



Abstract—Reproductive data collected through anatomical dissection, from 48 female and 66 male tiger sharks (*Galeocerdo cuvier*) captured in the western North Atlantic Ocean, were used to assess stage of maturity. The fork length (FL) of examined females and males ranged from 88 to 318 cm and from 84 to 349 cm, respectively. Median length at maturity (L_{50}) was calculated by using binomial maturity data from dissections in addition to maturity assignments based on clasper condition examination of 320 males (46–280 cm FL) and published maturity data for 14 males (170–313 cm FL) and 28 females (242–312 cm FL). Further, sex-specific median age at maturity (A_{50}) was calculated by using direct age estimates and the aforementioned binomial maturity data from the dissected specimens. Females reached L_{50} at 261.4 cm FL and A_{50} at 11.6 years. Males reached L_{50} at 258.9 cm FL and A_{50} at 9.5 years.

Updated reproductive parameters for the tiger shark (*Galeocerdo cuvier*) in the western North Atlantic Ocean

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The tiger shark (*Galeocerdo cuvier*) is a large, opportunistic predator that is common globally in warm temperate and tropical marine waters (Bigelow and Schroeder, 1948). Off the east coast of North America, within the western North Atlantic Ocean (WNA), the species ranges from Nova Scotia, Canada, to Texas, including in the Gulf of Mexico and the Caribbean Sea (Kohler and Turner, 2019).

In the WNA, tiger sharks are commonly caught in commercial and recreational fisheries but are usually released alive (Natanson et al., 1999). The WNA had an increase in recreational shark fishing in the 1970s, followed by the expansion of the directed shark fishery in the 1980s (Stone et al., 1998); these fisheries peaked in the late 1980s, after which abundance of tiger sharks declined by an estimated 80% into the early 1990s (Musick et al., 1993). After the implementation of the National Marine Fisheries Service Shark Management Plan in 1993, increases in tiger shark

abundance were observed throughout the late 1990s and 2000s (Peterson, 2017). Although information is available on various aspects of the biology of tiger sharks, such as diet and growth dynamics, and the size of the smallest mature fish in the sample or *size at maturity* has been reported from several studies (Springer, 1960; Clark and von Schmidt, 1965; Branstetter et al., 1987; Castro, 2011), median length and age at maturity (L_{50} and A_{50}) have not been calculated for this species.

Information pertaining to the reproductive biology of tiger sharks is largely limited to reports of examined specimens or anecdotal observations included in other studies (e.g., Bigelow and Schroeder, 1948; Springer, 1960; Clark and von Schmidt, 1965). For example, worldwide, female tiger sharks are thought to reproduce biennially and reported brood sizes range from 6 to 104 embryos, although most commonly they have a brood size of 30–40 embryos (Springer, 1938; Baughman and Springer, 1950; Rivera-López, 1970;

Dodrill, 1977; Applegate et al., 1979; Simpfendorfer, 1992; Castro, 2011). Simpfendorfer (1992) found a significant relationship between litter size and maternal length, a result that, along with the possibility of spontaneous abortion due to capture, may explain the smaller litter sizes occasionally observed.

Reliable estimates of L_{50} and A_{50} are critical to gaining a complete understanding of ontogenetic shifts in behavior, migratory patterns, diet, and habitat utilization, including identification of pupping, nursery, and mating areas (e.g., Natanson et al., 2020). Of equal, and perhaps greater importance, is an understanding of the reproductive potential of the population and how long it will take an exploited population to rebuild under different management strategies. Reproductive information on the tiger shark in the WNA is primarily from Branstetter et al. (1987), who reported that maturity occurs at approximately 256.9–261.1*¹ cm fork length (FL) and 252.6* cm FL for females and males, respectively. Although size at maturity was not mentioned as different between the areas, ages at maturity differed between the Gulf of Mexico and the rest of the WNA because of growth rate differences in that study.

Shields (2018) studied the maturation of the tiger shark in the WNA, using plasma hormone concentrations supplemented by clasper calcification and ultrasonography methods for males and females, respectively. She reported that males mature between 210.2* and 244.2* cm FL and females mature between 218.7* and 252.6* cm FL, ranges that fall below those reported by Branstetter et al. (1987) for tiger sharks from this region. However, this difference in length at maturity could be related to differences between the 2 studies in the methods used to assess maturity (dissection versus noninvasive sampling), as the hormonal methods have yet to be validated. Although it is possible that size at maturity for tiger sharks has changed over the 3 decades separating the 2 studies, direct comparison between maturity estimates through the use of lethal (anatomical dissection) and nonlethal (sex steroid analysis) methods cannot be made until it has been validated that both sampling strategies accurately assign maturity status. For example, sperm has been observed in the tiger shark prior to maturation of requisite secondary sex characteristics, such as calcified claspers (Clark and von Schmidt, 1965). Although a metric, such as sex steroid concentration, from a nonlethal method could indicate the commencement of spermatogenesis, an immature male would not be capable of copulation without possessing calcified claspers. Similarly, a female could be undergoing vitellogenesis prior to the maturation of the reproductive tract and be erroneously considered mature through the use of sex steroid analysis when actually incapable of reproducing.

In this study, we updated the reproductive parameters of both male and female tiger sharks from the WNA, using measurements obtained through anatomical dissection. Additionally, we produced sex-specific, quantitatively

derived estimates of L_{50} and A_{50} for the tiger shark that can be used to generate maturity schedules, which are a vital component of age-structured stock assessments.

Materials and methods

Tiger shark specimens were collected by using rod and reel during recreational fishing tournaments or longline gear during research surveys and commercial fishing operations. Upon landing, FL was measured (in centimeters) over the body (OTB) (Natanson et al., in press) from the tip of the snout to the fork in the caudal fin. Sex was assigned to all individuals on the basis of the presence or absence of claspers. Selected moribund or dead individuals were dissected to collect a suite of reproductive data upon which maturity status was assigned. All dissections were conducted by biologists from the Apex Predators Program, NOAA Northeast Fisheries Science Center, all of whom are experienced with reproductive dissection methods, using a standardized sampling protocol. We used standardized terminology for anatomical measurements from Hamlett (1999) and Hamlett and Koob (1999).

Because of difficulty in obtaining accurate weights for tissues collected aboard vessels, we relied upon linear measurements of various tissues within reproductive tracts and direct observation of external sexual characters (i.e., clasper condition) to assess the maturity of tiger sharks. All internal measurements (in millimeters) were taken from the right side of each shark at the widest portion of the organ and following the protocols detailed in Natanson and Gervelis (2013). For females, internal measurements included the anterior oviduct width, oviducal gland width, uterus width and length, ovary width and length, and diameter of the largest yolked oocyte. Internal measurements taken from male specimens included testis diameter and length, epididymis width, and ampulla epididymis width. Additionally, when functional, the right siphon sac length was measured. Siphon sacs are blind sacs between the dermis and the abdominal musculature and are requisite reproductive structures that are only functional when a male is mature or reaching a mature state. Further, the outer clasper length from the insertion to the posterior tip was measured and clasper condition was noted (i.e., uncalcified, transitional, or calcified). Assignment of male maturity for our study required fully calcified claspers that freely rotated 180° from their natural position and rhipidions that could be readily splayed opened (e.g., Clark and von Schmidt, 1965). Males that were approaching maturity as indicated by elongating yet flaccid claspers were considered to be transitional and classified as immature.

Pregnant and postpartum females, as indicated by the presence of embryos within the uteri or distended uteri, were assigned a mature status. Those that had given birth, with indications of recovery, were considered mature and in a resting (reproductively inactive) stage (Castro, 2009). Assignment of female maturity required ovaries capable of producing vitellogenic follicles and a fully developed

¹ An asterisk (*) denotes that the fork length has been converted from a total length.

reproductive tract (i.e., ovary, oviducts, oviducal glands, and uteri). Morphometric measurements of the reproductive organs of both sexes were plotted against FL to show how growth of the reproductive organs changed as an individual approached maturity. In most cases, determination of stage was made during dissection by using these criteria. For specimens that were not classified at the time of dissection, maturity status was later assigned by using the relationships between FL and organ measurements and the detailed notes taken at dissection. This process helped differentiate maturing or transitional nulliparous females from those that were truly mature.

Because of the overall small sample size and limited data for specific size classes, additional maturity data were obtained from the literature and used for analyses of L_{50} . All published data were carefully scrutinized to ensure that we agreed with the author's criteria for maturity and that the measured (i.e., not estimated) length and maturity status of individuals were explicitly stated. Published values originally reported in straight total length (TL_{STR}) were converted to FL_{OTB} by using a conversion from Natanson et al. (in press):

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

coefficient of determination (r^2)=0.996,

number of samples (n)=605.

Converted values are denoted with an asterisk throughout the text. All measurements are presented in FL_{OTB} unless otherwise noted. Additional maturity data were obtained from live males tagged and released during

bottom longline surveys conducted by the NOAA Southeast Fisheries Science Center between July and September off the east coast of Florida and in the northern Gulf of Mexico, with maturity status assigned solely on the basis of clasper condition.

For both sexes, L_{50} was estimated by using logistic regression fit to measured length and binomial maturity data (i.e., 0=immature, and 1=mature). Similarly, A_{50} was estimated by using a subset of the binomial maturity data that had corresponding ages from Kneebone et al. (2008), as both studies used many of the same specimens. Logistic models were fit to data for each sex separately through maximum likelihood methods by using functions available in R (vers. 4.1.3; R Core Team, 2022) as per Natanson et al. (2020). Confidence intervals (CIs) of 95% around L_{50} and A_{50} were bootstrapped from fits of a binomial generalized linear model to 1000 resamples of the maturity data (Harry et al., 2013) by using the boot package (vers. 1.3-28.1; Canty and Ripley, 2022) in R. For all models, normalized diagnostic plots of the residuals were examined visually to evaluate the appropriateness of model assumptions (Zuur et al., 2010).

Results

Dissections were conducted on 66 female and 48 male tiger sharks to assess their state of maturity and reproductive condition. Females and males ranged in size from 84.0 to 349.2 cm FL and from 88.3 to 318.0 cm FL, respectively (Fig. 1). The majority of specimens were collected between

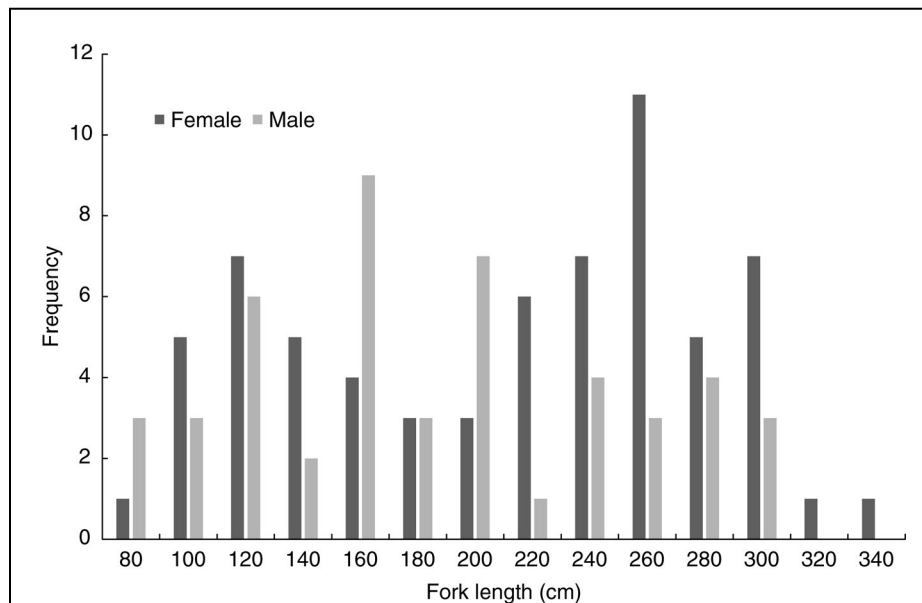


Figure 1

Size-frequency histogram for female and male tiger sharks (*Galeocerdo cuvier*) caught in waters from Massachusetts down along the Atlantic coast and into the Gulf of Mexico, between 1974 and 2019, and examined for reproductive condition.

1974 and 2019 from recreational anglers at shark fishing tournaments (60% of sexes combined, 59% of females, and 60% of males) and between May and June (78% of females and 85% of males) along the East Coast between Massachusetts and the west coast of Florida (Fig. 2). Females were caught from March through September, and males were caught from March through August.

Females

Among the females dissected, immature ($n=50$) and mature ($n=16$) specimens had size ranges of 84.0–279.4 cm FL and 270.0–349.2 cm FL, respectively. Results of regression analyses relating FL to reproductive organ measurements indicate that ovary width ($F=393.61$, $P<0.01$, $r^2=0.87$), ovary length ($F=177.19$, $P<0.01$, $r^2=0.74$), and uterus length ($F=100.22$, $P<0.01$, $r^2=0.79$) were not of value in assessing maturity as their relationships were linear and therefore isometric. The relationships between FL and anterior oviduct width ($F=278.89$, $P<0.01$, $r^2=0.82$; Fig. 3), oviducal gland width ($F=847.35$, $P<0.01$, $r^2=0.93$; Fig. 4), and uterus width ($F=401.14$, $P<0.01$, $r^2=0.87$; Fig. 5) were best fit with an exponential model and had inflection points at approximately 250 cm FL, indicating their utility for defining onset of maturation.

Immature females were characterized by undeveloped ovaries embedded within the epigonal organs, with the right ovary containing numerous macroscopically visible yet undeveloped oocytes that were white to clear in color.

The left ovary appeared inactive in all specimens and remained undeveloped through ontogeny. The anterior oviduct was thin and tubular, and the immature oviducal gland presented as a slight but discrete widening approximately midway along the length of the anterior oviduct. In the smallest individuals, the uteri were not differentiated from the anterior and posterior oviducts and were only slightly differentiated from the rest of the reproductive tract prior to onset of maturation.

The transitional length range, where individuals are approaching maturity, is bracketed by the sizes of the smallest mature female and largest immature female. The smallest mature female in our sample was 270.0 cm FL, which is substantially larger than the smallest mature shark from the literature at 241.6* cm FL (Clark and von Schmidt, 1965). The largest immature female in our sample was 279.4 cm FL. Maximum follicle diameter in the transitional range was 7.5–14 mm (Table 1). Measurements from transitional individuals overlap those of mature and immature individuals, and variation in the development rates of different organs make it difficult to differentiate maturity from only one organ. However, anterior oviduct and oviducal gland sizes greater than 18.6 and 69.1 mm, respectively, could be considered to be from mature females and those below 4.0 and 25.0 mm, respectively, could be considered to be from immature females with reasonable certainty (Table 1).

Mature females ranged from 270.0 to 349.2 cm FL ($n=16$). Of those sampled, 1 specimen was pregnant, 7 sharks were

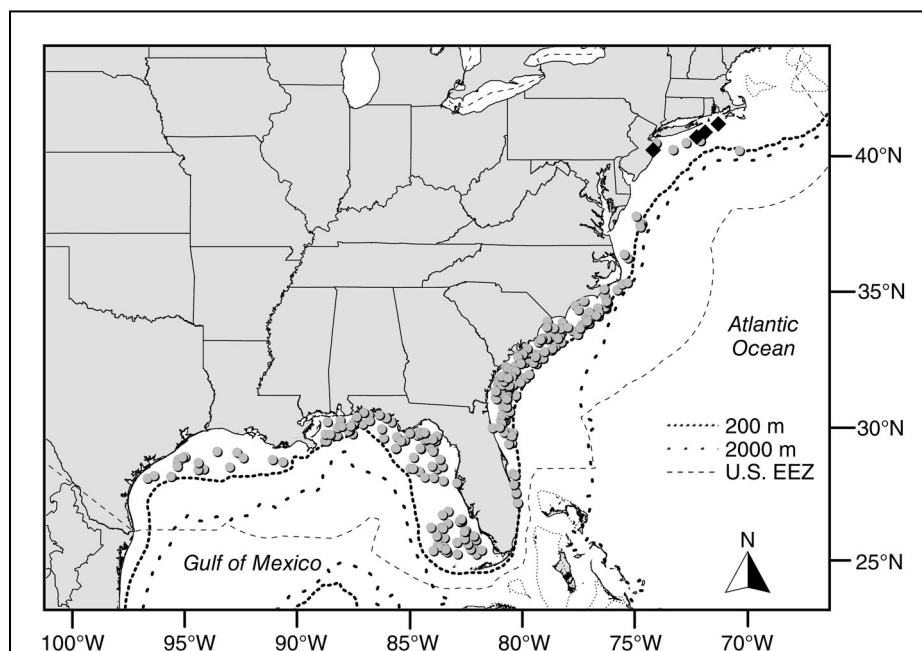


Figure 2

Map of the capture locations for tiger sharks (*Galeocerdo cuvier*) collected in the western North Atlantic Ocean, between 1974 and 2019, and examined for reproductive condition. Black diamonds represent the general locations where a total of 61 individuals were caught during 10 shark tournaments in the U.S. Northeast.

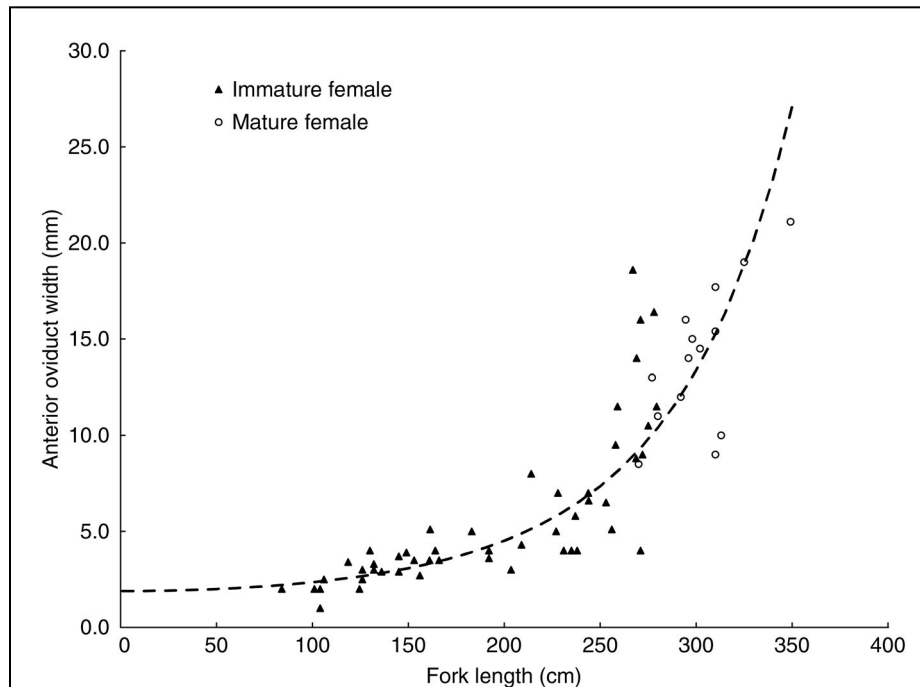


Figure 3

Relationship of anterior oviduct width (in millimeters) to fork length (FL, in centimeters) for female tiger sharks (*Galeocerdo cuvier*) ($n=63$) caught in waters from Massachusetts down along the Atlantic coast and into the Gulf of Mexico between 1974 and 2019. $Anterior\ oviduct\ width\ (mm) = \exp(0.0637934 + (0.000022 \times FL^2\ (cm)))$.

postpartum, and 8 females had just reached maturity or were resting. The pregnant female was 312.4 cm FL and was caught in June in the Gulf of Mexico with 19 embryos in each uterus. Postpartum females ranged in FL from 292.0 to 325.0 cm and were caught in June ($n=1$), July ($n=5$), and August ($n=1$). Five of the postpartum sharks were caught between Long Island, New York, and southern Massachusetts, and single individuals were caught off New Jersey and North Carolina and at an unknown location. Four of the 5 postpartum sharks were noted to be recently postpartum on the basis of the observation of flocculent materials in the uterus or organ condition (e.g., flaccid uteri), and no detailed information was available for the fifth one.

Males

Males that were dissected ranged in size from 88.3 to 318.0 cm FL. Immature ($n=40$) and mature ($n=8$) males had size ranges of 88.3–270.0 cm FL and 274.0–318.0 cm FL, respectively. The relationships between FL and testis length ($F=273.52$, $P<0.01$, $r^2=0.87$) and testes diameter ($F=164.31$, $P<0.01$, $r^2=0.80$) were significant but isometric and therefore not reliable in assigning maturity. The relationships between FL and epididymis width ($F=112.78$, $P<0.01$, $r^2=0.75$) and ampulla epididymis width ($F=108.43$, $P<0.01$, $r^2=0.73$) were exponential and also significant; however, there were no distinct inflection

points to indicate onset of maturity, and the widths of both organs vary widely at larger body sizes because of known seasonal regression and recrudescence of these tissues. Hence, these measures were also considered of minimal value in assessing maturity.

There was a significant exponential relationship between FL and clasper length ($F=1336.43$, $P<0.01$, $r^2=0.97$; Fig. 6) with an abrupt inflection point indicative of the onset of maturation. Clasper length gradually increased in size relative to FL until approximately 225 cm FL, when the clasper length increased more rapidly in growth, particularly after 250 cm FL; however, the small sample size for sharks in this length range makes interpretation difficult (Fig. 6). Claspers were not completely calcified until they were over 200 mm in length, although clasper size was not entirely indicative of calcification status or maturity. The smallest fully calcified clasper was 210 mm on a 290-cm-FL male. In contrast, claspers on 4 males ranging from 268 to 297 cm FL were large (217–235 mm), but these males were considered immature because of incomplete clasper calcification. The siphon sacs were only partially formed until a male had reached approximately 200 cm FL, at which point siphon sac length grew isometrically with body length (Fig. 7). Although the measurements of clasper length and siphon sac length had some overlap between stages, claspers greater than 225 mm and siphon sacs greater than 430 mm could safely be considered to be from

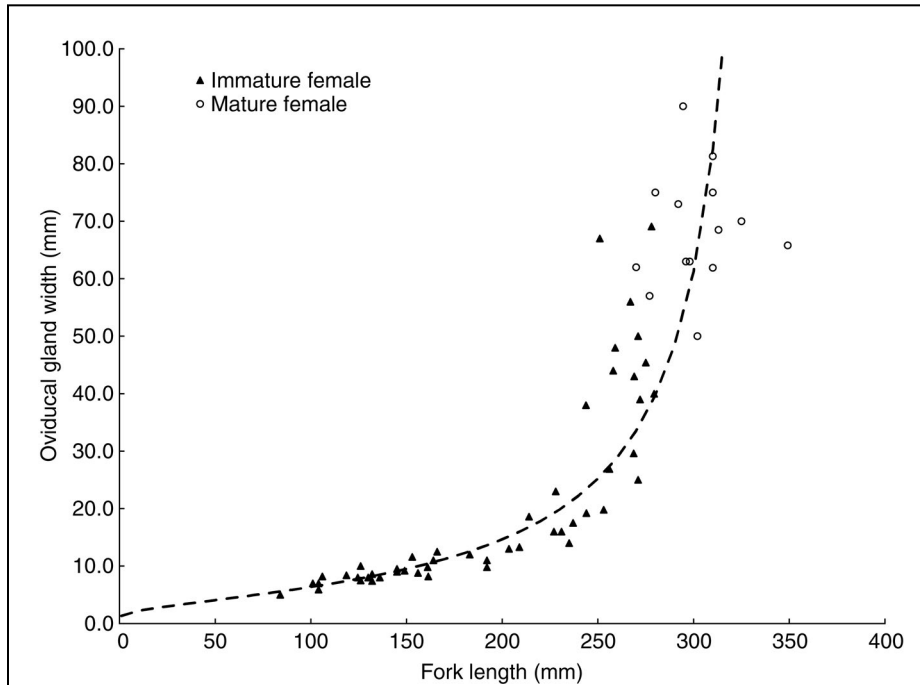


Figure 4

Relationship of oviducal gland width (in millimeters) to fork length (FL, in centimeters) for female tiger sharks (*Galeocerdo cuvier*) ($n=63$) caught in waters from Massachusetts down along the Atlantic coast and into the Gulf of Mexico between 1974 and 2019. $Ovi-$
 $ducal\ gland\ width\ (mm) = 1/(0.0747339 - (0.128163 \times \ln FL\ (cm)))$.

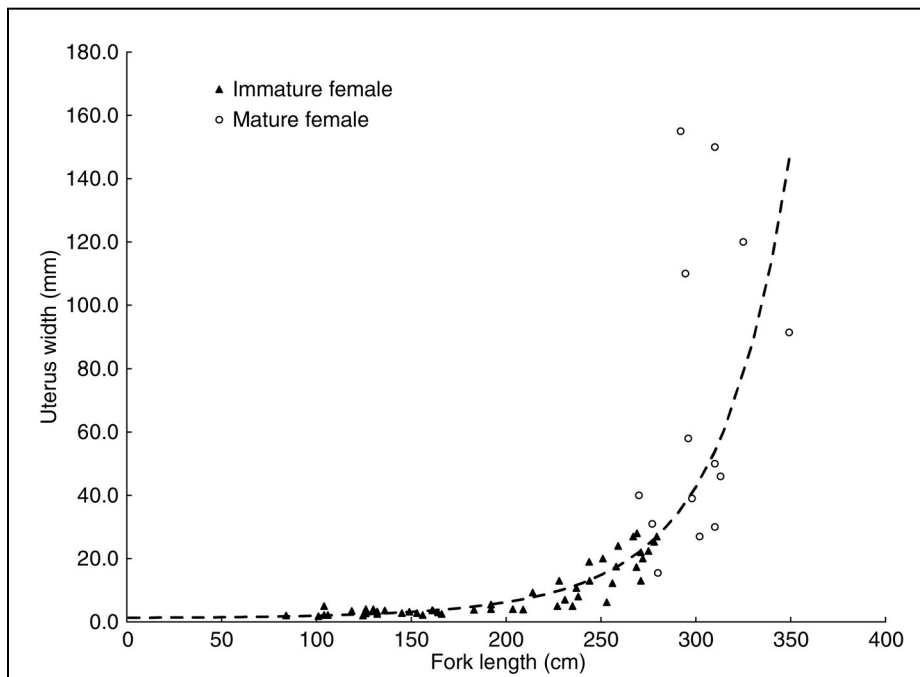


Figure 5

Relationship of uterus width (in millimeters) to fork length (FL, in centimeters) for female tiger sharks (*Galeocerdo cuvier*) ($n=63$) caught in waters from Massachusetts down along the Atlantic coast and into the Gulf of Mexico between 1974 and 2019. $Uterus\ width\ (mm) = \exp(0.285987 + (0.00038 \times FL^2\ (cm)))$.

Table 1

Comparison of measurements of female reproductive organs by stage for tiger sharks (*Galeocerdo cuvier*) collected in the western North Atlantic Ocean from 1974 through 2019. Stages are based on information from dissection. The measurements of the anterior oviduct, oviducal gland, and uterus are widths. FL=fork length; n=number of samples.

Maturity	Stage	Size range (cm FL)	Anterior oviduct (mm)			Oviducal gland (mm)			Uterus (mm)			Ovarian follicle diameter (mm)		
			Median	Range	n	Median	Range	n	Median	Range	n	Median	Range	n
Immature	Juvenile	<270.0	4.0	1.0–18.6	43	11.0	5.0–67.0	43	4.0	1.8–28.0	43	5.0	0.4–14.0	41
Immature	Transitional	≥270.0 to <279.4	10.5	4.0–16.4	7	50.0	25.0–69.1	7	22.4	13.0–40.0	7	9.6	7.5–14.0	6
Mature	Adult	≥279.4	14.5	9.0–21.1	13	68.5	40.0–90.0	13	50.0	15.5–155.0	13	10.0	6.0–14.7	13

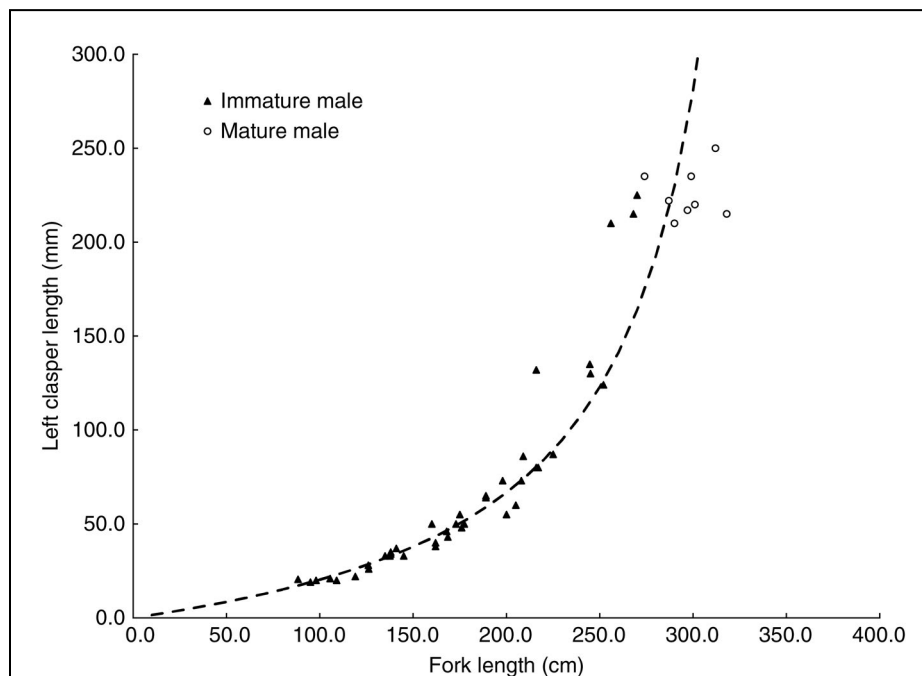


Figure 6

Relationship of left outer clasper length (in millimeters) to fork length (FL, in centimeters) for male tiger sharks (*Galeocerdo cuvier*) (n=48) caught in waters from Massachusetts down along the Atlantic coast and into the Gulf of Mexico between 1974 and 2014. $Left\ clasper\ length\ (mm) = 1/(-0.192966 + (6.85822/FL\ (cm)))$.

mature fish, and those less than 210.0 and 390.0 mm, respectively, could be considered to be from immature fish, particularly if there was information on clasper calcification (Table 2).

Because of a lack of samples in the size range at which male tiger sharks appear to be maturing, the exact size range at which transition occurred could not be defined from dissection data alone. We therefore examined data for 325 males, collected during Southeast Fisheries Science Center bottom longline surveys (n=322) or discussed

in the literature (n=3; Shields, 2018), that were staged on the basis of clasper condition alone. The fork lengths for 3 of these males (184.0, 210.2*, and 217.0 cm) were unrealistically low compared to dissection and published data and were therefore excluded from the ogive analysis. The remaining data indicate a lower size at maturity (232.0 cm FL) than previously published values, expanding the transitional maturity range to 232–280 cm FL, which is based on the size of the largest immature shark with uncalcified claspers (280 cm FL).

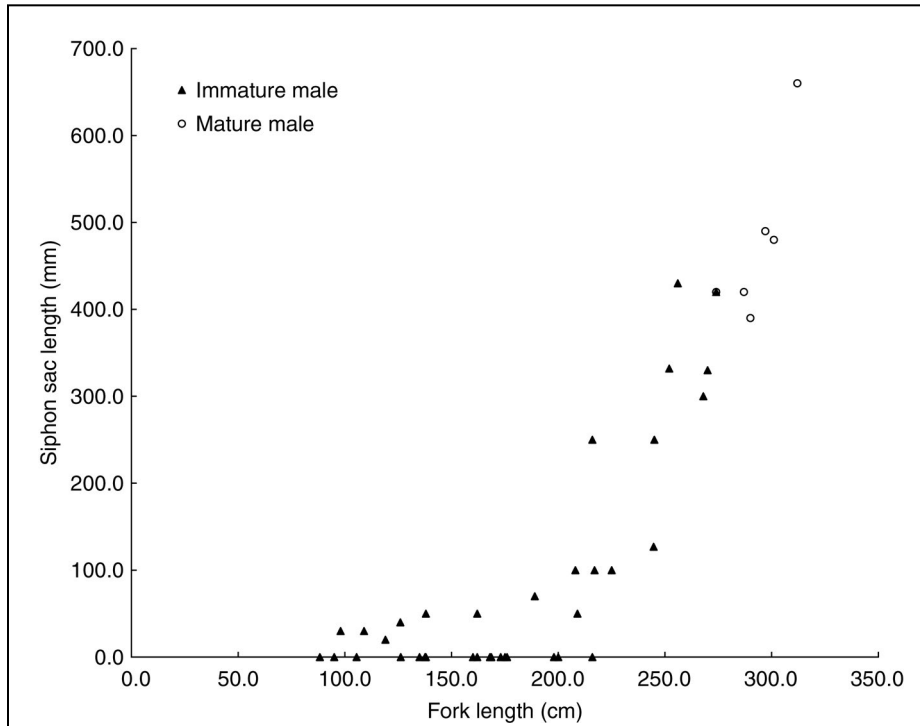


Figure 7

Relationship of siphon sac length (in millimeters) to fork length (in centimeters) for male tiger sharks (*Galeocerdo cuvier*) caught in waters from Massachusetts down along the Atlantic coast and into the Gulf of Mexico between 1974 and 2014.

Table 2

Comparison of length measurements of male reproductive organs by stage for tiger sharks (*Galeocerdo cuvier*) collected in the western North Atlantic Ocean from 1974 through 2019. Stages are based on information from dissection. Only one sample was determined to be in the transitional stage on the basis of our definition of the stage; therefore, data for this stage are not shown. FL=fork length; n=number of samples.

Maturity	Stage	Size range (cm FL)	Left clasper (mm)			Siphon sac (mm)		
			Median	Range	n	Median	Range	n
Immature	Juvenile	<274.0	50.0	19.0–225.0	40	25.0	0.0–430.0	34
Mature	Adult	≥280.0	220.0	210.0–250.0	7	480.0	390.0–660.0	5

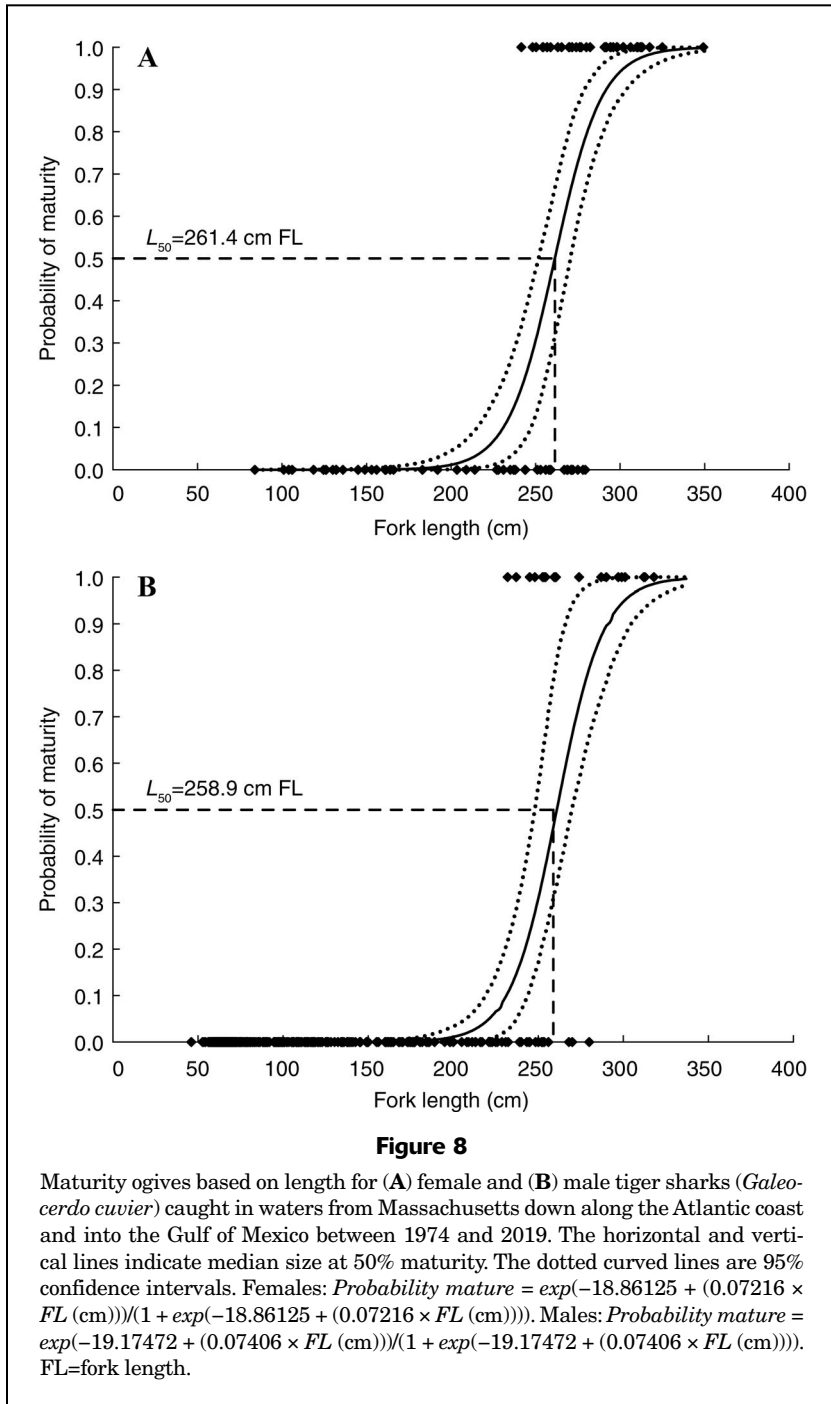
Median length and age at maturity

Data for the L_{50} analysis included the 320 males (46.0–280.0 cm FL) staged on the basis of clasper condition. To fill in other important size classes for which data were limited or missing, we also included data from 42 tiger sharks (14 males and 28 females, 170.4*–312.8* cm FL and 241.6*–311.9* cm FL, respectively) obtained from 5 publications (Clark and von Schmidt, 1965; Rivera-López, 1970; Dodrill, 1977; Branstetter et al., 1987; Castro, 2011). Combining all data sources, the estimated L_{50} for females was 261.4 cm FL (95% CI: 251.6–270.6 cm FL) (Fig. 8A). For males, the estimated L_{50} was 258.9 cm FL (95% CI:

247.9–269.8 cm FL) (Fig. 8B). The A_{50} for females estimated by using direct age data was 11.5 years (95% CI: 10.2–14.2 years) (Fig. 9A). For males, the estimated A_{50} was 9.5 years (95% CI: 8.6–12.3 years) (Fig. 9B).

Discussion

The data presented herein represent the largest compilation of reproductive samples for tiger sharks thus far available for this species in the WNA. Unfortunately, sampling issues common for large migratory species create limitations to these data. It is difficult to obtain an adequate



number of samples from all sizes and reproductive stages of a migratory shark, as access is often limited to shore-based or fishery-dependent sampling. Tiger sharks are known to be highly migratory and to have discrete pupping areas (Driggers et al., 2008; Kohler and Turner, 2019). Young tiger sharks are thought to be primarily coastal, and results from recent studies indicate that mature tiger sharks of both sexes are highly migratory (Hammerschlag et al., 2012; Lea et al., 2015; Rooker et al., 2019).

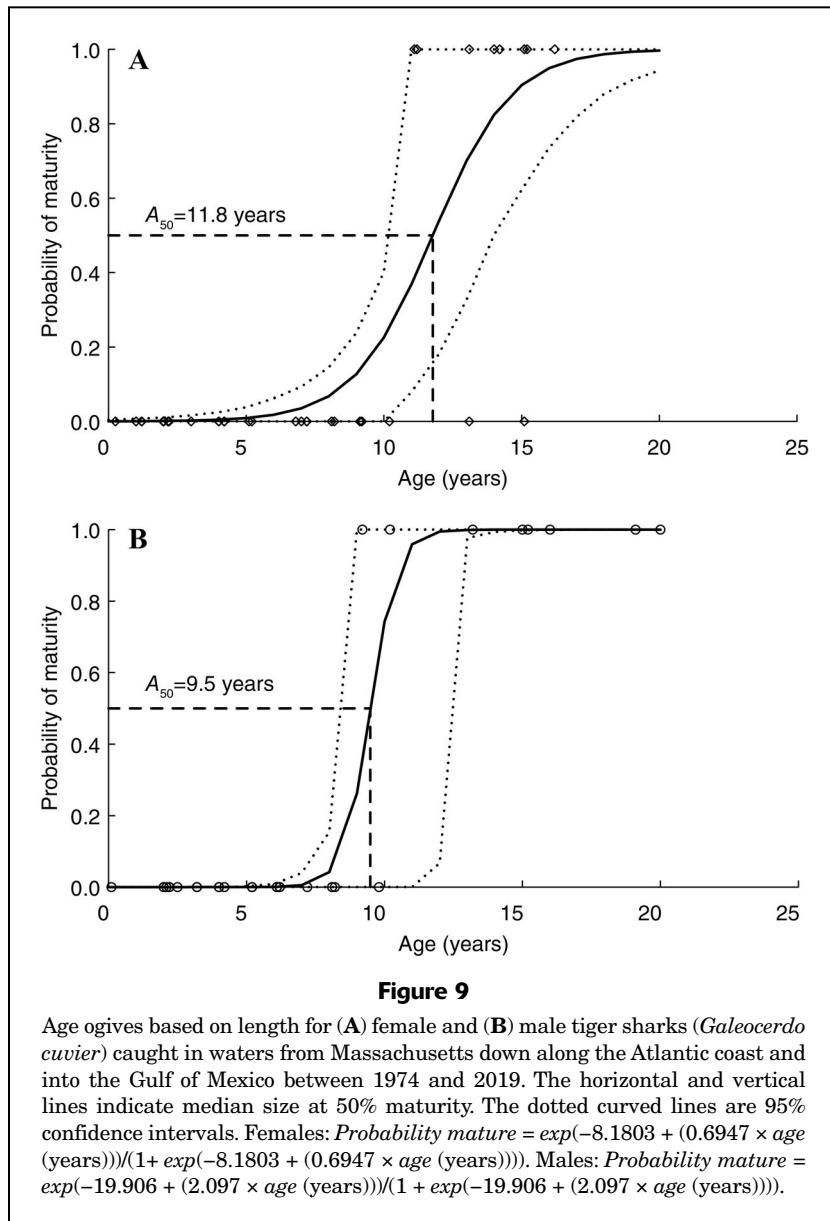
Our study was very fishery dependent. Over 60% of the sharks dissected were caught on recreational and

commercial vessels that were primarily in coastal waters. Fishing location likely limits the catch to mostly juveniles, as seen in this study. The smaller sample size of the maturing and mature fish was likely influenced by catch location and the effects of a commercial fishery that caused an 80% decline in the population in the 1990s (Musick et al., 1993), and the limited number of these fish may bias the sample. We attempted to mitigate this issue by adding data from published studies and research surveys, although the coastal nature of these surveys is very similar to the locations of recreational and commercial fishing. Despite these sampling limitations, our data encompass the full known size range of the tiger shark (Fig. 1) and the coastal geographic coverage of the WNA (Fig. 2); therefore, our estimates represent the portion of the tiger shark population in this region.

The size of the smallest mature female in our sample (270.0 cm FL) is within the range of worldwide estimates for the tiger shark (220.4–286.5* cm FL) (Kauffman, 1950; Fourmanoir, 1961; Stevens, 1984; Simpfendorfer, 1992; Whitney and Cowe, 2007; Shields, 2018). Incorporating data from other trusted sources into our ogive analysis decreased the size of the smallest mature female to 241.6* cm FL, presented by Clark and von Schmidt (1965), resulted in a range that more accurately represents the species in the WNA and improved ogive analysis.

It is interesting to note that more recent data contain information on several mature males that were substantially smaller than the smallest size estimates for mature males presented in Branstetter et al. (1987) (252.6* cm FL). Aside from the 3 males with fork lengths that were not used in our ogive (from surveys: 184.0 and 217.0 cm; from Shields, 2018: 210.2* cm), an additional

4 males (232.0–248.0 cm) from this study were staged mature at sizes less than those presented in the literature (Stevens, 1984; Branstetter et al., 1987; Whitney and Crow, 2007; Shields, 2018). The lengths of the latter 4 males were within the parameters of the dissection data and were included in the ogive. Alternatively, the size of the smallest mature female in our study was much higher than previously reported for this species in the WNA by Clark and von Schmidt (1965). Although these differences could be due to a response to environmental and fishing pressure affecting the size at maturation of



the tiger shark over time, they could also be due to sampling bias as discussed previously.

As is commonly the case for males, use of a combination of clasper length and stage of calcification is the most accurate method of determining maturity, and it is nonlethal (Clark and von Schmidt, 1965; Natanson and Gervelis, 2013). Mature males have rigid claspers, with the ability of the clasper to rotate freely and of the rhipidion to splay, whereas immature males have soft or plastic claspers that do not easily open or rotate (Clark and von Schmidt, 1965). Clasper calcification appears to be the last phase of maturation for the tiger shark on the basis of males that did not have fully rigid claspers having all of their other reproductive organs be visibly mature. Either the internal reproductive organs of the male tiger shark grew isometrically or there was no distinct inflection in their measurement, making them of

little value in quantitatively assessing maturity. In contrast, there was a very distinct inflection in siphon sac length at approximately 250 cm FL. The distinct siphon sac inflection has also been observed in the shortfin mako (*Isurus oxyrinchus*) and the porbeagle (*Lamna nasus*) (senior author, unpubl. data). Because of the presence of external reproductive organs in males, and the tendency for clasper calcification to be the last stage of maturation, assessing clasper condition is a viable alternative to lethal sampling. Nonlethal hormonal studies, however, still need to be validated, for both sexes, but particularly for females who have no external reproductive organs and go through several distinct stages.

Determining maturity from individual organ measurements can be complex. Quantitative overlap between organ measurements occurs between stages (Tables 1 and 2), and there is variation in organ growth between individuals. The internal reproductive organs of the female tiger shark were of varying use as indicators of maturity; therefore, the results from using one organ as an indicator of maturity could be misleading. Additionally, there is overlap in the measurements of individual reproductive organs between stages; in the transitional stage, maturity is particularly difficult to determine from examination of a single organ (Tables 1 and 2). Overlap in measurements between maturity stages is not uncommon and has been found in the sandbar shark (*Carcharhinus plumbeus*) and the common thresher shark (*Alopias vulpinus*) (Baremore and Hale, 2012; Natanson and Gervelis, 2013), among others. It is best to use a combination of observations and measurements when

assessing maturity (Baremore and Hale, 2012); however, if that is not possible, measurements from multiple reproductive organs need to be examined in concert. Additionally, the relationship of organ development to body length is species specific (e.g., in female common thresher sharks, measurements of all internal reproductive organs except the oviducal gland had an inflection [Natanson and Gervelis, 2013], but in the study described herein, the oviducal gland width did have an inflection). Although clasper development and calcification appear to be consistent indicators of maturity among species, a full analysis of species reproduction for both sexes is vital in determining maturity.

The estimates of L_{50} and A_{50} for the tiger shark provide information for management of this species and improve on previous information. Using updated reproductive data and direct estimates from paired ages and maturities, we

have refined the estimates and present A_{50} as 11.5 and 9.5 years for females and males, respectively. These estimates are similar to those of Kneebone et al. (2008), who estimated that the smallest mature female and male tiger sharks reached maturity at the age of 10 years on the basis of their validated growth curves and maturity estimates from Branstetter et al. (1987).

Brood size information was limited in this study to 1 shark with 38 young, but data from the WNA indicate a range of 18–70 young (Springer, 1938; Baughman and Springer, 1950; Dodrill, 1977; Castro, 2011). Worldwide, estimates of brood size reach 104 young (Applegate et al., 1979).

Conclusions

We examined the reproductive characteristics of the tiger shark in the WNA. Results of our analysis indicate that the values of L_{50} and A_{50} are similar to sizes and ages of the smallest mature individuals found in previous studies (Springer, 1960; Clark and von Schmidt, 1965; Branstetter et al., 1987; Kneebone et al., 2008; Castro 2011; Shields, 2018). Females reached L_{50} at 261.4 cm FL and A_{50} at 11.6 years. Males reached L_{50} at 258.9 cm FL and A_{50} at 9.5 years. This information can be used for input into species management in terms of maturity schedules and reproductive potential. These data are also useful in essential fish habitat analyses that may lead to management through the use of open and closed areas.

Resumen

Para evaluar el estado de madurez de tiburón tigre (*Galeocerdo cuvier*), se utilizaron datos reproductivos colectados mediante disección anatómica de 48 hembras y 66 machos capturados en el océano Atlántico noroeste. La longitud furcal (FL) de las hembras y machos examinados varió de 88 a 318 cm y de 84 a 349 cm, respectivamente. La longitud mediana de la madurez (L_{50}) se calculó utilizando datos binomiales de madurez a partir de disecciones en conjunto con asignaciones de madurez basadas en la condición del gonopterigios (cláspers) de 320 machos (46–280 cm FL) y datos de madurez publicados para 14 machos (170–313 cm FL) y 28 hembras (242–312 cm FL). Además, para cada sexo, se calculó edad mediana de madurez (A_{50}) utilizando estimaciones directas de la edad y los datos binomiales de madurez antes mencionados de los especímenes disectados. Las hembras alcanzaron la L_{50} a los 261.4 cm FL y la A_{50} a los 11.6 años. Los machos alcanzaron la L_{50} a los 258.9 cm FL y la A_{50} a los 9.5 años.

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