THE REPRODUCTIVE BIOLOGY OF THE ATLANTIC SHARPNOSE SHARK, *RHIZOPRIONODON TERRAENOVAE* (RICHARDSON)

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ABSTRACT

Atlantic sharpnose sharks, *Rhizoprionodon terraenovae* (Richardson), were collected in the north central Gulf of Mexico from June 1979 to May 1980. The principal sampling devices employed were longline, trawl, and rod and reel. From a total of 215 Atlantic sharpnose sharks obtained during the study, 144 were female and 71 were male, ranging from 30 to 107 cm total lengths. The reproductive anatomy of both male and female sharpnose sharks is described. Atlantic sharpnose sharks differ from other carcharhinids in that the ovary is developed on the left side in females and overlapping siphon sacs are present in males. Clasper development suggests that males mature at about 80 cm total length, while ovarian egg diameters show that female maturation occurs at about 85 cm. Matings occur primarily between mid-May and mid-July. Embryonic growth is rapid immediately after fertilization during summer and fall but declines during winter and spring. Gestation requires 10 to 11 months and parturitions probably peak in June. Pups are released near shore at an average total length of 32 cm. Statistical analyses reveal a positive relationship between adult total length and litter size, with the largest individuals being the most fecund. An inverse relationship was observed between the numbers of embryos per uterus and embryo size. Mechanical "packing" within the uterus is proposed to explain the relationship.

The seasonal distribution of sharpnose sharks was found to be determined by an inshore-offshore migration. The data indicate that during winter months in deeper offshore waters, aggregates of predominately adult female sharpnose sharks may be encountered. The sex ratio at birth was found to be 1:1 but among adults collected a 1:2.8 ratio was observed.

Studies dealing with the reproductive biology of elasmobranchs have fallen far behind the voluminous amount of data that have accumulated on reproduction in the teleostean fishes. The northern Gulf of Mexico has been an area of particular neglect with only a few rather generalized studies (Springer 1938, 1940, 1950; Baughman and Springer 1950). Springer's (1960) classic work on the natural history of the sandbar shark, *Carcharhinus milberti* (*Eulamia milberti*), contains a great deal of reproductive information that might be applied to carcharhinid sharks in general. Likewise, Clark and von Schmidt's (1965) survey of the sharks of the central gulf coast of Florida provided valuable reproductive data. The understanding of the life history of the blue shark, *Prionace glauca*, was furthered by Pratt's (1979) examination of its reproductive biology.

Data concerning the life history of *Rhizoprionodon terraenovae* are scarce. *Rhizoprionodon* species are believed to be born in the late spring and summer. Bigelow and Schroeder (1948) reported that recently born specimens can be collected from Florida in July and that they were also present off the mouth of the Mississippi River in August. Skocik (1969) reported that pups are usually born in the spring but no data were available on mating season or gestation period.

Rhizoprionodon species are viviparous, the embryos obtaining nourishment via a placental connection (sometimes called a "pseudo- or yolk-sac placenta") between mother and embryo. Fecundity in *Rhizoprionodon* has been variously reported. Baughman and Springer (1950) reported four embryos for *R. terraenovae*. Bass et al. (1975) found an average of 4.7 embryos with a range of two to eight in *R. acutus*. Skocik (1969) reported a litter size of 12 for *R. terraenovae*, while Bigelow and Schroeder (1948) reported the same number for *R. terraenovae* taken around Cuba. Clark and von Schmidt (1965) briefly surveyed *R. terraenovae* off Englewood, Fla., and found one 83 cm female with five eggs. They also reported that all adult females examined had functional left ovaries. Compagno (1978) reported a range of one to four embryos for *R. porosus*. The pups of *R. terraenovae* have been reported to be 11 to 16 in (27.9 to 40.6 cm) at birth (Baugh-

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Manuscript accepted June 1982.
FISHERY BULLETIN: VOL. 81, NO. 1, 1983.

man and Springer 1950). Bigelow and Schroeder (1948) reported that specimens from Texas showing traces of the umbilical scar were from 280 to 407 mm long.

Among *R. terraenovae* populations, adults are commonly 26 to 30 in (66 to 76 cm) total length (TL) (Baughman and Springer 1950), but the size at which male and female Atlantic sharpnose sharks mature is unknown. In his revision of the genera *Scoliodon*, *Loxodon*, and *Rhizoprionodon*, V. G. Springer (1964) reported that insufficient information was available to establish the size at which males first mature but it appeared that maturation occurs at >640 mm TL. Bass et al. (1975) reported that male *R. acutus* mature between 68 and 72 cm and females at 70 to 80 cm TL.

The present study is an attempt to clarify some of the known aspects of *R. terraenovae* reproductive biology as well as to provide additional information. The reproductive "strategy" of the Atlantic sharpnose shark is also examined.

METHODS AND MATERIALS

Atlantic sharpnose sharks, *Rhizoprionodon terraenovae* (Richardson), were collected in the north central Gulf of Mexico from June 1979 to May 1980. The principal sampling devices employed were longline, trawl, and rod and reel.

Floating longline generally gave the best results (Table 1). The technique, as used by Japanese fishermen, is described by Lopez et al. (1979). Because of the hazard to navigation that a floating longline represents, longlining operations were undertaken exclusively in deep waters offshore (Fig. 1). Longline sets were made in 10 to 28 fathom (18 to 51 m) depths, approximately due south of Dauphin Island, Ala. A trawl was used to collect specimens both inshore as well as offshore. Rod and reel, gill net, and seine were used exclusively inshore.

Specimens were immediately weighed and sexed. Total, fork, and standard lengths were measured to the nearest 0.1 cm. Lengths of the claspers and siphon sacs were measured on all male specimens. All specimens were dissected immediately in the field by an incision starting at the cloaca and extending to the midpectoral region. Notes on reproductive condition in males

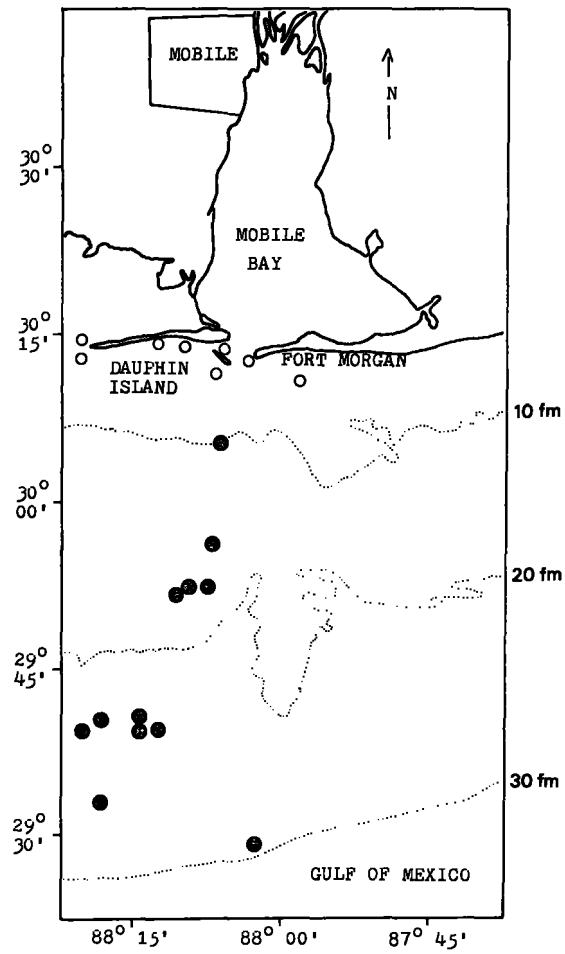

FIGURE 1.—Coastal Alabama study area of the Atlantic sharpnose shark. Offshore points (closed circles) represent longline and trawl sites. Inshore points (open circles) represent trawl, gill net, rod and reel, and seine sites.

TABLE 1.—Landings of Atlantic sharpnose sharks by month and by method. Longline and trawl produced more than 60% of the sharpnose shark specimens. Sharpnose sharks were collected in 10 of the 12 mo of the study period. — indicates no collections; 0 indicates collections attempted but no sharks landed.

	Jan.	Feb.	Mar.	Apr.	May	June	July.	Aug.	Sept.	Oct.	Nov.	Dec.	Totals
Longline	—	1	—	2	0	—	—	14	—	4	19	35	75
Trawl	—	1	—	21	8	—	6	8	6	0	9	0	59
Rod/reel	—	0	—	0	8	1	38	1	2	0	0	0	50
Gill net	—	—	—	2	15	0	4	4	—	—	—	—	25
Seine	—	—	—	—	—	6	0	—	—	—	—	—	6
Totals	—	2	—	25	31	7	48	27	8	4	28	35	215

were taken, using those indicators of maturity reported by Clark and von Schmidt (1965). Dissections of males allowed examinations of the reproductive systems and measurements of testicular length, weight, and volume.

Testes and epididymides were removed from some specimens, preserved in 10% Formalin[2], and returned to the laboratory. Histological sections of testes as well as epididymides were prepared. The tissues were embedded in paraffin, sectioned at 7 μm, stained with hematoxylin and eosin, and examined with phase contrast microscopy. Sperm smears were also examined under the microscope.

After obtaining weight and total, fork, and standard lengths, female specimens were dissected and their reproductive organs examined. Ovarian lengths as well as the number of ovarian eggs and their diameters were recorded. When embryos were present, the number, sex, total length, and wet weight were determined for each uterus.

When appropriate, the data were keypunched and statistically evaluated, using the McGill University System for Interactive Computing (MUSIC) time sharing system. The STATPAK computer program, a statistical package containing 23 statistical analyses and data modification routines, was used to analyze the data.

RESULTS AND DISCUSSION

Reproductive Anatomy

Ovarian Structure

Forty-two Atlantic sharpnose shark ovaries were examined during the study period. Elasmobranchs possess a great deal of variability in the structure of the ovary (Dodd 1972). The ovary of the adult Atlantic sharpnose shark is an unpaired, tear-shaped organ, 6 to 10 cm long and 3 to 5 cm wide. Unlike other carcharhinids, the ovary of the sharpnose shark is developed on the left side only. Structure and location of the sharpnose shark ovary (aside from its position on the left side of the body cavity) are similar to that found in the blue shark (Pratt 1979). The adult sharpnose shark's ovary, during most of the year, is filled with many small (ca. 2.0 to 5.0 mm) oocytes embedded in dense connective tissue. Outside the breeding season the ovary of the adult female contains an average of about 30 oocytes greater than ca. 2 mm in diameter. These oocytes serve as a "pool" from which the next generation of eggs will be drawn. In some ovaries, unusual, bright red, fluid-filled structures were found, ranging from about 2 to 8 mm in diameter (Fig. 2). These structures are assumed to be oocytes in a state of atresia that had failed to ovulate during the most recent breeding period. These preovulatory structures may be "corpora atretica," which are derived from egg-containing follicles. In *Cetorhinus maximus* the corpora atretica are believed to arise from follicles that have attained a diameter of about 1.0 mm (Dodd 1972). The corpora atretica consist of vacuolated peripheral cells and a central cavity and are well vascularized (Dodd 1972).

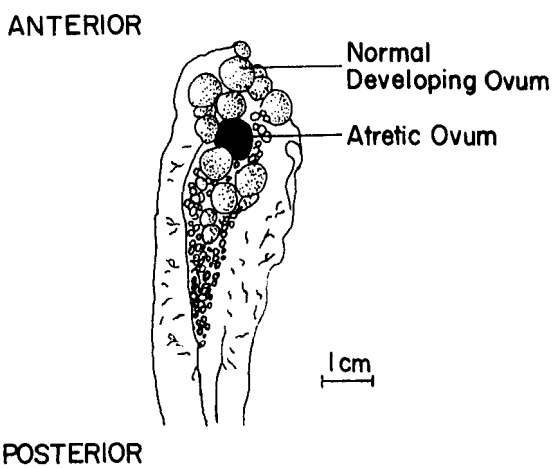

FIGURE 2.—Diagram of an Atlantic sharpnose shark ovary taken in December from a 93 cm gravid female. A red, fluid filled (atretic?) ovum can be seen in the center of the ovary.

Ovulation

As ovulation approaches, rapid yolk deposition occurs in four to eight of the many smaller oocytes. The "selected" oocytes are preferentially yolked, while the others undergo atresia. At or near ovulation the ovary appears highly vascularized and the large, yellow oocytes fill the entire ovary (Fig. 3). Measurements of both ovarian and uterine oocytes suggest that ovulation occurs at an egg diameter of about 20 mm.

After ovulation, the eggs move through the body cavity into the ostium tubae which forms the anterior end of the oviduct. In most cases

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

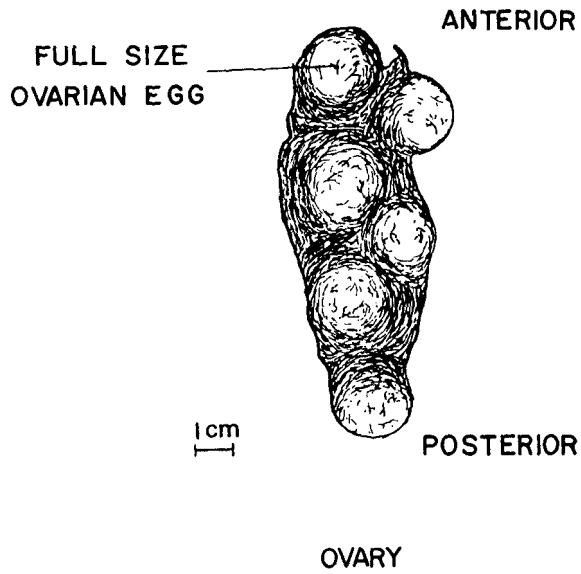

FIGURE 3.—"Ripe" ovary of an Atlantic sharpnose shark. The ovary contains ca. 20 mm ova that are ready to ovulate.

an equal number of ova enter both oviducts, although in some instances greatly disproportionate numbers of embryos were found between right and left uteri. The eggs move through the oviducts to the oviducal gland where fertilization probably takes place. The oviducal gland (Fig. 4) in the Atlantic sharpnose shark is a paired structure located at the forward end of the oviduct. The oviducal glands are the source of the egg case, and in some sharks the glands may be the site of long-term sperm storage (Pratt 1979). Viable sperm can be found within the lumen of those tubules within the gland which secretes the egg shell (Wourms 1977). As no histological sections of adult sharpnose sharks' oviducal glands were prepared, the question of sperm storage in sharpnose sharks remains unresolved. Prasad (1944), however, noted the presence of spermatozoa in the oviducal glands of *Scoliodon sorrakowah*, a closely related Indian Ocean species. This observation suggests that the oviducal gland may have at least a short-term storage capacity.

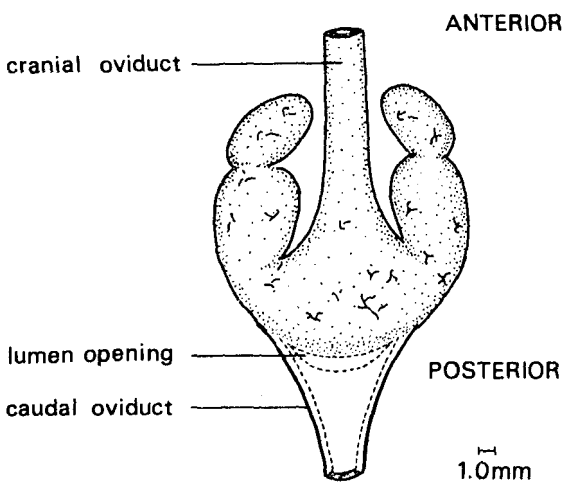

FIGURE 4.—Diagram of an oviducal gland taken from a mature female Atlantic sharpnose shark.

After moving through the oviducal gland the fertilized eggs then move to the uterus where they become implanted in depressions in the uterine wall. At this point the eggs are found encased in a thin, yellowish shell with pointed ends (Bigelow and Schroeder 1948). Within the uterus the eggs are elongate, averaging about 18 mm wide and about 32 mm long. Fertilization is apparently very efficient since in examination of 315 embryos only two unfertile eggs were noted (0.6%).

Placentation and Structure of the Umbilical Cord

During the first 2.5 to 3.0 mo of gestation, the Atlantic sharpnose shark embryos depend upon the yolk sac for nourishment. After about 3 mo the yolk sac has become intimately associated with the uterine wall to form a yolk-sac placenta. October embryos, i.e., 3 mo old, were ca. 16 to 20 cm and had well-developed placentas with little yolk material remaining. By November, 4 mo into gestation, embryos were 19 to 23 cm long and no yolk material remained in the placenta. In a related Indian Ocean species, *Scoliodon sorrakowah*, Mahadevan (1940) described a very thick vascularized area of the uterine wall, referred to as a trophonematous cup, which forms to receive the yolk sac of the foetus. This vascularized area was also noted in the Atlantic sharpnose shark.

Development of the umbilical cord closely parallels placentation. The umbilical cord is connected on the embryo's ventral surface in the midpectoral region. Very early in development the umbilical cord is virtually naked. By the time the embryos have grown to about 6.0 cm TL the umbilical cord has developed many knoblike appendages which give it a "pipe-cleaner" appearance. The appendages are about 1 mm long, and terminate in one or a cluster of several grapelike

distentions. Budker (1971) suggested that in addition to placentally derived nutrients, these appendages may allow the embryo to absorb directly nutritive substances that are secreted by the uterine lining. This type of nutrition is termed histotrophic. As gestation progresses the appendages of the sharpnose shark's umbilical cord lengthen and change morphologically. Full-term embryos possessed umbilical cords about 10 to 12 cm long with appendages about 10 mm. The projections at this time have a foliose appearance, i.e., flattened, extensively branched, and terminating in rounded, flat expansions. This differs from the fingerlike shape described for the projections found on the umbilical cord of *Sphyrna tiburo* (Schlernitzauer and Gilbert 1966).

Structure of Claspers and Siphon Sac

The paired claspers of the adult male Atlantic sharpnose shark are much the same as those of other carcharhinid sharks. The claspers are rigid, calcified, intromittent organs that rotate freely around their attachment base. The tip, or rhipidion, expands whereupon the rigid cartilages of the tip are directed at right angles to the main axis of the clasper. This expansion is believed to function as an anchor, holding the clasper in the oviduct during copulation. Under normal circumstances the claspers are directed posteriorly. Springer (1960) has suggested that just prior to mating the claspers of large carcharhinid sharks such as *Eulamia milberti* (*Carcharhinus milberti*) rotate in and forward. Expansion of the rhipidion occurs independently after insertion of the clasper into the oviduct of the female. This apparently also occurs in the Atlantic sharpnose shark, since a live specimen captured in December had one clasper oriented in this fashion, with the rhipidion expanded, probably a result of trauma. The clasper gradually returned to normal after about 3 min.

The siphon sac in the adult Atlantic sharpnose shark is a muscular, subdermal organ which begins at the base of the claspers, extends anteriorly along the ventral surface, and ends just short of the coracoid bar. The sac in adults ranges from about 20 to 28 cm long and 1 to 2 cm wide. Unlike other shark species which have paired separate siphon sacs, Atlantic sharpnose sharks possess overlapping sacs which communicate with the claspers via an opening located at the base of each clasper. Springer (1960) suggested that the siphon sac is filled with water just prior to mating and is used to flush sperm along the clasper groove and into the oviducts during copulation. The clasper siphon of adult spiny dogfish, *Squalus acanthias*, has been found to be a rich source of serotonin. This suggests that the siphon-sac secretion may play a role in affecting the mechanism of copulation and ejaculation in the male, or by eliciting contractions of the female reproductive tract, thus influencing passage of sperm and fertilization (Mann 1960).

Structure of the Testes and Epididymides

The testes in the adult male Atlantic sharpnose sharks are paired, elongate, flattened organs (Fig. 5). Depending on the season and the size of the adult, the testes range from 13 to 20 cm long, 1 to 2 cm wide, and 0.5 to 1.0 cm thick. The testes are located dorsal to the lobes of the liver at the anterior end of the peritoneal cavity. The organs are supported here by a mesorchium.

Microscopic examination of a mature testis of the sharpnose shark shows that the organ is filled

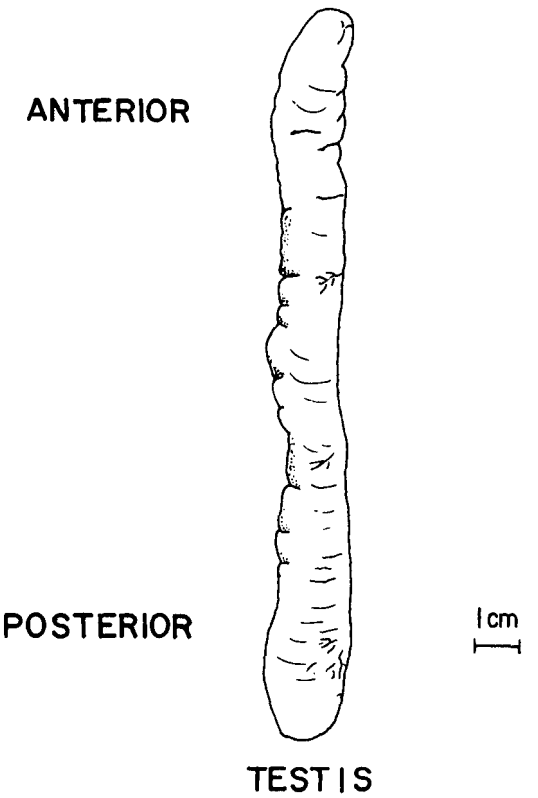

FIGURE 5.—Diagram of a "ripe" Atlantic sharpnose shark testis. The testis is turgid indicative of the reproductively active condition.

with spherical seminiferous ampullae, much the same as are found in spiny dogfish (Simpson and Wardle 1967) and blue shark (Pratt 1979). Histological sections of mature testes demonstrate that these ampullae contain spermatozoa in various stages of development (Fig. 6). Viewed in cross section, the heads of the mature spermatozoa are arranged in discrete groups around the periphery of the spherical ampullae.

The spermatozoa leave the testis by way of the efferent ductules and enter the epididymis. The epididymis is a paired organ located above the testis against the dorsal wall of the abdominal cavity. The sharpnose shark's epididymis is about 15 cm long, 1.0 cm wide, and 0.5 cm thick. Histological sections of an epididymis from a reproductively active sharpnose shark reveal great numbers of spermatozoa present in the tubules of the organ (Fig. 7).

Maturation

Males

Maturity in animals can generally be determined by comparing external secondary sex characters in adults with the same characters in smaller individuals. Using two indicators of sexual maturity (i.e., clasper growth and siphon-sac development), it was determined that maturation of the male Atlantic sharpnose shark begins at about 60 to 65 cm TL and is complete at about 80 cm.

At <65 cm TL the clasper length represents about 2.5% of the adult total length. Regression analysis shows that the claspers undergo a period of rapid growth with a major inflection in the line occurring at 65 to 70 cm TL (Fig. 8). The claspers quickly elongate, growing 3 cm within a short period of time to represent 7 to 8% of the total length. The smallest mature males examined were about 80 cm long and their claspers represented about 7.8% of total length. There were many individuals examined between 75 and 80 cm TL that possessed elongated claspers, but incomplete calcification of the claspers indicated that the specimens were not mature.

The clasper grows faster than the total length at the onset of maturation and for a short period into adult life. Regression analysis indicates that from about 85 to 95 cm TL the relationship is unchanging, but after 95 cm there is a period of

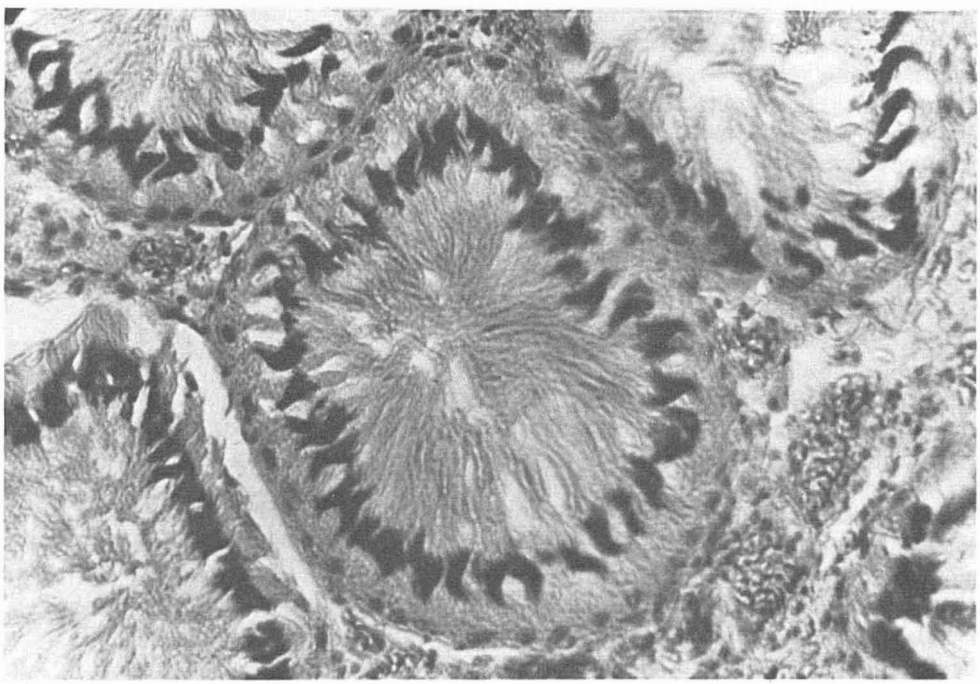

FIGURE 6.—Histological section of a testis from a mature Atlantic sharpnose shark (×440). The cross sections show that the heads of the mature spermatozoa are arranged in discrete groups around the periphery of the spherical seminiferous ampullae.

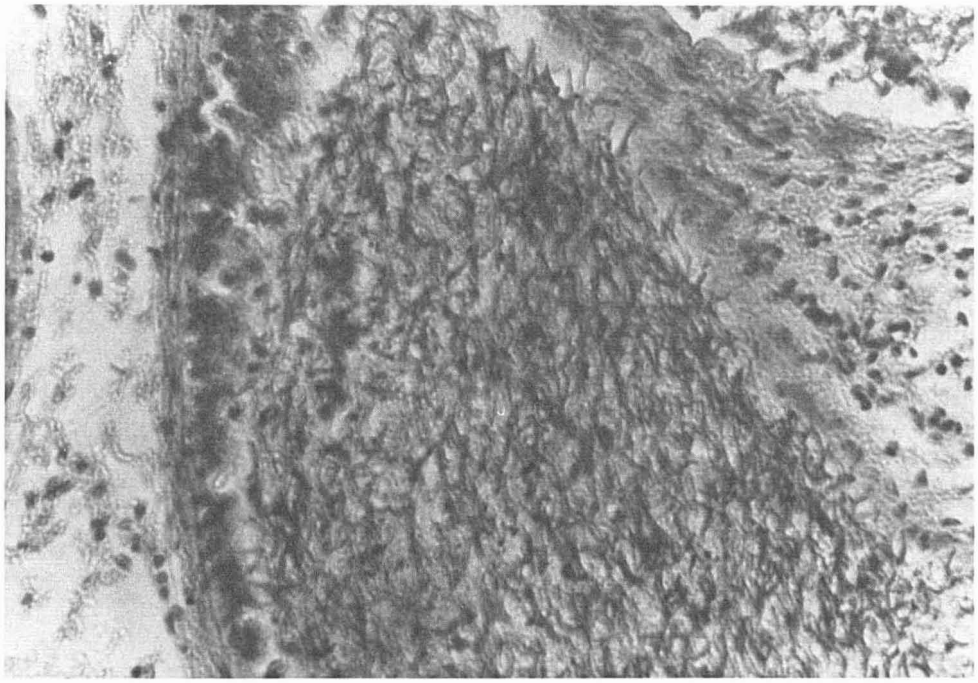

FIGURE 7.—Histological section of an epididymis from a mature Atlantic sharpnose shark (×140). Large numbers of spermatozoa are present within the tubules of the structure.

negative allometric growth. The claspers, after attaining their functional length, do not continue to grow or at least grow very little. This is a tenable hypothesis since continued growth would not necessarily enhance the claspers' utility.

Development of the siphon sacs coincides closely with the rapid increase in clasper length (Fig. 9). This muscular, subdermal organ is nonexistent until the onset of maturity. The siphon sacs develop quickly and represent about 28% of the

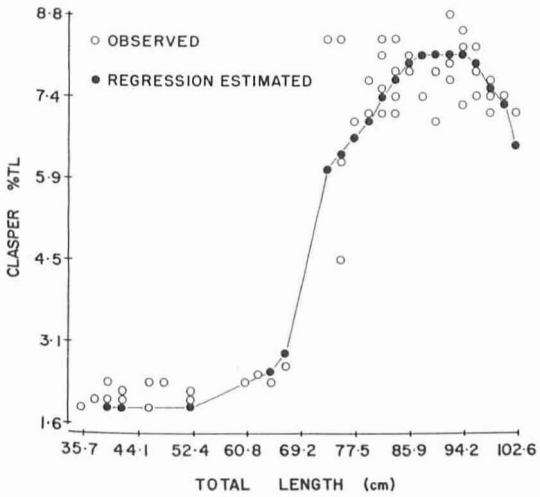

FIGURE 8.—The maturation of male Atlantic sharpnose sharks as evidenced by clasper development. The regression line indicates that maturation occurs between 80 and 85 cm total length, $N = 70$.

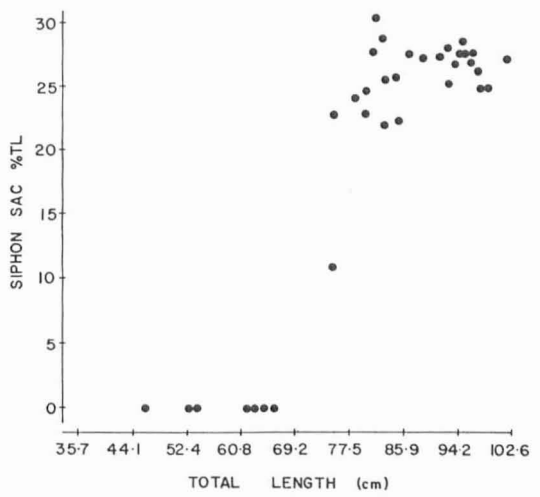

FIGURE 9.—The maturation of male Atlantic sharpnose sharks as evidenced by siphon-sac development. The scatter diagram suggests that maturation occurs at about 80 cm total length, $N = 35$.

total length at maturity. The smallest mature individuals were about 80 cm and possessed siphon sacs about 23% of total length.

Females

Maturation in females was determined by examining the developing ovary and ovarian eggs. Females were found to mature at a greater total length than males. The ovary does not begin to develop until the individual reaches about 60 cm TL. Figure 10 shows that development reaches an asymptote between 85 and 90 cm TL. Even among individuals of the same size taken during the same month there is a high degree of variation in ovarian length. For this reason ovarian length is not considered a good indicator of maturity in Atlantic sharpnose shark.

Changes in the diameter of ovarian eggs were found to be a reliable indicator of the beginning of maturation. Figure 11 shows the first generation of ovarian eggs produced by the subadult population. Increase in egg diameter begins at 60 to 65 cm TL, at about the same time the length of the ovary begins to increase. The eggs increase in diameter until the first ovulation, which occurs at about 85 to 90 cm TL. Most female sharpnose sharks mature within this size range.

Several female sharpnose sharks that had recently matured were examined. One individual of 88 cm TL, collected in late May, had full-sized ovarian eggs and had apparently recently mated due to the numerous mating scars that were observed in the region between the first and second

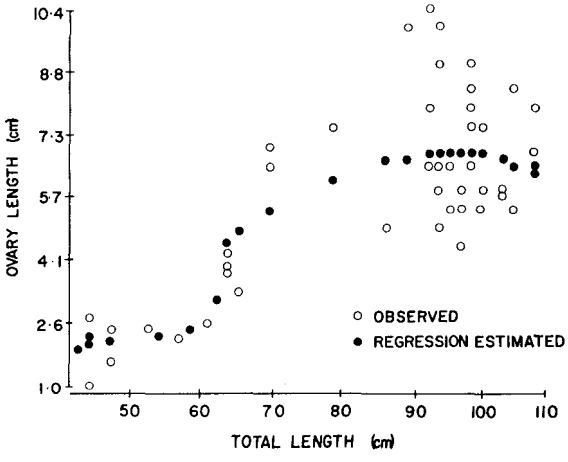

FIGURE 10.—Regression analysis showing development of the ovary in Atlantic sharpnose sharks, $N = 42$. Maturation is estimated to be complete at 85 to 90 cm total length.

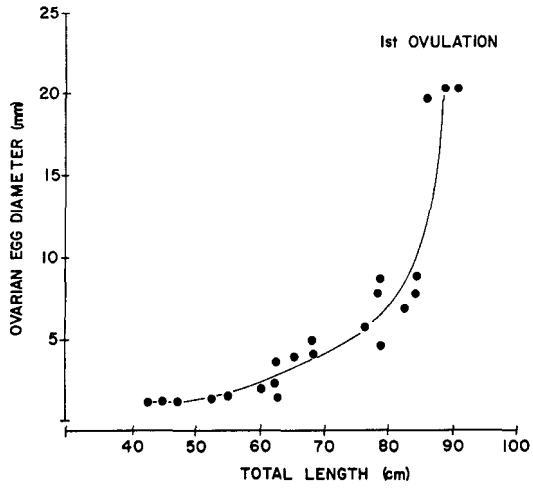

FIGURE 11.—Maturation of female Atlantic sharpnose sharks as evidenced by the increase in ovarian egg diameter. Hand-fit curve approximates the increase in ovarian egg diameter from juvenile to first ovulation, $N = 63$.

dorsal fins. An 86 cm individual, collected in early July, possessed six ova (8 to 10 cm), while another 89 cm female, collected in mid-July, possessed uterine eggs. In late August, all mature females examined contained embryos. The smallest gravid specimens were 87, 88, and 89 cm TL and contained 11, 8, and 6 cm embryos, respectively. These observations further support the 85 to 90 cm estimated size at maturity.

Mating Season

Twenty-three reproductively active male Atlantic sharpnose sharks were examined to delineate the mating season. A gonadosomatic index (GSI), testis weight expressed as percent total body weight, was found to be the best indicator of mating season.

The GSI provided a defined mating season for male sharpnose sharks (Fig. 12). Reporting on central gulf coast of Florida populations, Clark and von Schmidt (1965) suggested that small shark species (such as *Mustelus norrisi* and *Scoliodon terraenovae* = *Rhizoprionodon terraenovae*) mate and bear young in the late winter and early spring. In the north central gulf, contrary to Clark and von Schmidt's findings for Florida, male sharpnose sharks appear to be reproductively active during late spring and summer. From about September to March, the GSI was found to be low, 0.2 to 0.37. During these months specimens were observed to have reduced testes

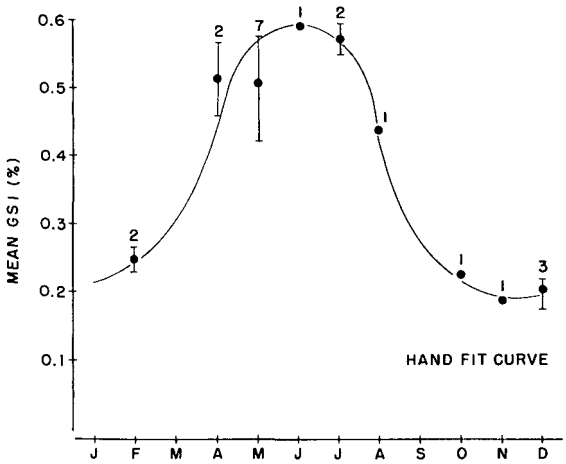

FIGURE 12.—Mating season of adult male Atlantic sharpnose sharks as evidenced by the seasonal increase in gonadosomatic index (GSI). The data suggest that male sharpnose sharks are reproductively active during late spring and summer. The closed circles represent mean values and the numbers indicate sample sizes, $N = 20$.

and no visible sperm or semen in the seminal vesicles. In late April the GSI had risen to 0.51, but there was little sperm present in the seminal vesicles. During mid- to late May the GSI averaged 0.47. All mature individuals had enlarged testes, turgid seminal vesicles, and copious amounts of sperm present in the claspers as evidenced by microscopic examination. This condition was found to persist through June and July with GSI equalling 0.59 and 0.57, respectively. Several adult males examined in August were found to have large quantities of sperm in the seminal vesicles. A single GSI determination indicated a slight decline from previous months.

The mating season in female sharpnose sharks was evidenced by an increase in ovarian egg diameter (Fig. 13). From August to December the average egg diameter increased from ca. 3.0 to 4.2 mm. In almost every ovary examined during November and December, a few eggs were beginning to visually dominate the other oocytes. In February, the mean oocyte diameter equalled 5.0 mm, with some eggs reaching 11 mm. In February, all mature ovaries contained four to eight oocytes that were noticeably larger than surrounding eggs. From mid-February to late May or June, there was a rapid increase in egg diameter to about 20 mm at ovulation.

The information indicates that the mating season for male and female sharpnose sharks in the northern Gulf of Mexico coincides, although male sharpnose sharks are reproductively active earlier in the year. Assuming that females do not mate when gravid and that ovulations occur after copulation, then the mating season must occur between mid-May and mid-July. Most adult females still carried near-term embryos in mid-May, and by mid-July all females examined had uterine eggs. Considering the peak of parturition for gravid females (see Embryonic Growth and Development section), the subsequent appearance of uterine eggs, and the occurrence of the first detectable embryos, the peak of mating most likely occurs from mid-June to mid-July.

Embryonic Growth and Development

Embryos representing various stages of development were weighed, sexed, and measured in total length. Conceptions were estimated to be at a peak in early to mid-July. At this time several sharpnose sharks that possessed recently ovulated uterine eggs but no visible embryos were examined. In late August, gravid females were collected, and they contained embryos ranging from about 4 to 11 cm TL. The smallest embryos examined were still dependent upon the yolk sac. They had prominent branchial gill filaments, undeveloped fins, and the anterior end was enlarged in relation to the rest of the body. Pratt (1979) suggested that growth of embryonic *Prionace glauca* is linear. Increase in length of sharpnose shark's embryos approximates a sigmoid curve as evidenced by polynomial regression

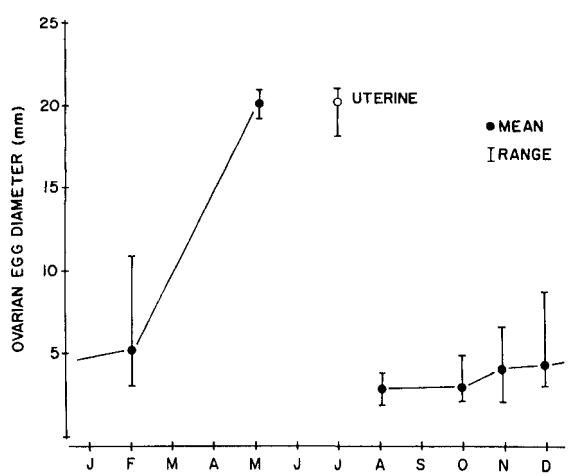

FIGURE 13.—Mating season of adult female Atlantic sharpnose sharks as evidenced by the seasonal increase in ovarian egg diameter, $N = 1,260$. The data suggest that the mating season for females occurs from mid-June to mid-July.

analysis (Fig. 14). After conception there is a period of rapid growth through the remainder of the summer and fall. By November the embryos have attained an average of 21.3 cm and appear almost completely developed. There is a noticeable inflection in the regression line in November. The increase in length declines through the winter and spring months, although a slight increase may occur just before parturition in May or June. Pups are born at an average of about 32 cm TL. Skocik (1969) reported a total length of 25 cm for sharpnose shark at birth, and Bigelow and Schroeder (1948) stated that newborn sharpnose sharks are generally about 275 to 400 mm long. The largest embryo recorded during the study period was 36 cm TL and the smallest free-living specimen was 32 cm.

Increases in weight of the sharpnose shark's embryo differed from the increases in total length (Fig. 15). Embryo weight increased slowly during the period from estimated conception (mid-July) to October. Thereafter, however, until parturition in late May or June, an almost linear increase of about 16 g/mo occurred. Parturition occurs most likely between about 95 and 150 g.

By using the above information, it was possible to estimate the gestation period. Atlantic sharpnose shark's embryos require a 10 to 11 mo gestation period, beginning in July or August and ending in May or June of the following year.

Relationships Between Adult Females and Embryos

A significant relationship was observed between total length of the gravid female and the number of offspring produced. This is noteworthy since other works have failed to show such a relationship among carcharhinids (Springer 1960; Clark and von Schmidt 1965). Figure 16 shows that the total length of the adult is correlated with litter size (ANOVA significant at <0.01). There is a direct relationship between fecundity and the size of the adult with the largest individuals being the most fecund. Gravid females produce an average of 5 pups/litter per year (one to seven), but in most cases either four or six embryos will be present.

It was anticipated that a relationship between litter size and embryo size could be detected. An optimal clutch size has been demonstrated in some species of birds (Lack 1954, 1966, 1968). Compared with small and large clutches, intermediate-sized clutches leave proportionately

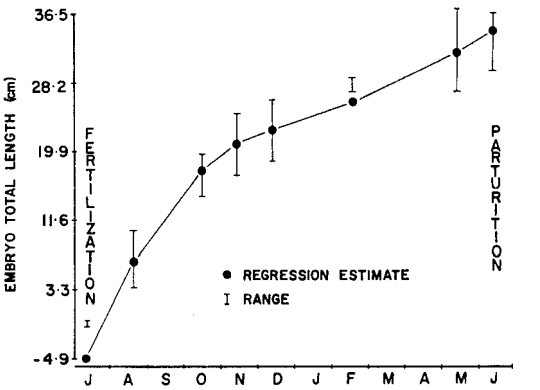

FIGURE 14.—Growth of embryonic Atlantic sharpnose shark. Regression analysis shows the increase in embryo total length from fertilization to parturition, $N = 300$.

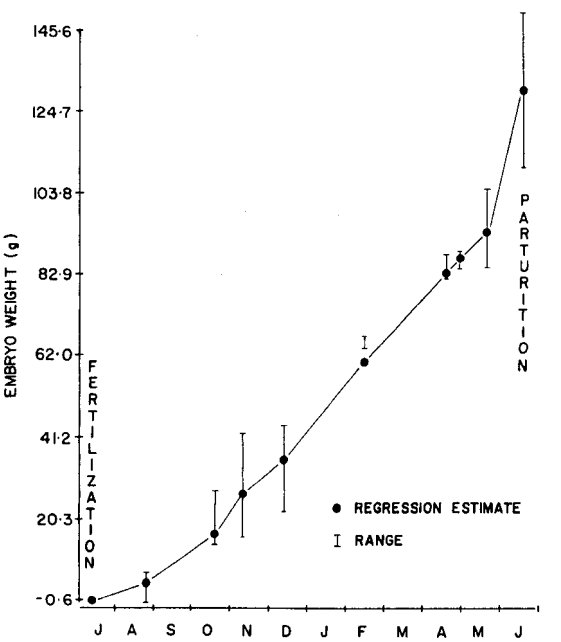

FIGURE 15.—Growth of embryonic Atlantic sharpnose shark. Regression analysis shows the increase in embryo weight from fertilization to parturition, $N = 300$.

more offspring that survive to maturity. Birds from large clutches are smaller in size than birds from intermediate-sized clutches. After evaluating the data, an "optimal litter size" could not be demonstrated for the Atlantic sharpnose sharks. However, when the right and left uteri of adults collected during a single sampling trip (to cancel out seasonal differences) were treated separately, an inverse relationship was observed between the numbers of embryos per uterus and

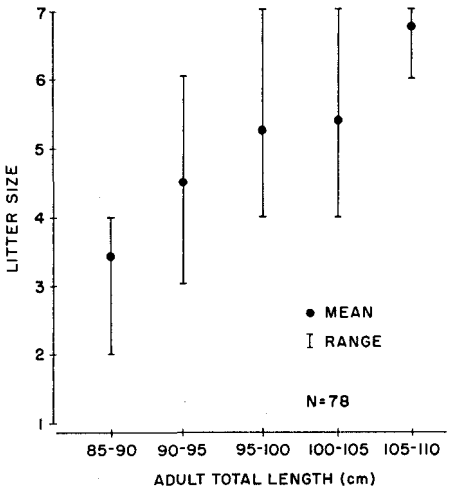

FIGURE 16.—Relationship between adult total length and litter size of the Atlantic sharpnose sharks. The plot indicates that fecundity increases significantly as adult total length increases ($F = 9.216$, $P<0.00001$).

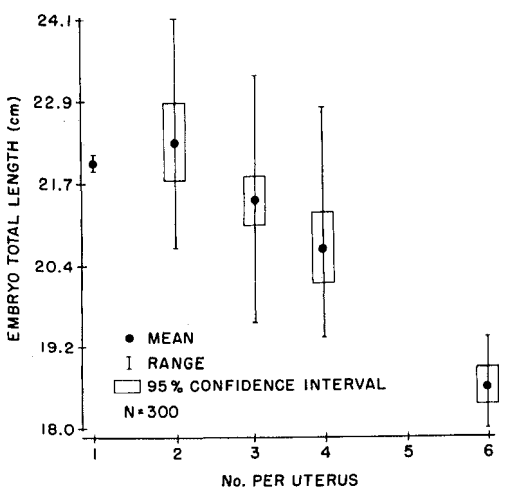

FIGURE 17.—Relationship between numbers of embryos per uterus and embryo total length of the Atlantic sharpnose sharks. Embryo total length decreases significantly with increasing number per uterus, $N = 89$.

embryo size (Fig. 17). The figure indicates that at the 95% confidence limits significant differences exist between the total lengths of the embryos. Embryos were found to be largest when one or two are present per uterus. However, in only one case was there a single embryo found within a uterus.

It is conceivable that mechanical "packing" within the uterus causes "intra-uterine competition" for nutrients. As already discussed, in addition to placentally derived nourishment, sharpnose shark embryos may be able to absorb directly nutrients which are produced by the uterine epithelium. An increase in the number of embryos within the uterus above some optimal value might result in competition for this "uterine milk" and a decrease in embryo size.

In sharpnose sharks, the parents that produce what might be termed an "optimal" number of embryos per uterus are producing the largest embryos. If we assume that these size differences are retained until birth, and thereafter, these larger embryos will result in progeny of highest individual fitness. Larger offspring cost more to produce, but they are also worth more (Pianka 1978).

It would be interesting to examine the reproductive strategy of tropical sharpnose shark populations, since these sharks have been reported to have litters with as many as 12 embryos (Bigelow and Schroeder 1948; Skocik 1969). Based on this study, it would be a logical extrapolation to predict that these litters would result in smaller offspring. A litter of 12 must be approaching maximum fecundity for sharpnose sharks.

Seasonal Distribution

In this study it was determined that migratory behavior of the Atlantic sharpnose shark is primarily limited to an inshore-offshore movement. From late April to September of 1979, 93 sharpnose sharks were collected from shallow inshore waters. During the period from late October 1979 to April 1980, despite numerous attempts, no sharpnose sharks were collected inshore. Sharpnose sharks may be encountered offshore year-round; however, the data indicate that the concentration of sharks is greatest during the fall and in particular, winter months. From October 1979 to February 1980, 59 sharpnose sharks were collected during offshore longlining. Figure 18 shows that the number of sharpnose sharks landed in deep water, as well as the catch per unit effort (CUE), is low in spring and summer (CUE = 1.2 and 2.4, respectively) and increases to a high in winter (CUE = 7.3).

The above data suggest that the migration from inshore to offshore begins around October or November. Atlantic sharpnose sharks apparently remain in deeper waters during the colder months and return inshore again in April and May.

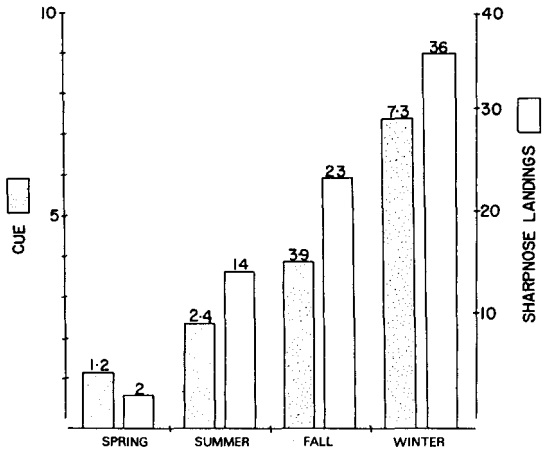

FIGURE 18.—Catch per unit effort (CUE) in sharks/100 hooks per hour and number of Atlantic sharpnose sharks landed during longline operations. Ninety percent of these offshore landings were gravid females.

Since adult female Atlantic sharpnose sharks were collected inshore only during summer months, the data suggest that females migrate inshore in late spring or summer to pup and mate, whereupon they return offshore again to overwinter. During June and July sharpnose shark pups with a fresh umbilical scar (in some cases the scar was actually an open slit) could be collected from the littoral zone. It is likely that special nursery areas exist for many shark species (Springer 1967), although the existence of specific pupping or nursery grounds for the Atlantic sharpnose sharks could not be conclusively established from this study. However, since newborn pups were never taken from deep waters in spite of intensive trawling, it is reasonable to suppose that the pups were born in shallow water. Perhaps the shallows of the northern Gulf of Mexico's extensive barrier island system serve as pupping/nursery grounds for the Atlantic sharpnose shark.

Sex Ratio

Sex of the Atlantic sharpnose sharks could be determined by clasper examination in embryos as small as 5.0 cm TL. The sex ratio through most of gestation could therefore be determined. The sex ratio early in development and of near-term embryos was found to be 1:1. One-hundred and fifty male and 155 female embryos were examined. These data suggest that the sex ratio at parturition is also 1:1.

Among adults sampled, the sex ratio was found to be one sided in favor of females. During this study 33 adult male and 91 adult female sharpnose sharks were collected representing a 1:2.8 ratio. During offshore longlining 90% of the catch consisted of gravid adult female sharpnose sharks. This condition in sharpnose shark is not without precedent, as it has been observed in other shark species. Springer (1940), discussing *Carcharhinus milberti* and *Carcharhinus obscurus*, stated that in both species females outnumber males. Clark and von Schmidt (1965) found a similar situation in *Galeocerdo cuvieri*.

ACKNOWLEDGMENTS

This research was funded by a fellowship awarded to the author by the Dauphin Island Sea Laboratory. Robert Shipp provided helpful assistance. Special thanks are due David Nelson for reviewing the manuscript, Snead Collard for supplying shark rodeo data, Benny Rohr for supplying NMFS data, and John Gourley for supplying data.

I am also very grateful for the assistance provided by the faculty and staff of the Dauphin Island Sea Laboratory. Likewise, I wish to thank the graduate students of the University of South Alabama, especially Rick Blaise, Steve Branstetter, Don Marley, and Austin Swift.

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