compliance with all applicable guidelines and regulations, and the research was conducted under permits from the NMFS and the New York State Department of Environmental Conservation.

The overwinter period was defined as that from December through April on the basis of previous data (Curtis et al., 2018), and only tag detections from that period were analyzed. Acoustic detections were received from moored acoustic receivers (Vemco VR2W, Innovasea Systems Inc.) maintained by cooperating members of the Mid-Atlantic Acoustic Telemetry Observation System (MATOS) along the East Coast of the United States (e.g., Bangley et al., 2020a). Positions transmitted to Argos satellites with location quality classes of 0–3, A, and B (i.e., the highest quality locations, with estimated errors less than approximately 15 km) were chronologically combined with passive acoustic detections of tags received from the MATOS network to produce positions for each shark, following Shaw et al. (2021). Erroneous points, including points on land, and points with an Argos location quality worse than B were removed from the analysis. One unique tag transmission per shark per day was selected on the basis of location quality, and daily positions were made regular by interpolating positions to fill gaps up to 7 d between consecutive tag detections with the ArcMET extension for ArcGIS 10.3 (Esri, Redlands, CA) (Curtis et al., 2018; Shaw et al., 2021). No positions were interpolated for tag detection gaps greater than 7 d in duration.

Four environmental variables were used to characterize habitat use: SST, Chl-*a* concentration, sea-surface height (SSH), and bathymetry. Underlying depths were derived from the NOAA ETOPO1 Global Relief Model, a data set of land topography and ocean bathymetry with a 1-arcmin resolution (NOAA National Geophysical Data Center, available from website), and each depth was matched to a raw coordinate position in ArcGIS. Group for High Resolution SST Level 4 data from the Jet Propulsion Laboratory were compiled at a spatial resolution of 0.01° (available from website). Weekly Chl-*a* concentrations were compiled

[1] NMFS (National Marine Fisheries Service). 2019. Issues and options for research and data collection in closed and gear restricted areas in support of spatial fisheries management, 27 p. Natl. Mar. Fish. Serv., Silver Spring, MD. [Available from website.]

[2] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

from data from the NOAA Visible Infrared Imaging Radiometer Suite at a spatial resolution of 4.17 km (available from website). Daily SSH data were collected from the Naval Oceanographic Office Hybrid Coordinate Ocean Model and Navy Coupled Ocean Data Assimilation at a spatial resolution of 1/12° (available from website). Values for oceanographic characteristics were matched to daily shark positions by using the xtractomatic function in R, vers. 3.6.0 (R Core Team, 2019).

All location and environmental data were visualized by using ArcMap 10.7 (Esri). The overwinter cumulative activity space (i.e., home range) for the tracked sharks was characterized by using a minimum convex polygon. By using ArcMap, the resulting minimum convex polygon was compared to spatial management areas for highly migratory species, including to the boundaries of the current EFH for YOY white sharks (Federal Register, 2017) and to the Mid-Atlantic Shark Closure Area—an area off North Carolina that is closed to shark bottom longline fishing from 1 January through 31 July each year to reduce fishing mortality on overfished dusky (*Carcharhinus obscurus*) and sandbar (*C. plumbeus*) sharks (NMFS[1]).

Results

Twenty YOY white sharks were tagged near Montauk, New York, in August 2016 (number of samples [*n*]=9) and August 2017 (*n*=11). For 9 of those sharks, 1111 tag detections were recorded in their first overwinter period (2016: *n*=4; 2017: *n*=5) (Table 1). Analysis of habitat use was based on a total of 184 daily positions, including 19 detections from 16 acoustic receivers at unique locations in the MATOS network, 76 positions transmitted to Argos satellites, and 89 positions interpolated between tag detections. During both years, sharks occupied a similar distribution, mostly in continental shelf waters off the coasts of North and South Carolina (32–37°N) (Fig. 1A). The sharks traveled along the coastline mostly over depths <100 m, although a few excursions were made beyond the continental shelf break over bottom depths >2000 m. The mean depth associated with tag positions was 74 m (standard deviation [SD] 329) when these extreme depths are included. However, 92% of all positions occurred over depths <80 m.

The YOY white sharks were exposed to similar ranges of oceanographic conditions in their overwinter habitat. The SSTs ranged from 12.9°C to 23.4°C with a mean of 18.4°C (SD 2.5). The majority of observations (60%) fell within a range of 16.0–21.0°C. Despite their proximity to the Gulf Stream, the tagged sharks generally were not located in its warmer waters (Fig. 1A). The YOY sharks occurred in waters with a mean SSH of −0.5 m (SD 0.2) and rarely occurred in areas with positive SSH (e.g., the Gulf Stream) or in areas with SSH less than −0.9 m. Additionally, the sharks used somewhat productive areas with

Table 1

Descriptions of 9 young-of-the-year white sharks (*Carcharodon carcharias*) tracked in the Northwest Atlantic Ocean during winter months (December–April) between 2016 and 2018, as well as of their tracking and detected positions and of characteristics of the habitat they used. Mean and range of sea-surface temperature (SST), depth (bathymetry), chlorophyll-*a* (Chl-*a*) concentration, and sea-surface height (SSH) are provided with standard deviations in parentheses. Shark IDs correspond to the individual sharks described in Shaw et al. (2021).

Shark ID	Total length (cm)	Sex	Tracking period	No. daily positions	SST (°C)	Depth (m)	Chl-*a* (mg/m^3)	SSH (m)
WS1	142	F	8-Dec-2016 to 29-Jan-2017	13	15.3 (0.9) 14–16.5	90 (89) 14–339	0.7 (0.6) 0.3–2.3	−0.6 (0.1) −0.7–0.5
WS2	158	M	17-Jan-2017	1	20.4 –	27 –	1.0 –	−0.6 –
WS7	162	F	10-Mar-2017	1	17.9 –	39 –	1.2 –	−0.7 –
WS8	162	M	4-Dec-2016 to 20-Apr-2017	17	18.6 (2.0) 13.5–21.7	30 (5.5) 18–41	1.3 (0.7) 0.6–3.2	−0.6 (0.1) −0.9–0.4
WS9	150	M	22-Dec-2017 to 5-Mar-2018	43	19.5 (2) 14.6–22.8	45 (57) 7–342	0.7 (0.6) 0.3–3.2	−0.5 (0.1) −0.9–0.2
WS11	166	M	5-Dec-2017 to 8-Mar-2018	70	18.6 (2.3) 12.9–23.4	124 (527) 1–3283	0.8 (0.9) 0.2–6.1	−0.5 (0.2) −0.8–0.1
WS13	147	M	2-Dec-2017 to 2-Apr-2018	16	14.9 (1.3) 13.5–17.1	13 (4) 6–20	1.8 (0.6) 0.8–2.7	−0.4 (0.2) −1.0–0.1
WS16	154	F	5-Dec-2017 to 1-Apr-2018	8	16.4 (1.0) 15.5–17.8	9 (5) 5–14	2.8 (1.3) 1.4–4.0	−0.4 (0.2) −0.7–0.1
WS17	152	F	2-Feb-2018 to 16-Feb-2018	15	21.2 (0.6) 19.4–22.0	57 (30) 27–134	0.4 (0.1) 0.3–0.7	−0.6 (0.1) −0.7–0.5

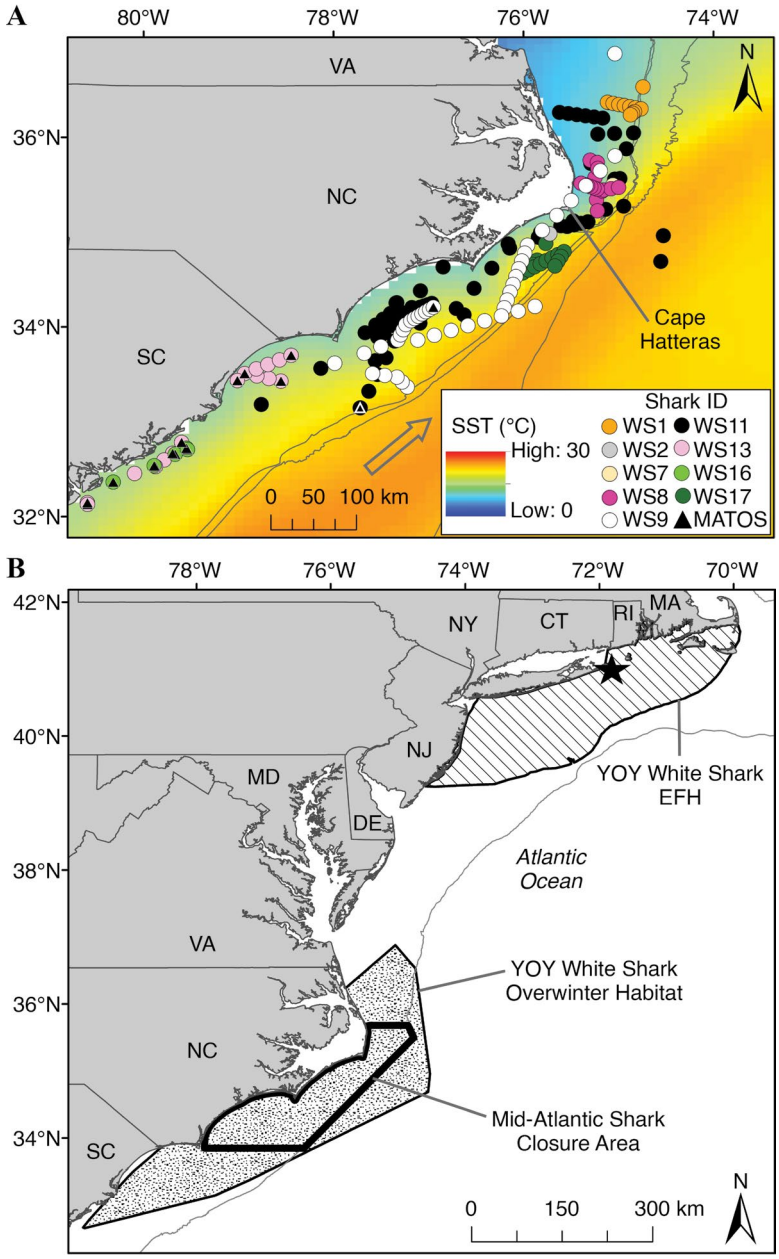

Figure 1

Maps showing (**A**) daily positions (colored circles) and (**B**) the minimum convex polygon that delineates the area of cumulative activity space (i.e., home range; stippled area) based on detections of tags attached to or implanted in 9 young-of-the-year (YOY) white sharks (*Carcharodon carcharias*) tracked off the East Coast of the United States from December through April during 2016–2018. In panel A, positions are shown over average winter sea-surface temperatures (SST) and the 100-m, 200-m, and 2000-m isobaths (gray lines). Triangles indicate the locations of acoustic receivers in the Mid-Atlantic Acoustic Telemetry Observation System (MATOS), and the open arrow denotes the location and direction of the Gulf Stream. Shark IDs correspond to individual sharks described in Shaw et al. (2021). In panel B, the area of cumulative activity space of tracked sharks is compared to the 200-m isobath (gray line), to the current essential fish habitat (EFH) area designated by the National Marine Fisheries Service for YOY white sharks (hatched area), and to the Mid-Atlantic Shark Closure Area (polygon outlined with a thick black line). The black star in the EFH denotes the location where sharks were tagged in August 2016 and 2017.

Chl-*a* concentrations of 0.2–6.1 mg/m^3 (mean: 1.0 mg/m^3 [SD 0.9]).

Overwinter distribution relative to key fisheries management boundaries varied. Positions of YOY white sharks did not overlap at all with the current EFH designated for this life stage, and they actually extended up to 960 km beyond the current EFH boundary (Fig. 1B). In contrast, the overwinter distribution of YOY white sharks significantly overlapped with the Mid-Atlantic Shark Closure Area. Over half (54%) of the daily positions indicate that tagged sharks were within the boundaries of the closure area during the time the closure was in effect (from 1 January through July 31).

Discussion

The results of this study improve the understanding of overwinter distribution and habitat use of YOY white sharks in the Northwest Atlantic Ocean, and this advancement is important because YOY is a life stage that has been historically little studied in this region (Curtis et al., 2018; Shaw et al., 2021). Preliminarily, results from analysis of tracking data for 9 individuals from 2 cohorts indicate that YOY white sharks make seasonal migrations to the coastal waters of North and South Carolina during their first winter period (from December through April). The combination of both satellite and acoustic tag technologies provided more insight into overwinter habitat use than either technology would have on its own, as has been recently reported for habitat use of YOY white sharks in their summer nursery area in the New York Bight (Curtis et al., 2018; Shaw et al., 2021).

The data presented herein support the hypothesis that the area occupied by these tracked YOY white sharks represents an overwinter nursery area. The area meets the shark nursery area criteria proposed by Heupel et al. (2007): our data indicate that YOY white sharks occur more frequently in this area than in other areas during winter (criterion 1), they remain in the area for an extended period (criterion 2), and they use the same area repeatedly across years (criterion 3). However, this information is based on only the movements of 9 individuals across 2 years, and 2

individuals were detected only on a single day. Unlike that for the summer nursery area used by white sharks in the New York Bight, the historical data that support any of the nursery area criteria for the habitat used in winter is minimal (Casey and Pratt, 1985; Castro, 2011; Curtis et al., 2014, 2018). Additional research is needed to more fully address whether coastal waters of North and South Carolina include overwinter nursery habitat for YOY white sharks, although the region appears to contain similar habitats and environmental conditions selected by YOY and juvenile white sharks in other regions (Weng et al., 2007; Bruce et al., 2019; White et al., 2019; Shaw et al., 2021).

There was some overlap, but YOY white sharks occurred in geographic areas different from those where larger juveniles (>2.5 m TL) and adults occurred during winter months (Curtis et al., 2014; Skomal et al., 2017; Curtis et al., 2018). Specifically, larger white sharks typically move through North and South Carolina as they migrate south during fall and winter, and they generally overwinter off the Atlantic and Gulf coasts of Florida (Casey and Pratt, 1985; Adams et al., 1994; Castro, 2011; Curtis et al., 2014; Skomal et al., 2017). Despite acoustic receiver coverage south of the area occupied by the tagged individuals (Bangley et al., 2020a), YOY white sharks did not appear to migrate as far south as most larger white sharks (Skomal et al., 2017), thereby maintaining a level of size-based spatial segregation in the population. Although this segregation may be the result of smaller body sizes and the related physiological constraints to migration for YOY white sharks, it could also reflect local resource availability or an evolutionary adaptation that reduces predation risk. Larger white sharks, dusky sharks, tiger sharks (*Galeocerdo cuvier*), and bull sharks (*Carcharhinus leucas*) are the most likely predators of YOY white sharks in this region. Numerous shark species seasonally co-occur with YOY white sharks, but such large predators appear to be uncommon in waters of North and South Carolina during the winter (Lea et al., 2015; Skomal et al., 2017; Calich et al., 2018; Kohler and Turner, 2019; Bangley et al., 2020b; Logan et al., 2020). The reduced predation pressure from the segregation of life stages of white sharks provides further support for the notion that this region may serve as a nursery through enhanced survival of young white sharks (Heupel et al., 2007).

Fisheries and environmental resource managers can use the increased understanding of seasonal distribution from this study to improve conservation of YOY white sharks and to evaluate the effects of human activities on their overwinter habitat. Although the current EFH for YOY white sharks does not encompass the overwinter habitat areas identified in this study, it was established by using observations compiled prior to any significant electronic tagging and tracking research on this life stage of this species (Federal Register, 2017). Our results may inform future reviews and updates to EFH by the NMFS and may allow improved mitigation of anthropogenic effects on these important habitats by state and federal agencies. Already, YOY white sharks appear to benefit incidentally from the current Mid-Atlantic Shark Closure Area, which minimizes bottom longline fishery bycatch during the period YOY white sharks occur in that area. Telemetry has revealed that other regional shark species also benefit from this time-area closure, providing empirical evidence that could be used to improve the timing and location of such areas (Calich et al., 2018; Bangley et al., 2020b; Logan et al., 2020). In this case, hypothetically shifting the closure period to start and end one month earlier (i.e., to occur from 1 December through 30 June) would increase overlap of the closure with YOY white sharks by an additional 6%. Additional research will help further refine spatial management and estimate bycatch susceptibility of white sharks across seasonal habitats.

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