Journal of Fish Biology (2007) **70,** 428–440
doi:10.1111/j.1095-8649.2007.01314.x, available online at http://www.blackwell-synergy.com

Reproductive cycle of the blacknose shark *Carcharhinus acronotus* in the Gulf of Mexico

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(Received 17 January 2006, Accepted 27 September 2006)

The reproductive periodicity of blacknose sharks *Carcharhinus acronotus* in the northern Gulf of Mexico was determined by examining reproductive tissues from specimens collected monthly from 2002 to 2005. Monthly changes in shell gland mass, right ovary mass and ovarian follicle diameter were assessed for 74 mature females. Temporal changes in testes mass, testes width and proportion of mature spermatocysts were examined for 64 mature males. Trends in female reproductive tissues suggested an annual peak in reproductive activity during June and July, while trends in male variables suggested an annual reproductive peak during May and June. Although male and female reproductive activity peaked in different months, a strong synchronicity existed between the proportion of mature spermatocysts and the diameter of the largest ovarian follicle. Based on these results, the mating season of blacknose sharks lasts from mid-May to July in the Gulf of Mexico. Maximum embryo sizes were observed in May, which suggested that partition occurs during late May or early June. Results indicate that blacknose sharks have a clearly defined annual cycle in the Gulf of Mexico. This conclusion is further supported by the complete absence of gravid females without vitellogenic ovarian follicles among all mature females examined.

Key words: blacknose shark; Carcharhinidae; elasmobranch; reproduction.

INTRODUCTION

A Fishery Management Plan For Sharks (NMFS, 1993), was developed in 1993 for the management of shark populations in U.S. territorial waters of the Atlantic Ocean and Gulf of Mexico (NMFS, 1993). Because species-specific catch and life-history information was limited, sharks were grouped and managed under three categories: large coastal, small coastal and pelagic. Recent studies focusing on sharks species within the small coastal shark complex [*i.e.*

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blacknose *Carcharhinus acronotus* (Poey), finetooth *Carcharhinus isodon* (Müller & Henle), Atlantic sharpnose *Rhizoprionodon terraenovae* (Richardson) and bonnethead *Sphyrna tiburo* (L.) sharks] indicate the possibility of intraspecific regional variability in important life-history characteristics such as growth and reproduction (Carlson *et al.*, 2003; Lombardi-Carlson *et al.*, 2003; Loefer & Sedberry, 2003; Driggers *et al.*, 2004*a, b*). Due to the importance of biological data as inputs in demographic and population models (Cortés, 2002), it is imperative to accurately describe the life history of each species throughout its range.

The blacknose shark is distributed throughout the western Atlantic Ocean from North Carolina to Brazil, including the Gulf of Mexico (Compagno, 1984). The life history of the blacknose shark has been previously investigated, however, dissimilarities in some variable estimates, such as growth, age and size-at-maturity, gestation periods and reproductive periodicity, exist among studies. For example, depending on geographic area, the size-at-maturity for blacknose sharks varies, with estimated size-at-maturity ranging from 887 to 918 mm fork length (L_F) for males and between 886 and 1005 mm L_F for females (Clark & von Schmidt, 1965; Dodrill, 1977; Schwartz, 1984; Driggers *et al.*, 2004*a*). Lengths at maturity were reported in total length (L_T) by some authors and were subsequently converted to L_F (M. Grace, unpubl. data). Variability in age-at-maturity has also been observed, with estimates ranging from 2 to 3 years in the Gulf of Mexico (Clark & von Schmidt, 1965; Carlson *et al.*, 1999) and from 4 to 5 years in the western North Atlantic Ocean (Driggers *et al.*, 2004*a*). As the spatial stock structure of blacknose sharks is poorly understood, Driggers *et al.* (2004*a*) noted that is unknown if variability in important life-history parameters is due to genetic differentiation or phenotypic plasticity.

In the western North Atlantic Ocean, Dodrill (1977) and Driggers *et al.* (2004*a*) reported that female blacknose sharks reproduce biennially with a gestation period of 10–11 months, while Schwartz (1984) proposed an annual reproductive cycle and a 9 month gestation period. After examining blacknose sharks collected from the coastal waters of Brazil, Hazin *et al.* (2002) were unable to resolve the reproductive cycle of females but hypothesized that gestation lasts for *c.* 8 months with adult females reproducing annually.

Within the Gulf of Mexico, there is inadequate information on the reproductive biology of blacknose sharks, particularly as it applies to their reproductive cycle. Branstetter (1981) reported on the simultaneous collection of gravid and non-gravid female blacknose sharks in the north central Gulf of Mexico, and based on his limited sample size suggested a biennial reproductive cycle. Branstetter (1981), however, also reported that he examined two near-term female blacknose sharks collected in the same region which had large vitellogenic ovarian follicles, suggesting an annual reproductive cycle. Given the disparity in the reproduction within and among regions, the purpose of this study was to examine the reproductive cycle of blacknose sharks in the northern Gulf of Mexico.

MATERIALS AND METHODS

Blacknose sharks were collected in the Gulf of Mexico between 2002 and 2005 during National Marine Fisheries Service, Mississippi Laboratories, bottom longline surveys and aboard commercial fishing vessels by fishery observers. All specimens were collected above 24°36′ N and between 84°48′ and 97°08′ W within the United States Exclusive Economic Zone. The L_F and L_T of all collected specimens were measured to the nearest mm.

To assess the reproductive cycle of males, the gross morphology of testes was examined and spermatogenesis was investigated histologically. After making an incision through the abdominal musculature, testes were removed, blotted dry and mass was calculated to the nearest g. The right testis width was measured at its widest section. Histological processing followed the protocol of Sulikowski *et al.* (2004, 2005). Briefly, a 2–3 mm thick segment was removed from the central portion of a single lobe in the medial section of a testis, placed in a tissue cassette and fixed in 10% buffered formalin until processed by the University of New Hampshire's Veterinary Diagnostic Laboratory. There, the sample was dehydrated, embedded in paraffin, sectioned and stained with haematoxylin and eosin.

Among the stages of spermatogenesis described in other elasmobranchs, hormone analyses have confirmed that stage VI (mature spermatocyst) is associated with reproductive readiness (Cuevas & Callard, 1989; Du Bois *et al.*, 1989; Heupel *et al.*, 1999; Tricas *et al.*, 2000; Sulikowski *et al.*, 2004), therefore, efforts were focused on this stage. Prepared slides of testicular tissue were examined and the mean proportion of mature spermatocysts was measured along a straight line across one representative full testis lobe cross-section. Stage VI spermatocysts were identified by the organization of spermatozoa into tightly shaped packets arranged spirally along the periphery of the spermatocysts (Hamlett & Koob, 1999).

To determine the reproductive periodicity of females, temporal changes in the size of reproductive tissues were examined. After exposing the body cavity, the right ovary, shell glands and uteri were removed, blotted dried and mass was calculated to the nearest g. Temporal fluctuations in ovarian follicle dynamics were evaluated by examining the changes occurring in the single largest follicle found in the right ovary of each blacknose shark (Driggers *et al.*, 2004*a*; Sulikowski *et al.*, 2004, 2005). Thus, changes in mean ovary and shell gland mass and the size of the largest vitellogenic follicle were used to assess temporal patterns during the reproductive cycle. The uteri, if developed, were dissected to determine if embryos or uterine eggs were present. If embryos were present their stretch total length (L_{ST}) was measured and sex was recorded. The L_{ST} was measured from the anterior most point of the snout to the posterior most point of the upper lobe of the caudal fin while fully extended. The L_{ST} was used as the standard length measure for embryos because caudal fin morphology changes during development.

CRITERIA FOR SHARK MATURITY

Females were considered mature if they were gravid. During the months immediately following parturition, females whose reproductive tracts contained uterine eggs with a minimum diameter of 20 mm and had a shell gland mass of at least 2·4 g were considered mature. Males with calcified claspers ≥120 mm long with a testes mass of ≥1·5 g and testes width of ≥7 mm were considered reproductively capable of fertilizing an ovulated follicle. These criteria are consistent with previous studies that reported similar characteristics for other mature elasmobranch species (Koob *et al.*, 1986; Heupel *et al.*, 1999; Conrath & Musick, 2002; Sulikowski *et al.*, 2004) and for those used by Driggers *et al.* (2004*a*) for blacknose sharks in the western North Atlantic Ocean.

STATISTICAL ANALYSES

ANOVA followed by a Tukey's *post hoc* test (Zar, 1974) was used to determine if there were significant differences in reproductive variables (*i.e.* testis mass, testes width, ovarian follicle diameter, ovary and shell glands mass and embryo size) by month. The results are presented as a mean ± S.E. To determine whether a relationship existed between the measured reproductive variables, a Pearson correlation (*r*; Zar,

1974) was performed. The proportion of mature spermatocysts was transformed to arcsin values before the statistical analyses were performed. The relationship between maternal L_F and litter size was compared using ANOVA and linear and non-linear regression.

RESULTS

Female blacknose sharks ($n = 74$) ranged from 850 to 1100 mm L_F (mean ± s.e. = 961 ± 50 mm) while males ($n = 68$) ranged from 820 to 1010 mm L_F (904 ± 47 mm). Samples were obtained during all months of the year except for December.

In male blacknose sharks, a strong correlation existed between the proportion of mature spermatocysts and testis mass ($r = 0{\cdot}63$, $P < 0{\cdot}001$) and testis width ($r = 0{\cdot}63$, $P < 0{\cdot}001$) over the course of the sampling period. Testis mass [Fig. 1(a)], testes width [Fig. 1(b)], and proportion mature spermatocysts [Fig. 1(c)] displayed an increasing trend in males collected from January to May before declining through to November. Statistical analyses (ANOVA, Tukey's *post-hoc*, $P < 0{\cdot}05$) revealed that testes mass from males in May were significantly different from those captured in all other months [Fig. 1(a)]. Testes width followed a similar trend, with the testes from males captured in May being wider (ANOVA, Tukey's *post-hoc*, $P < 0{\cdot}05$) than in those from mature male blacknose sharks captured in all months except for June [Fig. 1(b)]. The proportion of mature spermatocysts in May, June and July, were also significantly higher (ANOVA, Tukey's *post-hoc*, $P < 0{\cdot}05$) than in all other calendar months [Fig. 1(c)].

Among females, a strong correlation existed between shell gland mass and ovary mass ($r = 0{\cdot}76$, $P < 0{\cdot}001$) but only a moderate correlation existed between shell gland mass and the mean size of the largest follicle ($r = 0{\cdot}35$, $P < 0{\cdot}05$) over the course of the sampling period. Ovary mass [Fig. 2(a)], shell gland mass [Fig. 2(b)], and diameter of the largest follicle [Fig. 2(c)] displayed an increasing trend for females collected from January to July before declining through to November. Statistical analyses revealed that shell gland mass and diameter of the largest follicle were significantly larger in July (ANOVA, Tukey's *post-hoc*, $P < 0{\cdot}05$) than in all other months [Fig. 2(b), (c)]. Ovary mass followed a comparable trend, with the right ovary of females captured in May, June and July being heavier (ANOVA, Tukey's *post-hoc*, $P < 0{\cdot}05$) than in those from blacknose sharks captured in January, February or November.

A total of 106 pups from 38 litters were analysed. The mean ± s.e. number of pups carried by each female was 3·13 ± 1·07. The maximum observed number of pups was five and the minimum one. By September, the yolk sac and stalk had differentiated into the placenta and umbilical cord. Embryo growth was initially slow, but became more rapid after placental attachment from September to January and culminated with the largest embryo size being observed in May (Fig. 3). This growth suggests a 9–10 month gestation period. The growth of embryos was best described by the formula $L_{ST} = e^{[4{\cdot}05 - (3{\cdot}09a^{-1})]}$ ($r^2 = 0{\cdot}94$) where a = age (Fig. 3). There was no significant relationship between maternal length and the number of pups per litter (ANOVA, $P > 0{\cdot}05$).

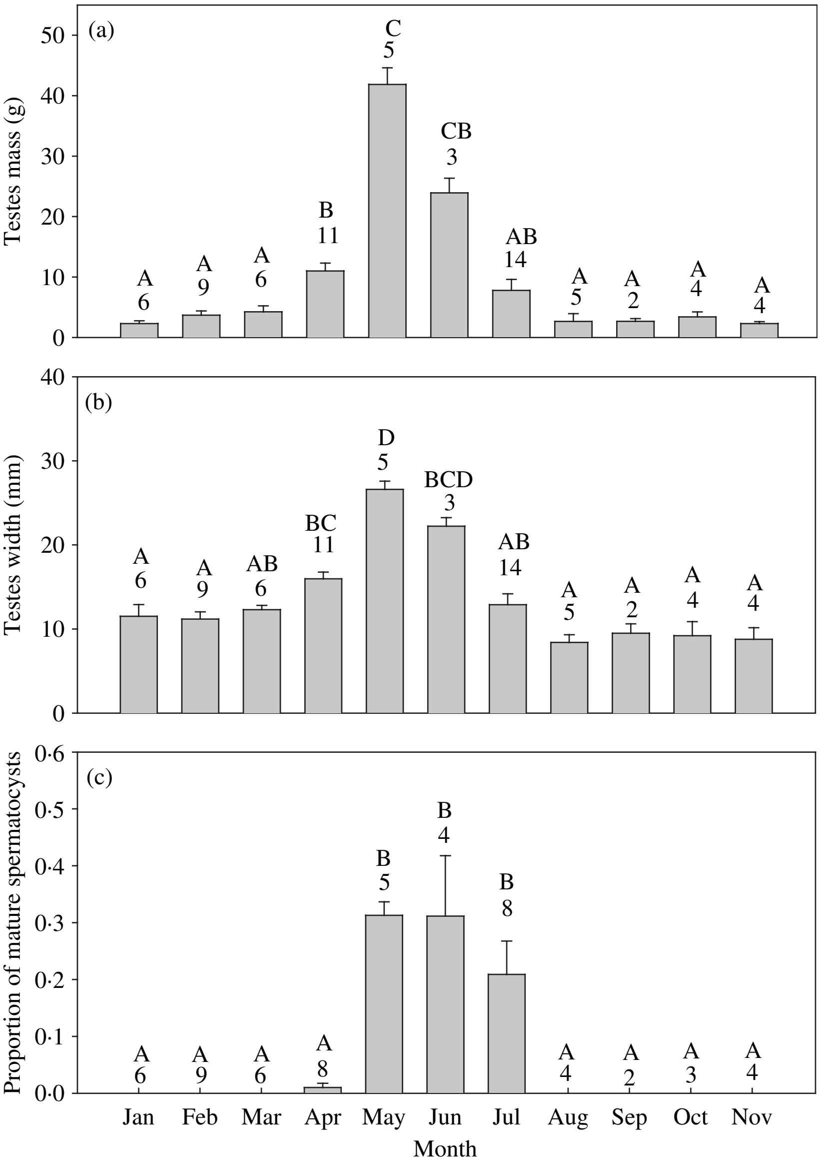

FIG. 1. Monthly changes in male blacknose shark reproductive tissues and spermatocysts: (a) testes mass, (b) testes width and (c) mean proportion of mature spermatocysts along a transect line across one representative full lobe cross-section of a testis. Values are expressed as mean + S.E. Sample sizes are indicated above each month. Values designated with different uppercase letters are significantly different from each other ($P < 0·05$).

Given that embryos reached maximum size in May, parturition was assumed to occur in late May or in early June (Fig. 4). This event coincided with the formation of large pre-ovulatory follicles (Fig. 5). Peaks in the proportion of mature spermatocysts suggested that copulation occurred shortly thereafter and continued until July (Fig. 4). Based on follicle size, ovulation appeared

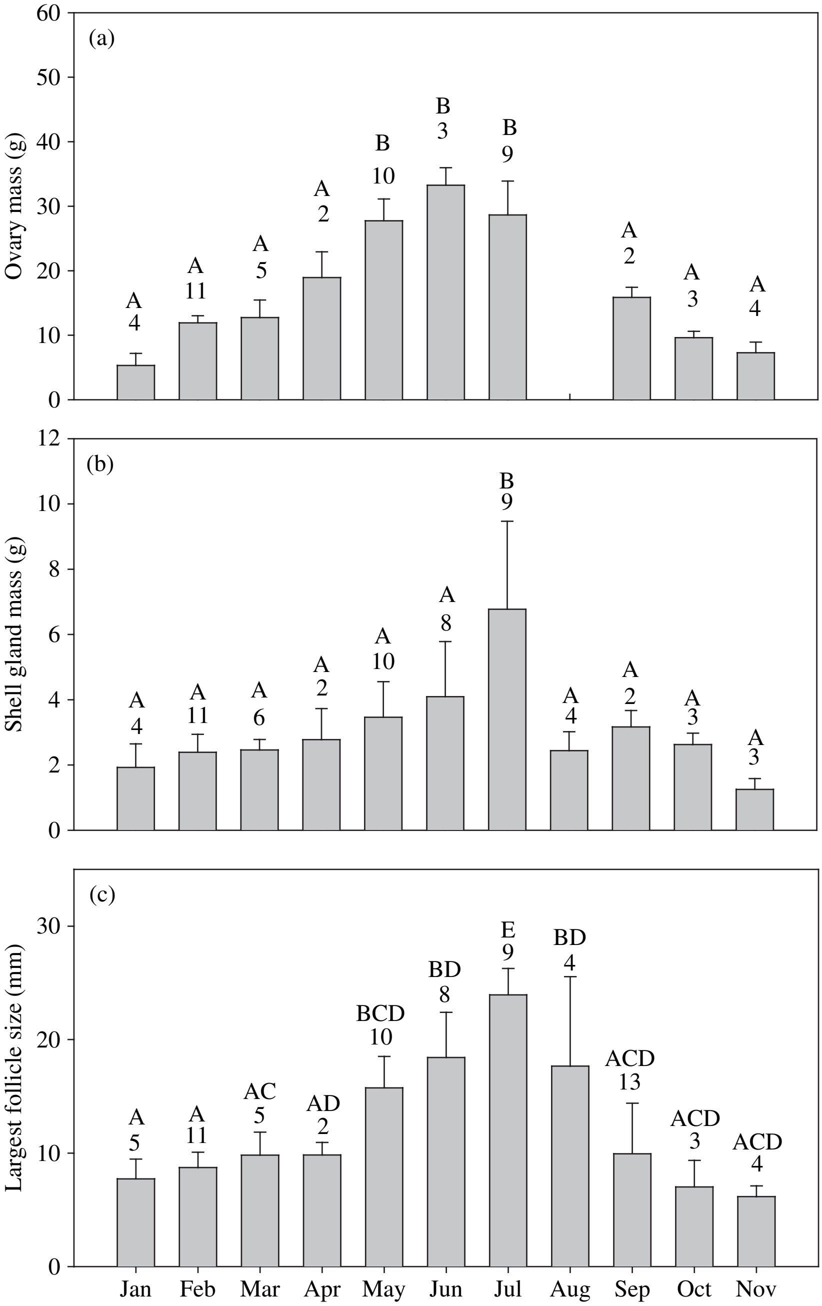

FIG. 2. Monthly changes in female blacknose shark reproductive tissues: (a) ovary mass, (b) shell gland mass and (c) diameter of the largest follicles. Values are expressed as mean + S.E. Sample sizes are indicated above each month. Values designated with different uppercase letters are significantly different from each other ($P < 0{\cdot}05$).

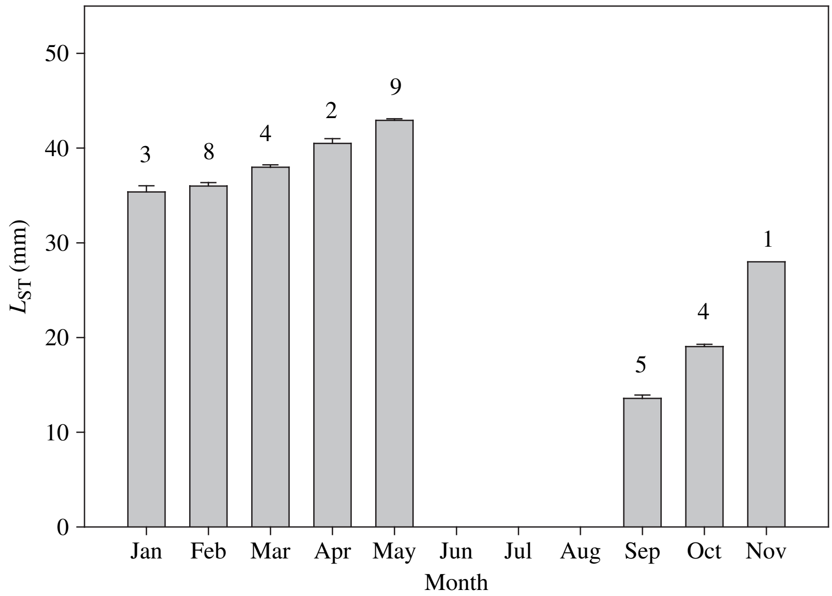

FIG. 3. Mean + S.E. stretch total length (L_{ST}) of blacknose shark embryos by month. Number of litters examined per month is given above each bar.

to commence in June, peaked in July, then began to wane in August (Fig. 4). In addition to the observed trends, a strong synchronicity ($r = 0{\cdot}45$, $P < 0{\cdot}01$) existed between the proportion of mature spermatocysts and the diameter of the largest follicle over the course of the yearly cycle. When the results of analyses of reproductive tissues were combined with the monthly change in embryo growth a clear annual cycle was observed.

DISCUSSION

A wide range of complex reproductive strategies are displayed within the sub-class Elasmobranchii (Wourms & Demski, 1993; Hamlett & Koob, 1999). These strategies are associated with one of the three basic types of reproductive cycles: 1) reproduction throughout the year, 2) a partially defined annual cycle with one or two peaks and 3) a well-defined annual or biennial cycle (Wourms & Demski, 1993; Hamlett & Koob, 1999). Research conducted thus far suggests that all of the species within the genus *Carcharhinus* inhabiting the western North Atlantic Ocean fit into the third category, exhibiting a distinct biennial reproductive cycle. For example, blacknose, finetooth and blacktip *Carcharhinus limbatus* (Müller & Henle) sharks were found to exhibit consecutive, year-long ovarian and gestation cycles off the coast of the south-eastern United States (Castro, 1993, 1996; Driggers *et al.*, 2004*a*).

Results from the analyses of male and female reproductive tissues conducted during the current study, indicate that blacknose sharks have a clearly defined annual cycle in the Gulf of Mexico. This conclusion is based on the co-ordinated waxing and waning of male and female reproductive variables,

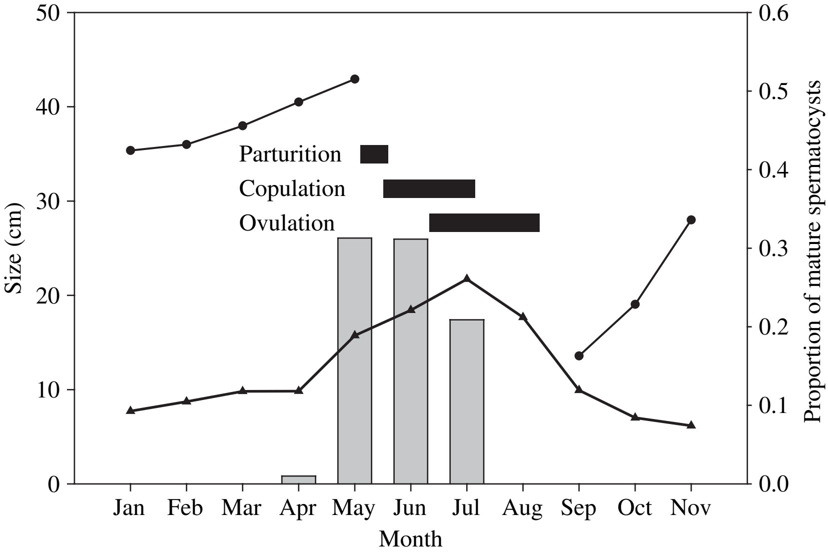

FIG. 4. Summary diagram of embryo growth and the associated reproductive events for the study population of blacknose sharks. Maximum pup size [stretch total length (L_{ST}) ●] peaks in May suggesting that parturition occurs in late May or early June. Peaks in the proportion of mature spermatocysts (▨) indicate that copulation occurs shortly thereafter and continues until July. Ovulation (follicle size, ▲) appears to commence in June, peak in July then begin to wane in August.

embryo growth and time of parturition (*c*. 9–10 months), and is based on analyses from a robust sample size of specimens collected during all seasons over a consecutive 3 year period. This conclusion is further supported by the complete absence of non-gravid mature females examined in the current study and

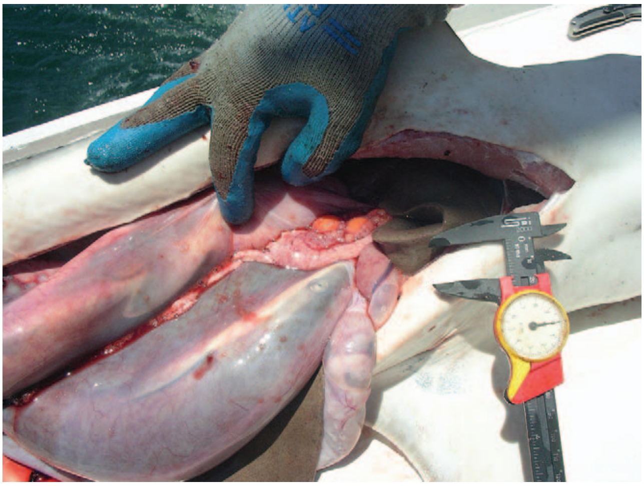

FIG. 5. The right uterus and ovary of an adult female blacknose shark (979 mm L_F), captured on 18 May 2006. The simultaneous formation of near-term pups and pre-ovulatory follicles within the reproductive tract denotes the existence of an annual reproductive cycle.

free swimming neonates (48·5 cm L_{ST}) captured in June as part of the NMFS inshore fishery-independent surveys in the north-east Gulf of Mexico.

It is unclear why disparity in the reproductive cycle for blacknose sharks exists between the western North Atlantic Ocean and the Gulf of Mexico, however, geographic variations in sample collection between studies must be considered. Several studies have demonstrated the effect of geographic variation, particularly latitude, on life-history traits in elasmobranchs. These effects have been attributed to phenotypic plasticity resulting from abiotic environmental factors, such as temperature (Lombardi-Carlson *et al.*, 2003). For example, a difference in five degrees of latitude had measurable effects on the maximum size, size-at-maturity and size of near-term embryos for bonnethead sharks in the eastern Gulf of Mexico (Lombardi-Carlson *et al.*, 2003). Studies focusing on other shark species also noted an increase in size with increased latitude (Taniuchi *et al.*, 1993; Yamaguchi *et al.*, 1998; Horie & Tanaka, 2002). While reproductive traits, such as fecundity or spawning season length, are known to vary with latitude for some teleost species (Conover, 1990; Fleming & Gross, 1990; Castro & Cowen, 1991), such variability has not been widely reported to occur in elasmobranchs. Observed latitudinal disparities in intraspecific life-history variables are thought to be adaptive responses to different environmental conditions (Conover, 1990). If latitudinal variation does affect the reproductive periodicity of sharks the annual reproductive cycle of blacknose sharks proposed by Hazin *et al.* (2002) seems probable. The mechanisms underlying the differences, however, are not well understood (Conover, 1990) and further investigation of the observed differences in reproductive cycles in female blacknose sharks must be conducted before any conclusions can be drawn.

Another cause for the disparity in the reproductive cycle for blacknose sharks in the western North Atlantic Ocean and the Gulf of Mexico could be related to the energetics of movement patterns. Off the east coast of central Florida, Dodrill (1977) reported that blacknose sharks are abundant from September until May and absent in these waters from July until late August. Blacknose sharks occur in South Carolina waters from May to November (G. Ulrich, pers. comm.) and in North Carolina waters from July to September (Schwartz, 1984). That blacknose sharks occur in Florida waters during the autumn, winter and spring, and that they are first seen in the spring and absent during the winter in the coastal waters of the Carolinas indicates that this species migrates annually up and down the east coast of the U.S. with the distance from the coastal waters of central Florida to those of North Carolina being in excess of 1500 km. This migratory pattern is further supported by limited tag recapture data (Kohler *et al.*, 1998; N. E. Kohler, pers. comm.). Studies on salmonids suggest that these teleosts must have sufficient energy reserves in place to fuel migration, and support the behaviours and morphological changes associated with courtship and spawning (Burgner, 1991; Brett, 1995). Moreover, a disproportionately high level of energy used during migration has been shown to cause premature mortality in these fishes (Rand & Hinch, 1998). While this phenomenon has yet to be studied in sharks, the additional energy expenditure needed by blacknose sharks in the western North Atlantic Ocean may limit the energy they can invest in the development of reproductive tissues. Therefore, it is possible that an annual reproductive cycle would be detrimental to female survival and thus limits them to reproducing in alternate years. Conversely, in the Gulf of Mexico if the seasonal migration of blacknose sharks is more spatially limited the energy conserved could be used for the annual reproductive processes such as vitellogenesis, shell gland enlargement and embryo nourishment. While there is scant information on the migratory pattern of blacknose sharks in the Gulf of Mexico evidence exists suggesting that their seasonal movements are more limited than is observed in the western North Atlantic Ocean. During the spring, summer and autumn blacknose sharks are frequently caught in the coastal waters of the central northern Gulf of Mexico. During the late autumn and early winter blacknose sharks migrate out of these waters as indicated by a precipitous decline in catch rates (W. B. Driggers, unpubl. data; E. Hoffmayer, pers. comm.). While the migratory patterns of this species are unknown in the Gulf of Mexico, the capture of 16 blacknose sharks, *c.* 110 km due south of Pascagoula, Mississippi, during March of 2003 suggests that this species moves offshore during the late autumn, winter and early spring months (W. B. Driggers, unpubl. data). If migrations are relatively spatially limited in the Gulf of Mexico then energy that would be used in more large scale migrations could be utilized for somatic or reproductive growth. Future investigations are needed before any definitive conclusions concerning the mechanisms controlling the causes of the regional variability in reproductive periodicities can be drawn.

Relatively few studies have assessed whether the recrudescence and regression of reproductive tissues are co-ordinated between males and female elasmobranchs over the course of their reproductive cycles. Among those species that have been studied, corresponding peaks in male and female gonad mass were found in winter skates *Leucoraja ocellata* (Mitchill) (Sulikowski *et al.*, 2004), thorny skates *Amblyraja radiata* (Donovan) (Sulikowski *et al.*, 2005) and epaulette sharks *Hemiscyllium ocellatum* (Bonnaterre) (Heupel *et al.*, 1999). Information pertaining to Atlantic sharpnose sharks collected from the Gulf of Mexico (Parsons, 1983) suggests males and females follow the same trends over a calendar year. In contrast, the reproductive cycles of male and female Atlantic sharpnose sharks in the western North Atlantic Ocean lack a direct synchronicity in reproductive seasonality. Analyses of male and female gonadosomatic indices (I_G) revealed that male I_G values are highest in April while female I_G values were highest in May and June (Loefer & Sedberry, 2002). Similarly, Driggers *et al.* (2004*a*) reported a comparable trend for blacknose sharks in the same region with male I_G values being highest in May while female I_G values peaked in June. The reproductive cycles of male and female blacknose sharks from the current study were also phase lagged by a period of *c.* 1 month. Although spermatogenic and vitellogenic activity peaked in different months, they were correlated over the course of the reproductive cycle and elevated levels of these variables persisted from May to July. Based on these results, it would appear that the mating season of the blacknose shark lasts from mid-May to July in the Gulf of Mexico.

Although not specifically investigated in this study, sperm storage in female elasmobranchs has been documented (Pratt, 1993; Maruska *et al.*, 1996). Results from the current study indicate that the testes of male blacknose sharks stopped producing viable sperm during July. Based on ovarian follicle dynamics, females were still producing large vitellogenic follicles at this time, suggesting that some mechanism for sperm storage, either in males or females, exists. Driggers *et al.* (2004*a*) determined that females ovulate, and ova are fertilized, in late June to early July while males were only reproductively active during the beginning of June. These observations suggest that female blacknose sharks in the western North Atlantic Ocean store sperm for at least a 2 week period prior to ovulation. This is consistent with Pratt (1993) who demonstrated that other carcharhinids are capable of storing sperm from weeks to months in the shell glands.

The regional variability in the reproductive cycle of female blacknose sharks stresses the importance for regionally based life-history studies, especially given the importance of vital rates in demographic models (Cortés, 1999). For example, Driggers *et al.* (2004*a, b*) determined that female blacknose sharks off the coast of South Carolina mature at an age of 4·5 years, have a theoretical longevity of 19 years and give birth to an average of 3·53 pups every other year. Based on these criteria, and ignoring senescence, a 19 year-old female would have the potential to reproduce seven times resulting in an average 24·71 pups over the span of her life. In contrast, data from Carlson *et al.* (1999) and the current study suggest that female blacknose sharks in the Gulf of Mexico mature at an age of 3 years, have a theoretical longevity of 16·5 years and give birth to an average of 3·13 pups every year. Based on these criteria, a 16·5 year-old female would have the potential to reproduce 13 times resulting in the production of an average of 40·69 pups over her lifetime. If the reproductive biology of the blacknose shark was generalized over the entire range of the species, either an over or underestimation of recruitment potential would be obtained.

As evidence for regional variability in important life-history variables continues to increase more effort should be focused on examining the life history of all commercially and recreationally important shark species on a regional basis throughout their range. To successfully ensure the sustainability of shark stocks, accurate information pertaining to the life history of the species of concern will need to be incorporated into the stock assessments upon which management strategies are based.

We would like to thank M. Grace, E. Hoffmayer, L. Jones, D. Landi and G. Ulrich for help in collection of sharks and providing data. Thanks are further extended to A. Piercy and T. Keller for help in the processing of samples, B. Snelson for reviewing an earlier version of the manuscript, and to N. Kohler and L. Natanson from the NMFS Apex Predators Program for providing tag and recapture data. This study was partially supported by funds from NOAA/NMFS to the National Shark Research Consortium.

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