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SPECIAL SECTION: ELASMOBRANCH LIFE HISTORY

Variability in the Reproductive Biology of the Atlantic Sharpnose Shark in the Gulf of Mexico

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Abstract

The reproductive biology of the Atlantic Sharpnose Shark *Rhizoprionodon terraenovae* in the Gulf of Mexico was investigated by examining 1,306 specimens (693 females, 613 males) collected from the Florida Keys to waters off Brownsville, Texas. The results of this study confirm the annual reproductive cycle established for this species; however, there was a significant amount of variability within the cycle. Ovulatory and postovulatory females were present from March to October, indicating that mating and ovulation were occurring over a more protracted period than previously described (e.g., May to July). The occurrence of postpartum females from April to September, the varying sizes of the embryos across several months, and the occurrence of mature spermatozoa in the testes of adults from March to November also corroborate the evidence of reproductive plasticity in this species. This observed variability in the reproductive cycle indicates that the Gulf of Mexico Atlantic Sharpnose Shark population is not completely synchronous in regards to mating, ovulation, and parturition, as a portion of the population is demonstrating reproductive asynchrony. Although the cause of this asynchrony remains unclear, it may be related to the environmental conditions of the Gulf of Mexico, which could provide water temperatures that are optimal for the reproduction of this species through much of the year (i.e., March to October), resulting in a protracted reproductive cycle. Given the results of the current study, the reproductive cycles of other carcharhinid species in this region should be examined in more detail to determine whether there is asynchrony in them as well, as this phenomenon could impact future management strategies.

Important intraspecific differences in the reproductive biology of some carcharhinid shark species in the western North Atlantic Ocean have been noted (Loefer and Sedberry 2003; Driggers et al. 2004; Sulikowski et al. 2007; Driggers and Hoffmayer 2009). For example, Driggers et al. (2004) determined that Blacknose Sharks *Carcharhinus acronotus* reproduce biennially in the Atlantic, whereas Sulikowski et al. (2007) found the reproductive periodicity of this species to be annual in the Gulf of Mexico. Driggers and Hoffmayer (2009) provided the first evidence that plasticity in elasmobranch reproductive cycles can exist within a discrete region, as the typically biennially reproductive Finetooth Sharks *C. isodon* of the Gulf of Mexico were found to also exhibit an annual reproductive cycle. In addition, Loefer and Sedberry (2003) compared their

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data with those of Branstetter (1987) and Parsons (1983) and reported that female Atlantic Sharpnose Sharks *Rhizoprionodon terraenovae* mature at smaller sizes and greater ages in the Atlantic than in the Gulf of Mexico. Although studies examining the reproductive biology of sharks in the western North Atlantic Ocean are limited, the fact that differences in important reproductive characteristics have been documented for several carcharhinid species suggests that this phenomenon is more widespread among sharks, especially tropical species (Mattos et al. 2001; Castro 2009), than currently recognized.

The Atlantic Sharpnose Shark occurs in the coastal waters of the western North Atlantic Ocean from Canada to Mexico (Compagno 1984) and is the most abundant shark species throughout most of its range, including the Gulf of Mexico (Branstetter 1990). Its close proximity to shore and high abundance have made this shark an ideal subject for many ecological and biological studies (e.g., Parsons and Hoffmayer 2005; Hoffmayer et al. 2006, 2010). Similar to previously documented intraspecific reproductive differences, several discrepancies in life history parameters have been identified for specimens collected from the same geographic area. For example, Parsons (1983) found that the gonadosomatic index (GSI) of male Atlantic Sharpnose Sharks caught in the Gulf of Mexico peaked from June to August, while Hoffmayer et al. (2010) reported that it peaked from March to May, suggesting either that there was a temporal shift in the reproductive cycle or that there is a protracted mating season. In addition, Carlson and Baremore (2003) reported that Atlantic Sharpnose Sharks sampled in the Gulf of Mexico from 1998 to 2001 were maturing at smaller sizes and younger ages than they were 20 years earlier (1979–1980; Parsons 1983).

In addition to the discrepancies identified by Carlson and Baremore (2003) and Hoffmayer et al. (2010), several recent observations of females mating and ovulating outside the known mating season for Atlantic Sharpnose Sharks in the Gulf of Mexico (E. R. Hoffmayer, unpublished data) suggest that this species exhibits reproductive plasticity. Understanding the reproductive biology of elasmobranchs is required for successful management, as several reproductive parameters are required for current stock assessment models and changes in these parameters could significantly alter the outcome of these assessments (Walker 2005). The objectives of the current study were to examine the reproductive biology of the Atlantic Sharpnose Shark over a large spatial scale in the Gulf of Mexico, develop up-to-date reproductive parameter estimates for stock assessment models, and describe the species' reproductive cyclicity.

METHODS

Sample Collection

Atlantic Sharpnose Sharks were collected from the Florida Keys to the waters off Brownsville, Texas (Figure 1) between March 2008 and February 2012 during fishery-independent research surveys or commercial fishing operations. The largest part of the specimens were provided by the National Marine Fisheries Service's (NMFS) Congressional Supplemental Sampling Program (48.6%), followed by the University of Southern Mississippi's Gulf Coast Research Laboratory shark surveys (34.4%), NMFS bottom longline and bottom trawl surveys (10.5%), and commercial fishers (6.5%) (Table 1). Few reproductive samples were obtained during winter (December,

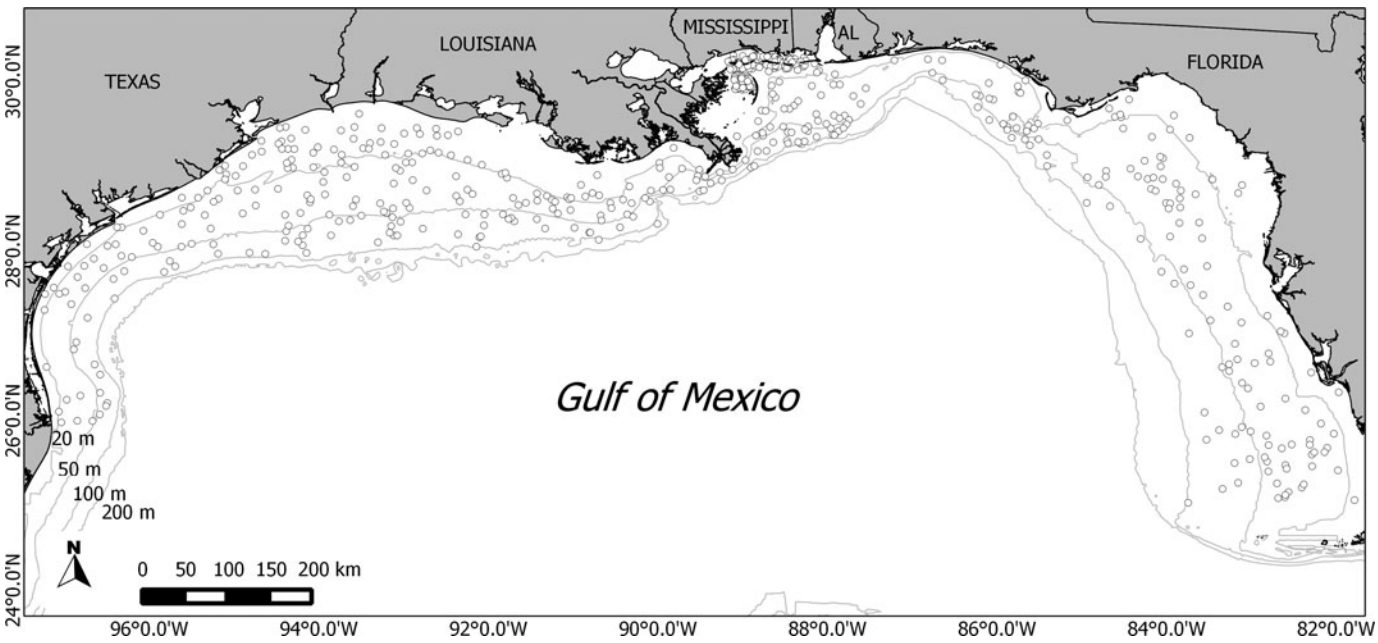


FIGURE 1. Locations in the Gulf of Mexico where Atlantic Sharpnose Sharks were collected from 2008 to 2012.

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TABLE 1. Surveys from which specimens of Atlantic Sharpnose Sharks were collected in the Gulf of Mexico. Survey abbreviations are as follows: CSSP = Congressional Supplemental Sampling Program, USM GCRL = University of Southern Mississippi's Gulf Coast Research Laboratory, and NMFS = National Marine Fisheries Service. Operation times indicate when the fishery independent surveys are conducted and when opportunistic samples were obtained from commercial fishers. Gear types include bottom longlines (BLL; Driggers et al. 2008) and bottom trawls (BT; Driggers et al. 2010). The sampling areas included either the entire northern Gulf of Mexico (GOM) or the north-central part of it.

Survey	Operation times	Years	Gear types	Sample area
NMFS CSSP	Apr–Oct	2011	1.6-km BLL	Northern GOM
USM GCRL	Mar–Oct	2008–2012	1.6-km BLL	North-central GOM
NMFS BLL	BLL: Aug–Sep	2008–2009	1.6-km BLL	Northern GOM
NMFS BT	BT: Oct–Nov	2008–2009	12.2-km BT	Northern GOM
Commercial fishers	Nov–Mar	2009–2012	1-km gill net	North-central GOM

January, and February) as none of the fishery-independent surveys were conducted during this time and severe weather conditions and management closures prevented sample collection by commercial fishers.

Sex was determined for all retained specimens, along with the precaudal length (PCL; the length from the tip of the snout to the anterior margin of the precaudal pit), FL (the length from the tip of the snout to the posterior notch of the caudal fin), TL (the length from the tip of the snout to the posterior tip of the caudal fin in its natural position), and stretch total length (STL; the length from the tip of the snout to the posterior tip of the fully extended caudal fin) to the nearest millimeter and weight to the nearest 0.1 kg. All measurements were taken on a straight line along the axis of the body. Specimens were then frozen whole or stored on ice (up to 24 h) prior to further processing.

Sexual Maturity

Males.—Maturity in males was determined by the presence of calcified claspers that rotated 180° relative to their normal position and had a freely opening rhipidion (e.g., Clark and von Schmidt 1965). Clasper length was measured from the cloacal apex to the tip of the clasper. To conduct gross examinations of internal reproductive tissues, an incision was made from the cloacal origin to the pectoral girdle. Once exposed, the right testis was excised from the epigonal organ and the length, width, and weight were measured. A 2–3-mm-thick cross section was removed from the medial section of the right testis, placed in a tissue cassette, and fixed in 10% buffered formalin. The sample was dehydrated, embedded in paraffin, sectioned, and stained with hematoxylin and eosin following the protocol of Sulikowski et al. (2004, 2005). Prepared slides were examined to assess spermatogenic development based on the criteria outlined by Maruska et al. (1996). Specifically, the mean proportion of the testes that was occupied by mature spermatocysts along a straight-line distance across the medial section of the right testis was determined. Mature spermatocysts were histologically identified by the organization of spermatozoa into tightly shaped packets that were arranged spirally along the periphery of the spermatocysts. Once exposed, the condition of the epididymides, ductus deferentes, and seminal vesicles was noted as turgid or regressed. In addition, the seminal vesicles were inspected for the presence of seminal fluid.

Females.—Females were considered sexually mature if they were gravid or they possessed developed oviducal glands, uteri, and vitellogenic follicles. An incision was made from the cloacal origin to the pectoral girdle to expose the reproductive organs. The widths of the right oviducal gland and right uterus (only in nongravid females) were measured. The left ovary (the only functional ovary) was excised and weighed, and the diameters of all exposed follicles were measured to the nearest millimeter. The stage of each exposed follicle was classified as undeveloped, developing, vitellogenic, or atretic. The uteri were dissected to determine whether embryos or fertilized oocytes were present. Embryos were counted and the mass, length (STL), and sex were recorded for each. Mature females were further divided into five reproductive stages, namely, nulliparous, ovulatory, postovulatory, gravid, and postpartum. Nulliparous females included nongravid individuals that were close to the size of maturity. Ovulatory females included individuals with fertilized uterine oocytes and large (>20 mm) vitellogenic follicles. Postovulatory females were characterized by the possession of fertilized uterine oocytes and small (<10 mm) nonvitellogenic follicles. Gravid females possessed macroscopically visible embryos (>4.0 mm), while postpartum females had empty uteri with stretched, vascularized walls (width, >15 mm) and distinct placental scarring.

Statistical analysis.—A variety of analyses were conducted to gain a better understanding of the reproductive biology of this species. Gonadosomatic indices were calculated to estimate the timing of vitellogenesis and ovulation in females and spermatogenesis in males. The GSI for each shark was calculated as 100 × [gonad mass / (mass of animal – gonad mass)]. Linear regressions of PCL, TL, and STL on FL were performed to facilitate comparison with other studies. To determine size at which 50% of the population was mature, a logistic model,

$$Y = \left[1 + e^{-(a+bx)}\right]^{-1},$$

where Y is the proportion mature and x is the FL, was fitted to binomial maturity data using a least-squares nonlinear regression. Median FL at maturity was determined as $-ab^{-1}$ (Mollet et al.

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2000). A one-way analysis of variance (ANOVA) followed by a Tukey's post hoc test (Zar 1999) was used to determine whether there were significant differences in reproductive variables (i.e., testes length, testes width, male and female GSI, maximum follicle diameter, and embryo size) by month. If the assumptions of normality or equal variances were not met, the data were transformed. If the assumptions were still violated, the nonparametric Kruskal–Wallis ANOVA followed by a Tukey's post hoc test was performed (Zar 1999). Regional and interannual variability were investigated as potential factors influencing the protracted mating period observed in this study. The Gulf of Mexico was divided into three regions: east (83–88°W), central (88–92°W), and west (92–97°W), and the monthly occurrences of ovulatory and postovulatory females were compared across regions. In addition, since the largest number of samples was collected during 2009 and 2011, the monthly occurrences of ovulatory and postovulatory females were compared across these 2 years. The relationship between maternal FL and brood size was compared using a linear regression analysis. The numbers of developing embryos occurring in the left and right uteri were compared with a Mann–Whitney *U*-test, as the samples were not normally distributed. The sex ratio of the embryos was calculated and compared using a chi-square test with Yates correction. The results are presented as means ± SEs. All statistical tests were done with SigmaStat 3.5 and considered significant at $\alpha = 0.05$.

RESULTS

A total of 1,306 Atlantic Sharpnose Sharks were collected during this study, ranging from 316 to 935 mm FL and from 0.2 to 7.5 kg (Figure 2). The relationships between FL and the other three length measures and weight are reported in Table 2.

TABLE 2. Length–length and length–weight relationships for Atlantic Sharpnose Sharks collected in the Gulf of Mexico. All lengths are in millimeters, all weights in kilograms; PCL = precaudal length and STL = stretch total length.

Conversion	*n*	Equation	r^2
FL to PCL	1,299	$(0.9421 \times FL) - 16.673$	0.99
FL to TL	846	$(1.1135 \times FL) + 45.679$	0.96
FL to STL	1,279	$(1.167 \times FL) + 36.993$	0.99
FL to weight, males	608	$1 \times 10^{-8} (FL^{2.9554})$	0.97
FL to weight, females	693	$1 \times 10^{-9} (FL^{3.3071})$	0.95
FL to weight, all	1,301	$3 \times 10^{-9} (FL^{3.1592})$	0.95

Males

A total of 613 male (143 immature, 470 mature) Atlantic Sharpnose Sharks (316–875 mm FL; 0.22–6.8 kg) were sampled for reproductive analyses (Figure 2). Mature males were collected during each month of the study except for December, January, and February. Clasper length exhibited a sigmoidal relationship with FL and was best described by the equation: CL = exp(6.28204–127.77/FL) (Figure 3). Claspers grew gradually in sharks <550 mm FL, followed by rapid growth until 650 mm FL, which is the onset of maturity. Mean clasper length was 12.7 ± 0.1% of FL once maturity was reached ($n = 470$), at which point the claspers were fully calcified and able to rotate and the rhipidions were fully functional. The length at 50% maturity for male Atlantic Sharpnose Sharks was 629 mm FL ($a = -104.559$, $b = 0.166$, $r^2 = 0.81$; Figure 4). The smallest fully mature male was 595 mm FL, and the largest immature male examined was 663 mm FL.

The monthly mean male GSI exhibited a prominent peak (April) during the reproductive cycle (Figure 5) and was significantly higher ($H = 241$, df = 8, $P < 0.001$) during spring (March–May; 0.3–0.4%) than in summer and fall

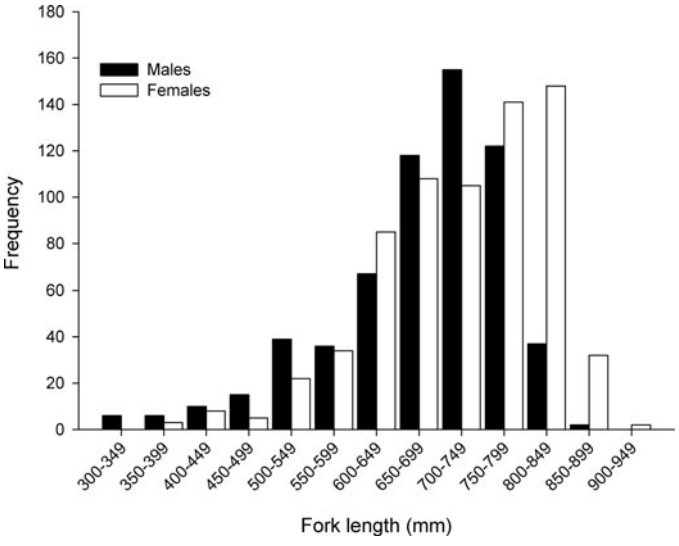


FIGURE 2. Length frequencies of male and female Atlantic Sharpnose Sharks caught in the Gulf of Mexico from 2008 to 2012.

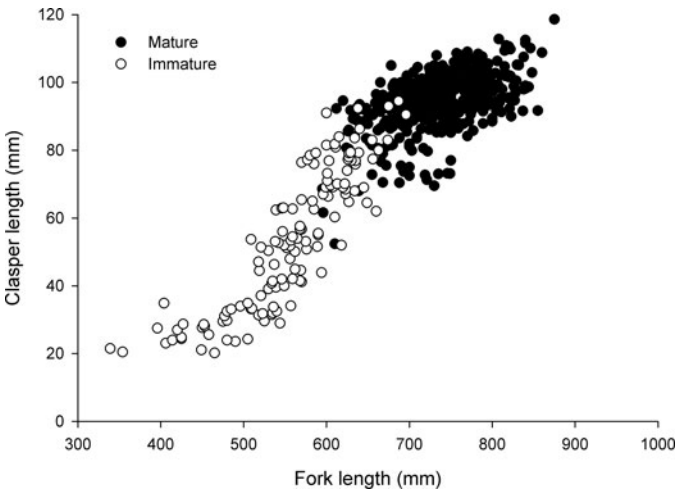


FIGURE 3. Relationship between FL and clasper length for mature and immature male Atlantic Sharpnose Sharks.

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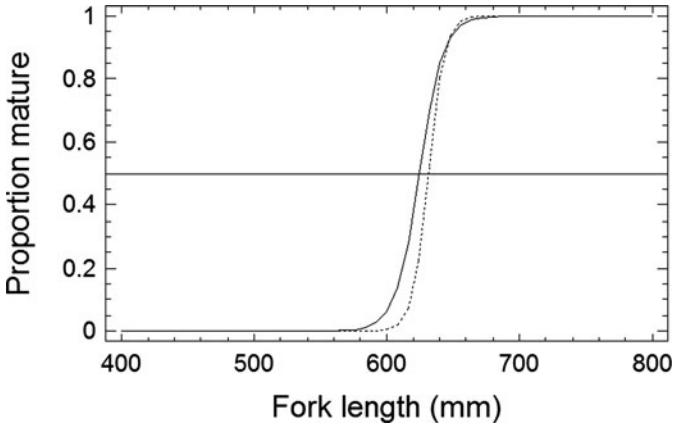


FIGURE 4. Proportion mature versus FL for male (solid line) and female (dashed line) Atlantic Sharpnose Sharks. The bold horizontal line represents the lengths at which probability of being mature is 0.50.

(June–November; 0.15–0.2%). Testis length did not significantly change over the annual cycle ($F_{448} = 0.99$, $P = 0.441$; Figure 5); however, testis width followed a trend similar to that of GSI, with significantly higher values during spring (13–16 mm) than in summer and fall (11–12 mm; $H = 114.1$, df = 8, $P < 0.001$; Figure 5). Histological analysis revealed that mature spermatozoa were present in male Atlantic Sharpnose Shark testes from March to November (Figure 6a). Based on GSI, histology, and testis width data, March through May is the peak time for spermatogenesis. The epididymides, ductus deferentes, and seminal vesicles remained turgid and full of seminal fluid after testicular regression began (Figure 6b). In addition, seminal fluid was present in 99% of the mature males examined from March to November.

Females

A total of 693 female (113 immature, 580 mature) Atlantic Sharpnose Sharks (384–935 mm FL; 0.25–7.2 kg) were sampled for reproductive analyses (Figure 2). Mature females were collected during each month of the study except for December and January. The length at 50% maturity for female sharks was 632 mm FL ($a = -156.274$, $b = 0.247$, $r^2 = 0.71$; Figure 4). At approximately 550 mm FL, the oviducal gland began to rapidly increase in size (Figure 7), from a mean width of 8.6 ± 0.3 mm to 15.4 ± 0.1 mm for the newly mature females. The smallest mature female was 581 mm FL, and the largest immature female was 665 mm FL.

Ovarian cycle.—The monthly mean GSI for mature females changed significantly throughout the reproductive cycle (ANOVA: $F_{9, 566} = 32.8$, $P < 0.001$) with two significant peaks, a primary peak that occurred in May and a secondary peak that occurred in September (Figure 8a). However, a scatterplot of GSI by month revealed a considerable amount of variability from April to October, with the largest variability occurring during June (0.07–1.0%; Figure 8b). Gonadosomatic index values were variable and ranged from 0.03% to 0.73% for gravid, from 0.02% to 0.61% for postovulatory, from 0.10% to 0.82% for ovulatory, and from 0.17% to 1.0% for postpartum females (Figure 8b). Maximum follicle diameter ranged from 1.8 to 30.8 mm, and ovulation occurred when follicles were between 25 and 30 mm. Similar to GSI, the monthly maximum follicle diameter changed significantly over the reproductive cycle (ANOVA: $F_{9, 571} = 16.1$, $P < 0.001$), with peaks occurring in May and September (Figure 9a). A scatterplot of maximum follicle diameter by month revealed a large amount of variability from March to October, with diameters ranging from 1.6 to 25 mm monthly during this time (Figure 9b).

Of the 580 mature females examined, 19 (3.3%) were nulliparous, 56 (9.7%) were ovulatory, 110 (19.0%) were postovulatory, 368 (63.4%) were gravid, and 27 (4.7%) were postpartum. Gravid females were encountered during each month and were numerically dominant, except in June (Figure 10). Almost half (44%) of the postpartum females were encountered outside the previously documented time of parturition for this species (Parsons 1983; Loefer and Sedberry 2003; Figure 10). Ovulatory and postovulatory females were encountered from March to November and ranged from 5% to 83% of the females encountered by month (Figure 10). When data were analyzed by region (east, central, west) and year (2009 and 2011), it was still apparent that a large percentage (25–59%) of the females in mating condition were encountered outside the known mating season (Parsons 1983); however, due to the small and inconsistent sample sizes across regions and years, no spatiotemporal correlations could be determined. Of the 94 ovulatory and postovulatory females encountered outside the known mating window, most were thought to be nulliparous females; however, the majority (60%) were larger than the size at 50% maturity. Three postovulatory females from March 2009 had mating scars, recently fertilized uterine oocytes, and no vitellogenic follicles (Figure 11a). In addition, several ovulatory and postovulatory females from October 2009 were examined, in particular, one specimen that had fresh mating scars and two fertilized oocytes transiting between the oviducal gland and the uterine horns (Figure 11b).

Brood size.—A total of 1,658 embryos (711 males, 755 females, 192 undetermined) from 368 broods were analyzed. Brood size ranged from one to nine individuals, and increased significantly with maternal FL ($F_{382} = 484.15$, $P < 0.001$, $r^2 = 0.56$; $y = 0.0221x - 12.887$; Figure 12). Brood size was 4.5 ± 0.1 embryos, and significantly more embryos were found in the left uterus (56%; 2.4 ± 0.06 embryos) than in the right one (44%; 1.9 ± 0.05 embryos) (Mann–Whitney test: $U = 42{,}136.5$, df = 382, $P < 0.001$). The ratio of male to female embryos was 1 : 1.06, which was not significantly different from 1:1 ($\chi^2 = 1.229$, $P = 0.268$). Unfertilized oocytes were present in 9.8% of the gravid females.

Embryos ranged from 4.4 to 380 mm STL (0.1–250 g). By late September, the yolk sac and stalk had differentiated into the placenta and umbilical cord for most of the embryos. Starting in July, uterine growth was rapid until November but then slowed from February to June (Figure 13). Given that the majority of the embryos reached maximum size in May and June, parturition was assumed to primarily occur in late May and early June

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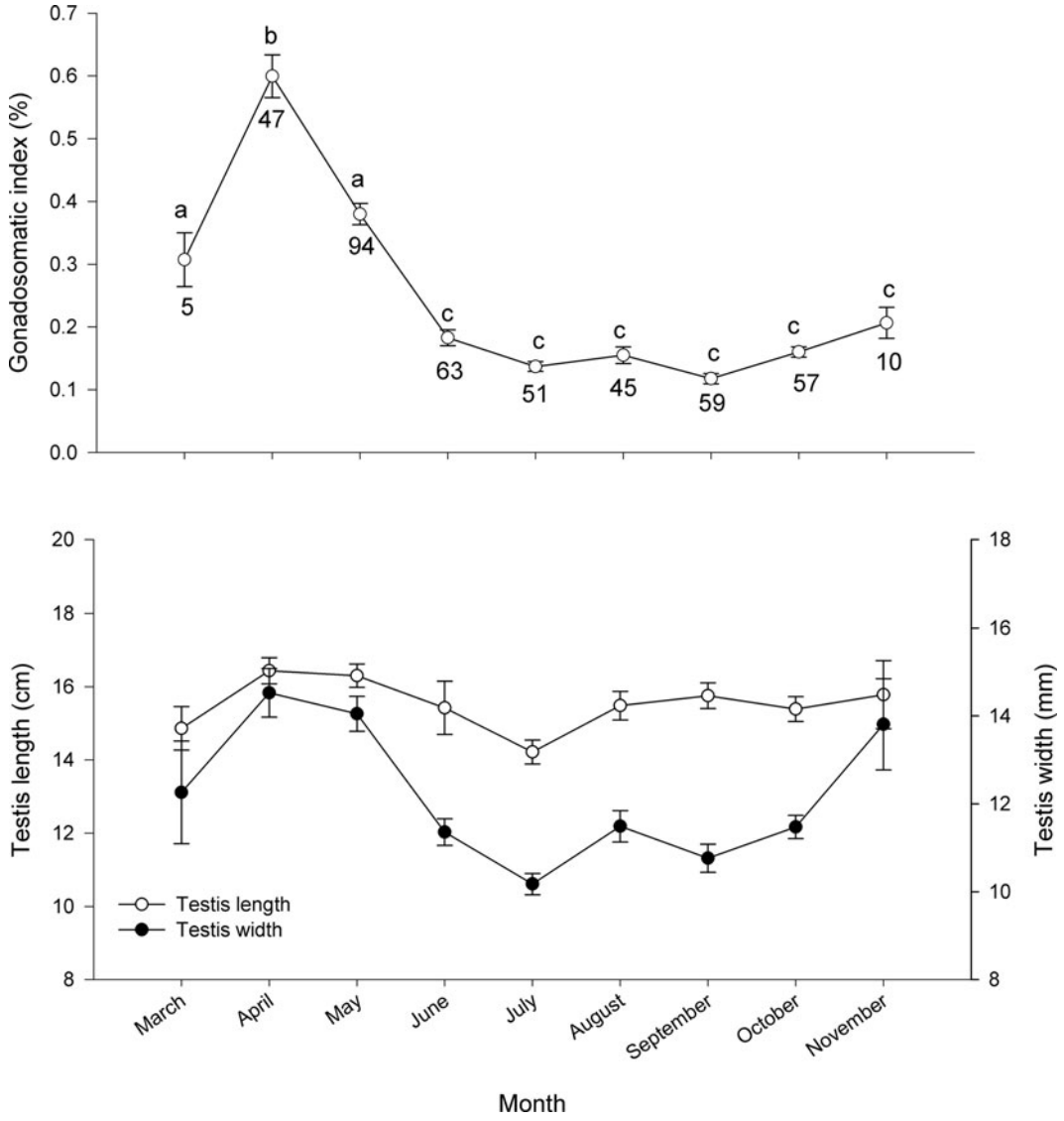


FIGURE 5. Variation in the mean value of the gonadosomatic index (upper panel) and in testis length and width (lower panel) for mature Atlantic Sharpnose Sharks, by month. Points with different letters are significantly different at $\alpha = 0.05$. Sample sizes are given beneath the points in the upper panel; error bars = SEs.

(Figure 13). The mean size of embryos close to parturition was 329 ± 3 mm STL and 154 ± 7 g. The growth rate of the embryos observed in this study suggests a 10–11 month gestation period. Similar to the variability observed with the timing of mating and ovulation in the females, a large amount of variability was found in monthly embryo length (Figure 13). For example, six gravid females sampled over a 10-d period in September 2009 had embryos ranging in size from 80 to 150 mm STL, along with fertilized oocytes (Figure 14).

DISCUSSION

It has been accepted as dogma that most carcharhinid and sphyrnid sharks exhibit a synchronous cycle in which mating, ovulation, and parturition occur over a short period of time (Wourms and Demski 1993; Hamlett and Koob 1999). Researchers have speculated that this short opportunistic window evolved to maximize the reproductive success of these species by increasing the survival of the young (Castro 2009). Despite the general acceptance of this view of carcharhinid reproductive strategy, the information on which it is based has been obtained from only a few species, largely ones from the temperate waters of the western North Atlantic Ocean, including the Atlantic Sharpnose Shark (Parsons 1983; Loefer and Sedberry 2003), Blacktip Shark *Carcharhinus limbatus* (Castro 1996), Finetooth Shark (Castro 1993), Blacknose Shark (Driggers et al. 2004; Sulikowski et al. 2007), Sandbar Shark *C. plumbeus* (Baremore and Hale 2012), and Bonnethead *Sphyrna tiburo* (Parsons 1993).

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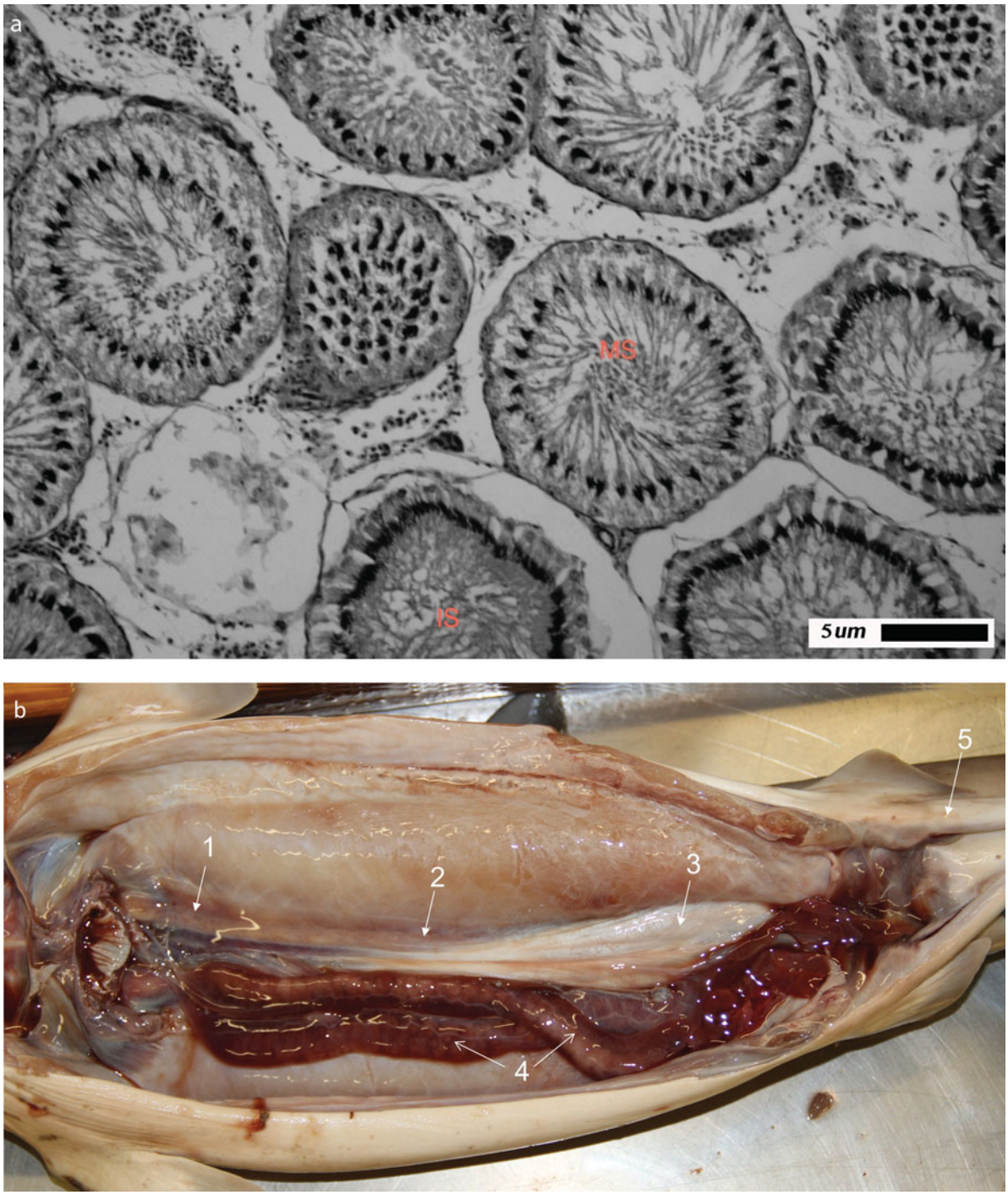


FIGURE 6. Panel **(a)** shows a representative histological section of the right testis of an Atlantic Sharpnose Shark from the Gulf of Mexico stained with hematoxylin and eosin; MS indicates a mature spermatocyst and IS an immature spermatocyst. Panel **(b)** shows the gross reproductive anatomy of a mature male (73 cm FL) Atlantic Sharpnose Shark; 1 = epididymis, 2 = ductus deferens, 3 = seminal vesicle, 4 = testes, and 5 = clasper.

In addition, several of these studies have lacked sample sizes and intervals adequate to fully assess the potential reproductive patterns and/or anomalies that could exist within a population. The surprising variability observed in the current study could be due, in part, to such shortcomings in previous studies of the reproductive biology of carcharhinid sharks.

Parsons (1983) first described the reproductive biology of Atlantic Sharpnose Sharks in the Gulf of Mexico and documented

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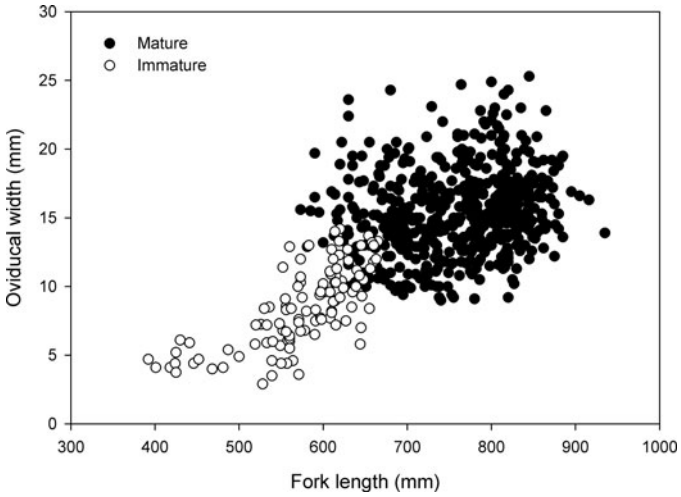


FIGURE 7. Relationship between FL and oviducal width for mature and immature female Atlantic Sharpnose Sharks.

an annual, synchronous reproductive cycle in which a clearly defined timing of mating, ovulation, and parturition were observed. However, this study was limited by its small sample size (33 mature males, 30 mature females) and discrete spatial scale; all sharks were collected in coastal and offshore waters off Alabama. Based on the broad spatial coverage and large sample

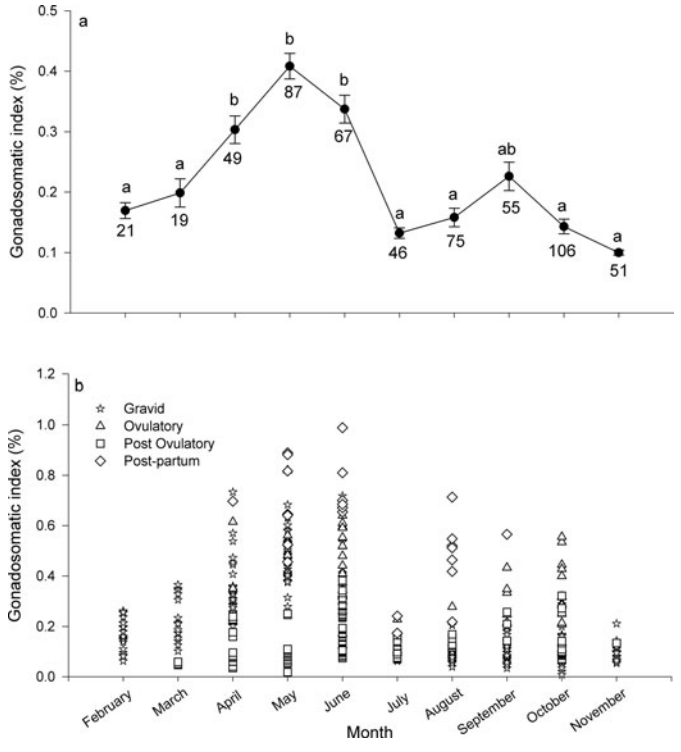


FIGURE 8. **(a)** Mean gonadosomatic index (GSI) and **(b)** a scatterplot of GSI by reproductive phase for female Atlantic Sharpnose Sharks, by month. Points with different letters are significantly different at $\alpha = 0.05$. Sample sizes are given beneath the points in the panel (a); error bars = SEs.

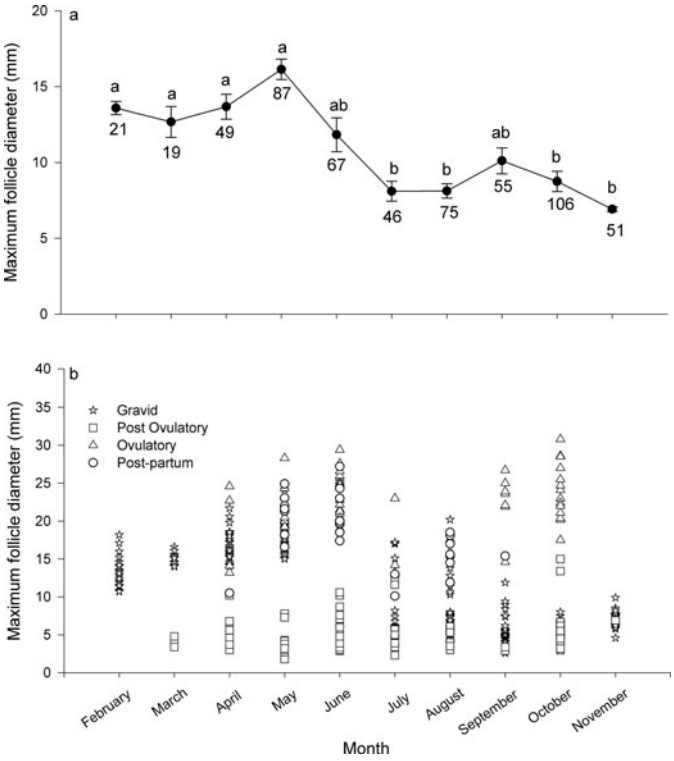


FIGURE 9. **(a)** Mean maximum follicle diameter and **(b)** a scatterplot of maximum follicle diameter by reproductive phase for Atlantic Sharpnose Sharks, by month. Points with different letters are significantly different at $\alpha = 0.05$. Sample sizes are given beneath the points in the panel (a); error bars = SEs.

sizes, our results represent the most comprehensive reproductive analysis for Atlantic Sharpnose Sharks in the Gulf of Mexico to date. Like Parsons (1983), the current study reports that females simultaneously carry term embryos and vitellogenic follicles, which confirms the proposed annual cycle; however, it is clear from the current data that some degree of asynchrony also exists within a portion of the population. For example, ovulatory and postovulatory females, which would only be expected to occur

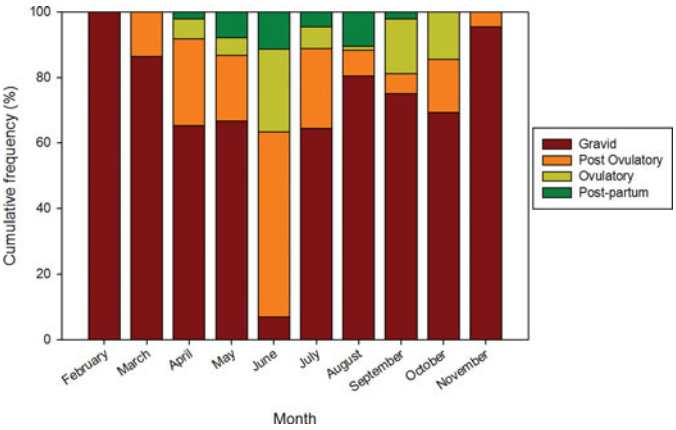


FIGURE 10. Percentages of mature female Atlantic Sharpnose Sharks in the Gulf of Mexico that were in each reproductive phase, by month.

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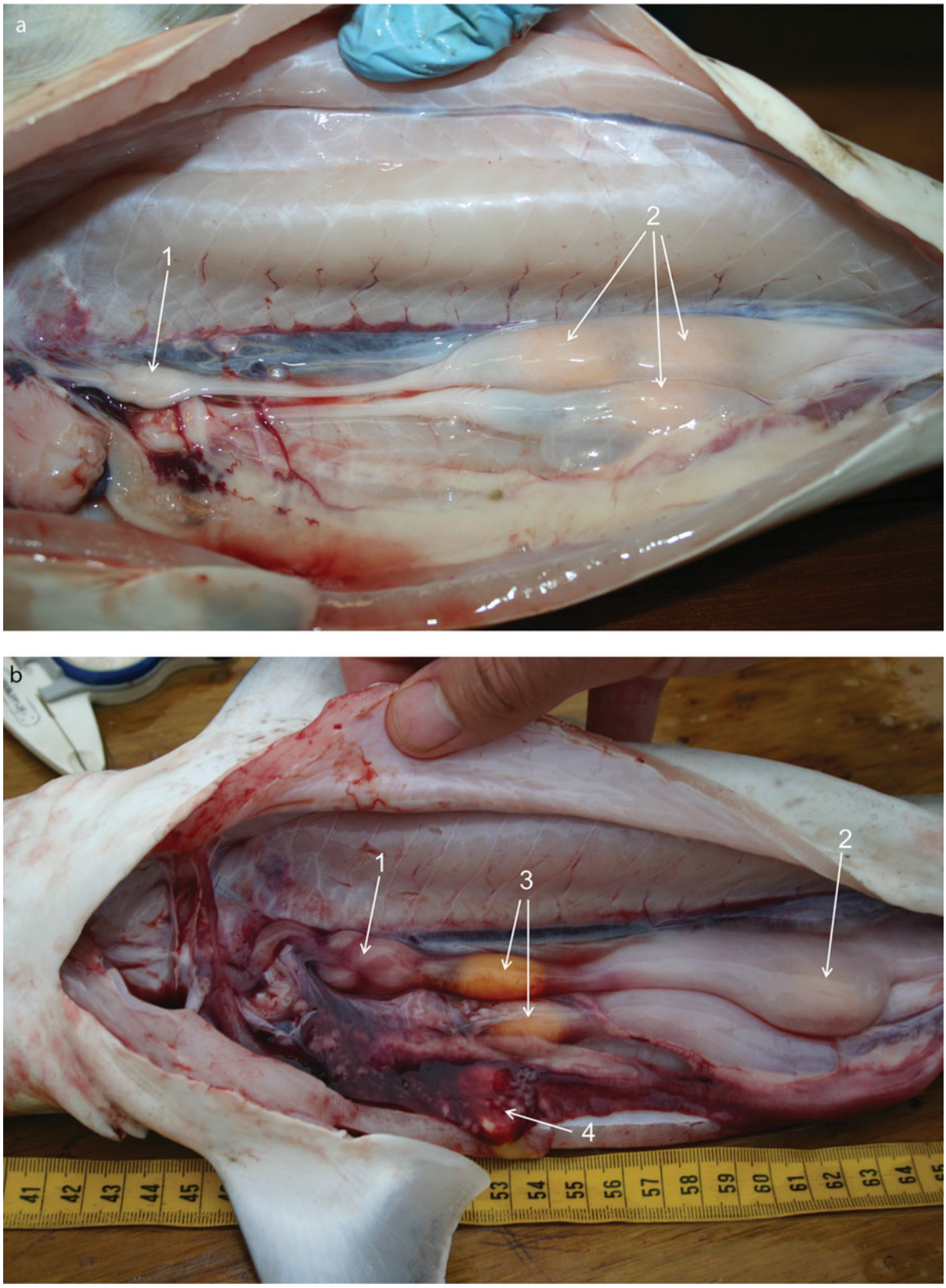


FIGURE 11. Illustration of asynchrony in female Atlantic Sharpnose Sharks: photograph **(a)** is from a postovulatory female collected on March 13, 2009, showing oocytes in the uteri; photograph **(b)** is from an ovulatory female collected on October 2, 2009, showing two fertilized oocytes en route to the uteri. Both sharks had numerous mating scars on their bodies. The oviducal gland (1), uterus with fertilized oocytes (2), and fertilized oocytes between oviducal glands and uteri (3) are identified.

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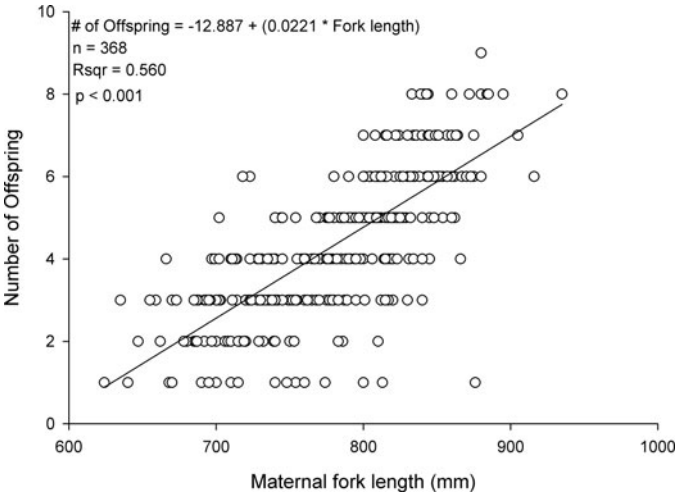


FIGURE 12. Relationship between maternal FL (mm) and the number of Atlantic Sharpnose Shark offspring.

from May to July in a synchronous population (Parsons 1983; Loefer and Sedberry 2003), were observed in high numbers nearly year-round. In addition, this asynchrony was observed along with maximum follicle diameter, as ovulatory females (with large vitellogenic follicles) were collected during September and October, 2–3 months after the known timing of ovulation for this species. The cumulative result of these observations was the documentation of two peaks in mean female GSI values, one

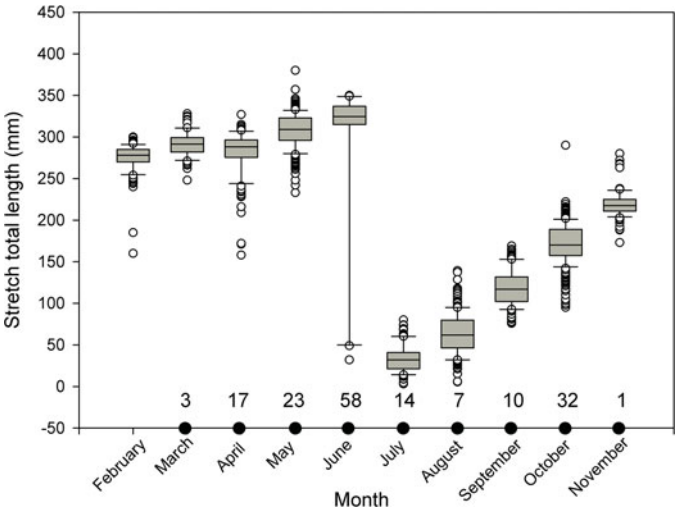


FIGURE 13. Box-and-whisker plot of the stretch total lengths of Atlantic Sharpnose Shark embryos, by month. The upper and lower boundaries of the boxes represent the 25th and 75th percentiles, and the line within the box represents the median. The error bars above and below the box represent the 90th and 10th percentiles, and the white circles indicate outliers. The black circles on the *x*-axis indicate recently fertilized oocytes found within postovulatory females, which were present from March to November, indicating a protracted mating season and most likely an asynchronous cycle. The number above each black circle is the number of postovulatory females.



FIGURE 14. Image of five Atlantic Sharpnose Shark embryos and one fertilized oocyte that were collected from six adult females during a 10-d period in September 2009. The embryos range in size from 80 to 150 mm STL.

in May and another in September, suggesting that a significant portion of the population was ready to mate and ovulate outside the previously described reproductive period (Parsons 1983).

Asynchrony in elasmobranch reproductive cycles can also be defined by the presence of embryos at various stages of development, with no coordinated pattern of growth among months (Castro 2009). For example, this developmental pattern has been observed in the embryos of Caribbean Sharpnose Sharks *Rhizoprionodon porosus* collected in waters off northern Brazil, which entailed the presence of full-term embryos over a protracted period (Mattos et al. 2001). Although the current study found a general increasing trend in embryo length from July to the following June, a significant amount of variability was observed among embryos. For example, embryos between 40 and 60 mm STL were found in gravid females during June, July, and August. In addition, gravid females collected in September possessed embryos at various stages of development, from recently fertilized oocytes to embryos with an STL of 150 mm (Figure 14). Previous studies suggest that embryos of

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this size would range between 40 and 120 d old (Parsons 1983; Loefer and Sedberry 2003), suggesting a protracted mating season occurring between April and July. Interestingly, mature spermatozoa were present in the testes and semen was present in the seminal vesicles nearly year-round (March to November). This is in contrast to the results of previous studies that have shown that male Atlantic Sharpnose Sharks only have semen present in the their reproductive tract for a few months following peak GSI (Parsons 1983; Loefer and Sedberry 2003; Castro 2011). Thus, based on our findings, male Atlantic Sharpnose Sharks in the Gulf of Mexico appear to have the ability to mate over most of the year, which is in agreement with the protracted mating season observed in the females.

Although variability in the reproductive cycle of sharks has been documented in the past, it has been limited to a few studies. For example, Walker (2007) found that although Gummy Sharks *Mustelus antarcticus* off southern Australia had a high degree of synchrony in their reproductive cycles, several individual females were out of phase by up to 3 months. Similarly, although female Great Hammerhead Sharks *Sphyrna mokarran* in northern Australian waters exhibited relatively synchronous reproductive cycles, variability was observed in the timing of mating and ovulation, suggesting that ovulation could take place over an extended period (~6 months; Stevens and Lyle 1989). Baremore and Hale (2012) reported variability in the reproductive cycle of the Sandbar Shark by documenting postpartum females from April to September and females with sperm present in their uteri from April to August. Thus, variability in the reproductive cycle of carcharhinid sharks may be more common than previously documented; however, the source of this variability needs further investigation.

It is unclear why a significant amount of variability is present in the reproductive cycle of Atlantic Sharpnose Sharks in the Gulf of Mexico. Nulliparous females could account for some of the variability, however. Castro (2009) reported that nulliparous female Atlantic Sharpnose Sharks in waters off South Carolina would mate 2–3 weeks prior to the larger females that had completed at least one reproductive cycle. Motta et al. (2007) suggested a similar protracted mating season for the Brazilian Sharpnose Shark *R. lalandii*, in which mating takes place between April and June for nulliparous females and between July and September for postpartum females. This phenomenon is most likely occurring in the Atlantic Sharpnose Shark population in the Gulf of Mexico and could, in part, explain the more protracted mating season observed in the current study. Based on the aforementioned studies, it was anticipated that the majority of the ovulatory and postovulatory females collected outside the known mating season would be nulliparous females; however, this group only accounted for approximately 40% of the females in the current study, suggesting that some other phenomenon was responsible for the observed reproductive variability. We believe this variability in the reproductive cycle of Atlantic Sharpnose Sharks is real because 70% of the ovulatory and postovulatory females collected from August to November were larger than 650 mm FL, which is well above the size at maturity for this species.

Another potential source of this variability is the environmental conditions prevalent in the Gulf of Mexico. In more stable environments, such as tropical and deepwater regions, several species have been shown to display asynchronous reproductive cycles with protracted mating and parturition seasons (Mattos et al. 2001; Veríssimo et al. 2003; Braccini et al. 2006; Castro 2009). Environments such as these, which have stable conditions and ample food supplies, permit the expansion of the narrow windows of mating and parturition because there are no energetically limiting factors (Castro 2009). For example, environmental conditions have been shown to influence the reproductive periodicity of the Gummy Shark. Walker (2007) reported that the population of Gummy Sharks east of 138°E longitude displayed an annual cycle while the population west of 138°E displayed a biennial cycle and that this difference in reproductive cyclicity was explained by environmental differences, primarily water temperature, between the two regions. Additionally, Hoffmayer et al. (2010) suggested that increased sea surface temperatures in the north-central Gulf of Mexico from 1979 to 2009, particularly during spring, allowed males to become reproductively active earlier in the year. Since Atlantic Sharpnose Sharks have such a large distribution in the western North Atlantic Ocean (which spans both temperate and tropical regions), this species could exhibit both synchrony and asynchrony. The environmental conditions in the Gulf of Mexico, which is located between western North Atlantic Ocean and Caribbean Sea, could provide water temperatures that are optimal for the reproduction of this species over much of the year (e.g., March to October), resulting in the protracted reproductive cycle observed in this study. Due to varying oceanographic conditions among the eastern, central, and western areas of the Gulf of Mexico, the asynchronous reproductive cycle observed in this study could be accounted for, in part, by spatial variability. However, a detailed study that systematically collects specimens from all three regions of the Gulf of Mexico will be needed to determine whether this variability occurs on a finer scale than we observed.

In conclusion, the large amount of variability observed in both female GSI and maximum follicle diameter over an extended temporal period (March to October) as well as the presence of mating scars throughout this period indicate that mating and ovulation are occurring over a more protracted period than previously described for Atlantic Sharpnose Sharks. The occurrence of postpartum females from April to October and the varying sizes of the embryos across several months also support this hypothesis. Finally, the occurrence of spermatogenesis in the testes of adult male sharks from March to November corroborates the reproductive plasticity observed in this species. Thus, based on the findings presented herein, the observed variability in Atlantic Sharpnose Shark reproduction is a result of asynchrony in mating, ovulation, and parturition within a portion of the population.

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