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ARTICLE

Reproduction of the Sandbar Shark in the Western North Atlantic Ocean and Gulf of Mexico

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Abstract
The reproductive parameters of 1,194 sandbar sharks *Carcharhinus plumbeus* (701 females, 493 males) were examined for stock assessment. Size and age at 50% maturity was 151.6 cm FL (12.1 years) for males and 154.9 cm (13.1 years) for females; however, the size and age at which 50% of females were in maternal condition was 162.0 cm FL (15.5 years). Males and females showed distinct seasonal reproduction patterns, with peak mating and parturition occurring from April through July. The majority of near-term pregnant and postpartum females were observed in the Florida Keys, which is an extension of the previously reported nursery grounds for sandbar sharks in the western North Atlantic Ocean. Female fecundity averaged 8.0 pups, and there was a significant increase in fecundity with length and age. The ovarian cycle is at least biennial, although there is evidence that some females have triennial cycles.

Reproductive characteristics vary greatly among shark species within the same genus and can even differ among the same species throughout its range. Growth rates, the availability of mates, resource competition, food availability, and the removal of individuals can all affect the periodicity and success of reproduction in fish (Pianka 1970; Winemiller 2005). While parameters such as size and age at maturity, seasonality, periodicity, and fecundity are vital to modern stock assessment models, these estimates can be difficult to obtain for large, highly mobile marine species (Carrier et al. 2004). Even more difficult is the task of maintaining current life history information to assess how populations respond to factors such as sustained fishing mortality (Sminkey and Musick 1995; Carlson and Baremore 2003). Stock assessment scientists often rely on decades-old life history information to determine current stock status for shark species.

The sandbar shark *Carcharhinus plumbeus* is a common coastal species in the U.S. waters of the western North Atlantic Ocean and Gulf of Mexico (Springer 1960; Compagno and Niem 1998). Until recently, it was the most important commercial shark species in the United States, but management initiatives (NMFS 2008) in response to the 2006 stock assessment (SEDAR 2006) put the sandbar shark on the prohibited species list (no landings allowed). Currently, a small number of specially permitted vessels in a research fishery are allowed to land sandbar sharks. All vessels in the research fishery must carry a fisheries observer when targeting sandbar sharks.

Age at maturity has been previously investigated for the sandbar shark in the western North Atlantic Ocean (Casey et al. 1985; Casey and Natanson 1992; Sminkey and Musick 1995; Merson 1998). These studies were primarily age and growth papers and produced widely varying estimates, with age at maturity for females ranging between 12 (Casey et al. 1985) and 30 years (Casey and Natanson 1992). In addition to the range of ages, all published age-at-maturity estimates in this region were back-calculated using estimated size at maturity rather than assessing the maturity state of each aged shark.

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Thorough reproductive studies on the sandbar shark in the western North Atlantic are limited to Springer (1960) and two dissertations (Merson 1998; Piercy 2009), with shorter contributions on the subject (Clark and von Schmidt 1965; Lawler 1976). Size at maturity was estimated as 148–157 cm FL, though sexes were combined by Springer (1960) and Merson (1998). Piercy (2009) and Merson (1998) estimated fecundity to be 9.6 and 8 pups, respectively, and no relationship between maternal size and fecundity was found (Piercy 2009). All three studies suggested that the reproductive cycle was biennial, but Piercy (2009) and Merson (1998) also brought forth evidence of a triennial cycle. Both Gulf of Mexico and Atlantic sandbar sharks were included in Piercy's (2009) study, which reported that there was no difference in the timing of the reproductive cycle between the two areas.

The largest nursery area for sandbar sharks in the western North Atlantic is reported to be in the Chesapeake Bay (Springer 1960; Musick and Colvocoresses 1988), with known smaller nursery areas along the Atlantic coast in New York, Delaware, Virginia, South Carolina, and mid-Florida (Springer 1960; Castro 1993; Merson 1998; Merson and Pratt 2001; Grubbs et al. 2007), though it has been suggested that the pupping range has contracted (Merson 1998; Grubbs et al. 2007). Springer (1960) reported that the area from Cape Cod, Massachusetts, to Cape Canaveral, Florida, was the primary nursery range for the species, and secondary nursery grounds existed in the western Gulf of Mexico. It was postulated that the secondary nursery area was not self-sustaining but resulted from breakoff groups from the larger migration of adults from the western North Atlantic (Springer 1960). However, Carlson (1999) reported juvenile and neonate sandbar sharks in the eastern Gulf of Mexico, suggesting that nursery areas in this region are more extensive than previously thought.

Sandbar sharks are known to move large distances, with seasonal north–south migrations off the U.S. eastern coast and into the Gulf of Mexico, as demonstrated by extensive tagging studies (Casey and Natanson 1992; Kohler et al. 1998). Genetic analyses indicate that sandbar sharks in the western North Atlantic and Gulf of Mexico are of one stock (Heist et al. 1995; Heist and Gold 1999); therefore, gene flow likely occurs between the two areas. For this reason, sandbar sharks in the U.S. Atlantic and Gulf of Mexico are managed and assessed as one stock (SEDAR 2010).

The sandbar shark stock in the western North Atlantic and Gulf of Mexico undergoes assessment for stock status approximately every 4 years (Cortés et al. 2002; SEDAR 2006, 2010). The reproductive parameters used in shark stock assessments include size and age at first maturity, overall fecundity, fecundity as it relates to maternal size and age, periodicity of the ovarian cycle, duration of the parturition–reproductive season, size and age of females in maternal condition, sex ratio of pups, and gestation period (Walker 2005; SEDAR 2006; Brooks et al. 2010). The objectives of this study were to provide comprehensive and updated reproductive parameters for the sandbar shark for stock assessment and to provide the first direct estimates of age at maturity in the western North Atlantic Ocean and Gulf of Mexico.

METHODS

Sampling

The sandbar sharks examined for reproductive analysis were sampled by certified at-sea observers aboard commercial longline vessels that targeted sharks; most samples were from vessels participating in the sandbar shark research fishery (NMFS 2008). The observers sampled sandbar sharks in an opportunistic fashion, when sea conditions were favorable and fishing operations allowed. All sampled sandbar sharks were measured in a straight line, from the tip of the nose to the fork in the tail (FL; cm). Only FL was measured because of the time constraints of sampling during commercial operations; this measurement is common in the literature and is known to be less variable than total length (Francis 2006). Reproductive organs were removed as the carcass was processed by the fishers, and a 10-cm segment of the vertebral column was also removed. Because the carcasses were commercial products, the vertebrae were sampled from the discarded portion of the shark, in the cervical region of the spinal column. The observers also sampled the ovary, both oviducal glands, and both uteri from females, and both testes, epididymedes, the seminal vesicle, and claspers from males when possible. Samples were either frozen on board until they could be shipped or were immediately shipped on ice to the National Marine Fisheries Service (NMFS) Panama City Laboratory for processing.

Because sandbar sharks caught by commercial fishers were mostly >130 cm FL, fishery-independent surveys were utilized to capture smaller individuals. While not assessed for reproductive characteristics, these juveniles were used to inform the size- and age-at-maturity schedules. The surveys that provided juvenile sharks were the South Carolina Department of Natural Resources (SCDNR) survey in South Carolina waters of the Atlantic Ocean and the Cooperative Gulf States Shark Pupping and Nursery (GULFSPAN) survey in Florida waters of the eastern Gulf of Mexico (Figure 1). The SCDNR survey employed a mixture of longlines and gill nets, while the GULFSPAN survey was strictly a gill-net survey. Two additional fishery-independent samples were collected by a survey using a hydraulic longline in the Gulf of Mexico. A complete description of the gear utilized to obtain sandbar sharks from fishery-dependent and -independent sources can be found in Hale and Baremore (2010). Approximately five to ten vertebrae were removed from a region just anterior to the dorsal fin from fishery-independent sources. Although it is preferable to use vertebrae from a standardized location on the spinal column, Piercy et al. (2006) found that growth ring formation was not variable along the spine of sandbar sharks.

Vertebral samples were catalogued and frozen whole until processing. All sandbar sharks included in reproductive analyses were aged using vertebral band pair counts. All

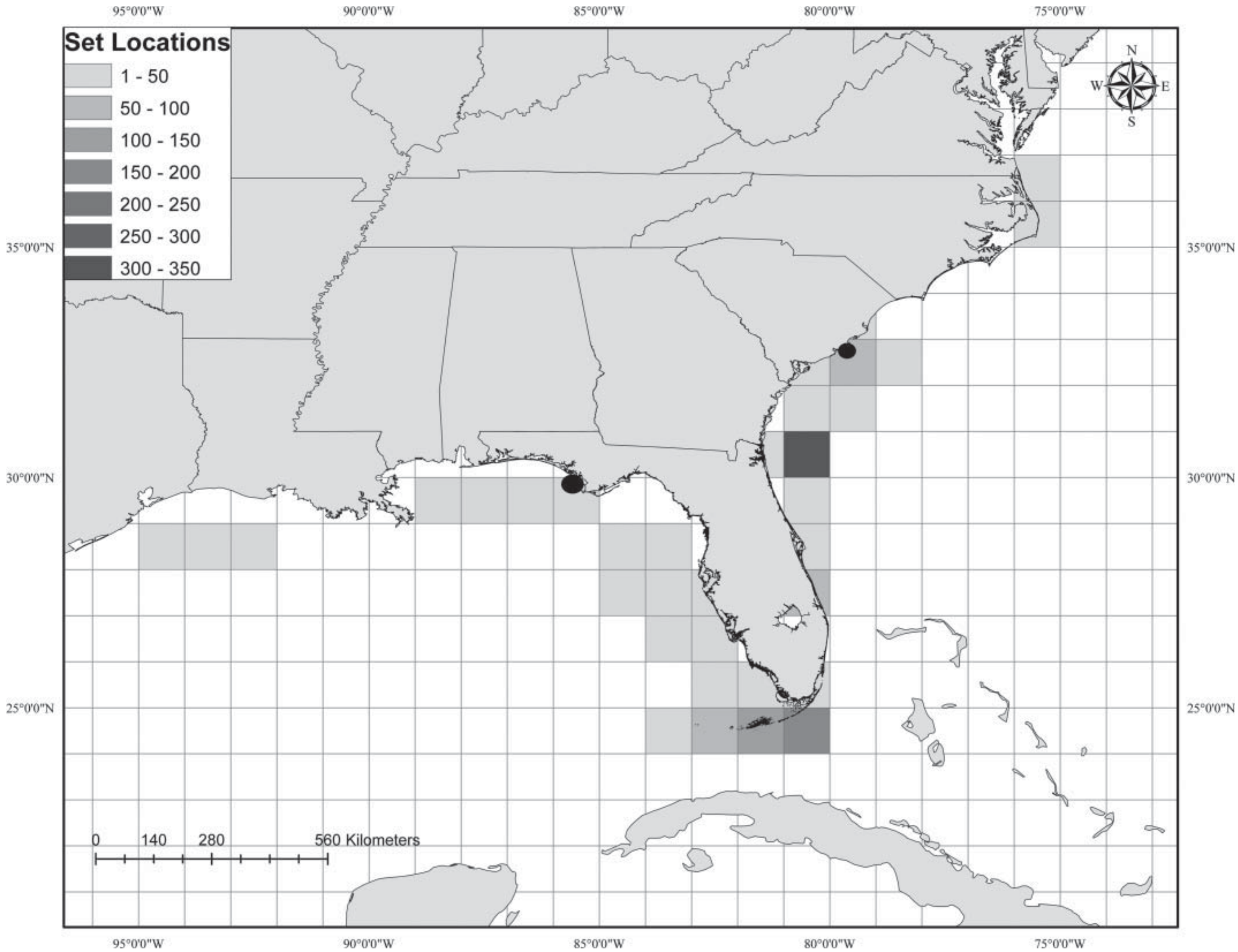

FIGURE 1. Capture locations for all sandbar sharks assigned ages from the western North Atlantic Ocean and U.S. Gulf of Mexico, 2006–2010. Shading indicates the number of sandbar sharks sampled. Circles indicate the locations of the fishery-independent surveys.

vertebrae were sectioned at 0.6 mm, and band pair counts were enumerated using a dissecting microscope under transmitted light. Assigned ages were band pair count less 1 (i.e., the number of band pairs counted less the birth mark). For full vertebrae processing and aging processes, see Hale and Baremore (2010).

Reproductive Analyses

Female reproductive measurements and stages.—For females, ovary weight (OW; g) was measured, along with the oviducal gland width (OG; mm) and uterus width (UW; mm). The maximum ovarian follicle diameter (MFD; mm) was measured unless one follicle was notably larger than the majority of the other follicles, in which case the second largest follicle was also measured. These singular large follicles were notable because they tended to occur in gravid females during the late summer months; almost all were flaccid and grayish in color and were most likely unovulated follicles that were being reabsorbed. Including these singular follicles in analyses would misrepresent the overall condition of the ovary and its follicles. Uteri from nongravid females were dissected to identify sperm packets or umbilical scarring. When present, sperm packets were visible in the lining of the uteri and were approximately the size and shape of large grains of rice. For gravid females, pups were removed and enumerated by uterus, then sexed, weighed (g), and measured for FL and stretch total length (STL; cm). When only blastodiscs were visible, STL was recorded as 0.

Maturity stage for females was determined by examining the oviducal, ovarian, and uterine development and using stage designations (1–7) established from the measurements described in the previous paragraph (Table 1; Walker 2005; McAuley et al. 2007). Stage 1 females had very thin, white uteri, the oviducal glands were generally the same diameter as the uterus, and ovarian follicles were granular and clear. Stage 2 females' uteri and oviducal glands were distinct, and yellow follicles

TABLE 1. Stages and maturity classifications for female sandbar sharks based on qualitative and quantitative observations.

Stage	Classification	Ovary weight (g)	Maximum follicle diameter (mm)	Oviducal width (mm)	Uterus width (mm)
1	Juvenile, no development	<100	<10	<20	<20
2	Juvenile, developing	<180	<15	<25	<30
3	Mature, resting	>180 OW <550	>15 MFD <40	>25 OD <65	>30 UW <50
4	Mature, sperm present	>180 OW <550	>15 MFD <40	>25 OD <65	>30 UW <80
5	Mature, ovulating	>180 OW <400	>25 MFD <55	>25 OD <65	>50 UW <100
6	Mature, pregnant	>100 OW <220	>15 MDF <50	>25 OD <50	>50 UW <350
7	Mature, postpartum	>100 OW <220	>15 MDF <50	>25 OD <40	>50

<10 mm were often present in the ovaries. Females classified as being in stage 3 or higher were considered mature. Many of the measurements of the mature female stages overlapped, so qualitative evidence (e.g., pups present in the uterus) was used in conjunction with the measurements to distinguish the stages of these females. Stage 3 females were not pregnant and had OW > 180 g, MFD > 15 mm, OG > 25 mm, and uterus width > 30 mm. When sperm packets were visible in the uterine lining, females were considered to be in stage 4. Females undergoing ovulation were classified as being in stage 5 and had both newly fertilized eggs in the uterus and yolked follicles in the ovary > 25 mm. Stage 6 females were pregnant, and postpartum females (uterus width >50 mm, visible umbilical scars) were considered in stage 7 (Table 1). The definitions given in Table 1 were guidelines to assigning maturity state; inherent natural variation among females and measurements will produce some overlap in the measurements (e.g., juvenile females with MFD >10 mm); however, taking all measurements and qualitative evidence into account improved the accuracy of the maturity classifications.

Females were considered to be in maternal condition (Walker 2005) when gravid (stage 6) or expected to be gravid within the reproductive year (MFD > 20 from January to June). Because nongravid females did not show follicular development from July to December (i.e., it was not possible to determine whether they would reproduce the following spring), their reproductive condition was considered to be nonmaternal. Maternal condition is used to identify the portion of the female population that is actively reproducing; this is to ensure that population productivity estimates are not biased by the inclusion of nonreproducing females in stock assessment models.

Male reproductive measurements.—Testis width and weight (g) were measured, along with the epididymis width. Clasper calcification was noted, as was the presence and nature of semen in the seminal vesicle. Male sandbar sharks were considered to be mature when the claspers were fully calcified and were in reproductive condition when the seminal vesicles were engorged and contained ropy packets of spermatozoa.

Seasonal trends in reproduction and periodicity.—Monthly plots of mean MFD and OW were examined to determine the seasonal mating patterns of mature female sandbar sharks. For males, testis weight and epididymis width were likewise plotted by month. Because the sandbar sharks were processed at sea, carcass weights were not taken and therefore gonadosomatic indices were not calculated. Analysis of variance (ANOVA) tests were used to test for differences among months for each plot. Levene's test (Levene 1960) was used to test for homogeneous variance, and Tukey's honestly significant difference (HSD) test was used for pairwise comparisons among months when ANOVA results were significant. Stage 6 (pregnant) females were plotted but not included in the analyses because they did not exhibit vitellogenesis during pregnancy and therefore did not follow the seasonal variation of the nongravid females. Likewise, stage 5 (ovulating) females were plotted as reference points but not included in analyses because these females were technically pregnant. The percentage of mature females in each stage (3–7) was plotted by month to further elucidate the reproductive season.

Scatterplots of individual MFD values from mature, nongravid females (stages 3–5) were examined closely in spring months (January–June) to infer the periodicity of the ovarian cycle. Spring months were chosen because the months leading up to the peak mating time are the only period when nongravid, resting females can be distinguished from nongravid females that will be able to reproduce that year (Walker 2005). Resting females will show no increase in MFD and the follicles will remain a whitish color as the time of mating and ovulation approaches, while those ready to mate have bright yellow follicles and show a rapid increase in MFD prior to ovulation (Lutton et al. 2005; Walker 2005; Castro 2009).

Gestation period and embryo characterization.—A scatterplot of mean embryo length by month was used to investigate the length of gestation, time of parturition, and size at birth. Linear regression analyses were used to determine the relationships between litter size and maternal length as well as litter size and maternal age. The sex ratio of embryos and the number of embryos in each uterus per female were tested for significant differences from a 1:1 ratio with chi-square tests.

Maturity and maternity ogives.—Logistic curves using binomial maturity data (0 = juvenile, 1 = mature) were used to analyze size and age of maturity for males and females, that is,

$$y = \frac{1}{(1 - e^{(a+bx)})}$$

where x = FL or age. The sizes (L_{50}) and ages (A_{50}) at which 50% of the individuals were mature were calculated ($y = -a/b$), as were standard errors (SEs) of the estimates. An additional maternity ogive was plotted to assess the size and age of females in maternal condition, with binomial maternity data (0 = juvenile or mature but not in maternal condition, 1 = mature in maternal condition; Walker 2005). The logistic curves for the females in maternal condition were scaled by the proportion of gravid females in the sample to account for the periodicity of the ovarian cycle. Logistic analysis was performed using the lrm procedure in Program R (R Development Core Team 2009). Likelihood ratio tests were used to test for differences in the curves between males and females and between females in maternal condition and females overall.

RESULTS

Seasonal Trends in Reproduction and Periodicity

A total of 1,194 sandbar sharks (701 females, 493 males) were collected for age and maturity analyses from July 2006 through January 2010. Females ranged in size from 54 to 202 cm FL and males from 77 to 176 cm FL (Figure 2). Only mature animals were used for reproductive analyses (325 females, 214 males), while all sandbar sharks were used to produce maturity ogives.

Females.—Mature, stage 3 female sharks showed strong seasonal trends in reproduction, with increases in MFD and OW occurring from January to June and a significant decline in July (ANOVA: $P < 0.0001$; Tukey's HSD: $P < 0.05$; Figure 3), indicating that peak ovulation occurred from June to July. Stage 4 (sperm in uterus) and stage 7 (postpartum) females were first observed in April, while stage 5 (ovulating, with fertilized ova) females were only reported in June and July (Figure 4). Stage 6 (pregnant) females were observed year-round, though fewer were recorded in June and July than in other months (Figure 4) and none of those had measurable ovaries or follicles due to the condition of the samples (Figure 3). This indicates that full-term females had most likely pupped and that ovulating females were in the process of mating during these months. While reproductive activity was apparent (sperm present, ovulation occurring) from April to September, the vast majority of females appeared to mate in June and July. Both the MFD and OW values of stage 3 females were statistically similar for the months of July

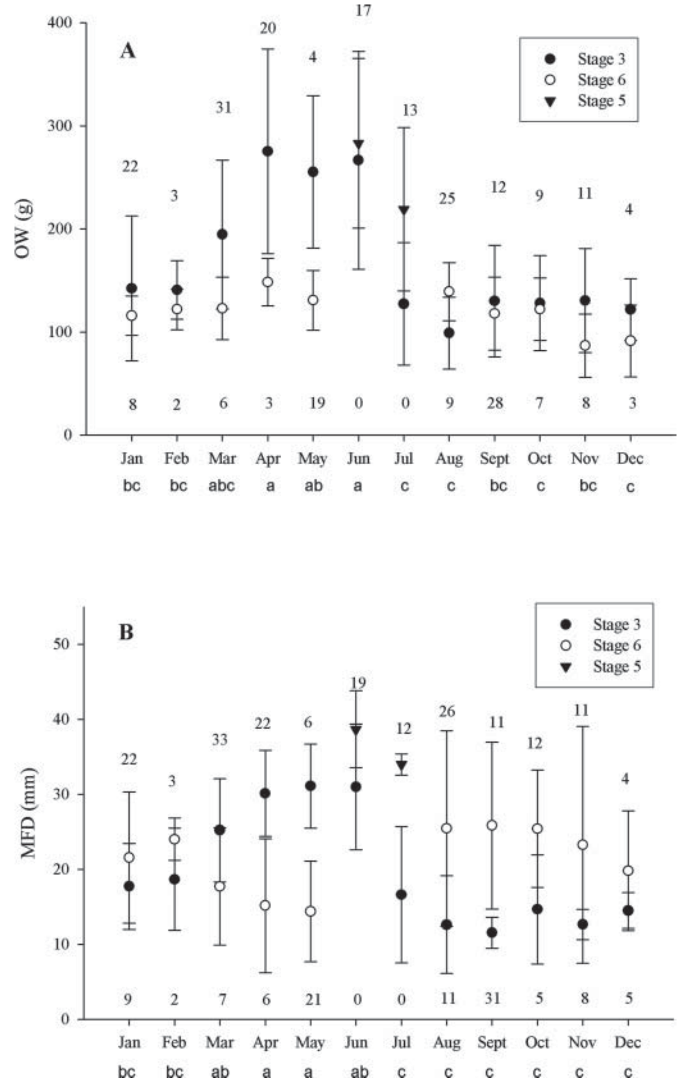

FIGURE 3. **(A)** Mean ovary weights (OW) and **(B)** maximum follicle diameters (MFD) for stage 3 ($n = 171$), stage 5 ($n = 7$), and stage 6 ($n = 120$) female sandbar sharks, by month. The error bars represent SDs. The numbers above the error bars are sample sizes for stage 3 females, while those below the error bars are sample sizes for stage 6 females. The letters below the months indicate statistical equivalence according to Tukey's HSD test ($\alpha = 0.05$).

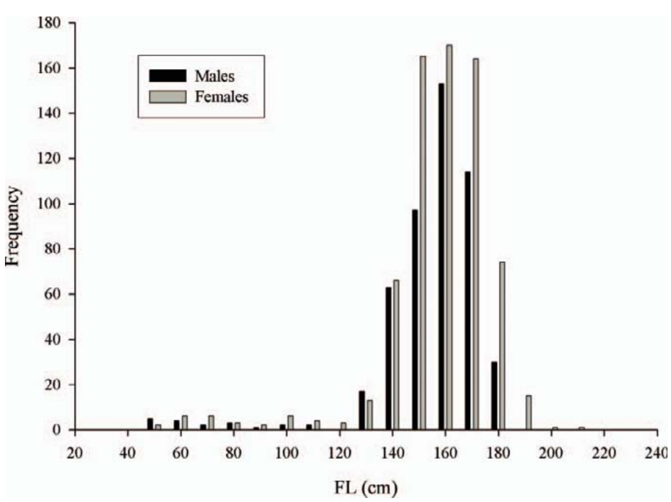

FIGURE 2. Length-frequency distribution of all sandbar sharks assessed for maturity state (n = 701 females, 493 males).

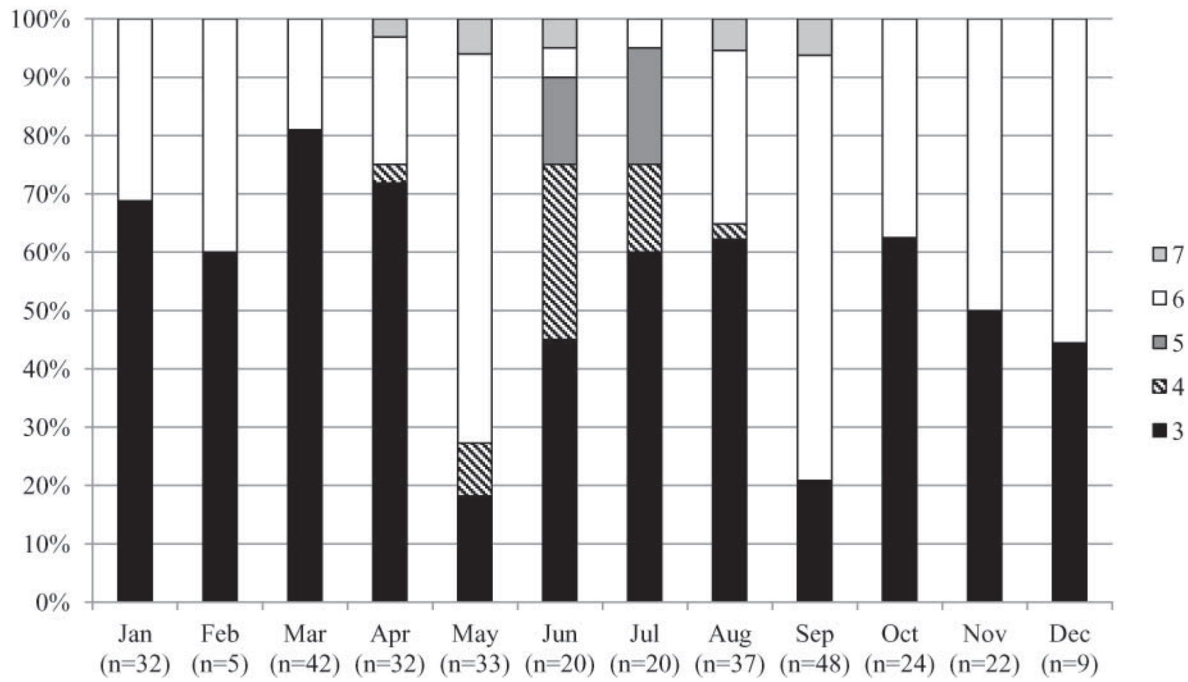

FIGURE 4. Cumulative frequencies of mature female sandbar sharks stages, by month. Stage 3 = mature, nongravid; stage 4 = sperm in uterus; stage 5 = ovulating; stage 6 = pregnant; and stage 7 = postpartum.

through February (Tukey's HSD: $P > 0.05$; Figure 3), indicating that vitellogenesis occurred from March through June. Females ovulated at MFD values of 30–40 mm and OW values >250 g.

Females did not exhibit any signs of vitellogenesis during or shortly after gestation, indicating that the ovarian cycle is at least biennial. However, while the mean MFD values of nongravid females showed a distinct increase during the months leading up to ovulation, when examined individually there is evidence that nongravid females did not undergo vitellogenesis during this time period (Figure 5). These females had MFD values <20 mm

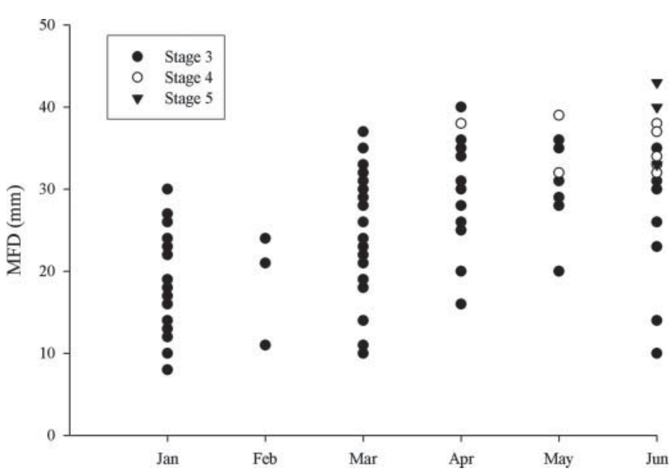

FIGURE 5. Scatterplot of maximum follicle diameter (MFD) values for stage 3–5 female sandbar sharks during spring months (January–June).

and the follicles were not the telltale bright yellow (Figure 6A), but a whitish color (Figure 6B), and their ovaries were similar in appearance to those of near-term gravid females (Figure 6C). Approximately 37% of mature females were gravid overall.

Males.—Male testis weight peaked in April, while epididymis width was highest in June (Figure 7). Changes in testis width were significant by month (ANOVA: $P < 0.001$; Figure 7A), and spring values (February–June) were significantly higher than those from July to January. While epididymis widths also showed similar seasonal variation (Figure 7B), overall epididymis width values were not significantly different among months (ANOVA: $P > 0.10$). Males in reproductive condition (engorged seminal vesicles) were found from April through June.

Gestational Period and Embryo Characterization

A total of 123 stage 6 females were observed during all months of the year, with 121 having embryos that were measured and 99 having intact uteri that were used for statistical analyses. Gestation was approximately 12 months; the first fertilized embryos were observed in June, and the largest near-term embryos were found in May and June (Figure 8). Pups were between 48 and 64 cm STL (39–55 cm FL) at birth, with an average of 57 cm STL (46 cm FL). Embryo STL was plotted because forks in the tail were not developed in embryos <2 cm. The average number of viable pups per female was 8.0 (SD, 2.39), with a range of 3–12. The sex ratio of in utero pups was not significantly different from 1:1 among uterine branches

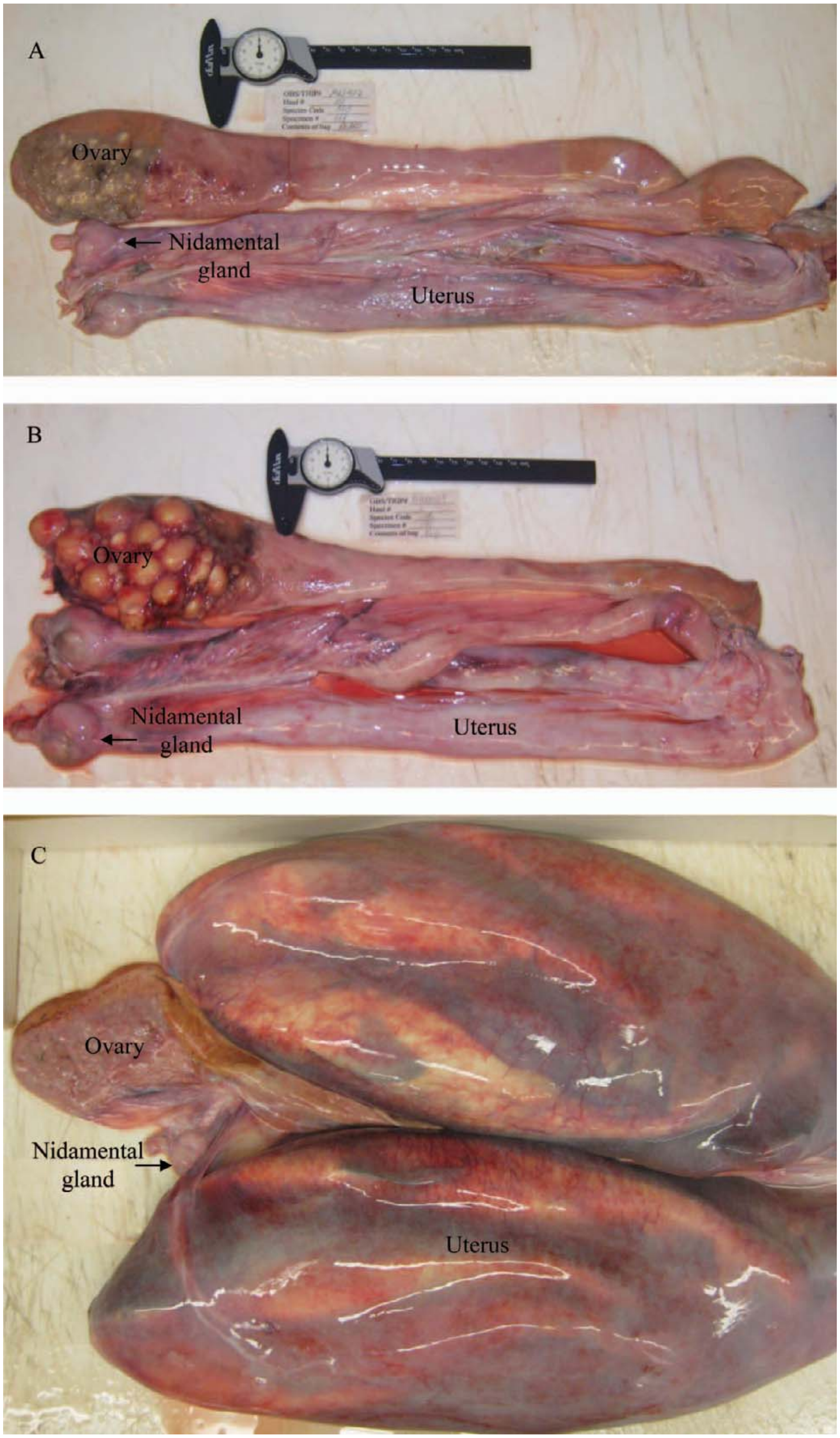

FIGURE 6. Reproductive tracts of female sandbar sharks exhibiting different stages of the ovary and uterus. Panel **(A)** shows a specimen collected off the east coast of Florida (Atlantic) on March 20 (155 cm FL; MFD = 14 mm), panel **(B)** a specimen collected off the Florida Keys (Atlantic–Gulf) on March 21 (156 cm FL; MFD = 33 mm), and panel **(C)** a specimen collected off the west coast of Florida (Gulf) on May 1 (166 cm FL; MFD = 12 mm).

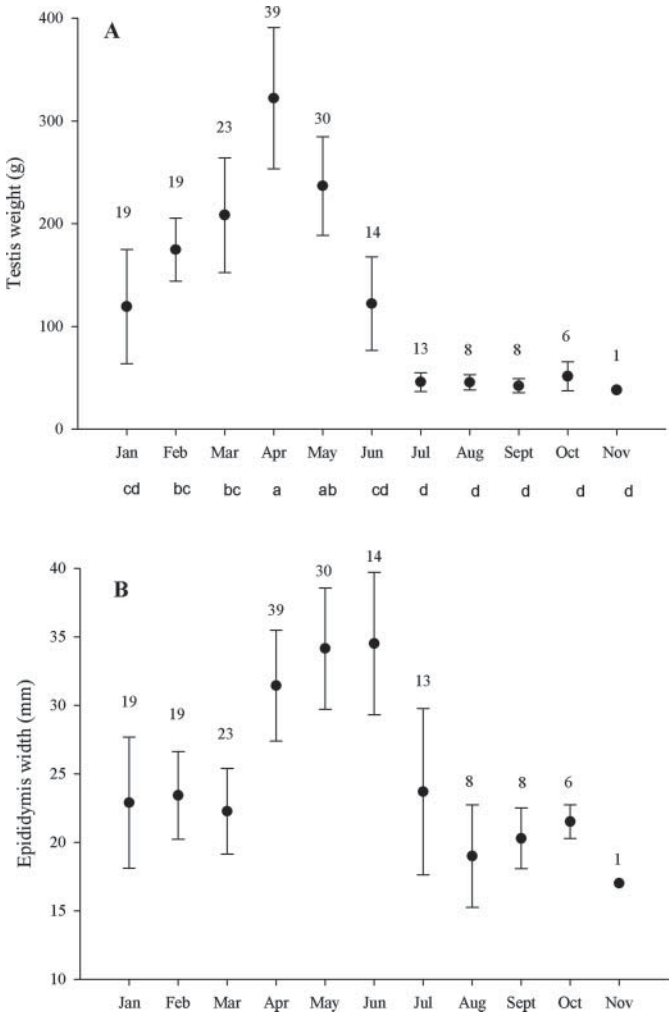

FIGURE 7. **(A)** Mean testis weight ($n = 174$) and **(B)** mean epididymis width ($n = 173$) values for male sandbar sharks, by month. Error bars are SDs. The numbers above the error bars are sample sizes, and the letters below the months indicate statistical equivalence according to Tukey's HDS test ($\alpha = 0.05$).

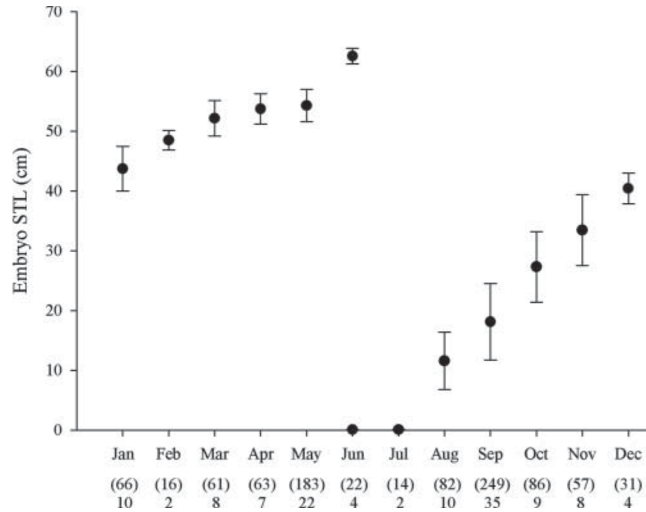

FIGURE 8. Mean stretch total length (STL) of in utero sandbar shark embryos, by month. The error bars are SDs. The numbers in parentheses are the numbers of embryos measured; the others are the numbers of litters examined.

($\chi^2 = 1.27$, df = 1, $P = 0.25$) or overall among females ($\chi^2 = 0.83$, df = 1, $P = 0.36$). The relationship between maternal FL and the number of offspring per cycle was weakly correlated but significant ($R^2 = 0.06$, $P < 0.05$, $n = 99$ females; Figure 9A). The relationship between maternal age and the number of offspring had a higher coefficient of correlation and was highly significant ($R^2 = 0.37$, $P < 0.001$, $n = 99$; Figure 9B).

Of the 99 pregnant (stage 6) females, 34% contained at least one unfertilized egg in one uterus. When present, females had on average 1.3 unfertilized eggs. Unfertilized eggs were characterized by a grayish color and chalky texture and were out of sync with other uterine contents (i.e., viable embryos were also present) but were similar in appearance to newly ovulated eggs. There were three cases of fetal mummification, two of which were from the same litter. In this instance, the mummified fetuses and unfertilized ova were in the same uterus (left), while the right uterus of the same female contained three well-developed embryos.

Maturity and Maternity Ogives

The L_{50} values were 151.6 ($n = 449$) and 154.9 ($n = 658$) cm FL for males and females, respectively (Table 2; Figure 10A). The A_{50} values were 12.1 years for males ($n = 449$) and 13.1 years for females ($n = 656$) (Table 2; Figure 10B). The size at which 50% of females were in maternal condition was 162.0 cm FL ($n = 645$) or 15.5 years of age ($n = 640$). The maternity curves were multiplied by 0.37 to scale them to the proportion of gravid females overall (Figure 10C, D). Likelihood ratio tests showed significant differences in the logistic regressions for both size and age at maturity between sexes ($P < 0.05$). Likewise, size at maternal condition was significantly greater than size at maturity for all females ($P < 0.05$).

DISCUSSION

The results from this study provide the most comprehensive reproductive analysis for sandbar sharks in the western North Atlantic Ocean and Gulf of Mexico to date. Additionally, this study provides the first age-at-maturity estimates obtained from directly aged sharks in this region. Though the geographic range of sampling was limited to the southeastern United States, mature females were captured in all months of the year and all stages of reproduction were represented by robust sample sizes.

Mating and parturition were highly seasonal, with the peak of mating occurring from May to July and parturition taking place in May and June. The MFD and OW values of stage 3 females were highest in June, with significant declines from June to July. Ovulating females were observed in June and July, and sperm was identified in the uteri of females beginning in

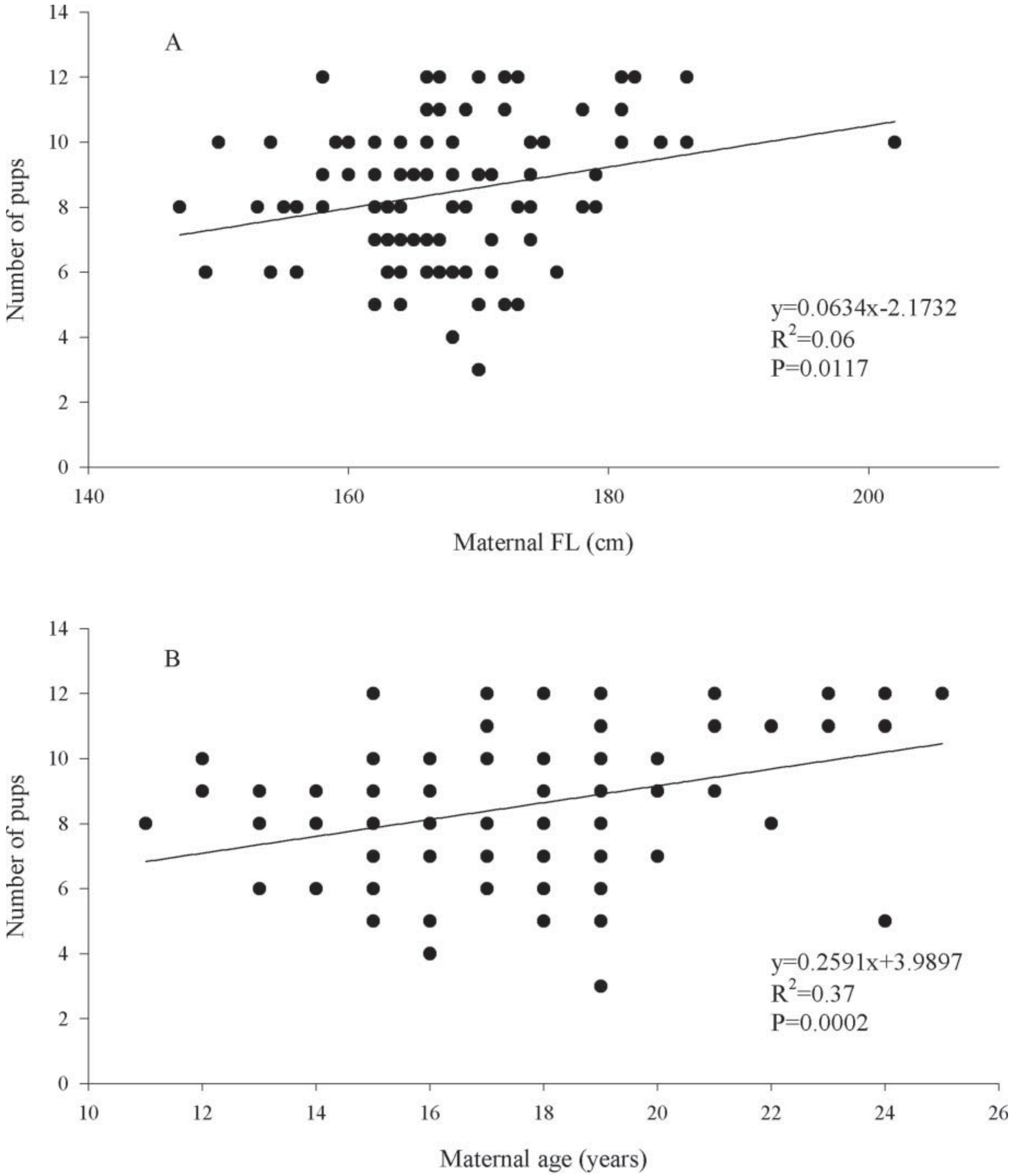

FIGURE 9. Scatterplot and regression analysis of the number of sandbar sharks pups relative to **(A)** maternal fork length ($n = 99$) and **(B)** maternal age ($n = 99$).

April. While the first postpartum female was observed in April and the last in September, no near-term pups were observed after June. Because reproductive analysis was conducted via internal examination of females only, the presence of mating scars could not be confirmed. With the exception of a few individuals, reproductive timing was relatively succinct. These observations agree with earlier reports of the timing of parturition from Virginia (Medved and Marshall 1981; Musick and Colvocoresses 1988) and South Carolina (Castro 1993), though parturition appears to begin nearly 1 month later in the more northerly Delaware Bay (Merson and Pratt 2001). This is not uncommon, however, as latitudinal variation in life history characteristics is known to occur in shark species over a range of a few hundred kilometers (Lombardi-Carlson et al. 2003).

TABLE 2. Parameter estimates and standard error (SEs) for maturity and maternity logistic regressions for sandbar sharks.

	Maturity: females		Maturity: males		Maternity	
Parameter	Estimate	SE	Estimate	SE	Estimate	SE
FL						
a	−36.55	2.84	−43.35	4.23	−24.59	2.01
b	0.24	0.02	0.29	0.03	0.15	0.01
Age						
a	−8.61	0.72	−11.39	1.18	−6.45	0.51
b	0.66	0.51	0.94	0.09	0.41	0.03

Males likewise showed seasonal trends in reproductive condition. Epididymis width peaked in June, though testis weight was highest in April. The lag in these trends likely corresponded to peak spermatogenesis in the testes just prior to mating, with the maximum in epididymis width being consistent with the climax of the mating period (Engel and Callard 2005). Males with engorged seminal vesicles and large quantities of semen were observed in April, May, and June.

While the Chesapeake Bay is most likely the largest pupping and nursery area for sandbar sharks in the U.S. Atlantic Ocean, perhaps dozens of smaller nursery areas exist along the U.S. East Coast and Gulf of Mexico (Springer 1960; Clark and von Schmidt 1965; Carlson 1999; Grubbs et al. 2007). Cape Canaveral, Florida, has historically been reported as the southernmost boundary of the sandbar shark pupping range (Springer 1960), though it has been suggested that the boundary has moved north to South Carolina (Merson 1998; Grubbs et al. 2007). However, we found that all near-term females (those captured in May and June with average embryo STL >55 cm) were captured in the waters offshore of Florida, with 21 females collected in the Florida Keys, one off the coast of Ft. Pierce, and one off the coast of Jacksonville. The postpartum females

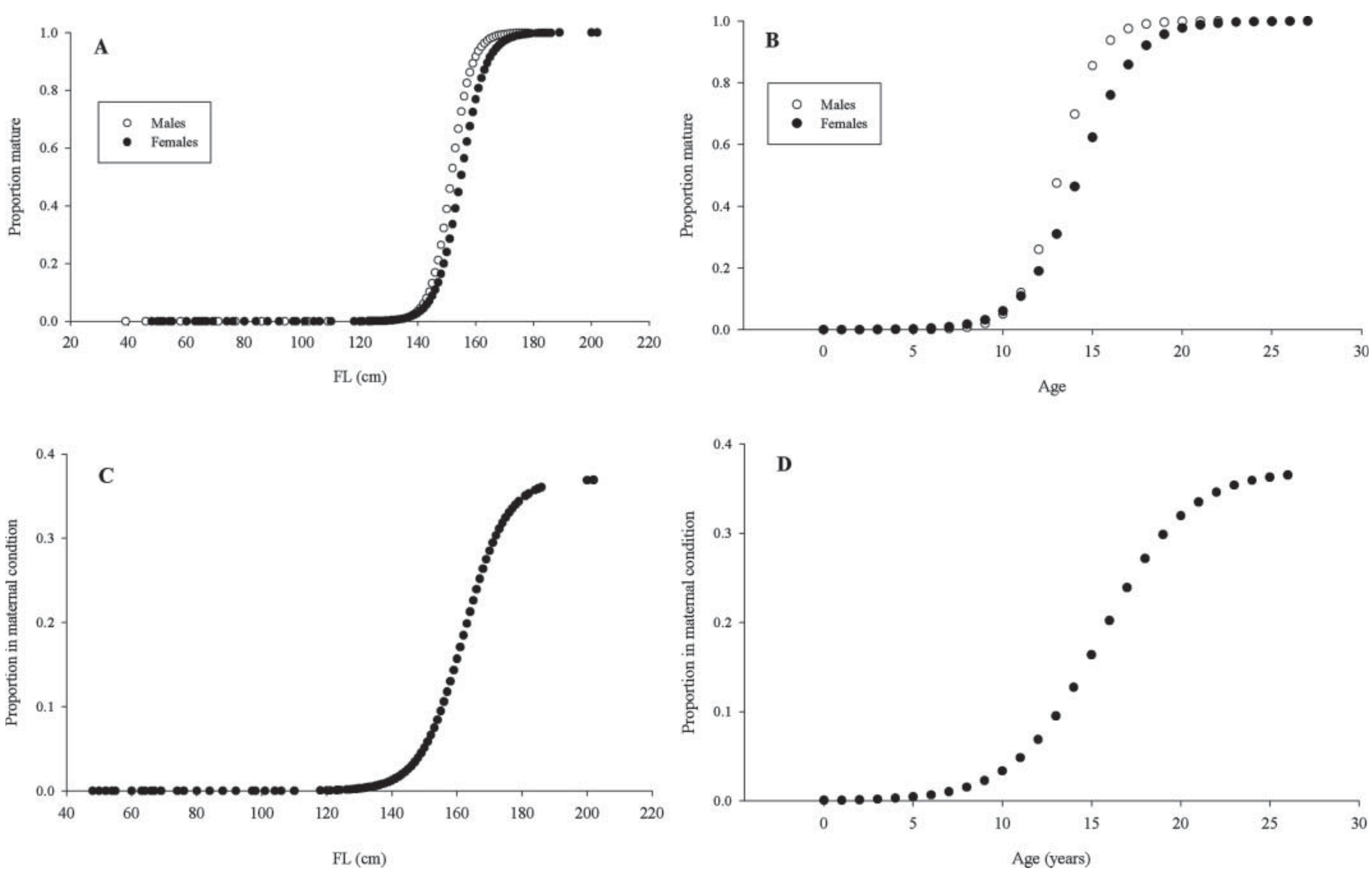

FIGURE 10. Logistic curves for sandbar sharks by **(A)** size and **(B)** age at maturity for males ($n = 493$) and females ($n = 701$) and **(C)** size and **(D)** age at maternal condition ($n = 646$) for females. The curves for panels (C) and (D) were scaled to 0.37 (the proportion of gravid females in the population).

examined ($n = 11$) were likewise collected from Jacksonville through Key West, and one female was sampled in the northeastern Gulf of Mexico. Newly pregnant females (captured June–September with embryos <30 cm STL) were observed from North Carolina through the Florida Keys. It is therefore clear that while some of the sandbar sharks sampled in this study were probably migrating, both mating activity and parturition were taking place as far south as Key West. What is unclear is whether these females were residents that did not take part in the northern migration or migrants from the Gulf of Mexico or another population in the south. Long-term telemetry studies of mature female sharks are needed to clarify these issues.

Pregnant females did not show any signs of vitellogenic development during gestation, indicating that the periodicity of the ovarian cycle is at least biennial in sandbar sharks. Typically, shark species with a seasonal, biennial reproductive cycle can be expected to follow predictable patterns (Castro 2009). For example, it would be expected that approximately 50% of mature females would be pregnant at any given time and that the majority nongravid mature females would undergo vitellogenesis during the months prior to ovulation and mating. We found that approximately 37% of mature females were pregnant overall, and during the months leading up to the peak of ovulation several mature females appeared to be in "resting" condition. No previous studies in the same region that examined the ratio of pregnant females to nonpregnant ones reported numbers close to the expected 50% ratio. In the western North Atlantic, the percentage of mature females examined that were pregnant has been reported as 17–18% (Springer 1960) and 27% (Clark and von Schmidt 1965); in Australia, the number was around 30% (McAuley et al. 2007). However, 56% of mature female sandbar sharks were pregnant in South African waters (Cliff et al. 1988). These factors indicate that the sandbar sharks in some regions may not have a strictly biennial cycle but that some females might maintain a resting condition for 2 years between pregnancies. Other authors have reported differences in ovarian cycles among shark species from different regions (Sulikowski et al. 2007; Walker 2007). Though sampling bias cannot be ruled out, it is reasonable to assume that while sandbar sharks are likely capable of reproducing every 2 years, factors such as energetic condition and food availability could lead to a delay in reproduction.

The presence of mature females in resting condition during the peak of reproduction was seen most clearly in the plot of individual MFD values during the months of January–June (Figure 5) and by comparing the ovarian and uterine conditions of females captured during the same time period (Figure 6A, B). Examining MFD values among months, it appears that vitellogenesis takes place over approximately 4 months (March–June) because the MFD values of nongravid females from July to February were <20 mm and the average MFD was not significantly different by month. This was also supported by the females in each stage by month (Figures 3, 4): ovulating females were only observed in June and July. Therefore, the presence of mature females with MFD values <20 mm from March to June warranted closer examination. As parturition also occurred during this time period, the width of the uterus and presence of placental scars were used to distinguish postpartum females (stage 7) from those in resting (stage 3) condition. Other authors have suggested a triennial cycle for this species (Merson 1998; Hazin et al. 2001; Piercy 2009), and Piercy (2009) showed an even stronger bimodality in the MFD during spring months. In light of this evidence, the most recent sandbar shark stock assessment (SEDAR 2010) base model used a 2.5-year reproductive cycle in place of the 2-year cycle that was assumed for previous assessments (Cortés et al. 2002; SEDAR 2006). Further investigation is needed to fully understand the periodicity of the ovarian cycle of the sandbar shark because reproductive output parameters directly affect stock assessment models and can change stock status (I. Baremore and K. Andrews, National Marine Fisheries Service, unpublished). Future studies should focus on the histology and movement patterns of mature females in nursery areas over a period of several years.

Fetal mummification has been reported in sandbar sharks (Springer 1960; Clark and von Schmidt 1965). We found three cases of fetal mummification and that ovulated but unfertilized ova were present in 34% of pregnant females. The cause of these reproductive failures is unclear, but it could be due to a lack of male genetic material. Sandbar sharks exhibit multiple paternity in some areas, though genetic monogamy was found to occur between 15% and 50% of the time (Daly-Engel et al. 2007; Portnoy et al. 2007). Although multiple paternity is thought to increase reproductive success and/or genetic diversity, it appears that multiple paternity is due to male coercion and conflict rather than reproductive benefit (Portnoy et al. 2007). The overall rate of unfertilized–mummified embryos was very low and the phenomenon seems to be common in shark species; however, future researchers may want to take this into account to ensure that rates of infertility are not increasing.

Most of the mature sandbar sharks sampled for this study were collected exclusively from commercial bottom longline fisheries, while the majority of juveniles were captured during fishery-independent surveys using anchored gill nets and small-scale longlines. The difference in sampling gears could have had a size-selective effect on the age and growth estimates (Thorson and Simpfendorfer 2009). However, the robust sample size of the age estimates and the methodology used to produce the growth parameters (Hale and Baremore 2010) likely minimized these effects. Reproductive analysis was conducted almost exclusively on sandbar sharks collected by commercial bottom longlines, so differences in gear selectivity did not have an effect on current results.

This was the first study to find a statistically significant relationship between litter size and increasing maternal age in an elasmobranch. Litter size was also positively correlated with FL, though the correlation was weaker than it was for maternal age. Because viviparous sharks produce large, well-developed young, the prevailing theory is that maternal body size has the greatest effect on reproductive output (Carrier et al. 2004).

However, most carcharhinid sharks do not dramatically increase fecundity or the quality of offspring (i.e., size of pups at birth) with size (Carrier et al. 2004). Very few reproductive studies on sharks to date include aged animals, so little else is known about potential differences in reproductive output and quality as sharks age. Our findings indicate that, like many teleost fishes, older female sandbar sharks may be more reproductively fit than younger females. In teleost fishes, both the quantity and quality of eggs are known to increase as females grow in size and age (Chambers et al. 1989; Marteinsdottir and Steinarsson 1998; Berkeley et al. 2004). Studies on teleost fishes have shown that older females produce offspring that have higher survival rates than those of younger females. Sandbar shark embryos exhibit placentation, whereby embryos receive sustenance by maternal uterine secretion and eventually placental nourishment (Hamlett 2005). With an average of eight pups per litter, each reaching nearly 60 cm STL, maternal energetic investment is likely high. In the case of sandbar sharks, older females are approaching asymptotic growth, and are therefore able to devote more energy to reproduction than younger females. This could account for the increase in fecundity with age for sandbar sharks.

Size at maturity for males and females was smaller than reported by Piercy (2009) in the same region but well within the range reported by authors in other regions (Cliff et al. 1988; Joung and Chen 1995; Merson 1998; Saïumldi et al. 2005; Hazin et al. 2007; McAuley et al. 2007; Diatta et al. 2008). This study provides the first maternity ogive for the species, a parameter which is becoming important in stock assessments because it takes into account the periodicity of the reproductive cycle by excluding those females not actively reproducing. Overall landings of sandbar sharks in the western North Atlantic and Gulf of Mexico have been drastically reduced since the sandbar shark research fishery was established. As a result, the stock appears to be recovering and was most recently assessed as overfished but with no overfishing occurring (SEDAR 2010). Because the stock has undergone severe declines (Sminkey and Music 1995; SEDAR 2006), it is important to evaluate how density dependence affects life history parameters as the population continues to recover. Periodic reassessment of reproduction, along with as continued monitoring of the age structure of sandbar sharks removed by the fishery, will ensure that assessment scientists and managers have the best data possible.

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