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Distribution of the tiger shark (*Galeocerdo cuvier*) in the North Atlantic Ocean by season, sex, and life stage, based on tag and recapture data

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Abstract—Movements of the tiger shark (*Galeocerdo cuvier*) by life stage are largely unknown yet are necessary to determine essential fish habitat and sustainable fishery management practices. In an effort to elucidate distribution and movements of the tiger shark, we analyzed fishery-dependent and -independent tag (sample size [*n*]=10,516) and recapture (*n*=762) records for sharks caught in the North Atlantic Ocean during 1963–2018. Seasonal distribution of the tiger shark was examined by life stage—young of the year, juveniles (immature), and adults (mature)—and distribution patterns were used to identify potential nursery habitat. Tiger sharks were caught over a wide area from the Grand Banks of Newfoundland, Canada, south to Brazil and from coastal to offshore waters and into the eastern North Atlantic Ocean. Seasonal north–south movements were observed in all life stages, and 14 immature sharks were found to have migrated from the western to the eastern North Atlantic Ocean. A broad nursery area and a potential birthing area were identified on the continental shelf between Florida and Georgia on the basis of the repeated presence of neonates in summer across years and of the recapture of multiple tagged young-of-the-year sharks from the same location over a period of at least 2 years.

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The tiger shark (*Galeocerdo cuvier*) is a wide-ranging, globally distributed predator found in tropical and warm temperate waters (Bigelow and Schroeder, 1948). Tiger sharks make extensive migrations in many parts of the world, and the range of this species is considered both coastal and oceanic (Heithaus et al., 2007; Ferreira et al., 2015). In the western North Atlantic Ocean (WNA), the tiger shark is known to undertake seasonal inshore–offshore movements in the Gulf of Mexico (GOM) and seasonal north–south movements along the East Coast of the United States (Lea et al., 2015; Ajemian et al., 2020). Evidence also exists for basin-wide migrations in the North Atlantic Ocean (Kohler et al., 1998; Kohler and Turner, 2019). Tiger sharks have been found in water temperatures ranging from 4.0°C to 34°C (Afonso and Hazin, 2015; Hammerschlag et al., 2022), but in the WNA they seem to prefer water temperatures between 26°C and 28°C, regardless of season (Hammerschlag et al., 2022). Because of its broad distribution, this species occurs in the waters of many countries and crosses numerous management boundaries. Therefore, understanding the movements of tiger sharks in general, and by life stage, is important to international management.

Tiger sharks are caught in commercial and recreational fisheries throughout the North Atlantic Ocean (Natanson et al., 1999; Domingo et al., 2016). The tiger shark is currently listed on the IUCN Red List of Threatened Species as near threatened globally (Ferreira and Simpfendorfer, 2019). However, in the North Atlantic Ocean, shark vulnerability to pelagic longline gear has been estimated to be low to moderate on the basis of an ecological risk assessment based on the species' productivity and susceptibility to the gear (Cortés et al., 2015). Furthermore, increases in tiger shark abundance in the WNA have been documented since the early 1990s, a trend attributable to the implementation of the National Marine Fisheries Service (NMFS) Shark Management Plan in 1993 (Carlson et al., 2012; Peterson et al., 2017).

Life history studies of tiger sharks have expanded in recent years. Results of the most recent study on growth dynamics, in which ages validated with bomb radiocarbon techniques were used, indicate a longevity of 27–29 years and an age at maturity of 10 years for both sexes (Kneebone et al., 2008). Updated reproductive parameters corroborated these estimates, indicating a size and age at median maturity of

258.9 cm in fork length (FL) and 9.5 years for males and of 261.4 cm FL and 11.6 years for females (Natanson et al., 2023). Tiger sharks are well known as generalist predators (Lowe et al., 1996), and they have a high trophic level indicative of a top predator (Cortés, 1999). They are considered an important component of the trophic structure for reef systems and other coastal habitats (Heithaus, 2001; Ruppert et al., 2013), and results of studies indicate that ontogenetic shifts in their diet may partly result from sharks of different sizes or sharks in different life stages occupying different habitats (Lowe et al., 1996; Aines et al., 2018).

Movement and migration information on the tiger shark is limited to discrete studies in which high-technology tagging methods were used with limited numbers of satellite or acoustic tags. The results of these studies indicate that seasonal migrations to higher latitudes are common and that, although there are resident individuals, migrations over long distances are also undertaken (Sulikowski et al., 2016; McClain et al., 2022). In some studies, longer migrations have been attributed to males (Lea et al., 2015), but more recent data indicate that they are undertaken by both sexes (McClain et al., 2022) and are likely related to foraging, especially in relation to turtle nesting sites (Fitzpatrick et al., 2012), temperature (Papastamatiou et al., 2013; Lea et al., 2018; Hammerschlag et al., 2022), or important habitats related to life stage (e.g., birthing and nursery areas) (Meyer et al., 2018). Data from these types of studies, however, are limited by the number of tagged individuals and a lack of representation by all life stages, and such data may not provide a complete picture of movements for the species (Meyer et al., 2018; Sequeira et al., 2019).

In this study, we used updated reproductive parameters (Natanson et al., 2023) in conjunction with conventional tagging data to examine the demographic characteristics of the population of tiger sharks in the North Atlantic Ocean. Specifically, we looked at potential variation in spatial and seasonal distributions and migrations by sex and life stage, young of the year (YOY), juveniles (immature), and adults (mature). We also examined locations of mature females and neonate individuals (<66.2*[1] cm FL) from March through August by using estimated time and size of birth (Castro, 2011) to identify possible areas of parturition and by using the distribution of YOY to identify potential nursery areas for the tiger shark. Information on movements by life stage can be used in management to understand essential fish habitat and to help define protected areas or other approaches to protect vulnerable portions of the population.

Materials and methods

Mark and recapture

Tag and recapture data from the NMFS Cooperative Shark Tagging Program (CSTP), for the period 1963–2018, were used with published maturity estimates (Natanson et al., 2023) to investigate distribution and movements of tiger sharks by sex and life stage. Tiger sharks were tagged by cooperating commercial and recreational fishermen, scientists, and fisheries observers. Tagging methods and quality control have remained consistent since the inception of the CSTP and are detailed in Casey and Kohler (1992) and Kohler and Turner (2019). Distances between release and recapture locations are expressed in straight-line nautical miles (nmi). Tag and recapture data were reported in FL, total length (TL), or weight (WT) and as measured or estimated. Lengths are presented in centimeters, and weights are provided in kilograms. All tagging and recapture data were converted to FL_{OTB} (i.e., from the tip of the snout to the fork in the tail, over the body [OTB]) by using the I-MARK web application (Kohler and Turner, 2019) and conversions from Kohler et al. (1996). Published straight-line TL (TL_{STR}) data were converted to FL_{OTB} (these converted values are indicated with asterisks) by using the conversion from Natanson et al. (2022):

$$TL_{STR} = 11.90 + 1.18(FL_{OTB}),$$

coefficient of determination [r^2]=0.996, n=605.

Unless otherwise noted, all lengths are presented in FL_{OTB}.

Demographic structure

To investigate the spatial distribution of the population, tiger shark catch records of tagging and recapture events were divided into subsets by sex and life stage, where possible. Classification into stages was done by length. Sharks ≤106 cm FL were considered YOY (Natanson et al., 1999), sharks >106 cm FL and less than the median size at maturity by sex (258.9 and 261.4 cm FL, for males and females, respectively; Natanson et al., 2023) were classified as juveniles (immature), and sharks greater than or equal to the median size at maturity were classified as adults (mature). For sharks for which no sex was recorded, maturity status was determined by using the more conservative, larger, female size at maturity. Additionally, locations at which sharks ≤66.2 cm FL (neonates) were caught from May through August were examined as possible locations of birthing areas on the basis of an extension of the timing of parturition from Castro (2011) (June and July) to account for early and late parturition. The length at birth was based on the range (57.7*–66.2* cm FL) provided by Castro (2011) with the assumption that any free-living shark <66.2 cm FL had just been born. A chi-square test was used to determine if there was a significant difference between the sample sizes of females and males in the tagging data.

To visualize potential variation in the spatial distribution of the life stages of tiger sharks, catch locations by sex, life stage, and season were mapped by using R (vers. 4.1.3; R Core Team, 2022). Seasons were defined as winter (December–February), spring (March–May), summer (June–August), and fall (September–November). The

[1] An asterisk (*) after a size value denotes a fork length that has been converted from a total length.

distribution of catch records for neonates, adult females, and YOY were examined for patterns related to birthing and nursery areas.

Results

Tagging and recapture

Tiger sharks (n=10,516) were tagged in coastal waters throughout the continental shelf in the WNA from the Grand Banks of Newfoundland, Canada, south to Brazil and in offshore waters (past the 200-m depth contour) to 40°W (Table 1, Fig. 1). The majority of tags (n=9211) were deployed along the East Coast of the United States from Cape Hatteras, North Carolina, down and into the U.S. waters of the GOM. Sharks tagged were primarily captured on longline gear (80.8%) during commercial (32.7%) or scientific (33.2%) fishing operations or by fisheries observers (17.0%), followed by recreational anglers using rod and reel (17.0%). All industries fished in the same general locations, although spatial effort varied between them (Table 1, Fig. 1). Recreational anglers, in general, fished closer to shore, and commercial and scientific operations fished both inshore and offshore, particularly between northeastern Florida and north of Cape Hatteras (Table 1). Commercial effort was primarily focused on the east coast of Florida, and the bulk of the scientific effort was evenly distributed along the coast from Cape Hatteras to the Florida Keys. Observer coverage was highest from Cape Hatteras to the border of Florida and Georgia, and although recreational fishing was highest north of Cape Hatteras, it was fairly evenly distributed south of the cape and into the GOM but very limited in the Caribbean Sea and the Bahamas (Table 1).

Sharks were captured in all months of the year. Lengths of tagged tiger sharks encompassed the entire size range of the species (from birth to 391.0* cm FL; Bigelow and Schroeder, 1948), with a range of 40.1–457.2 cm FL for both sexes combined and a mean of 120.2 cm FL (standard deviation [SD] 51.1) and 134.7 cm FL (SD 60.4) for males and females, respectively (Fig. 2A). The lengths of 5 individuals were greater than the published maximum size, but because these lengths were estimated, none can be considered a definitive new maximum size; 3 of these sharks were females, and 2 of them were of unknown sex. Although caution should be exercised in taking these values as a new maximum size for tiger sharks, the sharks would be classified as mature, and, for that reason, these lengths were included in our analyses. Of those tagged sharks for which sex was reported, the proportions of females (57.3%) and males (42.7%) were significantly different from the expected ratio of 1:1 ($X^2(1, n=9419)=200.14$, $P<0.05$).

A total of 762 tiger shark recapture events were reported between 1967 and 2018 throughout the North Atlantic Ocean (Fig. 3), with an overall recapture rate of 7.2%. Of these, 35 individuals were recaptured multiple times (3 sharks were recaptured twice, and 2 sharks were recaptured 3 times). For 13 recaptured sharks, no information was turned in at tagging and their tag data could not be used for movement analysis. In all but 5 cases, sex was reported the same at both tagging and recapture. Sex was reported as unknown at recapture for 2 of those exceptions, and sex was reported unknown at tagging for the other 3 cases. Similar to the proportions

Table 1

The numbers of tagged tiger sharks (*Galeocerdo cuvier*) from the western North Atlantic Ocean caught between 1963 and 2018 by area tagged for each sex, life stage, and tagger industry. Also provided is the percentage of tagged fish that were mature for each sex. Tagged sharks were classified into 3 life stages: young of the year (YOY), juveniles (immature [IMM]), or adults (mature [MAT]). The tagger industries include commercial (COM) and scientific (SCI) fishing operations, fisheries observers (OBS), and recreational anglers (REC). The latitudinal borders of the tagging areas are as follows (in decimal degrees): north of Cape Hatteras (35.2500–45.5833°N), from Cape Hatteras to Florida (35.2499–30.7167°N), east coast of Florida (30.7168–25.3400°N), west coast of Florida (25.3401–30.2600°N), rest of the Gulf of Mexico (GOM, 302601–21.0333°N), Caribbean Sea (15.5667–21.3000°N), and the Bahamas and adjacent waters (13.0000–25.0833°N). The total number of sharks tagged includes those of unknown sex or maturity and 2 fish caught outside the location parameters.

		Females				Males				Tagger industry			
Area	Total no. tagged	YOY	IMM	MAT	% MAT	YOY	IMM	MAT	% MAT	COM	SCI	OBS	REC
North of Cape Hatteras	1318	141	398	23	4.1	81	209	22	7.0	160	164	131	859
Cape Hatteras to Florida	3066	787	727	73	4.6	668	506	39	3.2	298	1424	1062	282
Florida East Coast	4692	1258	1125	95	3.8	1226	762	35	1.7	2808	1422	273	185
Florida West Coast	677	94	225	23	6.7	102	143	8	3.2	80	109	270	217
Rest of GOM	419	33	182	9	4.0	26	87	10	8.1	25	109	49	232
Caribbean Sea	113	3	41	11	20.0	4	28	5	13.5	44	64	1	4
Bahamas and adjacent waters	229	1	112	27	19.3	2	36	20	34.5	29	194	0	6
Total	10,516	2317	2810	262	4.9	2109	1771	139	3.5	3444	3486	1786	1785

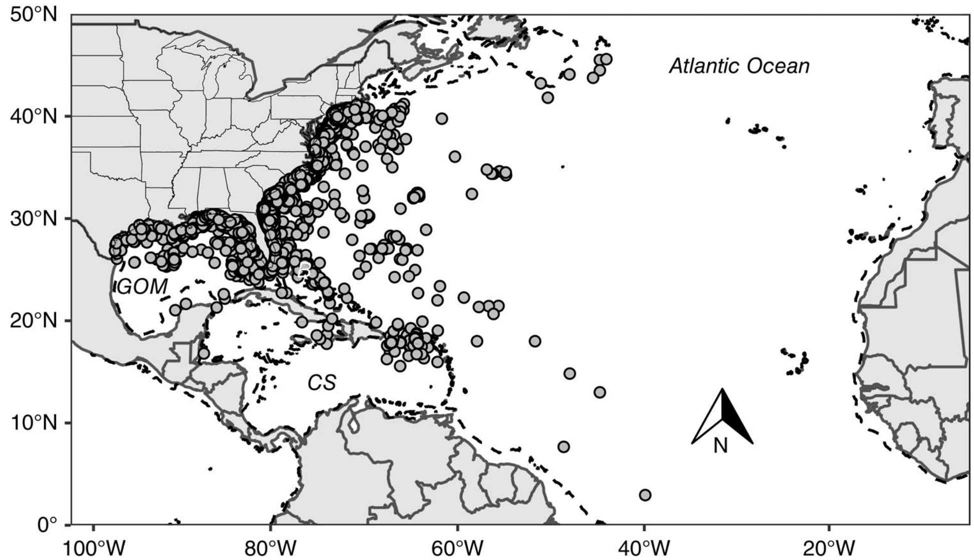

Figure 1

Map showing the distribution of all tiger sharks (*Galeocerdo cuvier*) tagged in the western North Atlantic Ocean by participants in the Cooperative Shark Tagging Program of the National Marine Fisheries Service between 1963 and 2018. Circles indicate locations where sharks were tagged. The dashed black line indicates the 200-m contour. GOM=Gulf of Mexico; CS=Caribbean Sea.

of tagged sharks, recaptured females (56.2%) outnumbered recaptured males (43.8%) for sharks for which sex was reported at recapture (n=714). Sizes of recaptured tiger sharks ranged from 66.0 to 373.0 cm FL with a mean of 142.8 cm FL (SD 50.4) and 154.7 cm FL (SD 56.6) for males and females, respectively (Fig. 2B), nearly representing the entire size range of this species. Commercial fishermen (69.3%) recaptured the majority of tiger sharks, followed by recreational anglers (18.0%), biologists (5.8%), fisheries observers (4.5%), unknown (2.4%), and educators (<1%). The majority of sharks recaptured were caught on longline gear (75.7%) during commercial fishing operations.

The range of overall time at liberty for tiger sharks was 0.0–13.4 years with a mean of 1.0 year (SD 1.4). Most sharks were at liberty less than a year (71.8%). Time at liberty varied depending on life stage, with mature males having a higher mean time at liberty (5.7 years [SD 3.9]) than the means for males at all other maturity stages (Table 2). Distance between tagging and recapture locations ranged from 0 to 3643 nmi with a mean of 243.2 nmi (SD 449.5). Although mean distance between tagging and recapture locations was higher for mature sharks of both sexes, immature fish had higher maximum distances (Table 2).

Recapture locations were concentrated close to the coast between Long Island, New York, and Florida, into the U.S. portion of the GOM. Additional recapture events occurred along the coast of Mexico in the GOM into the Caribbean Sea and south to Brazil. North of Long Island, sharks were recaptured farther offshore. The northernmost recapture was on the Grand Banks of Newfoundland, and the easternmost recapture was in the coastal waters of Guinea-Bissau, a country in West Africa (Fig. 3).

Tiger sharks transited throughout the WNA, including the GOM and Caribbean Sea (Fig. 3). A total of 37 sharks crossed between these water bodies. The majority of these individuals moved from the main body of the Atlantic Ocean into either the GOM (n=11) or the Caribbean Sea (n=14). Movement was also seen from the GOM into both the main body of the Atlantic Ocean (n=5) and the Caribbean Sea (n=5) and from the Caribbean Sea into both the main body of the Atlantic Ocean (n=1) and the GOM (n=1).

A total of 116 sharks, of both sexes, traveled more than 500 nmi; of these, 115 individuals had length data at tagging and 109 individuals had length data at both tagging and recapture. The majority of tiger sharks that travelled over 500 nmi were immature (82%, 84% including YOY), reflecting the prevalence of this life stage in the tagging data (Table 2). Even though adults account for only 5% of the total recapture events, this life stage had the greatest percentage of recaptured sharks that travelled over 500 nmi. (Table 2). Of those sharks that travelled >500 nmi, 23 individuals were tagged when YOY, 88 sharks were tagged when immature, and 4 fish were tagged when mature. Six fish were immature at tagging and mature at recapture. Two female tiger sharks recaptured in 1995 had traveled from the East Coast (off Frying Pan Shoals in North Carolina and off St. Augustine, Florida) across the middle of the Atlantic Ocean (45°W). One of these females, immature at both tagging and recapture, traveled to 41.5°W and was recaptured after 571 d at liberty. The other female was a YOY at tagging and still immature when recaptured

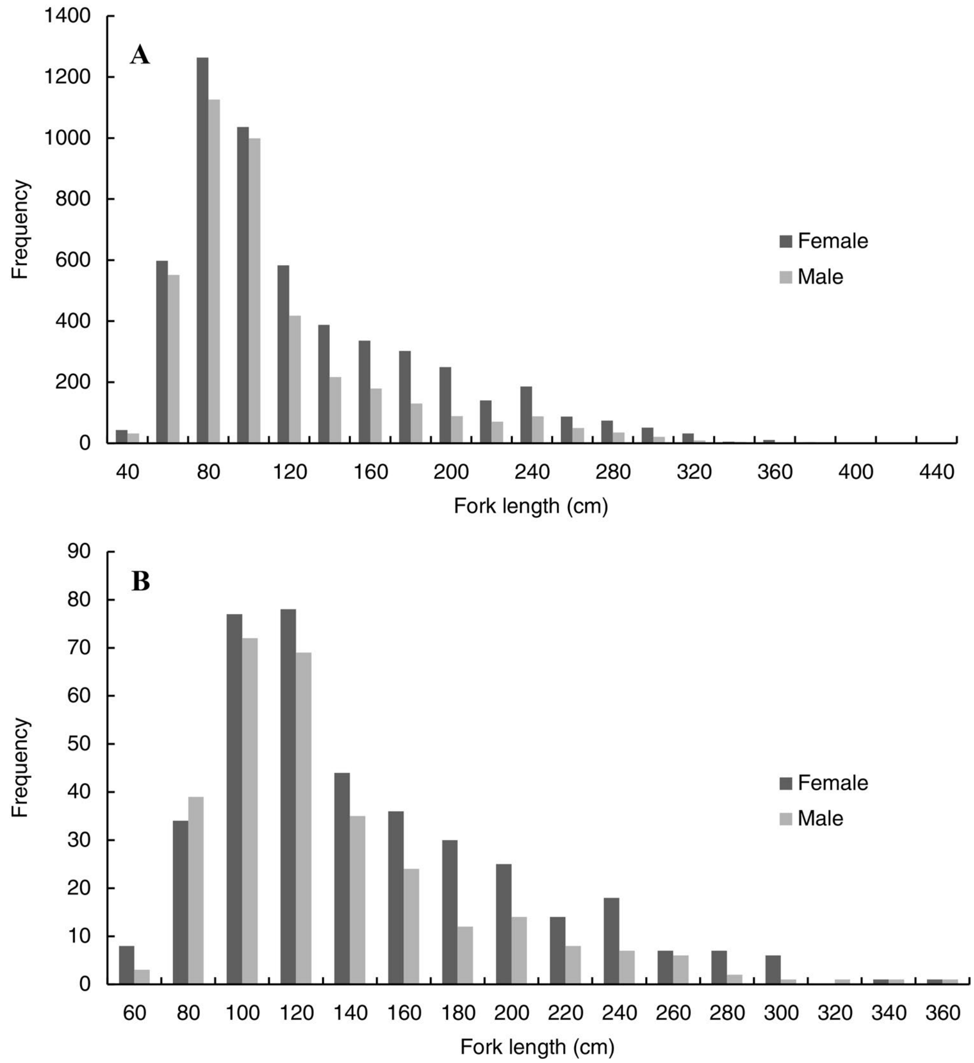

Figure 2

Size–frequency histograms for (**A**) tagged and (**B**) recaptured tiger sharks (*Galeocerdo cuvier*) from the North Atlantic Ocean for the period between 1963 and 2018.

off the coast of Guinea-Bissau at 17.5°W; the transit of this shark remains the longest distance traveled to date for a tiger shark in the CSTP (3643 nmi; Kohler and Turner, 2019) (Fig. 4). Since 1995, an additional 12 individuals that had been tagged in the coastal waters of the WNA have been reported to have been recaptured in the eastern North Atlantic (ENA). These sharks were all immature at tagging and recapture and consisted of 6 females, 5 males, and 1 individual of unknown sex (Fig. 4).

All of the 35 tiger sharks that were recaptured multiple times were immature at tagging and final recapture (Table 3). Twenty-two (63%) of these sharks were originally tagged as YOY. Multiple mark-recapture records indicate that individual tiger sharks tagged and recaptured as YOY, and up to 124 cm FL, were recaptured in the vicinity of their tagging location for up to 3 months and/or returned to the area where they were tagged for up to 2 years (Table 3). The continental shelf off northern Florida was used by YOY each month of the year. Several of the immature sharks also made long-distance movements; for example, a 91-cm-FL male was tagged off northern Florida in November, recaptured there the following May, and recaptured again in December nearly 1400 nmi away in the Caribbean Sea off Venezuela (Table 3). A 134-cm-FL female was tagged and recaptured off North Carolina in September of the same year and was recaptured again 2 years later east of the Mid-Atlantic Ridge (>2300 nmi away). Only 1 shark was recaptured multiple times in the GOM, a 156-cm-FL female at tagging that used the northeastern GOM over

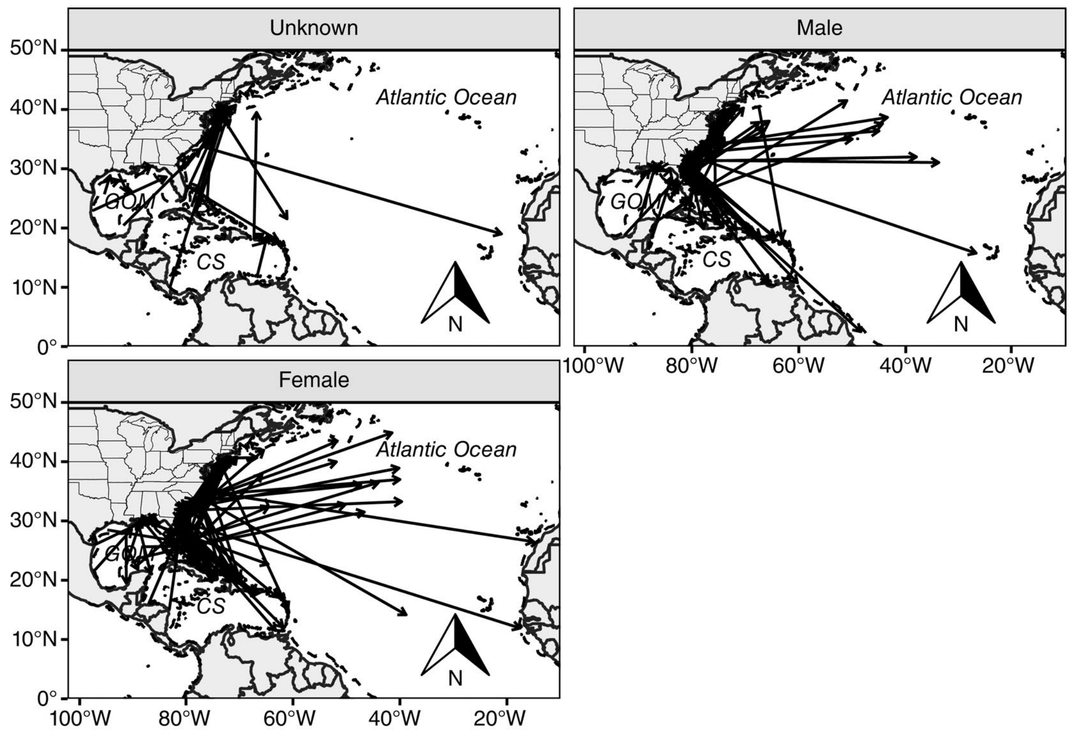

Figure 3

Maps showing the locations where tiger sharks (*Galeocerdo cuvier*), by sex, were tagged and recaptured in the North Atlantic Ocean between 1967 and 2018. The dashed black line indicates the 200-m contour. GOM=Gulf of Mexico; CS=Caribbean Sea.

multiple years (Table 3). The largest tagged tiger sharks with multiple recapture events were a 214-cm-FL female and a 223-cm-FL male (Table 3).

Demographic structure

Females with length information (n=5797), based on combined tag and recapture data, ranged in size from 48.0 to 457.2 cm FL. Of these, 284 females were classified as mature. Males with length information (n=4336) ranged in size from 41.8 to 373.0 cm FL. Of these, 153 males were considered mature. Sharks of unknown sex with length data (n=1132) ranged in size from 40.1 to 457.2 cm FL. Of these, 107 individuals were classified as mature. All of these samples were used in combined sex analyses.

Life stage—immature Across both sexes, 95.2% of the specimens (n=11,221, tagged and recaptured combined) were classified as a juvenile tiger shark (n=9654, including YOY); of these, immature females (56.9%) outnumbered immature males (43.1%) overall and in all seasons. Individuals of both sexes were found in the same general areas, although 2 immature males were caught off Brazil, the southernmost extent of where our data were collected, 311.6 nmi farther south than any female was caught (Figs. 5 and 6). Immature animals of both sexes were caught in all seasons from Cape Hatteras into the GOM and down in the Bahamas and the Caribbean Sea (Suppl. Figs. 1A and 2A). In winter and spring, immature individuals of both sexes were found concentrated in these areas, but in summer and fall, immature sharks ranged farther north and east, with females traveling up to Nova Scotia, Canada, and males moving up to Massachusetts.

Life stage—mature Adult females (n=284) outnumbered adult males (n=151) in all seasons, except in summer, although the largest difference was in spring. Mature fish of both sexes overlapped the range of immature fish; however, mature females had a slightly different seasonal distribution than mature males (Suppl. Figs. 1B and 2B). In fall, mature males were found up to Cape Hatteras, and mature females were found as far north as Long Island and slightly offshore. In winter, mature females were found as far north as North Carolina, and mature males were found only in the GOM and south. In spring and summer, mature fish of both sexes shared approximately the same range.

Life stage—young of the year The majority of YOY (n=4606) were encountered between the U.S. waters of the GOM and Long Island, although they were found as

Table 2

Summary of tag and recapture data by life stage for tiger sharks (*Galeocerdo cuvier*) from the western North Atlantic Ocean caught between 1963 and 2018. Tagged sharks were classified into 3 life stages: young of the year (YOY), juveniles (immature), or adults (mature). Mean distances traveled and times at liberty are provided with standard deviations (SDs) and maximum values. Other values include the number and percentage of tagged fish that traveled >500 nautical miles (nmi) and the number of tagged fish that crossed from the western to the eastern North Atlantic Ocean. The asterisk (*) indicates that this shark was tagged as a YOY and recaptured as a juvenile.

Life stage	No. of sharks tagged	No. of recapture events	Distance travelled (nmi)			No. >500 nmi	% >500 nmi	No. that crossed Atlantic	Time at liberty (years)		
			Mean	SD	Max				Mean	SD	Max
Females											
YOY	2317	64	72.7	176.6	1282	2	3.1	1*	0.3	0.2	0.8
Juveniles	2810	300	266.4	480.1	3643	56	18.7	7	1.0	1.3	8.2
Adults	262	22	300.0	424.7	1556	5	22.7	0	2.2	2.1	8.0
Males											
YOY	2109	61	60.2	88.1	494	0		0	0.2	0.2	1.3
Juveniles	1772	222	234.9	442.4	3018	30	13.5	5	0.8	1.0	6.0
Adults	138	12	525.3	533.6	1690	5	41.7	0	5.7	3.9	13.4
Unknown											
YOY	214	0				0		0			
Juveniles	769	42	431.6	630.4	3089	9	21.4	1	1.0	1.0	4.4
Adults	102	5	781.4	615.0	1623	3	60.0	0	3.1	2.8	7.5
Total	10,493	728	243.2	449.5	3643	116	15.9	14	1.0	1.4	13.4

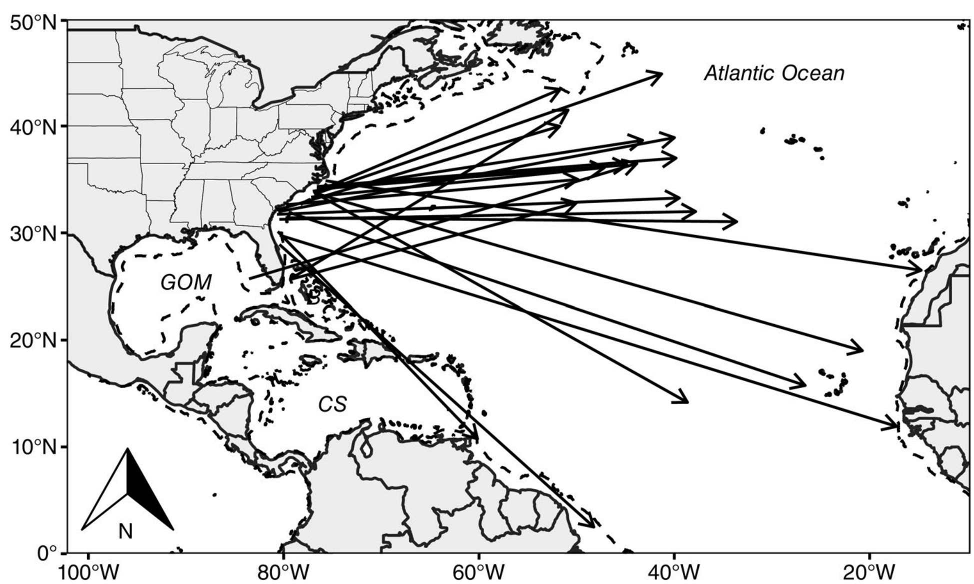

Figure 4

Map showing the locations where immature tiger sharks (*Galeocerdo cuvier*) that traveled east of longitude 60°W were tagged and recaptured in the North Atlantic Ocean between 1963 and 2018. The dashed black line indicates the 200-m contour. GOM=Gulf of Mexico; CS=Caribbean Sea.

Table 3

List of tagged tiger sharks (*Galeocerdo cuvier*) that were recaptured multiple times, by tagging location and month and by size in fork length (FL), sex, and estimated age at tagging calculated by using conversions from Kneebone et al. (2008). Records of sharks tagged and caught in the North Atlantic Ocean during 1963–2018 were used in this study. The letter *X* marks the month the shark was tagged and the following months in which it was recaptured. If there is no superscript character after the *X*, the tagging and recapture events occurred in the same location. A superscript numeral *2* denotes that the shark was recaptured in the same month as it was tagged or that it was recaptured twice in the same month. If the superscript *2* follows a superscript letter, both recapture events in that month occurred at the same location. The superscript letters *N*, *V*, *J*, *M*, *Z*, *C*, *F*, *S*, and *R* denote the following recapture locations, respectively: off North Carolina, Virginia, New Jersey, Maryland, Venezuela in the Caribbean Sea, northern Cuba, Florida's western panhandle, Florida's southern Atlantic coast, and east of the Mid-Atlantic Ridge. The asterisk (*) identifies a tiger shark that was recaptured 6 years following the tagging year in June, approximately 260 nautical miles north-northwest of Bermuda.

			Year 1												Year 2												Year 3												Year 4								
Size (cm FL)	Sex	Age (years)	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S
New Jersey																																															
107	M	1.4						X	X^N			X^N																																			
Maryland																																															
108	M	1.4							X																	X^N					X^N																
155	M	3.3										X							X^V														X^J														
North Carolina																																															
134	F	2.3									X^2																										X^R										
147	–	2.9	X		X						X^M																																				
South Carolina																																															
120	M	1.9	X						X^{N2}																																						
Northern Florida Atlantic coast																																															
72	F	0.3									X										X^2																										
76	M	0.4									X		X																			X^N															
77	M	0.4											X								X		X																								
79	M	0.5				X		X																			X																				
85	M	0.7											X								X								X^N																		
85	F	0.7											X		X					X						X																					
86	F	0.7												X						X								X																			
87	F	0.7												X							X	X																									
87	F	0.7	X								X	X																																			
90	M	0.8											X									X			X																						

(*Continued on next page*)

Table 3 (*continued*)

Size		Age	Year 1												Year 2												Year 3												Year 4								
(cm FL)	Sex	(years)	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S
Northern Florida Atlantic coast																																															
91	M	0.9											X							X						X^Z																					
93	M	0.9											X		X					X																											
94*	M	1.0				X		X																																							
96	M	1.0	X					X^2																																							
97	F	1.1				X			X^2																																						
98	F	1.1						X	X	X																																					X^C
99	F	1.1							X				X		X																																
100	F	1.2			X	X																	X																								
102	F	1.2					X^2			X																																					
103	F	1.3						X^2				X																																			
103	F	1.3							X					X								X^J																									
104	F	1.3			X							X	X																																		
109	F	1.5								X^2	X																																				
110	M	1.5		X	X	X																																									
114	M	1.6											X				X										X^N																				
124	F	2.0									X										X	X																									
Bimini Islands																																															
214	F	6.1				X^2		X																																							
223	F	6.7					X												X^{S2}																												
Alabama																																															
156	M	3.3											X									X																									X^F

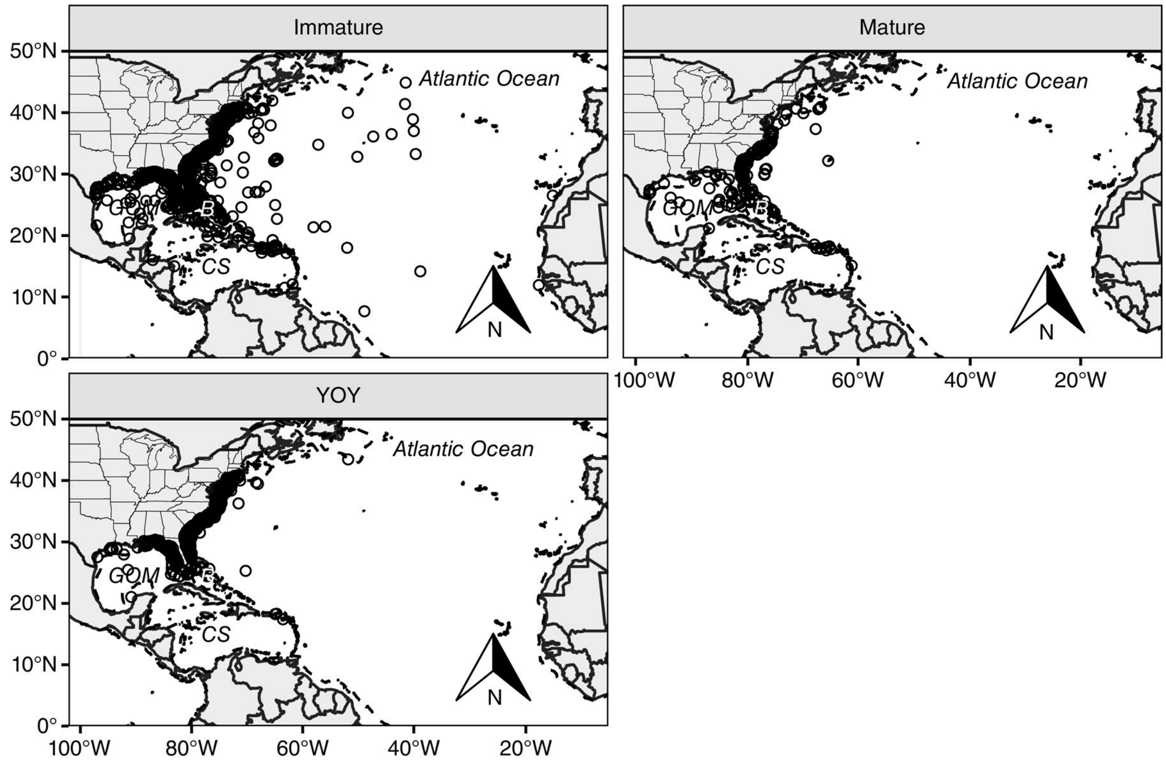

Figure 5

Maps showing the distribution of female tiger sharks (*Galeocerdo cuvier*) tagged and recaptured in the western North Atlantic Ocean between 1974 and 2018, by life stage, young of the year (YOY), juveniles (immature), and adults (mature). The dashed black line indicates the 200-m contour. GOM=Gulf of Mexico; CS=Caribbean Sea.

far north as the Grand Banks of Newfoundland (n=1) and as far east as Georges Bank (n=3) (Figs. 5 and 6). In spring, YOY were tightly clustered from the east coast of Florida up to Cape Hatteras and from off the west coast of Florida to the Florida Panhandle (Suppl. Figs. 1C and 2C). In summer, YOY were up the coast from Cape Hatteras, as far north as Massachusetts, and were found south in the GOM, but by fall, they appeared to be retreating south and, by winter, the majority were between Cape Hatteras and the tip of Florida, similar to the distribution of YOY in spring (Suppl. Figs. 1C and 2C). The majority of YOY (82.0%, n=3777) were caught between 29°N and 34°N, with a concentration (65.6%, n=3023) at 29–31°N. In the GOM, YOY (n=273) were found primarily along the coast between 80.3°W and 97.0°W, although one was captured in Mexico, and in winter, individuals of both sexes were found farther offshore (Figs. 5 and 6, Suppl. Figs. 1C and 2C).

Neonates and mature females In May–August, 225 neonates were caught from off eastern Florida up through New York. Although neonates were caught in all 4 months, the majority were caught in July (55.5%) and August (32.9%), and 86.2% of them were caught between Florida and Georgia (between 29°N and 32°N) (Suppl. Fig. 3). Mature females were primarily caught in May (50.4%) and were less concentrated in distribution than neonates; the majority of the mature female sharks in May (66.1%) were evenly distributed between 29.6°N and 36.8°N (Suppl. Fig. 4). Of those females caught in May, 24.2% were caught in the area of highest neonate abundance, and 43.5% of those females caught in June were caught in that area. In July and August, the portion of mature females caught in the area of neonate abundance decreased (to 21.4% and 20.0%, respectively). In these latter months, mature females were more spread out and distributed as far north as 40.9°N. No neonates were found in the northeast Caribbean Sea. Not enough samples were obtained from the GOM for neonate inquiry.

Discussion

The results of our analysis of 55 years of tag and recapture data advance our knowledge of the distribution and habitat use by life stage of tiger sharks in the North Atlantic Ocean. Conventional tagging relies on cooperation from commercial and recreational fishing industries, whether they participate as taggers or simply capture tagged sharks. Therefore, results include fishery-dependent data,

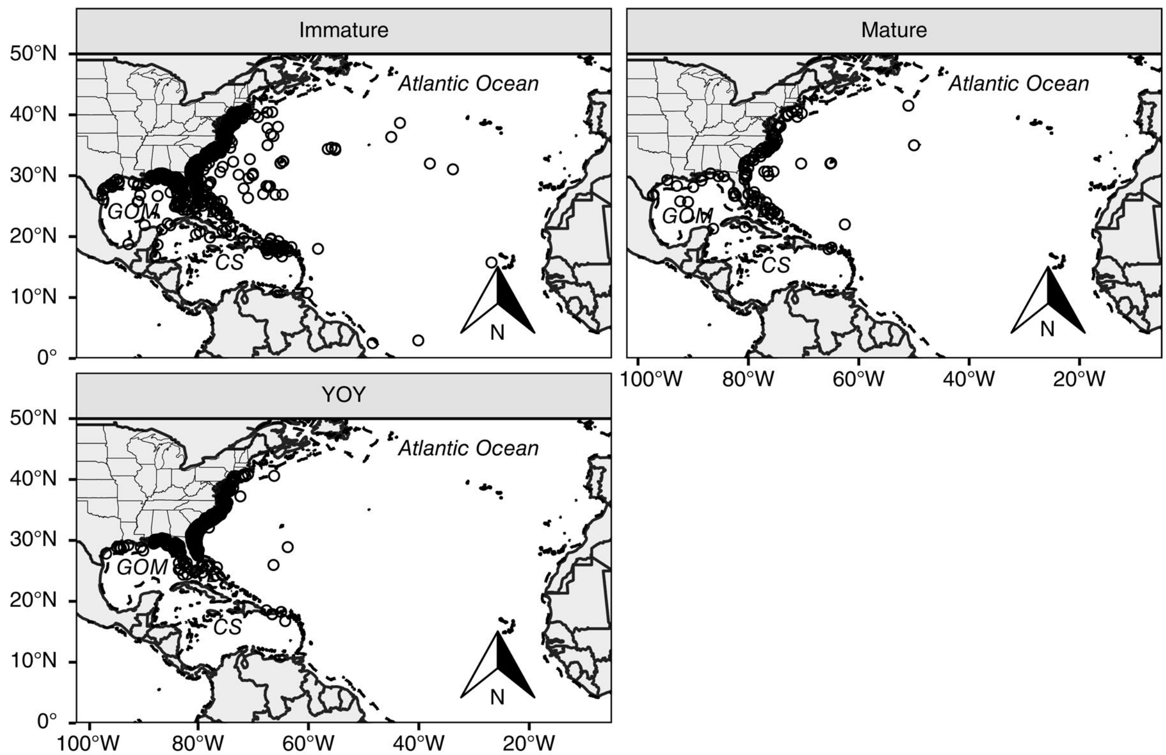

Figure 6

Maps showing the distribution of male tiger sharks (*Galeocerdo cuvier*) tagged and recaptured in the western North Atlantic Ocean between 1963 and 2018, by life stage, young of the year (YOY), juveniles (immature), and adults (mature). The dashed black line indicates the 200-m contour. GOM=Gulf of Mexico; CS=Caribbean Sea.

and the number of tagging and recapture events in an area may reflect fishing effort rather than fish distribution. Additionally, the CSTP is based in the United States, likely leading to a higher proportion of recapture events occurring in U.S. waters of the Atlantic Ocean, the GOM, and the Caribbean Sea. In this study, the tagging and recapture data that were analyzed are a compilation of fishery-dependent (from commercial and recreational fisheries) and fishery-independent (from research trips and surveys) sources. Differences in type and location of fishery, gear selectivity, and fishing method can influence the size and distribution of the individuals caught. For example, most of the fishing for all gears and industries occurred close to shore, leading to a higher likelihood of encountering immature sharks (Fig. 1) (Natanson et al., 2023). These same limitations have been noted in other studies on migratory sharks (Mucientes et al., 2009; Heupel et al., 2018; Natanson et al., 2020). Because the large amounts of data on such sharks are inaccessible when using other methods, the use of fishery-dependent methods will remain an important source of data.

Because fishery-dependent data could bias results if fishing occurred in areas of concentrated juveniles, or of single-sex groups, and because the inclusion of fishery-independent data from scientific surveys and comparisons to published data from the use of fishery-independent methods (i.e., electronic tagging) have their own inherent biases, it is necessary to use multiple sampling methods and gear types to mitigate much of such biases. It is also important to note that some of the fishery-independent data were obtained by using sampling of fixed stations, possibly contributing some bias due to site selection that may not result in sampling across the entire habitat (McClelland and Sass, 2012). The ability to use data from both fishery-dependent and -independent sources allowed us to have a broader geographic range and, as a result, a broader biological range (the entire size range for each sex) for examining this species (Natanson et al., 2023).

We observed substantial geographic overlap in the distribution of individuals of all life stages and of both sexes of the tiger shark. In particular, all life stages and both sexes spent considerable time between Cape Hatteras and northeastern Florida. The majority of our data are from immature sharks caught at depths less than 200 m. Driggers et al. (2008, fig. 3) found YOY and juvenile sharks in this same area as well. Our data also indicate that tiger sharks have some degree of seasonal north–south migration, a finding that corresponds with results of other studies that indicate similar migrations in the Atlantic Ocean (Lea et al., 2015; Ajemian et al., 2020) and that indicate that tiger sharks are capable of both making extensive migrations and having periods of residency (Sulikowski et al., 2016; McClain et al., 2022). Mature tiger sharks of both sexes were primarily caught in the GOM in winter, off the east coast of Florida and off North Carolina in spring, and ranged from the GOM to New England in summer. In fall, most catches of adults were off the coast from the east coast of Florida to North Carolina, although adult females were found as far north as Long Island. The observation of adult tiger sharks seasonally in the GOM is consistent with reports of mature tiger sharks in the GOM in spring and summer (Springer 1938, 1940; Baughman and Springer, 1950; Clark and von Schmidt, 1965; Dodrill, 1977).

Timing and location of mating cannot be determined with our data. Mature males and females overlap throughout the majority of their range in all seasons, except for in winter when overlap is limited and a low sample size for mature males in winter may bias this result. Results of previous studies indicate that a mating season occurs in spring in the GOM and the Caribbean Sea (Baughman and Springer, 1950; Clark and von Schmidt, 1965; Rivera-López, 1970). The Bahamas, in the vicinity of Tiger Beach, have been proposed as a mating area for tiger sharks in the Atlantic Ocean, on the basis of mating scars found on females in winter (Sulikowski et al., 2016). Lea et al. (2015) tracked mature males and found they routinely returned to this area in winter and suggested mating as a possible driver. Our data do indicate overlap of mature males and females in this region of the Bahamas during winter. Additionally, our data indicate some overlap in the GOM off the panhandle and west coast of Florida near Apalachicola and Englewood, respectively, in the spring, but no overlap in the Caribbean Sea during spring.

Pregnant females with embryos in various stages of development have been observed off the west coast of Florida in spring and early summer (Springer, 1938, 1940; Baughman and Springer, 1950; Clark and von Schmidt, 1965; Dodrill, 1977) and off southwest Puerto Rico in the Caribbean Sea (Rivera-López, 1970). Data from the CSTP indicate the presence of YOY in this area; however, there is no evidence of neonates, indicating that these YOY may move into these areas from the GOM or from the main body of the Atlantic Ocean after parturition. Sulikowski et al. (2016) suggested that the area off Tiger Beach may be a gestation area, given the consistent number of large females with an extended residency and observations of pregnant females. Smukall et al. (2022) reported captures of near-term and recently postpartum females, verified by ultrasonography, near the Bimini Islands in the Bahamas during late spring and summer. Additionally, Smukall et al. (2022) reported frequent catches of young-of-the-year tiger sharks, including neonate-size individuals, but acoustic data indicate limited residency, potentially meaning that YOY moved out of the area soon after parturition.

Because near-term pregnant females are found in the GOM and Atlantic Ocean, it is probable that they birth, and possibly gestate, in their respective water bodies, although we do not have direct data from the GOM to corroborate it for that area. Our data indicate that the highest concentration of neonates between March and August overlap the locations of mature females in the waters off the East Coast of the United States at this time (Springer, 1938; Clark and von Schmidt, 1965). The presence of postpartum females between New Jersey and southern New England during June–August indicates a northward movement of mature females after birthing (Natanson et al., 2023).

Seasonal north–south migrations were undertaken by tiger sharks in the YOY, juvenile, and adult stages. The YOY concentrate between the east coast of Florida and Cape Hatteras throughout the year, expanding north in summer and fall (Suppl. Figs. 1C and 2C). Natanson et al. (1999) reported concentrated catches of neonate and YOY tiger sharks on the continental shelf between 29°N and 33°N. Driggers et al. (2008), using data on catch per unit of effort of neonates, expanded this region to 27–35°N, with the area of 31–33°N as the most important. The majority of YOY (82.0%) in this study were caught between 29°N and 34°N, with a concentration between 29°N and 31°N (65.6%). In contrast, Driggers et al. (2008) found the highest concentration of YOY tiger sharks at 32°N in waters off the East Coast. The differences in these areas of high concentration for YOY between our study and Driggers et al. (2008) may be a result of timing and type of sampling. Data from this study were collected year-round and are a combination of 55 years of fishery-dependent and -independent (fixed-station and random-stratified surveys and targeted research sampling) data, and the data from Driggers et al. (2008) are temporally discrete (August–September) and based on 13 years of a single fishery-independent survey (with a random-stratified design). Additionally, the concentrations may shift depending on optimal environmental conditions for each stage in a given year.

Shark nursery areas can be detected by using the presence of gravid females with near-term embryos, neonates, and small juveniles for viviparous species (Castro, 1993). Although presence data can be used to detect nursery habitat, isolated events do not provide information on the importance of this habitat in supporting juvenile shark populations (McCandless, 2007). Monitoring through long-term fishery-independent surveys, conventional mark-recapture work, and acoustic telemetry studies can help develop a better picture of how nursery habitat is used (McCandless, 2007). With fishery managers in mind, Heupel et al. (2007) developed a quantitative definition for identifying important shark nursery areas by using 3 criteria for neonates and YOY: 1) these juveniles are more commonly encountered in the area than other areas, 2) they have a tendency to remain in or return to the area for extended periods, and 3) the area is repeatedly used across years.

On the basis of these criteria, the tagging and recapture data used in our study indicate that the area from off the east coast of Florida north of Cape Canaveral to off Jekyll Island in Georgia (between 29°N and 31°N) provides nursery habitat for tiger sharks. Data from multiple recapture events indicate that this area has concentrations of neonate- and YOY-size sharks, that these sharks spend several months there following parturition that occurs within the area or following migration to the area, and that these sharks repeatedly use this area across years. Expanding this region to Cape Island, South Carolina (33°N), incorporates data from Driggers et al. (2008) indicating the importance of this region for both neonates and YOY. Our data on neonates, YOY, and multiple recaptured immature tiger sharks, combined with data from Driggers et al. (2008) and McClain et al. (2022), support the existence of separate, broad birthing areas and nursery habitats in the GOM and in waters off the East Coast (Heupel et al., 2007; Driggers et al., 2008). Knowledge of defined areas of concentration informs management decisions regarding refinement of essential fish habitat and spatial management and conservation goals to protect the vulnerable life stages of this species (Heupel et al., 2007, 2018; Kinney and Simpfendorfer, 2009). The area of concentration for YOY in this study encompasses the range where neonates were concentrated.

This report is the first to document that immature tiger sharks undertook long-distance movements from the western to the eastern Atlantic Ocean. These data indicate movements of tiger sharks that are much broader and of longer distances and taken at smaller sizes than previously known for this species. Although results from other studies indicate that adult males and females and subadult (no longer a juvenile but not yet an adult) females undertake long-distance movements (Hammerschlag et al., 2012; Lea et al., 2015; Ajemian et al., 2020), the outcomes of many studies indicate that juvenile tiger sharks cannot undertake long-distance migrations because of inefficient swimming in the more anguilliform body of the young tiger shark (Lea et al., 2015, 2018; Aines et al., 2018) or because of the effect of environmental factors on body size (i.e., small sharks are less tolerant of low sea-surface temperatures) (Lea et al., 2018).

Our data indicate that YOY use coastal waters of the United States fairly continuously from Louisiana to Long Island, depending on the season, and are found offshore and north to New England in summer. Individual tiger sharks of both sexes tagged as YOY traveled >500 nmi, indicating that this life stage is capable of movements of longer distances than previously thought. For example, one YOY, was tagged in February and recaptured 6 months later southeast of Newfoundland, having traveled nearly 1300 nmi. Another was tagged in November and recaptured after 1 year in the Caribbean Sea off Venezuela, having traveled nearly 1400 nmi. By the juvenile stage, the range of tiger sharks becomes Atlantic basin-wide. The coastal range extends from New England down and into the Caribbean Sea. The north–south migration along the Atlantic coast of the northeastern United States taken by immature fish is complicated by offshore and transatlantic movements. These sharks move north in summer past New England to the east; some remain in coastal waters, and others venture offshore presumably with the Gulf Stream and as far north as the Grand Banks of Newfoundland. This northward offshore movement with the Gulf Stream has been documented for adult males (Lea et al., 2015, 2018) and for adult and subadult females (Hammerschlag et al., 2012) by using satellite tracking data, and results of our study indicate that immature tiger sharks of both sexes also follow this pattern. Additionally, our data indicate movement of immature tiger sharks, including YOY, into and out of the Caribbean Sea from both the main body of the Atlantic Ocean and the GOM.

It has been suggested that ontogenetic movements into more oceanic habitats are possibly related to foraging (Lowe et al., 1996; Lea et al., 2015), and more recently McClain et al. (2022) suggested a reproductive component to migration. On the basis of their electronic tagging data, Lea et al. (2018) further suggested an ontogenetic shift in foraging strategy and diet that leads to longer migrations by adult males. Although a foraging component may certainly drive these migrations, our data indicate that immature tiger sharks make extensive migrations throughout the Atlantic Ocean, refuting the ontogenetic component of the basis for longer distance migration. Long migrations are evident even for young juveniles; for example, the transatlantic migration of over 3600 nmi of a tiger shark tagged as a YOY and recaptured 2 years later.

In conjunction with the data we present on juveniles crossing the Atlantic Ocean, and data from other studies, we suggest that a northeasterly track could be the route that these sharks take to the eastern Atlantic Ocean. Following the major current system in the North Atlantic Ocean, this track starts with the Gulf Stream, moving north and east with the North Atlantic Drift and then south to the Canary Current before following the North Equatorial Current back to the WNA as has been previously postulated for the migration of the blue shark (Casey, 1985). Afonso et al. (2017) suggested an equatorial route for juvenile tiger sharks linking the eastern and western Atlantic Ocean. Additionally, Domingo et al. (2016), using observer data, documented that tiger sharks in the North Atlantic Ocean were more broadly distributed than previously thought. A limited number of mature sharks of both sexes (n=10; 2 males, 7 females, and 1 individual of unknown sex) in this study made movements greater than 500 nmi within the WNA, although none crossed the North Atlantic basin. Although mature individuals have not yet been documented to travel across the North Atlantic basin, they have been repeatedly shown to have the ability to travel the long distances required for this movement (Hammerschlag et al., 2012; Ferreira et al., 2015; Lea et al., 2015). The lower percentage of mature sharks in our sample may also be a factor in this result. Much of the data are limited to immature sharks crossing the North Atlantic basin, but these movements and distributions strongly indicate that there is only one population in the North Atlantic Ocean.

Conventional tags are significantly less costly than electronic tags; therefore, more individuals of a species can be tagged with them at various times, locations, and life stages. Additionally, long-term studies with increased numbers of recapture events can enhance the body of knowledge. Sample size is important in interpreting results from tagging studies, and an increase in sample size allows for a larger range and scope of questions that can be answered (Sequeira et al., 2019). When examining tagging data for population trends and movements, an increased number of tags makes it possible to see variation in movements between individuals, life stages, or sexes (Sequeira et al., 2019); it is therefore important to tag individuals of all sizes and sexes to obtain a complete overview of the movements of a species. Additionally, the duration of tag deployment and the location of release of tagged fish can influence movements for certain shark species (Rooker et al., 2019). It is apparent from studies of a variety of species, including the tiger shark, that individuals can be resident or migratory for given periods of time and stages of maturity.

Despite the number of tiger sharks tagged in the CSTP, it took 34 years and 5832 tiger sharks to be tagged before the first tiger shark tagged in the WNA was recaptured in the ENA. It is certainly doubtful that we have seen all possible scenarios, particularly with mature sharks. These recapture events are important not only in that the tiger shark can cross the North Atlantic Ocean, therefore indicating potential mixing within the population, but in that immature sharks are capable of this movement. Pooling all tagging data on the tiger shark in the WNA creates a better picture of the movements of this species than examining those studies individually. For example, Lea et al. (2015, 2018) stated that only mature males make long-distance migrations and that movements into and out of the Caribbean Sea were not observed; however, with the addition of Hammerschlag et al. (2012), Rooker et al. (2019), and Ajemian et al. (2020), it is apparent that females also travel long distances and exchange between these water bodies. Combining data from conventional and electronic tagging studies can provide a far more robust, comprehensive picture of the movements of a species and of the drivers for those movements than the representation formed when using data from just one type of tagging, leading to advancements in management measures (Hammerschlag et al., 2022) to better support sustainable fisheries.

Conclusions

We examined seasonal movement patterns of the tiger shark on the basis of sex and life stage and have added to the literature describing seasonal north–south movements of the tiger shark. Additionally, our data indicate that immature tiger sharks tagged in the WNA make long-distance migrations to the ENA. We propose that there is a potential route that runs up the coast of North America in the WNA and crosses over to the ENA, revealing potential mixing within the population not indicated by data from electronic tagging to date. We also identified a broad nursery area and potential birthing grounds off the East Coast of the United States. Tagged tiger sharks crossed multiple international jurisdictions, indicating that management measures need to have a basin-wide scale. The results of this project highlight the need for the use of more long-term, conventional tagging along with electronic tagging to fully understand the movements of shark species and to adequately implement management strategies.

Resumen

Los movimientos del tiburón tigre (*Galeocerdo cuvier*) durante las etapas de su vida, son en gran medida desconocidos. Sin embargo, es necesario conocerlos para determinar su hábitat esencial y las prácticas sostenibles de manejo pesquero. En un esfuerzo por dilucidar la distribución y los movimientos del tiburón tigre, analizamos datos de marcaje dependientes e independientes de la pesquería (tamaño de la muestra [*n*]=10,516) y registros de recaptura (n=762) de tiburones tigre capturados en el océano Atlántico norte entre 1963 y 2018. Se examinó la distribución estacional del tiburón tigre por etapa de vida—juveniles del año, juveniles (inmaduros) y adultos (maduros)—y se utilizaron patrones de distribución para identificar posibles hábitats de críanza. Se capturaron tiburones tigre en una amplia zona desde los Grandes Bancos de Terranova (Canadá) hacia el sur, en Brasil y desde la costa hasta alta mar y hacia el este del océano Atlántico Norte. Se observaron movimientos estacionales de norte a sur en todas las etapas de la vida, y se descubrió que 14 tiburones inmaduros habían migrado del océano Atlántico Norte occidental al oriental. Se identificó una amplia zona de crianza y una posible zona de nacimiento en la plataforma continental entre Florida y Georgia con base en recurrencia de neonatos en verano a lo largo de los años y en la recaptura de múltiples tiburones tigre juveniles del año marcados en el mismo lugar durante un periodo de al menos 2 años.

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