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Abstract—Improved understanding of the seasonal distribution, habitat use, and fishery interactions of the common thresher shark (*Alopias vulpinus*) in the western North Atlantic Ocean (WNA) is required for future management. We compiled and analyzed 3478 fishery-dependent capture records in the WNA between 1964 and 2019 to examine dynamics by sex and life stage (i.e., young of the year, juvenile, and adult). Sharks were captured over a broad geographic range from the Gulf of Mexico to the Grand Banks, primarily in continental shelf waters shallower than 200 m. Seasonal north–south movements along the east coasts of the United States and Canada were observed for all life stages and both sexes, with individuals generally occurring at more northerly latitudes in the summer and more southerly latitudes in the winter. Distinct areas of more frequent capture in fisheries were identified for all life stages throughout their range. Common thresher sharks were observed in waters with sea-surface temperatures of 4–31°C, most commonly of 12–18°C. The results of this study will help to identify essential fish habitat for each life stage of common thresher sharks along the U.S east coast and to develop management measures for the WNA population.

Seasonal distribution and habitat use of the common thresher shark (*Alopias vulpinus*) in the western North Atlantic Ocean inferred from fishery-dependent data

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The common thresher shark (*Alopias vulpinus*) is one of 2 species in the family Alopiidae that occurs in temperate and subtropical regions of the North Atlantic Ocean (Compagno, 2001). In the western North Atlantic Ocean (WNA), common thresher sharks are thought to represent a discrete population (Castro, 2011; Rigby et al., 2019) and occur from Cuba to Newfoundland, Canada (Compagno, 2001). There is currently no large-scale, directed commercial fishery for this species in the WNA, but common thresher sharks are often caught incidentally in pelagic longline and demersal gill-net fisheries and occasionally are retained for sale in the United States (NMFS, 2019a). The common thresher shark is also the target of an extensive recreational shark fishery from Virginia to Maine with the majority of sharks landed (NMFS, 2019a) because their flesh is considered excellent (Compagno, 2001).

There is limited and conflicting information on the status of the population of common thresher sharks in the WNA. Results of studies examining pelagic longline logbook data collected since the late 1980s for *thresher sharks* (i.e., the common thresher shark and the bigeye thresher, *A. superciliosus*, combined) indicate that their relative abundance has declined by 63–80%

over the time series (Baum et al., 2003; Cortés et al., 2007). In contrast, pelagic longline fisheries observer data indicate that relative abundance had either stabilized at low levels (Baum and Blanchard, 2010) or increased (Cortés et al., 2007) during the 1990s into the early 2000s. Results of recent analyses of pelagic longline logbook and observer data for common thresher sharks from the period 1992–2013 also indicate a stabilized trend in relative abundance at low levels (Young et al., 2016) to an overall increasing trend when temperature profiles are incorporated into the analyses (Lynch et al., 2018). Relative abundance indices derived from data from 5 long-term recreational sportfishing tournaments based out of New York and New Jersey also indicate an overall increasing trend but with high annual variability (Young et al., 2016).

Although recent analyses provide an optimistic outlook, the true extent to which these trends are representative of the population of common thresher sharks in the WNA remains unknown. For example, although observer data are often considered more reliable than fishery logbook data, especially for bycatch species, the sample size for observer data is much smaller and interactions of individuals with the pelagic longline fishery are likely limited by the coastal and temperate distribution of this species (Young et al., 2016). Nonetheless, this species is currently listed as vulnerable by the International Union for Conservation of Nature (IUCN) in the IUCN Red List of Threatened Species, with a decreasing population trend assumed throughout its global range (Rigby et al., 2019). There are also no formal stock assessments, international management measures, or species-specific quotas for common thresher sharks in the WNA, and there are only limited biological and ecological data for the development of domestic and international management policies.

Detailed information on seasonal distribution, habitat use, migration patterns, and population structure of common thresher sharks in the WNA is limited. Although records from fishery-dependent catch data support a north–south movement pattern along the U.S. east coast (e.g., Castro, 2011; Natanson and Gervelis, 2013), published movement data are limited to fishery-dependent data from the recapture of 2 individuals from the 230 common thresher sharks tagged by the National Marine Fisheries Service (NMFS) Cooperative Shark Tagging Program from 1962 through 2018 (tag return rate: ~0.9%). Both recaptured sharks had a north–south movement pattern along the northeastern coast of the United States (Kohler and Turner, 2019). However, the records of these recaptures provide minimal insight into the spatial and temporal extent of the annual movements of this species, given the extended times at liberty (1533 and 2934 d) and the fact that both recapture events occurred in June. Migratory routes are also poorly known (Castro, 2011), and only general descriptions of distribution and habitat use by sex or life stage have been presented from historical catch data.

Given the uncertainty over the status of the population of common thresher sharks in the WNA, there is a need to improve our understanding of this species' life history and general susceptibility to capture in commercial and recreational fisheries. Improved knowledge is needed considering that their life history parameters (i.e., relatively slow growth, late age to maturity, and low fecundity; Gervelis and Natanson, 2013; Natanson and Gervelis, 2013) increase their susceptibility to population decline (Smith et al., 1998) and that ecological data on their temperature and habitat preferences are few. Accordingly, we compiled and summarized fishery-dependent data on catch of common thresher sharks throughout the WNA 1) to document their seasonal distribution and habitat use by sex and life stage, 2) to better understand fishery interactions, and 3) to provide information that facilitates the identification of essential fish habitat (EFH) by life stage in U.S. waters.

Materials and methods

At-sea observer and other catch data on common thresher sharks originated mainly from the NMFS, specifically from the Northeast Fisheries Observer Program, Pelagic Longline Observer Program of the Southeast Fisheries Science Center, Shark Bottom Longline Observer Program, Cooperative Shark Tagging Program of the Apex Predators Program, Cooperative Tagging Center of the Southeast Fisheries Science Center, and Large Pelagics Survey. Additional records were obtained from the Industry Surveys Database of Fisheries and Oceans Canada (H. Bowlby, personal commun.), which is used to archive at-sea observer information from commercial fisheries. Data from each source were subjected to editing and quality control a priori by the provider and represent all records of common thresher sharks available in their respective databases through 2019. Data requested from each source include the date of capture, location of capture (i.e., latitude and longitude), shark sex, shark length (i.e., fork length [FL] and total length [TL]) and nature (i.e., measured or estimated) of the length, shark weight (i.e., whole [or round] and dressed) and nature (i.e., measured or estimated) of the weight, gear type used for capture, and the observed sea-surface temperature (SST, in degrees Celsius) at the time and location of capture.

Prior to analysis, records with no geographical information were removed, and a series of steps were taken to standardize and validate length and weight data among the various sources. All capture records for which a measured FL was provided were considered reliable and retained. Records with a measured or estimated TL or whole weight were converted to an estimated FL by using the appropriate conversion equation (TL to FL: coefficient of multiple determination [R^2]=0.83; whole weight [in kilograms] to FL: R^2=0.93; NMFS[1]). Reported weights were also used to

[1] NMFS (National Marine Fisheries Service). 2020. Unpubl. data. Apex Predators Program, Northeast Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, 28 Tarzwell Dr., Narragansett, RI 02882.

reconcile any lengths that appeared to have been inaccurately labeled (e.g., labeled as TL when the weight was more consistent with a fish near the same FL). Length data for any record that had a measured or estimated FL below the published size of near-term embryos (50 cm FL; Gervelis and Natanson, 2013) or markedly above the estimated maximum length (350 cm FL; Cailliet et al., 1983) were considered unreliable and excluded from ontogenetic analyses. Lastly, all common thresher sharks with a measured or estimated FL were assigned to 1 of 3 life stages, on the basis of published estimates of length at age (Gervelis and Natanson, 2013) and length at 50% maturity (Natanson and Gervelis, 2013) for individuals from the WNA: young of the year (YOY), if ≤100 cm FL; juvenile, for males 101–187 cm FL and for females 101–215 cm FL; and adult, for males ≥188 cm FL and for females and sharks of unknown sex ≥216 cm FL.

Distribution analysis

Spatial and temporal patterns in presence and fishery interactions of common thresher sharks by sex, life stage, and season were qualitatively analyzed following the general approach of Curtis et al. (2014). All analyses were performed in R (vers. 4.0.3; R Core Team, 2020). Maps and figures were created by using the tidyverse collection of packages (vers. 1.3.0; Wickham et al., 2019) and the sf package (vers. 0.9.6; Pebesma, 2018) in R. Seasons were classified as winter (January–March), spring (April–June), summer (July–September), or fall (October–December).

Because of the limitations of using presence-only data when detectability is unknown, location data over the full time series (1964–2019) were plotted by season, both in aggregate and by sex and life stage, to assess distribution patterns. To meet confidentiality requirements for commercially derived data, latitudes and longitudes (under the World Geodetic System 1984) were aggregated in a raster grid (0.5° × 0.5°) spanning the WNA, including the Gulf of Mexico. Grid cell counts (number of captures) were natural log transformed for plotting to increase contrast among small values.

Habitat use

Fishery-dependent records with a recorded SST were aggregated by month and summarized by using box plots to examine monthly and seasonal trends. To visually examine distribution of common thresher sharks in relation to typical seasonal SST conditions in the WNA, grid cells were plotted over NMFS Southwest Fisheries Science Center monthly composite climatologies (data set ID: erdAGsstamday_LonPM180; available from the ERDDAP server at website) averaged over the most recent years for which data were available (2009–2016); 62% of all capture events occurred over this period. The SST data were downloaded by using the rerddap package (vers. 0.6.5; Chamberlain, 2019) in R. To explore any association with bathymetry, the local depth was assigned to each record by using data from the NOAA ETOPO1 1 Arc-Minute Ocean Relief Model (NOAA National Geophysical Data Center, model available from website, accessed June 2019; Amante and Eakins, 2009) in the R package marmap (vers. 1.0.5; Pante and Simon-Bouhet, 2013). Histograms were used to examine SST and depth occupancy by life stage.

Results

A total of 3478 fishery-dependent records of the capture of common thresher sharks were compiled between 1964 and 2019, representing 1035 males, 1039 females, and 1404 sharks of unknown sex (Tables 1 and 2). The number of

Table 1

Source, number, and time period for fishery-dependent capture records compiled to examine spatial distribution and habitat use of common thresher sharks (*Alopias vulpinus*) in the western North Atlantic Ocean between 1964 and 2019. DFO=Department of Fisheries and Oceans; NMFS=National Marine Fisheries Service; SEFSC=Southeast Fisheries Science Center.

Data source	Number of records	Time period
DFO Canada: Industry Surveys Database	299	1982–2019
NMFS Cooperative Shark Tagging Program	235	1964–2019
NMFS Large Pelagics Survey	198	2002–2018
NMFS Shark Bottom Longline Observer Program	39	1996–2019
NOAA Northeast Fisheries Observer Program	2165	1990–2019
NOAA Southeast Pelagic Observer Program	526	1992–2017
NOAA SEFSC Cooperative Tagging Program	16	1978–1996
Total	3478	1964–2019

Table 2

Summary of fishery-dependent data by life stage and sex as well as the range of associated sea-surface temperatures (SST) and depths from capture records for common thresher sharks (*Alopias vulpinus*) in the western North Atlantic Ocean between 1964 and 2019. Ranges and means, with standard deviations in parentheses, are presented for SST and depth. YOY=young of the year; unknown=unknown life stage or sex.

	Number of records				SST (°C)		Depth (m)	
Life stage	Total	Male	Female	Unknown	Range	Mean	Range	Mean
YOY	1136	425	432	279	6–26	16 (3)	1–2077	21 (86)
Juvenile	1083	338	376	369	6–31	17 (4)	1–4535	262 (556)
Adult	423	182	83	158	5–30	18 (4)	1–5401	414 (902)
Unknown	836	90	148	598	4–30	18 (4)	1–5427	1197 (1581)
Overall	3478	1035	1039	1404	4–31	17 (4)	1–5427	434 (1039)

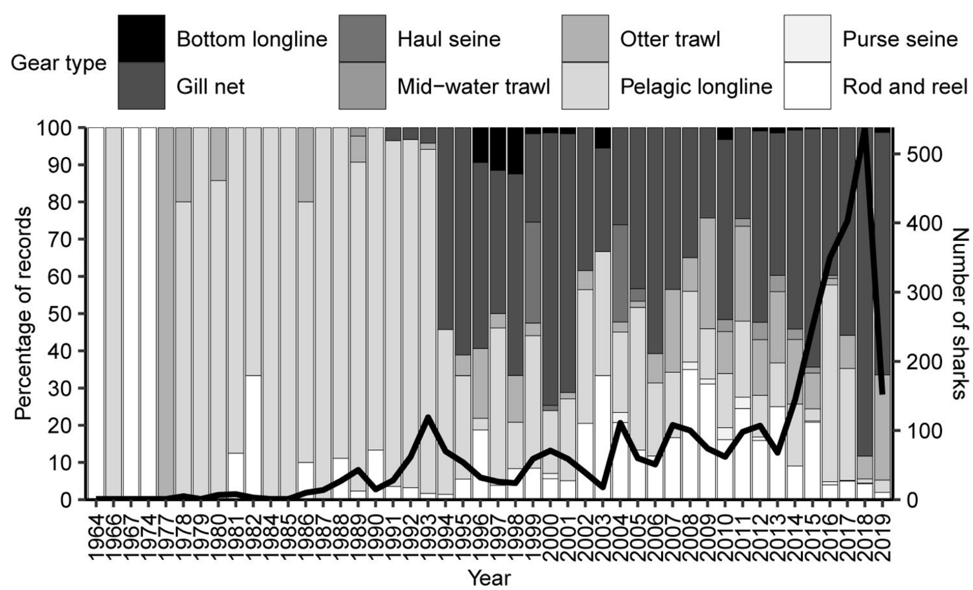

Figure 1

Percentage of the total number of capture records from fishery-dependent data, by gear type, and the total number of records, by year, for common thresher sharks (*Alopias vulpinus*) in the western North Atlantic Ocean from 1964 through 2019. The shade or pattern of each bar indicates gear type, and the solid line indicates number of records.

records obtained per year ranged from 1 to 538 (mean: 76 [standard deviation (SD) 109]) with 48.7% of all records occurring between 2015 and 2019 (Fig. 1). Lengths were available for 3072 (88.3%) individuals, including 1720 (49.4%) sharks that were measured and 1352 (38.9%) sharks whose lengths were estimated either at the time of capture or by a length conversion. Measured FLs ranged from 59 to 320 cm (mean: 125 cm [SD 48]), and estimated FLs ranged from 60 to 330 cm (mean: 160 cm [SD 56]) (Fig. 2). Five length records were eliminated because of biologically implausible length estimates or measurements. Life stage was assigned to 2642 (76.0%) sharks of which 1136 (32.7%) were YOY, 1083 (31.1%) were juvenile, and 423 (16.0%) were adult (Table 2, Fig. 2). Sex was noted for only 21 of the sharks captured in Canada; therefore, any comparisons among sexes and juvenile and adult life

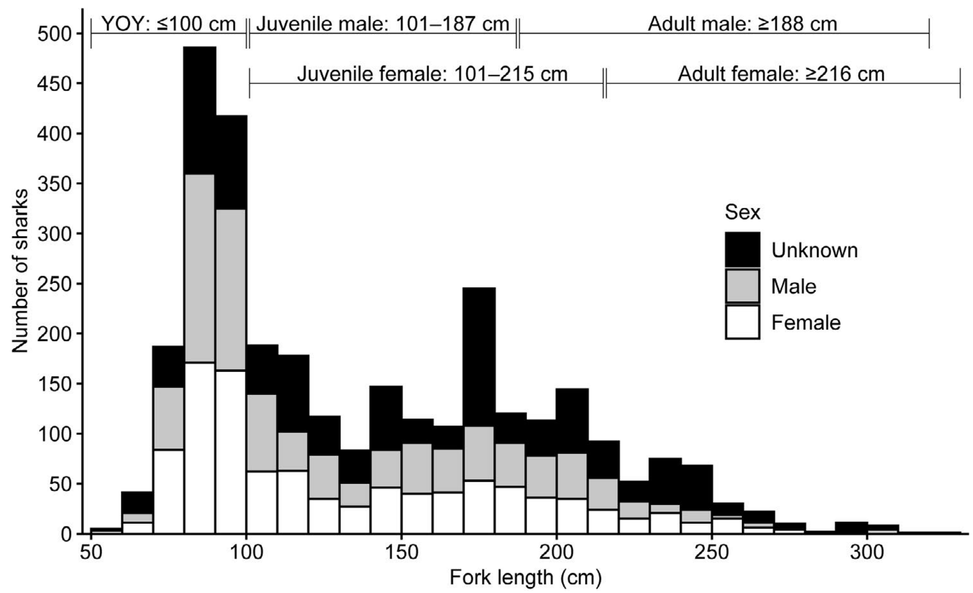

Figure 2

Length-frequency histogram for 3072 common thresher sharks (*Alopias vulpinus*), representing males, females, and those with unknown sex for which a measured or estimated length was available, captured from 1964 through 2019 in the western North Atlantic Ocean. The classification of life stages, based on sizes at 50% maturity from Natanson and Gervelis (2013), is provided at the top of the figure for males and females. YOY=young of the year.

stages almost exclusively represent sharks captured in U.S. waters.

Gear interactions

Common thresher sharks were captured with a wide range of gear types, including commercial bottom longline, pelagic longline, gill net (sink and floating), haul (beach) seine, purse seine, (bottom) otter trawl, mid-water trawl, and recreational rod and reel (Fig. 1). Of these gears, gill nets (50.0%; primarily sink gill nets) and pelagic longlines (27.1%) accounted for the majority of capture records, followed by rod and reel (10.4%) and otter trawl (9.2%). All other gears accounted for no more than 1.4% of the total number of records. The most common life stage of sharks captured by gill nets was YOY (88.4%), but YOY sharks were also caught by otter trawls, haul seines, and rod and reel (Fig. 3). Juveniles were captured by all gear types but were most commonly taken in gill nets (43.1%) and pelagic longlines (33.3%). Adults were captured by every gear type except haul seine, but they most commonly were taken by pelagic longline (39.2%) and rod and reel (26.7%).

Seasonal distribution

Common thresher sharks were captured over a broad geographic range extending from 23.9°N to 46.3°N and from 42.8°W to 95.1°W (Fig. 4). The majority of records (number of sharks [n]=2751; 79.1%) were from continental shelf waters shallower than 200 m; however, numerous individuals (n=727; 20.9%) were encountered in deeper (>200 m) offshore waters of the WNA. Records were available from all months and seasons with the greatest number of them from the winter (Table 2). The increase in capture records during winter was partially due to a large number of YOY and juveniles being taken in 2018 by gill-net fisheries off North Carolina.

Throughout the year, north–south changes in distribution along the east coasts of the United States and Canada were noted for common thresher sharks over all life stages. In general, individuals occurred at more northerly latitudes in the summer and more southerly latitudes in the winter (Fig. 4). During the winter, sharks were primarily encountered off the coast of North Carolina, both in the vicinity of Cape Hatteras and in waters near the edge of the continental shelf. A considerable number of specimens were also caught in continental shelf waters off the east coast of Florida during the winter. Sharks were distributed over the broadest area during the spring, with the center of distribution from North Carolina to Long Island, New York. During the summer, sharks were captured most commonly in continental shelf waters off the mid-Atlantic states, southern New England, and the Gulf of Maine, and sharks were rarely encountered south of Maryland. In the

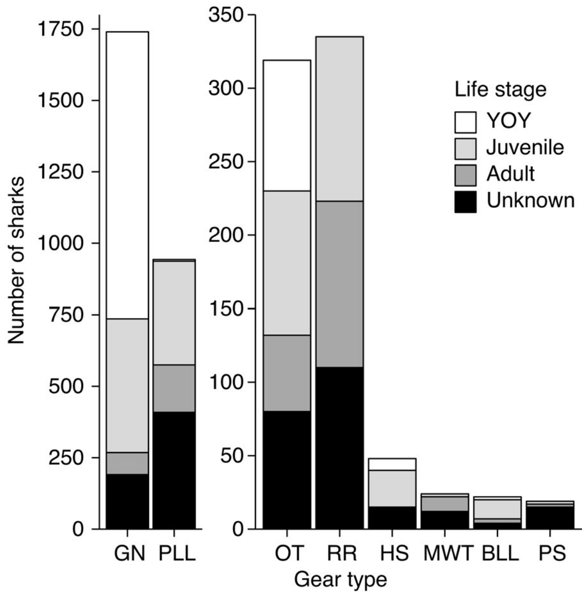

Figure 3

Number of common thresher sharks (*Alopias vulpinus*) caught in the western North Atlantic Ocean, based on compiled fishery-dependent data from 1964 through 2019. Sharks were captured with the following gear types: gill net (GN), pelagic longline (PLL), otter trawl (OT), rod and reel (RR), haul (beach) seine (HS), mid-water trawl (MWT), bottom longline (BLL), and purse seine (PS). Note the difference in scale between the y-axes. YOY=young of the year.

fall, 2 centers of distribution were evident: one from North Carolina to New Jersey and another off the Scotian Shelf in Canada.

Young of the year Common thresher sharks classified as YOY were distributed almost exclusively (99.1%) in continental shelf waters north of 33.5°N (Fig. 5). Only 6 individuals were captured south of 33.5°N, including a single record from the Gulf of Mexico (27.8°N, 88.6°W), which may have been a misidentification. Sharks of this life stage migrated along the coast in a north–south pattern, with overwintering grounds off Cape Hatteras. During the summer, sharks were most commonly taken off New Jersey and Long Island, New York, but their distribution ranged as far north as Cape Cod, Massachusetts. During the spring and fall, their distribution spanned between these summer and overwintering grounds.

Juveniles and adults Because of the inability to assign a life stage to all recorded common thresher sharks and the limited data from adults (Table 2), composite distribution maps were made for the juvenile and adult life stages (Fig. 6). The lack of sex data for sharks captured in Canada also precluded a thorough assessment of juvenile and adult distribution in waters of Canada, particularly along the Scotian Shelf. The winter distribution of these life stages occurred off the coast of North Carolina and the center of summer distribution extended from the mid-Atlantic states north to the Gulf of Maine. The distribution patterns of both juvenile and adult sharks are consistent with a seasonal, north–south distribution pattern along the east coasts of the United States and Canada, with extensive movements between the winter and summer habitat areas.

Males and females In general, the overall and seasonal distributions of male and female common thresher sharks were similar and followed the patterns previously described for this species and for each life stage (Fig. 7).

Habitat use

Sea-surface temperature at the time and location of capture was recorded for 2764 common thresher sharks and ranged from 4°C to 31°C (mean: 17°C [SD 4]) (Table 2); 78.2% of all records were for sharks captured in waters with temperatures of 10–22°C (Fig. 8). Young-of-the-year sharks were associated with the narrowest temperature range (6–26°C); however, each life stage and both sexes were generally associated with a similar range of SSTs (males: 5–30°C [mean: 17°C (SD 4)]; females: 6–30°C [mean: 17°C (SD 4)]). Monthly and seasonal fluctuations in SST at capture were evident for all life stages (Fig. 9). Sharks were taken in areas with depths ranging from 1 to 5427 m (mean: 433 m [SD 1032]), with 43.7% of all records from waters 10–25 m deep (Table 2, Fig. 8). In particular, 98.4% of YOY were caught in depths from 1 to 50 m, and 61.7% of juveniles were caught in depths from 10 to 100 m. Males and females were taken in areas with depths from 1 to 5427 m (mean: 165 m [SD 533]) and from 1 to 5401 m (mean: 146 m [SD 497]), respectively.

Discussion

The results of our analysis of over 50 years of fishery-dependent data advance the scientific understanding of the distribution and habitat use of common thresher sharks in the WNA and will improve our ability to assess and sustainably manage the population of this species nationally and internationally. Although trends of relative abundance for common thresher sharks in the WNA appear to have stabilized or slightly increased in recent years, current levels are still well below historic values of abundance (Young et al., 2016; Lynch et al., 2018) and fishery interactions are increasing across some gear types (Fig. 1) (Gervelis and Natanson, 2013; NMFS, 2019a). New insights into habitat use by sex and life stage will also promote the identification of EFH in U.S. waters. Accurate EFH designations allow potential effects on species in areas of proposed development or other activities to be considered before approval and provide a basis for

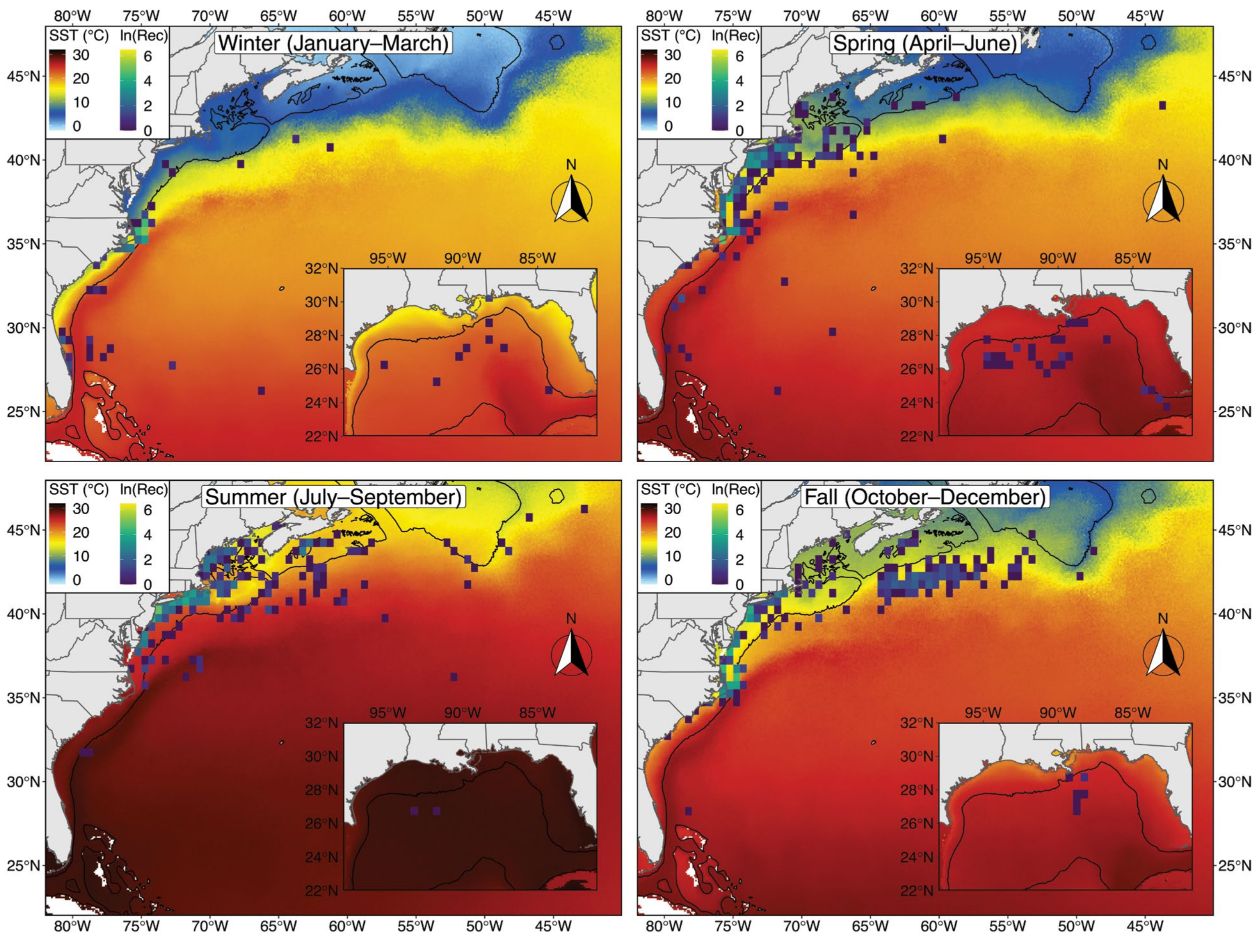

Figure 4

Distribution of common thresher sharks (*Alopias vulpinus*) in the western North Atlantic Ocean by season during 1964–2019 and in relation to average sea-surface temperature (SST) climatologies for the period 2009–2016. The number of capture records (Rec) in each grid cell (0.5° × 0.5°) is natural log transformed. Records from the Gulf of Mexico are presented in the inset. The 200-m depth contour delineates the boundary of the continental shelf.

evaluating time or area closures to assist in the recovery of overfished populations.

Analyses of presence-only data are a useful and cost-effective way to understand the distribution and habitat use of wide-ranging species for which limited species-specific survey data exist (Elith and Leathwick, 2009; Curtis et al., 2014). Their main limitation is the potential for bias due to spatial and temporal variability in fishing effort or in catchability by both gear type and life stage (Pearce and Boyce, 2006; Curtis et al., 2014). For example, common thresher sharks are the target of a relatively large, seasonal recreational shark fishery that operates from Virginia to Maine (Gervelis and Natanson, 2013), and >99% of the observed rod-and-reel capture events occurred over this geographic area. However, commercial fisheries data would be expected to be less biased, given that common thresher sharks are caught almost exclusively as bycatch in the WNA (Castro, 2011; Young et al., 2016) and that effort in trawl, gill-net, and pelagic longline fisheries is relatively consistent, widespread, and year-round along the U.S. east coast (Beerkircher et al., 2004; Guiet et al., 2019). Because 94.9% of records originated from a variety of commercial fisheries that operate throughout the range of this species, the overall and seasonal trends we report herein may largely reflect animal distribution. Nonetheless, spatial and temporal concentration in fishing effort may have influenced the number of captured sharks by season; for example, the large number of YOY observed off North Carolina during the winter and spring.

Seasonal distribution and habitat use

Our results are consistent with those of previous reports that indicate that the common thresher shark is primarily

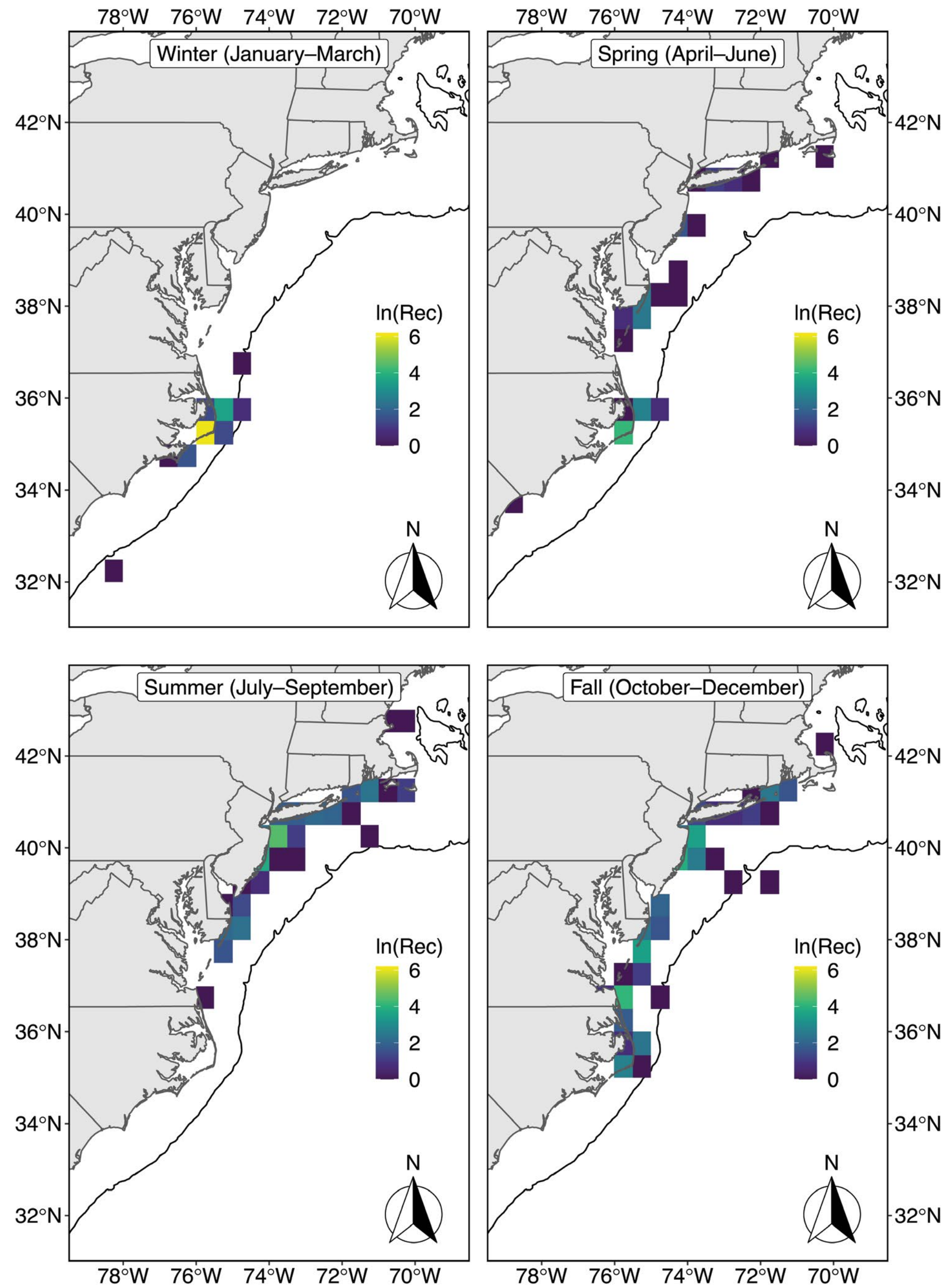

Figure 5

Distribution of young-of-the-year common thresher sharks (*Alopias vulpinus*) by season in the western North Atlantic Ocean between 1964 and 2019. The number of capture records (Rec) in each grid cell (0.5° × 0.5°) is natural log transformed. One record of a capture in the Gulf of Mexico is not presented because it may have been a misidentification. The 200-m depth contour delineates the boundary of the continental shelf.

distributed at depths <200 m in the continental shelf waters in the WNA but that its range seasonally extends farther offshore, closer to the northern edge of the Gulf Stream along the Scotian Shelf and Grand Banks (Fig. 4) (Castro, 2011). Although higher rates of observer coverage in coastal fisheries (NMFS, 2019b) would contribute to more frequent capture of common thresher sharks in continental shelf waters, their limited occurrence in the extensive and fairly well-monitored pelagic longline fisheries in offshore waters of the United States and Canada

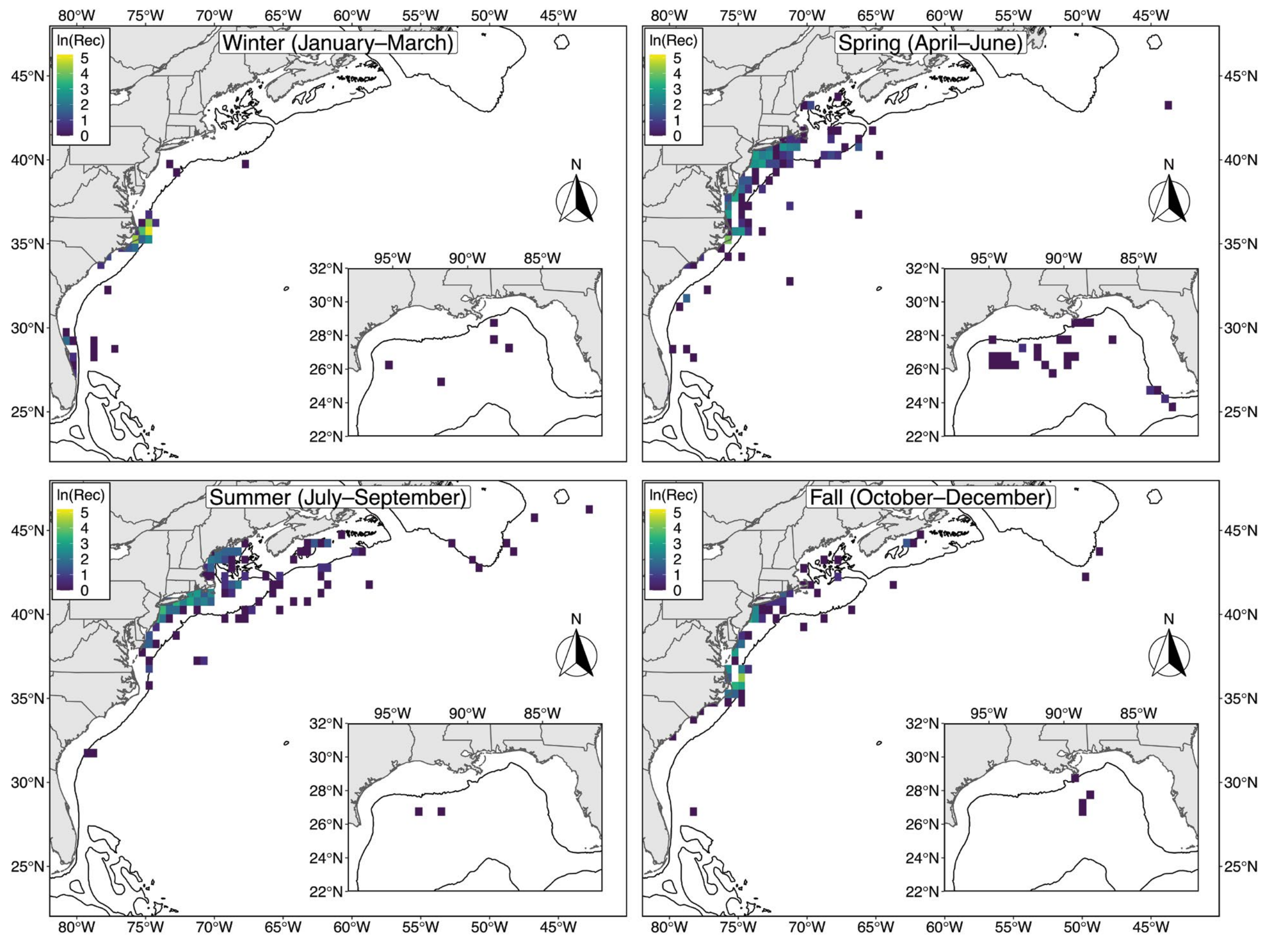

Figure 6

Distribution of juvenile and adult common thresher sharks (*Alopias vulpinus*) by season in the western North Atlantic Ocean between 1964 and 2019. The number of capture records (Rec) in each grid cell (0.5° × 0.5°) is natural log transformed. The lack of records in the maps for waters of Canada is a result of missing data on sex of sharks and the subsequent inability to assign a life stage to sharks captured in Canada. Records from the Gulf of Mexico are presented in the inset. The 200-m depth contour delineates the boundary of the continental shelf.

(Beerkircher et al., 2004; Hanke et al.[2]) indicates that this species does not occur as frequently in deep, offshore waters. Capture of common thresher sharks has been recorded sporadically throughout tropical offshore waters, including in the Gulf of Mexico. However, species identification could not be verified, and it is possible that some capture records represent misidentifications of bigeye thresher, the only other alopiid that occurs in the WNA (Compagno, 2001). Of note, misidentification would be most likely in the pelagic longline records from offshore areas in the Gulf of Mexico, where the distribution of bigeye threshers is well-documented (Fernandez-Carvalho et al., 2015) and the species tends to be encountered 4 times more frequently than the common thresher shark (Young et al., 2016).

Trends in distribution are consistent with a seasonal, north–south movement pattern in the WNA, with distribution focused shoreward of the continental shelf edge in depths <200 m along the east coasts of the United States and Canada. This distribution and movement pattern is similar to those of many other highly migratory species that inhabit the temperate WNA, such as the shortfin mako (*Isurus oxyrinchus*) (Vaudo et al., 2017) and bluefin tuna (*Thunnus thynnus*) (Galuardi et al., 2010), except with no evidence of frequent movements to the tropical Atlantic Ocean. It also aligns with the seasonal distribution and movements of common thresher sharks in the eastern Pacific Ocean, where northward (spring and summer) and southward (fall) movements occur between Baja

[2] Hanke, A. R., I. Andrushchenko, and G. Croft. 2012. Observer coverage of the Atlantic Canadian swordfish and other tuna longline fishery: an assessment of current practices and alternative methods. DFO Can. Sci. Advis. Secr. Res. Doc. 2012/049, 84 p. [Available from website.]

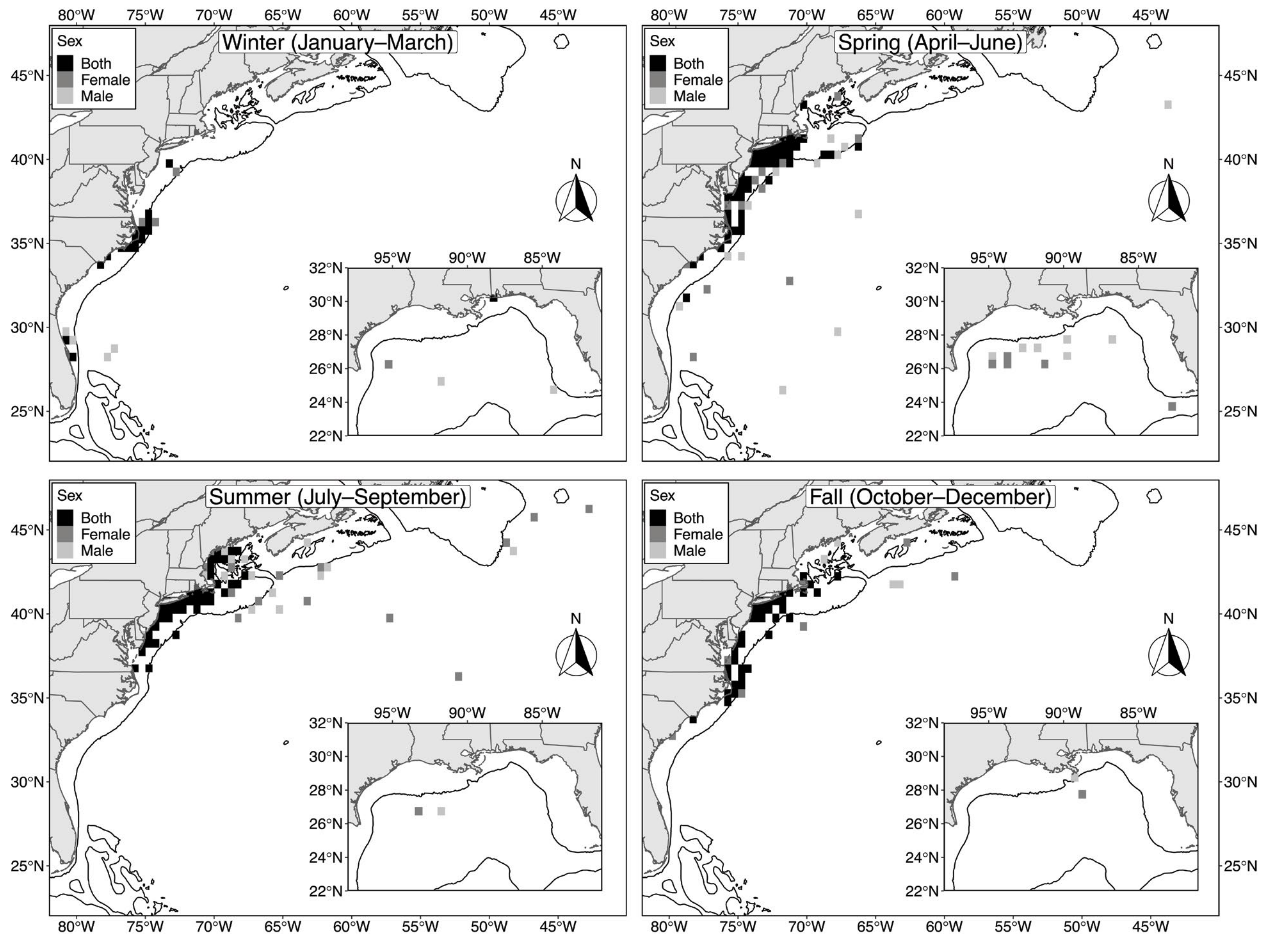

Figure 7

Distribution of male and female common thresher sharks (*Alopias vulpinus*) and of both sexes combined in the western North Atlantic Ocean between 1964 and 2019, by season and aggregated in grid cells (0.5° × 0.5°). The lack of capture records in maps for waters of Canada is a result of missing data on sex of sharks. Records from the Gulf of Mexico are presented in the inset. The 200-m depth contour delineates the boundary of the continental shelf.

California, Mexico, to as far north as British Columbia, Canada (Hanan et al., 1993; Cartamil et al., 2016; Kinney et al., 2020). The distribution of common thresher sharks in the WNA was more contracted during the winter than in any other season, with individuals being most commonly taken in relatively small areas off the coast from Virginia to North Carolina (outside of the barrier islands) and off the east coast of Florida.

The seasonal distribution of common thresher sharks changes markedly over ontogeny. Parturition for this species occurs from May through August in the mid-Atlantic states and in southern New England (Natanson and Gervelis, 2013; Young et al., 2016), consistent with the elevated occurrence of YOY throughout these areas during the summer months (Fig. 5). In the winter, YOY were taken almost exclusively in depths <50 m off the coast of North Carolina from Oregon Inlet to Cape Lookout. These results align with previous hypotheses that inshore waters from North Carolina to Massachusetts support nursery habitat for YOY and juvenile common thresher sharks (Natanson and Gervelis, 2013) and indicate that specific areas off New York, New Jersey, and Cape Hatteras (Fig. 5) may be of particular importance to individuals in these life stages. Investigation into why YOY occur more frequently in these areas than in others was beyond the scope of this study; however, their presence may be related to environmental preferences (see subsequent paragraphs) or prey distribution.

The distribution of common thresher sharks expands and individuals move into deeper waters of the WNA as they grow to maturity. A similar range expansion has been documented for juveniles and adults of this species off the U.S. west coast (Smith et al., 2008; Kinney et al., 2020) and may be related to changes in diet or physiological limitations imposed by environmental variation (Knip et al., 2010). Note that the inability to assign a life stage to

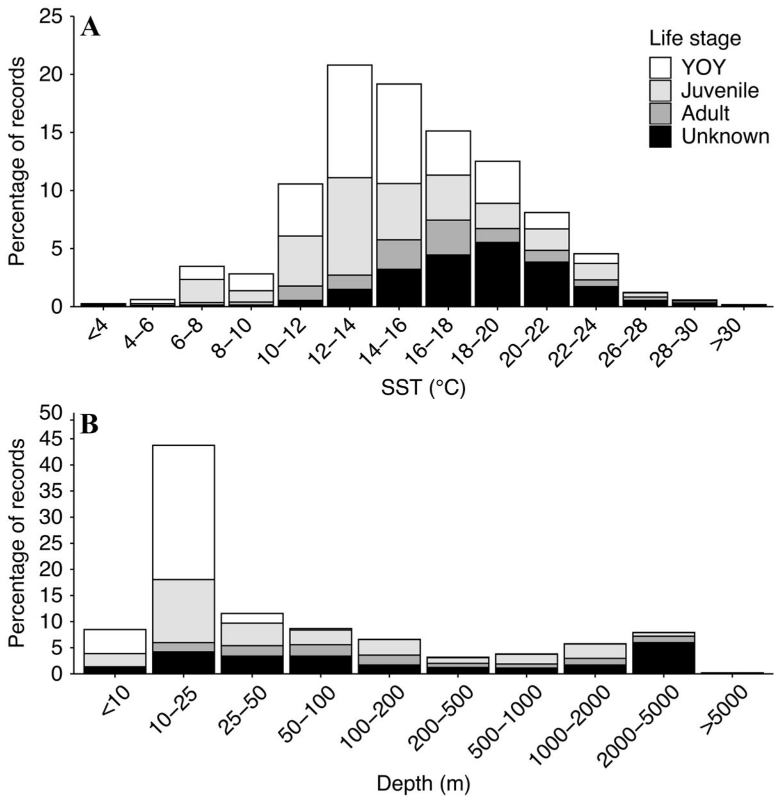

Figure 8

Percentage of the total number of capture records from fishery-dependent data of common thresher sharks (*Alopias vulpinus*) in the western North Atlantic Ocean between 1964 and 2019 by (**A**) sea-surface temperature (SST) and (**B**) depth for each life stage: young of the year (YOY), juvenile, adult, and unknown.

24.0% of the captured sharks and the low number of adults (i.e., 423 sharks) hindered our ability to describe the distribution and habitat use of sharks in these life stages, particularly in Canada. However, the clear association of YOY with shallow waters (depths <50 m) indicates that records from deep, offshore waters of Canada were of juveniles and adults. Difficulties measuring or estimating the total length of common thresher sharks and variability in size at maturity (Natanson and Gervelis, 2013) may have also led to the misclassification of life stage for some individuals and confounded our descriptions of distribution for each life stage.

Contrary to research in other regions (Moreno et al., 1989; Smith et al., 2008; Kinney et al., 2020), our results indicate that there is no strong evidence of sex-specific spatial or depth segregation of the population in the WNA. Segregation by sex tends to be most apparent in the adult life stage (Speed et al., 2010), and it is possible that we did not have sufficient information on this life stage for trends to be apparent. There is some evidence of sexual segregation of common thresher sharks in southern New England based on observations of large aggregations of predominantly female sharks in late summer (senior author and D. Bernal, unpubl. data).

Sea-surface temperatures recorded at the time of capture indicate that the common thresher shark occurs over a wide range of temperatures but is most commonly associated with temperatures from 10°C to 22°C. Previously, this species has been observed in SSTs ranging from 16.5°C to 19.8°C off the east coast of Florida (Castro, 2011), from 8°C to 28°C near the Republic of the Marshall Islands (Cao et al., 2011), and from 9°C to 21°C off the U.S. west coast (Cartamil et al., 2016). Preferred temperatures have been reported as 18–20°C (Cao et al., 2011) and 14–17°C (Cartamil et al., 2016), which are relatively similar to the temperature range over which the greatest number of capture events were recorded during this study (i.e., 12–18°C; Fig. 8). The overall range and mean SST at capture was also similar for all life stages (Table 2); however, YOY were observed over the narrowest temperature range. This result may be due to the lower capacity for metabolic heat retention in small individuals, which have a higher surface-to-volume ratio and therefore a decreased capacity to retain heat through regional endothermy (Bernal and Sepulveda, 2005).

The monthly and seasonal patterns in SST at capture indicate that temperature may be one of the key determinants of distribution and migration of common thresher sharks in the WNA. In general, captured sharks rarely occurred north of ~37°N in the winter and south of ~37°N in the summer (Fig. 4), the seasons during which the lowest and highest mean SSTs were observed, respectively (Fig. 9). This pattern is typical of migratory species that inhabit coastal waters of the WNA. By contrast, temperature was not one of the main factors driving movements and distribution off the U.S. west coast, with more broad-scale extrinsic seasonal factors (e.g., North Pacific Gyre Oscillation) being more influential (Kinney et al., 2020). Of note, the trends reported herein solely represent SST at the time and location of capture and do not necessary represent the temperatures that sharks experience at depth, which are likely the main drivers of movement and distribution. This is supported by Lynch et al. (2018), who demonstrated that water temperature profiles influenced catch rates for common thresher sharks in the pelagic longline fishery that operates off the Atlantic coast of the United States.

Fishery interactions and management implications

Capture records were available for common thresher sharks of all life stages; however, YOY was the most

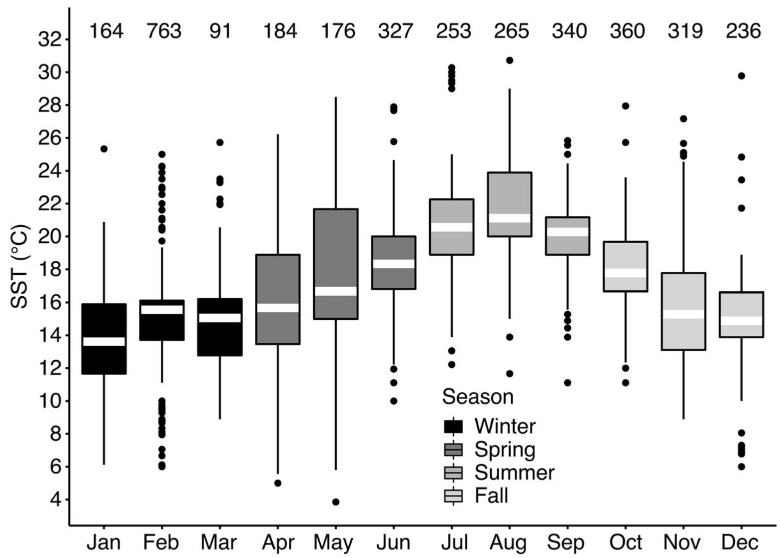

Figure 9

Box plot of sea-surface temperatures (SST) recorded, by month and season, as part of capture records from fishery-dependent data of common thresher sharks (*Alopias vulpinus*) in the western North Atlantic Ocean between 1964 and 2019. The numerals above the boxes indicate the number of records for each month. The upper and lower parts of each box represent the first and third quartiles (the 25th and 75th percentiles), and the horizontal white line is the median. The whiskers that extend above and below the box correspond to 1.5 times the interquartile range, and the black circles represent values outside this range.

commonly observed life stage, possibly because the restricted distribution of YOY in depths <50 m. There are no minimum commercial size limits for this species in the U.S. waters of the Atlantic Ocean and a review of the data provided by the Northeast Fisheries Observer Program indicate that many YOY are retained for sale. For example, between January and April 2018, at least 367 YOY were captured by gill nets during observed trips in the vicinity of Cape Hatteras. Assuming an average brood size of 3.7 young (Natanson and Gervelis, 2013), these captured sharks represent the reproductive output of approximately 100 adult females. Given the bi- or triennial reproductive cycle of this species in the WNA (Natanson and Gervelis, 2013) and the fact that the total number of YOY removed in the fishery may be many times greater than what was observed, such removals may represent a significant loss in recruitment in the WNA. However, because of their small size, landed weight of YOY common thresher sharks may not constitute a large percentage of the total quota for pelagic sharks in the Atlantic Ocean (i.e., 488.0 metric tons in dressed weight; NMFS, 2006).

Our results provide new insight into the environmental conditions and habitats used by common thresher sharks for each life stage and will assist managers in the designation of EFH by life stage off the U.S. east coast, as required under the Magnuson-Stevens Fishery Conservation and Management Act. Because of insufficient data on individual life stages, all life stages currently share a single EFH that spans continental shelf waters from Cape Lookout to Georges Bank and from Cape Ann, Massachusetts, to Bar Harbor, Maine (NMFS, 2017). However, our results provide information that should be sufficient to differentiate EFH for YOY. Although the extent of fishery-dependent data compiled for YOY common thresher sharks ranges from the Gulf of Maine to off South Carolina (consistent with Natanson and Gervelis, 2013), our analyses clearly identify areas of high levels of interaction off New York and New Jersey during the summer and off Cape Hatteras during the winter. Additional, direct information on the residency and movements of YOY common thresher sharks in these areas, however, is needed to confirm whether they warrant designation as nursery areas (Heupel et al., 2007). Additional fishery-independent (e.g., tagging and survey) data are also needed to better define juvenile and adult EFH and to confirm the broader conclusions regarding distribution and habitat use of common thresher sharks presented herein.

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