REPRODUCTION IN THE BLUE SHARK, *PRIONACE GLAUCA*

HAROLD L. PRATT, JR.[1]

ABSTRACT

In the male blue shark, *Prionace glauca*, paired testes produce spermatozoa year round which are stored first in the epididymides, then as spermatophores in the lower ductus deferentia. Spermatazoa are transferred to the female through paired claspers employed singly. Spermatozoa are injected into the upper vagina and pass through the uterus and isthmus into the shell (oviducal) gland, where they are stored until the female is ready for fertilization. Male blue sharks reach maturity at 183 cm fork length when 50% possess spermatophores. Females pass through a subadult phase (145-185 cm), when the organs for copulation and sperm storage are developed but the ova are undeveloped. During this phase females receive numerous toothcuts in their thickened dermis as a prelude to mating and frequently copulate.

I examined reproductive organs from 160 subadult female blue sharks, caught in shelf waters off southern New England during summer months, by histological sectioning to determine if spermatozoa were present. Of these females, 79 had spermatozoa in the oviducal gland, establishing successful copulation. Inseminated females then emigrate offshore where fertilization occurs the following spring during ovulation. Blue sharks are viviparous and bear young after 9 to 12 months gestation. Thirty-eight new or unpublished accounts of gravid females are investigated, as well as one 192 cm hermaphroditic blue shark.

In shelf waters during the summer the sex ratio for subadults is nearly equal while males dominate the adult sizes due to the emigration of inseminated females.

The blue shark, *Prionace glauca*, is the most abundant of the larger oceanic sharks in the Atlantic (Bigelow and Schroeder 1948). It is frequently among the incidental catch of tuna and swordfish longliners in temperate, subtemperate, and tropical parts of the world ocean. Nichols and Murphy (1916) reported seeing "hundreds, even thousands" of them swimming free and attracted by the activity of the sperm whale fishery in the tropical Atlantic. Longline fishing operations conducted by National Marine Fisheries Service biologists in the offshore areas between Cape Cod, Mass., and Cape Hatteras, N.C., reveal the blue shark to be more numerous in this area than any other large shark or big game fish (Casey and Hoenig[2]).

Like other elasmobranchs, blue sharks have a complex reproductive cycle which contributes to their success as a species. Suda (1953), Strasburg (1958), Aasen (1966), and Stevens (1974) have all contributed information about blue shark reproduction, but many of the details concerning anatomy, maturity, and the sexual cycle were incomplete. New information is presented on the mechanism of spermatozoa storage in the male and female blue sharks and adaptations for mating in the female.

In this study, the reproductive systems of western North Atlantic blue sharks have been investigated to better understand the life history of this important apex predator.

MATERIALS AND METHODS

Blue sharks sampled from October 1969 to April 1977 came from two sources: 1) longline catches made by research and commercial vessels and 2) anglers' catches landed during shark fishing tournaments. The area sampled extended from Cape Hatteras to east of Georges Bank, both on the continental shelf and in the Gulf Stream. Three fish were also collected north of St. Thomas, V.I.

Throughout this paper I use fork length (FL), a straight line measurement from the tip of the snout to the fork of the tail. Measurements involving the upper caudal (such as total length, TL) are variable due to its flexibility. Fork length is an easier and more accurate measurement for one person to make at sea. Many authors cited use

[1]Northeast Fisheries Center Narragansett Laboratory, National Marine Fisheries Service, NOAA, Narragansett, RI 02882.

[2]Casey, J. G., and J. M. Hoenig. 1977. Apex predators in deepwater dumpsite 106. *In* Baseline report of environmental conditions in deepwater dumpsite 106. NOAA Dumpsite Evaluation Report 77-1, p. 309-376.

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total length, defined by Bigelow and Schroeder (1948) as a caliper measurement along the body axis from the snout to a perpendicular extended from the upper caudal. I have converted all references to blue shark total lengths in the literature to fork lengths in centimeters using a regression[3] derived from a sample of 554 males and females between 93 and 282 cm FL (r = 0.995).

Clasper length (posterior free tip to the free trailing edge of the pelvic fin lateral to each clasper) and internal organs were measured with calipers to the nearest millimeter.

Sharks were dissected as soon as possible after being caught. Several adults were frozen whole and dissected in detail at the laboratory. Specimens for analysis and anatomical description ranged in size from 1.1 to 264 cm and included 210 females and 114 males.

A single ventral incision from cloaca to pectoral girdle permits access to the body cavity. The size and condition of internal organs of both sexes were noted. To determine maturity and insemination, both oviducal glands were excised carefully, without squeezing, with several centimeters of adjacent oviduct. Oviducal glands and other histological samples were preserved in Bouin's fixative because it is compatible with the primary stain (Mallory's Triple Stain). Larger organs were preserved in 10% Formalin.[4] Tissues were prepared by the paraffin method and sectioned to 10-15 μm. In the latter part of the study a smear technique was developed to quickly determine insemination. This new technique, which obviates the need for histological sectioning, is discussed in a later section.

RESULTS AND DISCUSSION

Male Anatomy

Testes and Epigonal Organ

The male blue shark has two equally developed testes each embedded in the anterior portion of a long irregular epigonal organ which has no known reproductive function other than to support the testes (Figures 1, 2). Dissected from the epigonal organ, the testis is cylindrical with rounded ends. It is packed with tiny spheres averaging 0.3 mm in

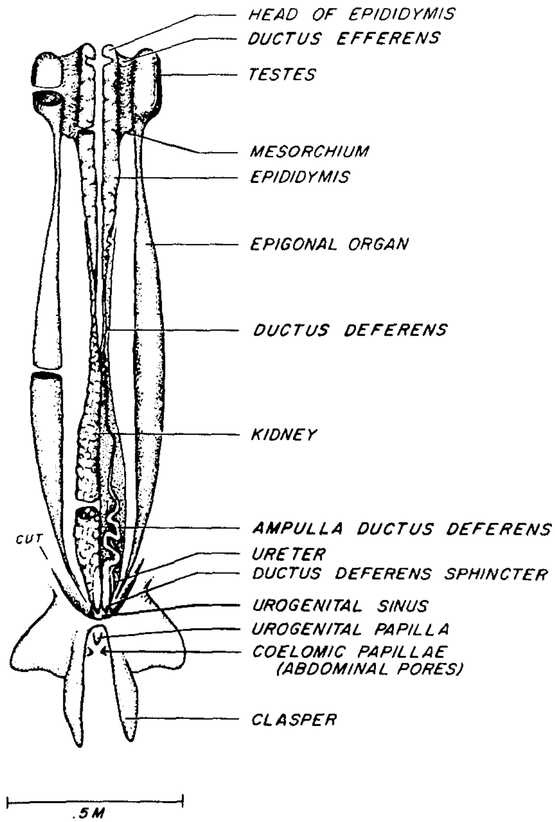

FIGURE 1.—Male reproductive system in the adult blue shark, general ventral view.

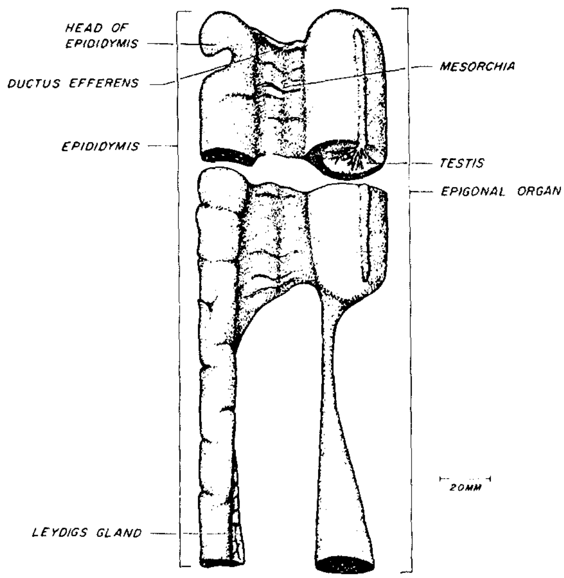

FIGURE 2.—Testes, epididymis, and epigonal organ of the adult male blue shark.

[3]Computed regression: FL = 1.73872 + 0.82995 TL.

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

diameter, the seminiferous ampullae (Figure 3). The only other macroscopic structures are supportive partitions of connective tissue radiating internally from a band on the mediolateral surface of the testes. A double mesorchia suspends the testes from the midline of the dorsal body wall. The ductus efferens is a series of fine tubules which crosses the mesorchium at its anterior edge and communicates with the head of the epididymis.

Epididymis

Above the testes on the dorsal abdominal wall lie the paired epididymides. They are attached on either side of the dorsal aorta in the hollow of the ventrolateral processes of the vertebral column. In the adult blue shark the epididymis is approximately 3 cm wide, 30 cm long, and 0.5 cm thick. In sharks captured from March to November it is turgid with spermatozoa in a matrix of supportive tissue secreted by accessory glands on the dorsal surface. The epididymis originates just forward of and adjacent to the testes as a firm subspherical "head" which narrows to a short "neck" and then expands to form a long straplike organ (Figure 2). The tubules of this organ describe a path of convolutions so complex that its surface appears cerebriform. Tubule diameters range from 1.5 to 1.75 mm adjacent to the testes, expanding to >2 mm at the junction of the ductus deferens. Here it enters Leydig's gland, the modified anterior section of the mesonephric kidney. At this level the function of the ductus changes from spermatozoa storage to spermatophore formation and storage.

Ductus Deferens

The ductus deferens (Figure 4) is the storage organ for male seminal products. The ductus gradually increases in diameter as it penetrates the kidney, finally enlarging in strong convolutions to form the ampulla ductus deferens which is 10-15 mm in diameter in the adult blue shark. The ampullae are lined with partitions or septa similar to those noted by Matthews (1950) in the basking shark, *Cetorhinus maximus*. The thin-walled ureter becomes entwined with the ductus deferens in the last 20 cm of its length and roughly parallels its sinuous course. The ureter and ductus deferens terminate in a common double papilla which projects into the anterior wall of the urogenital sinus. The ductus occupies the central orifice of the papilla and is closed by a sphincter muscle. The ureter has a crescent-shaped sphincterless duct on the dorsal edge of the cone of the papilla. The urogenital sinus vents into the common cloaca by means of a single large (2 cm) papilla that projects from the dorsal body wall.

FIGURE 3.—Seminiferous ampullae of mature testes in the blue shark (×160). Spermatozoa arranged radially inside spheres (seen in cross section).

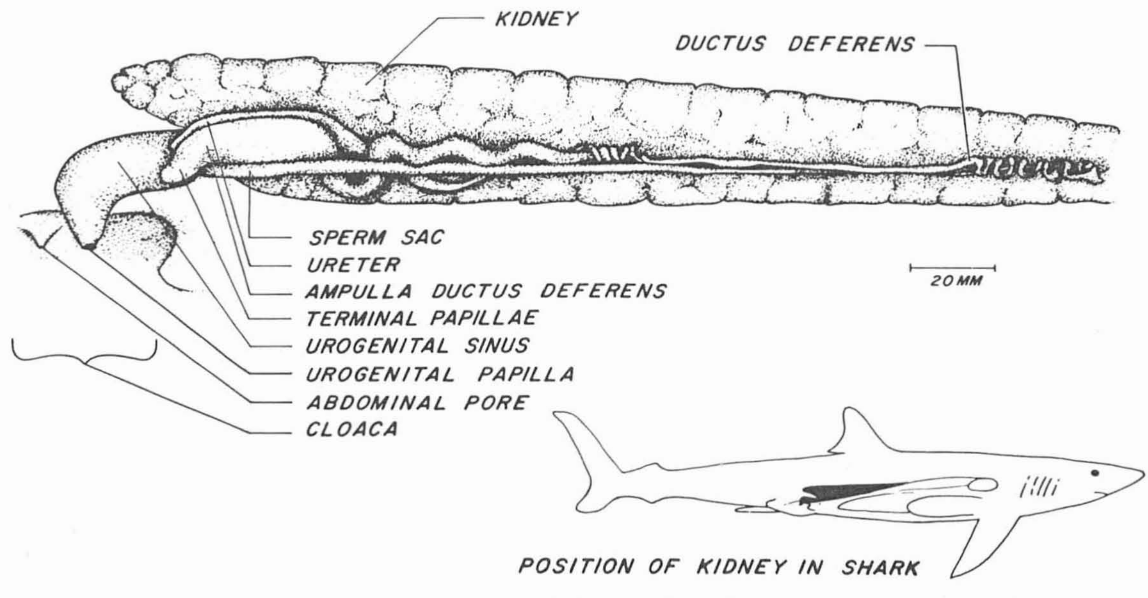

FIGURE 4.—Male urogenital complex in the blue shark.

Sperm Sac

The sperm sac (Figure 4) is not well developed in the blue shark. This paired organ communicates with the anterior end of the urogenital sinus through an opening between the paired terminal papillae of the ductus deferens. The diameter in a mature 200 cm male was 16 mm at the sinus. The sperm sacs lie along the dorsal midline of the body cavity and extend anteriorly into the kidney approximately 15 cm, where the tubes taper down to threads and end blindly.

Siphon Sacs and Clasper

In the adult blue shark the paired claspers are heavily calcified scroll-shaped appendages which transfer sperm from the lower ductus through the urogenital papilla to the vagina of the female during copulation. Propulsive force is provided by a water piston driven by the muscular subdermal siphon sac associated with each clasper. An accurate description of clasper morphology and function is given by Leigh-Sharpe (1920). The clasper is similar in form to that of the basking shark, which has been described in detail by Matthews (1950) and to the tope, *Galeorhinus galeus* (Leigh-Sharpe 1921). The blue shark lacks a distinct spur or clasper hook and uses instead the sharpened edges of the terminal parts, which are splayed open after insertion to secure the clasper in the

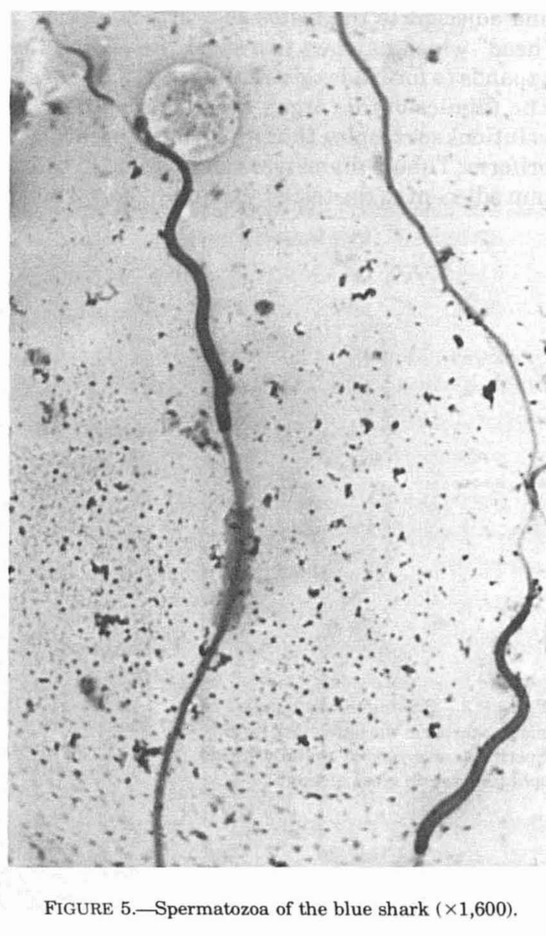

FIGURE 5.—Spermatozoa of the blue shark (×1,600).

vagina during copulation. The siphon sacs originate on the surface of the pelvic fin at the proximal end of the clasper and extend anteriorly under the dermis to end blindly just short of the pectoral girdle. They are approximately 25 mm in diameter and 60 cm long.

Spermatoza

Sperm cells (Figure 5) develop in expendable spheres of germinal tissue, the seminiferous ampullae described by Romer (1962). They form radially, then clump together in groups of 60-70 (Figure 6). When the sperm mature the ampullae disintegrate, liberating individual spermatozoa into the interstitial spaces of the testis. They pass through the ductus efferens (Figure 2) and into the epididymis. Secretions from the accessory glands flow into the epididymis and form a matrix which supports the individual spermatozoa. Spermatozoa are stored in the epididymis which usually appears swollen in adult males. This is the most convenient location to obtain a sperm smear. In the lower epididymis the spermatozoa again aggregate, with heads aligned parallel until groups of 60-70 are formed in the anterior section of the ductus deferens. Hundreds of these packets then aggregate into spermatophores (Figure 7), which are stored in the expanded terminal ampulla of the ductus deferens.

Spermatophores

In mature males the entire lumen of the lower ductus deferens is usually turgid with seminal products. Most noticeable macroscopically are snow-white clumps of a gelatinous substance 3-4 mm in diameter and containing no spermatozoa. This evidently is a supportive and possibly nutritive material for the smaller spermatophores. The blue shark spermatophore (Figure 7) is an ivory white ovoid, 0.5-2.0 mm across its largest diameter. When the ampulla is cut at midkidney, spermatophores flow freely and copiously from the incision and are interspersed with the white gelatinous clumps. Several hundred milliliters may be expressed from the two ductus deferens of an adult male.

Matthews (1950) gave a good account of the structures and functions involved in spermato-

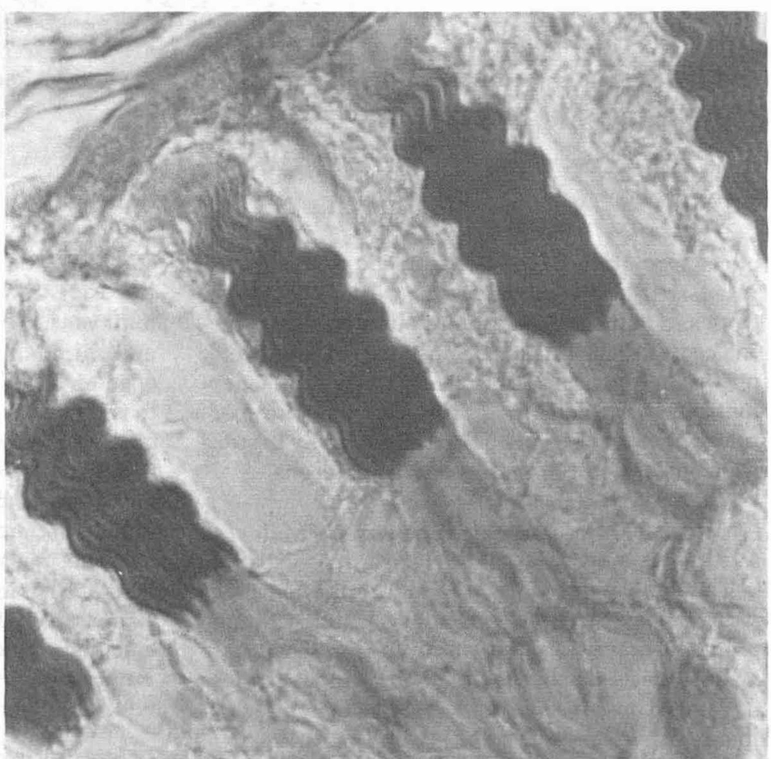

FIGURE 6.—Spermatozoa in seminiferous ampullae of the blue shark (×1,600).

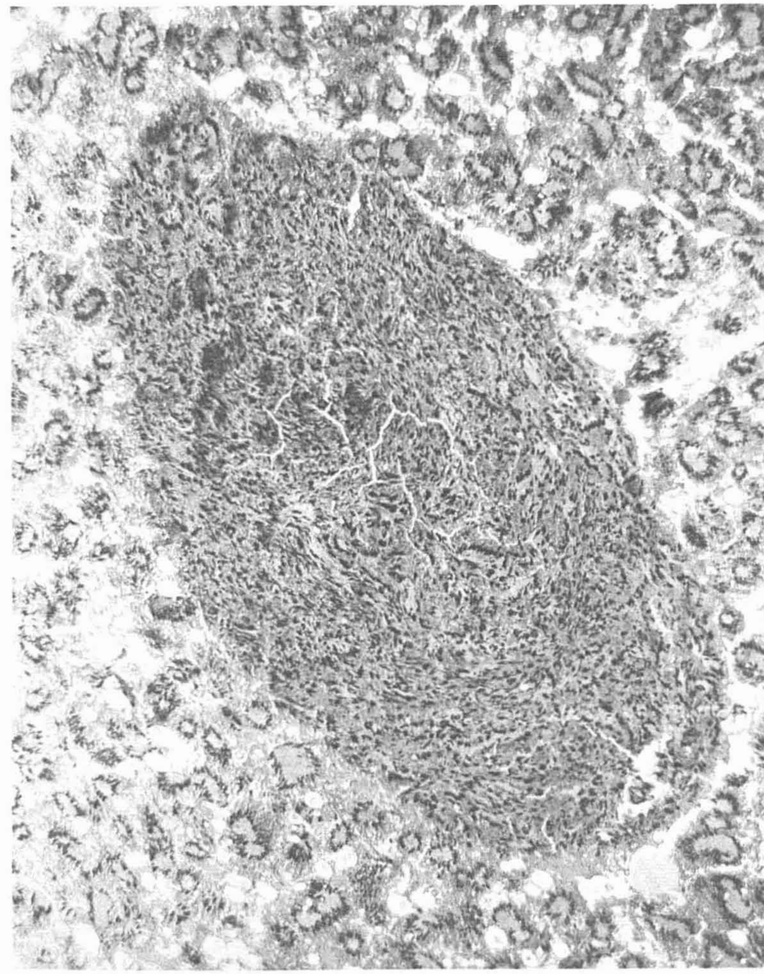

FIGURE 7.—Spermatophore of the blue shark (×100).

phore formation in the basking shark. He speculated that spermatophores preserve the sperm from loss in leakage to the surrounding water during copulation. Blue shark spermatophores break down in seawater, liberating individual spermatozoa, so rapid transfer is necessary. The spermatophore may simply be an efficient way to store spermatozoa in the male's ductus deferens.

Indicators of Sexual Maturity in Males

The simplest technique to determine maturity is to compare external secondary sexually dimorphic characteristics that occur in large animals with those same characters as they appear in less developed members of the species. In male elasmobranchs changes in relative size, hardness, and development of the claspers is the most frequently employed method for determining sexual maturity. Clark and von Schmidt (1965) considered a male mature when: 1) the distal end of the clasper and rhipidion are fully formed and can be spread open on a fresh specimen, 2) the clasper proximal to the head is rigid due to calcification of the supporting cartilage, 3) the base of the clasper rotates easily and the clasper can be directed anteriorly, and 4) the siphon sacs are fully elongated. Aasen (1966, footnote 5) used clasper length exclusively as a maturity index in his work on blue and porbeagle sharks. Springer (1960) noted that the claspers of the sandbar shark become hardened or calcified at about the same time that the testes enlarge.

[5]Aasen, O. 1961. Some observations on the biology of the porbeagle shark *Lamna nasus*, Bonnaterre. Int. Counc. Explor. Sea, C.M. 1961, 109:1-7.

Blue shark claspers exhibit these characteristics (Figure 8) in a gradual transition with body growth rather than the abruptness noted by Clark and von Schmidt (1965) for the carcharhinids. It is therefore difficult to distinguish maturity in subadult blue sharks based on external organs.

Another valid index of sexual maturity is the presence or absence of sex products such as eggs and sperm. Several authors have used the presence of male sexual products as indicators of maturity. Kauffman (1950) working on the tiger shark observed ". . . the release of milt from the gonoduct when pressure was applied." Matthews (1950) stated that a basking shark of 622 cm ". . . was just approaching sexual maturity, for though the testis was showing incipient activity, the ampullae of the ductus deferentia were rather small, completely empty of spermatophores and showing no signs of having contained any." Olsen (1954) recognized that maturity took place over a fairly extensive size range. He noted that in the school shark, *Galeorhinus australis*, seminal fiuid flows freely from the cut surface of the enlarged testes and the seminal vesicles contain active spermatozoa in early summer. In borderline cases Olsen histologically sectioned the testis. He considered those fish to be mature that had ". . . enlarged seminiferous tubules [sic] which carried bundles of ripe spermatozoa . . . ." Bonham et al. (1949) and Templeman (1944) working on the spiny dogfish, *Squalus acanthias*, combined clasper length with the presence of spermatozoa in the seminal vesicles to determine maturity.

In the blue shark, two organs which enlarge as the male matures are the testes and the epididymides. Unfortunately, testes length (Figure 9) and epididymis width (Figure 10) follow the same gradual size increase as the claspers (Figure 8). Because they do not exhibit major inflections, these relationships are of little use for determining the onset of sexual maturity.

The most reliable method that I have found for determining maturity in the difficult subadult to adult sizes is to assess the ability of a shark to produce spermatophores. Many sharks with claspers that appear mature lack spermatophores and have small ductus deferentia. The spermatophore is the last tissue to mature and it develops abruptly in blue sharks.

Of 193 male blue sharks examined, 74 (38.3%) contained some quantity of spermatophores. The sharp increase in spermatophore occurrence between 175 and 205 cm body length is the transition

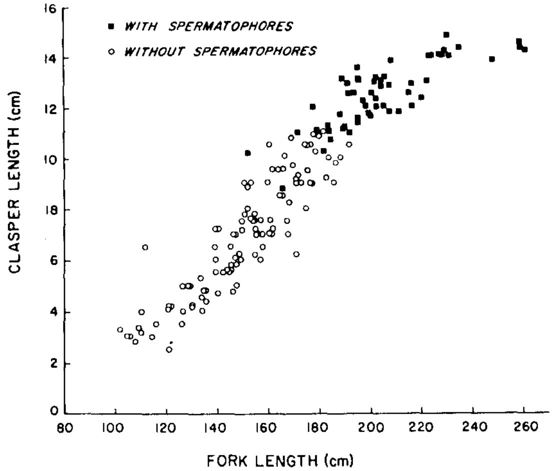

FIGURE 8.—Clasper-body length relationship compared with spermatophore development in the blue shark.

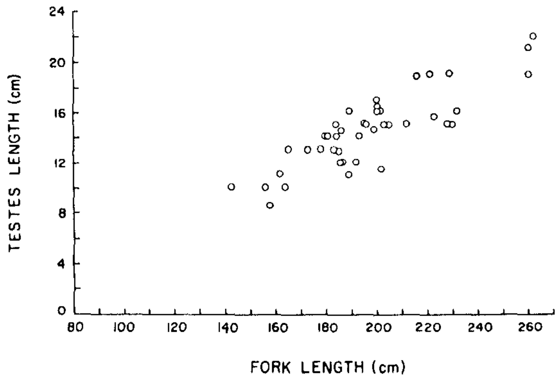

FIGURE 9.—Testes length-body length relationship in the blue shark.

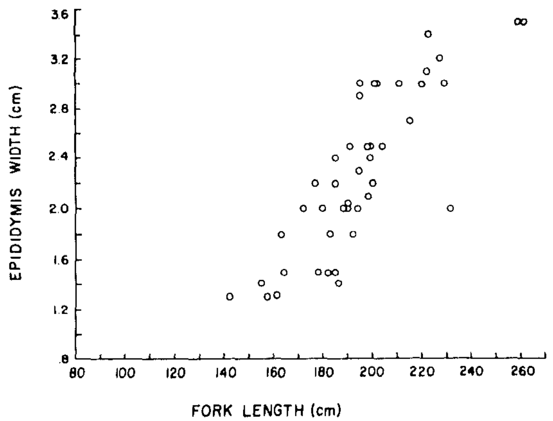

FIGURE 10.—Epididymis width-body length relationship in the blue shark.

zone between immaturity and maturity (Figure 11).

By this definition, the smallest mature blue shark (with spermatophores) in my sample was 153 cm and at 183 cm, 50% were mature. Judging from the radii of male tooth cuts on females (discussed below) and the condition of the clasper, 183 cm is the average size at which male sexual maturity is attained. Ninety-five percent of the males >205 cm and 100% >235 cm were mature.

These data agree well with Aasen's (1966) length at sexual maturity for the male blue shark. He cited 196.6 cm as the point of maturity as determined by an analysis of clasper length and my observations show 80% of the males contain spermatophores at this size. Stevens' (1974) sample contained only one mature male blue shark. He drew no conclusions regarding male maturity. Stevens speculated that all of his blue sharks were either immature or in a resting stage, except the largest one which was in poor condition. By my criteria, all of his sharks were immature except this individual. Bigelow and Schroeder (1948) suggested that both sexes mature in the range of 177-203 cm which agrees well with my finding of 183 cm.

A field test for the presence of spermatophores is accomplished by making a cross-sectional cut through the kidney at its thickest part. Four large (10-15 mm) ducts are visible ventral to the kidney at this level. Two of these are the thin-walled ureters, usually filled with a clear fluid. The thicker walled pair are the ampullae ductus deferens containing several hundred cubic centimeters of spermatophores, 0.5-2.0 mm in diameter, and their associated white flocculent supportive tissue. The presence or absence of spermatophores provides a positive answer to the question of sexual maturity in an individual male blue shark.

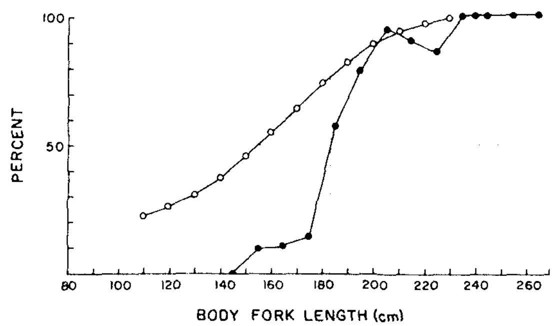

FIGURE 11.—Comparison of clasper length and spermatophore presence with body length. Circles are clasper growth as percent of largest clasper. Dots are percent of blue sharks with spermatophores. Dotted lines indicate coordinates for 50% maturity.

I observed no obvious seasonal fluctuations of sperm production in the blue shark as have been noted by Olsen (1954) and other authors for different species of sharks.

Female Anatomy

Ovary and Epigonal Organ

Only the right ovary of the blue shark is present and functional. It lies at the anterior end of the abdominal cavity adjacent to the liver and gall bladder (Figure 12). The ovary is a large organ (25 cm × 6 cm) adnate to the forward lateral surface of the right epigonal organ. It is roughly teardrop shaped, corresponding to the expansion of the epigonal organ as it reaches its forward terminus.

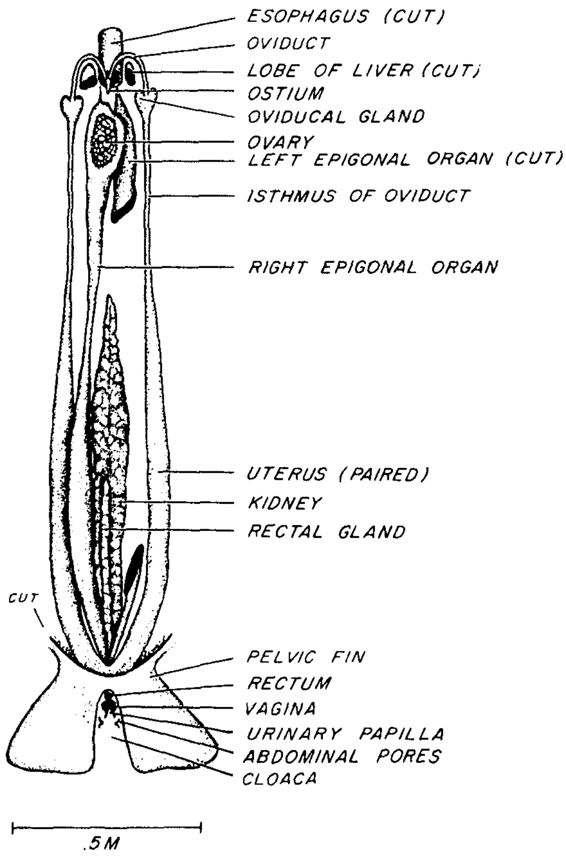

FIGURE 12.—Female reproductive system in the blue shark, general ventral view.

The ovary is composed of hundreds of follicles in a dense stroma of connective tissue. In the blue shark, follicles are contained in a single layer of generative tissue which blankets the ova as they develop.

The ovary of a full-term 243 cm gravid female, with 60 embryos "in utero," contained over 1,000 follicles (Figure 13). Although the average number of embryos seldom exceeds 54 (Bigelow and Schroeder 1948), this ovary contained 123 ripe eggs from 6 to 20 mm in diameter. Also present was a similar number of corpora lutea of various sizes, ranging from 1.2 to 7.5 mm in diameter, presumably from the generation then contained in the uterus. So-called corpora lutea are also found in the developing ovaries of immature blue sharks. It is likely that the 123 large ova constitute the next generation of 50-60 embryos, and that the balance would be reabsorbed. This would explain the presence of 120 corpora lutea found in the ovary of this female which, as determined by her size, was at the end of her first pregnancy. The next generation is recruited from those follicles currently in the 0.3-3.5 mm size class. No follicles were present between 3.5 and 6.9 mm diameter.

The epigonal organ is a paired straplike organ that extends the length of the peritoneal cavity. The anterior end is suspended from the dorsal body wall just behind the heart cavity near the origin of the liver and extends caudally, supported by a thin mesentery, to the insertion of the rectal gland. The organ is 3 cm in diameter in the central body cavity and gradually expands and flattens to 10-15 cm wide and 2-3 cm thick at each end. Matthews (1950) speculated that this is the site of erythrocyte production in elasmobranchs. It serves no reproductive function other than supporting the ovary.

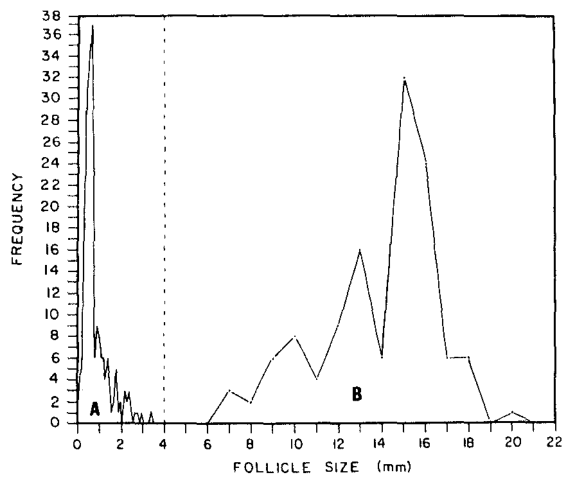

FIGURE 13.—Size/frequency population of ovarian follicles in a 243 cm gravid blue shark. A. 202 follicle subsample of an estimated 1,000 follicles in the ovary, grouped in 1.0 mm intervals. B. 124 maturing ova grouped in 10 mm intervals.

Ostium

The ostium is the anterior opening of the oviduct located at the forward end of the peritoneal cavity. It is a 10 mm long membranous funnel which bifurcates into the right and left oviducts. Lying between the ostium and the oviducal gland, the oviducts are firm white cylindrical tubes 10 mm in diameter. They traverse the curved mesentery that supports the liver to become attached to the dorsal peritoneal wall where the oviduct joins the oviducal gland.

Oviducal Gland and Isthmus

Approximately 80 cm from the ostium the oviduct expands to form the oviducal gland. It is heart-shaped, 3-4 cm in diameter, and 4-5 cm long. The oviducal glands of the adult female blue shark are small relative to other elasmobranchs. Externally, each is a symmetrical snow-white organ, with two short horns on the lateral anterior surfaces. The structure and function of this gland are discussed in a later section.

As it leaves the oviducal gland, the oviduct resumes its original diameter of 10 mm, but is now lined with longitudinal furrows and folds of tissue. This part of the oviduct is termed the isthmus (Figure 12) and runs for 15-20 cm from the oviducal gland to the uterus.

Uterus and Vagina

At the end of the isthmus the oviducts expand in diameter to 2 or 3 cm in nongravid adults and join the paired uteri (Figure 12). Each uterus is 50-60 cm long and supported by a mesometrium. In fish that have pupped recently the uterus is flaccid and much larger (5-15 cm diameter). Even at its smallest diameter the uterus of adult females is always thick-walled and oval in cross section. The uteri unite at their posterior end to form the common vagina. The length of the vagina is about 15 cm. Its distal end is demarcated by the hymen, a circular transverse fold. The hymen separates the vagina from the cloaca. In young females 82-120 cm the vagina is sealed or nearly sealed by a thin circular membrane originating from the hymen.

Cloaca

The rectum opens into the cloaca ventrally and forward of the vagina. A single urinary papilla is located on the dorsal wall of the cloaca just posterior to the hymen. Paired abdominal pores are found on the dorsal wall of the cloaca (Figure 12).

Copulation

During copulation spermatophores pass from the male ductus deferens to the urogenital sinus and sperm sac. They exit from the sinus through the common urogenital papilla which is positioned over the apopyle of the clasper and partially fill the clasper groove. The paired muscular siphon sacs drive a water piston past the apopyle to force the spermatophores through the clasper and into the common vagina of the female through the uterus and into the oviducal gland. Many females have been observed to contain spermatozoa packed in the greatly distended tubules of the oviducal gland (Figures 14, 15). The motility of individual spermatozoa may play a part in entering the inner tubules of the oviducal gland.

From the presence of vaginal scars, Matthews (1950) determined that the basking shark employs one clasper at a time in copulation. Leigh-Sharpe (1920) killed two tope "in copula" and observed both claspers inserted. I have found unpaired vaginal scars in female blue sharks caused by the employment of a single clasper. Judging from the size of the organs involved, the use of both claspers simultaneously may be an option only for young male blue sharks.

Mating Injuries

Wounds resulting from mating in large sharks have been described by several authors. Springer (1960) noted bite marks between the first and second dorsal fins of the female sandbar shark, *Carcharhinus milberti*. He stated, "These are never present on males or immature females and are obviously produced during courtship." Suda (1953) was the first to record tooth cuts on blue sharks. In the Pacific, tooth cuts appear as early as March and are most numerous from June to August. Stevens (1974) conducted a study of tooth cuts on blue sharks in British waters. He divided wounds into three types, semicircular impressions, tooth slashes, and individual tooth nicks, and recorded their distribution on the female. He found tooth cuts only on female sharks >150 cm and suggests that this is the size at sexual maturity for the blue shark.

Northwest Atlantic blue sharks bear dermal wounds similar to those described as courtship scars by Stevens (1974). Distinct tooth cuts have been observed on females of 134 cm. (The smallest female carrying sperm is 136.5 cm.) Occasionally slashes and wounds resembling mating marks occur on females as small 118 cm. External tooth cuts are most extensive in female blue sharks from 145 to 200 cm long (Figure 16). Pregnant females generally bear only older healed scars. Males of all sizes are usually free of cuts. Wounds are so consistently present on females that the fish being tagged during longline or sportfishing operations may be sexed from the dorsal surface without examination of the pelvic appendages.

To accommodate the male's aggressive mating behavior, the skin over most of the body of the mature female is more than twice as thick as that of the male (Figure 17). The skin is thicker than the males' teeth are long and only occasionally do the wounds penetrate the dermis and involve the musculature. Tooth cuts are generally punctures or slashes made by the upper jaw only. Resistance to infection and healing rates are apparently high in the blue shark. Despite injuries that seem very serious, evidence of infection and necrotic tissue are notably absent.

Matthews (1950) noted internal lacerations on the thick vaginal pads of female basking sharks. They are caused by the male's clasper claw, a structure common to several families of elasmobranchs.

The blue shark clasper does not bear a claw. After insertion, the terminal end of the clasper is flexed about 45°, unfolding and expanding the sharp-edged rhipidion to form an anchor in the vagina. The female often bears hematose abrasions on the otherwise light colored walls of the vagina as a result of copulation. Specimens from the Middle Atlantic Bight possess vaginal wounds during all seasons examined (March-October). Fresh marks are more frequent in summer months while older dark purple scars are observed in spring and fall. Spermatozoa have been found in young females lacking vaginal wounds indicating

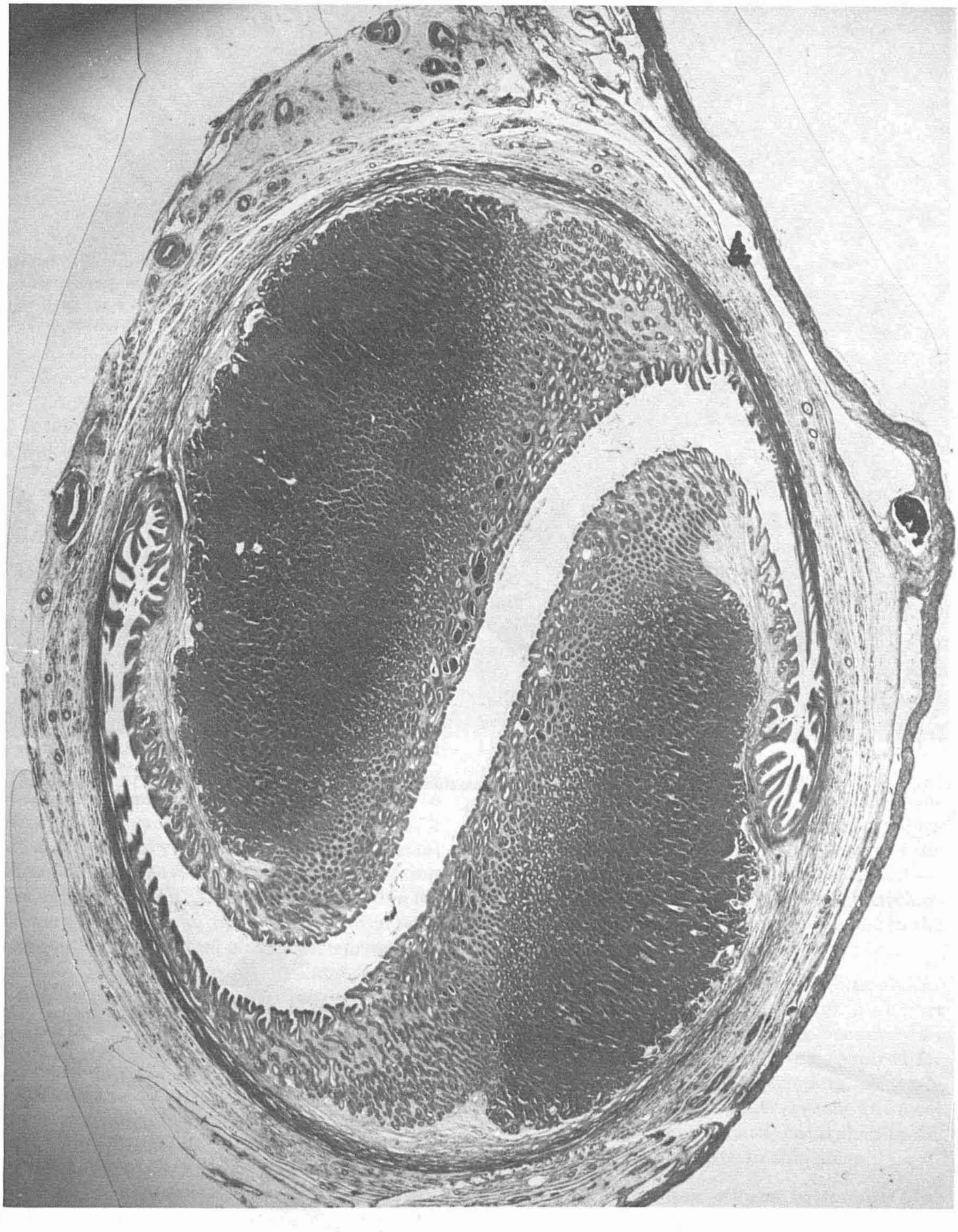

FIGURE 14.—Oviducal gland of female blue shark. Dark contents of central tubes are spermatozoan masses. Cross section (×8).

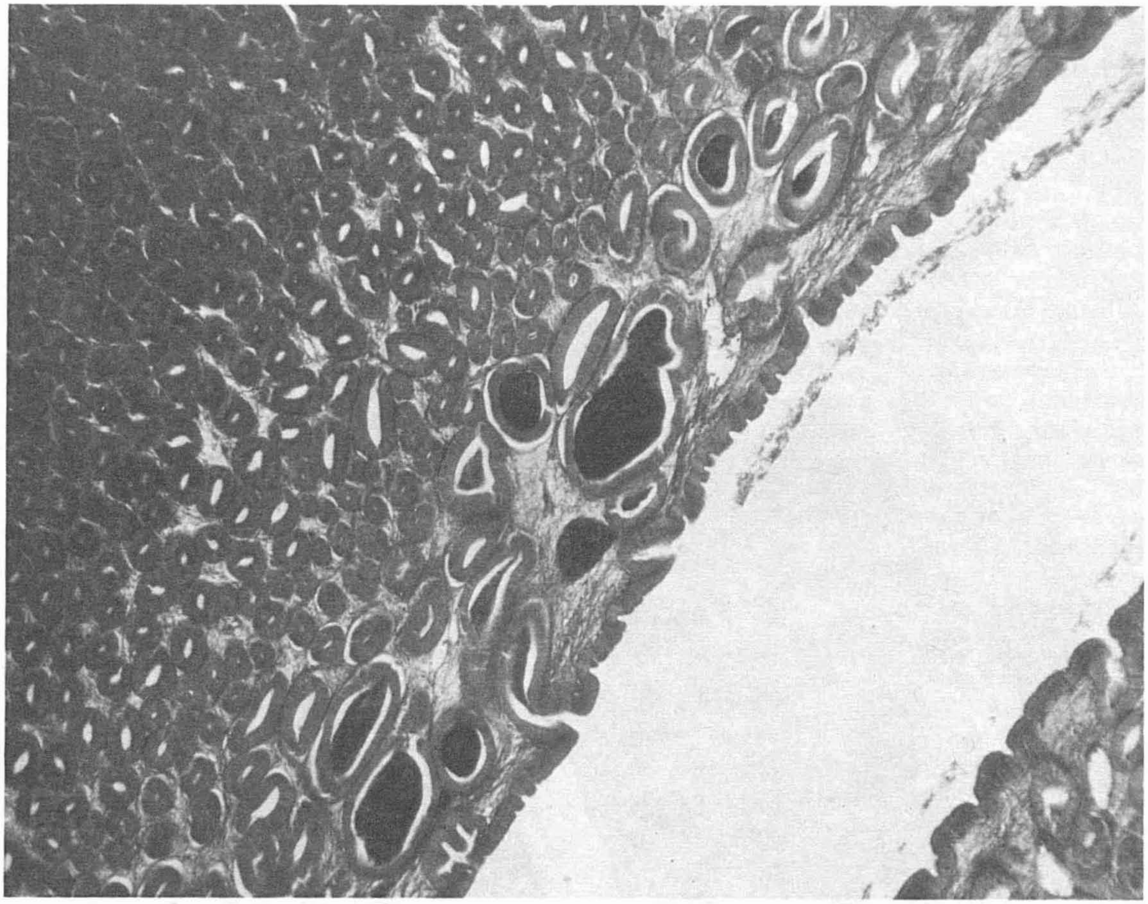

FIGURE 15.—Oviducal gland of female blue shark with spermatozoa clumped in tubules. Enlargement of Figure 14. Cross section (× 80).

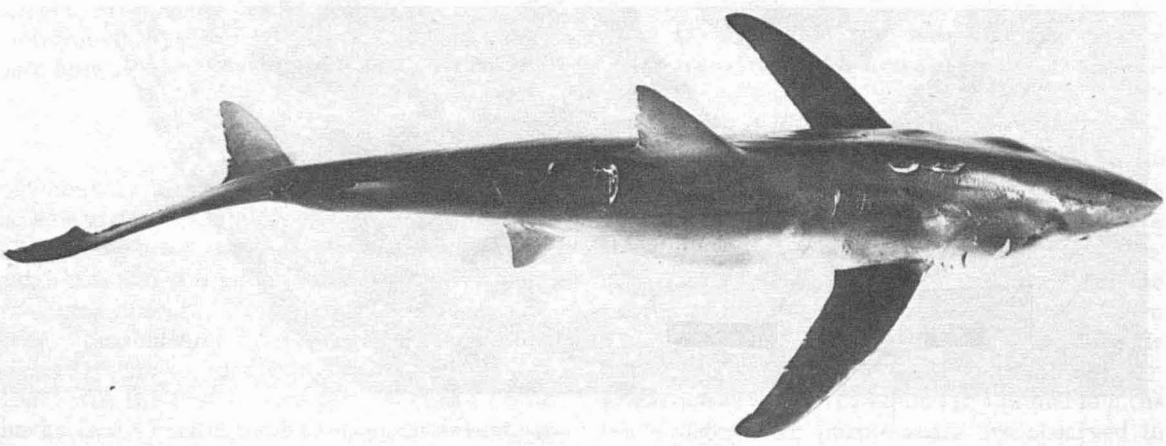

FIGURE 16.—Subadult female blue shark 185 cm FL with tooth cuts (mating scars).

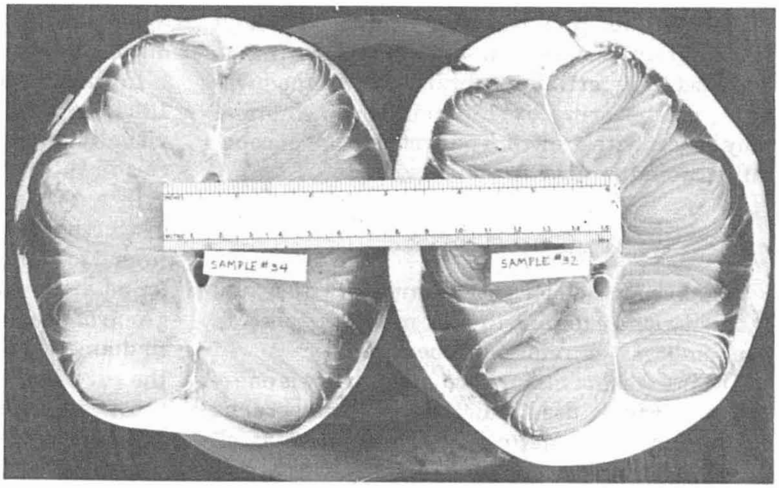

FIGURE 17.—Skin thickness comparison, cross sections of pelvic region of similar-sized male (left) and female (right) blue shark.

that insemination is not always accompanied by internal lesions.

Hermaphroditic Blue Sharks

Hermaphroditic blue sharks have not been mentioned in the literature and are apparently as rare as in other species of elasmobranchs. The only hermaphroditic blue shark I have examined was caught off central Long Island, 14 July 1973. It was 192 cm long and weighed 94 lb. There were many severe dermal lacerations (mating scars), some so recent as to be freshly clotted. There were two similar-sized claspers on the inner margin of the pelvic fins. They were much too short for the body length (17 mm from the margin of the fin to the free tip) and were not calcified. Internally, a small patch of ovary bearing four large (11 mm) ovarian follicles was found in the normal position on the epigonal organ. All of the reproductive organs were reduced; the upper oviduct diameter was 4 mm. Paired oviducal glands were present as 10 mm swellings in the oviducts. Caudally the 4 mm oviduct expanded to a 10 mm uterus. Two small testes were suspended in the usual position forward in the abdominal cavity. Histological sections revealed spermatozoa in the seminiferous ampullae of the testes. The epididymis and vas deferens were identifiable as undeveloped white tubes 1 mm in diameter. Judging from mating scars on the dorsal surface, this fish was treated by at least some of its conspecifics as a female. Although the ovary and testes were developed, the oviduct, ductus deferens, and claspers were too underdeveloped to permit this specimen to be functionally mature as either a male or female.

Indicators of Sexual Maturity in Females

Nearly every structure of the female reproductive tract has been used in the past to determine sexual maturity. Most authors rely on a combination of indicators that account for several stages in the reproductive cycle. Bonham et al. (1949) noted that the length of the ovary increased only slightly faster than did the body length of *Squalus acanthias*. Springer (1960) and Kauffman (1950) used the appearance of the elasmobranch ovary as an indicator of maturity. The development of the oviduct has been considered an index by Springer (1960) and Olsen (1954); the oviducal gland by Olsen (1954) and Nalini (1940); and the uterus by Olsen (1954), Templeman (1944), and Aasen (see footnote 5). In the carcharhinids studied by Clark and von Schmidt (1965), the development of the vaginal opening proved to be the most useful external indicator of maturity. In young carcharhinids the vaginal opening begins as a slit in the urinary papilla.

Defining sexual maturity in female blue sharks is difficult because they pass through a distinct subadult phase in which the organs necessary for copulation are developed and those required for generation are dormant or developing. The subadult stage lasts for two summer seasons and most female blue sharks on the continental shelf in the western North Atlantic are in this stage.

Examination of sex organs in female blue sharks of various sizes reveal that like the male claspers, growth is quite regular in the ovary and oviduct. The oviducal gland exhibits some differential growth after 100 cm body length is attained

(Figure 18), but growth is nearly constant through the subadult sizes. The vaginal opening is occluded by a partial membrane only in the juveniles, disappearing by 135 cm. The membrane may be lost with growth. The first attempt at copulation would remove it.

Sex Products

Another method for determining size at sexual maturity is to examine the sex products (follicles, ova, embryos) in relation to body length.

The presence of mature ova in the ovary is one of the most widely used indicators of elasmobranch sexual maturity. Metten (1941), Bonham et al. (1949), Kauffman (1950), Olsen (1954), and Springer (1960) have all partially utilized the condition of ovarian eggs for this purpose.

In the mature blue shark a generation of 100-130 large ova of fairly equal diameter (15-20 mm) visually dominate the hundreds of smaller follicles in the ovary.

In a 243 cm mature gravid female, the most distinctive ovarian features were 123 yolked ova from 6 to 20 mm in diameter. The larger ova were found at the anterior end of the ovary. A second group of nearly 1,000 follicles, from 0.1 to 1.0 mm in diameter, were found between and attached to the covering of the larger ova.

The diameter of the largest generation of ovarian eggs is a valid index of first maturity when compared with body length (Figure 19). First

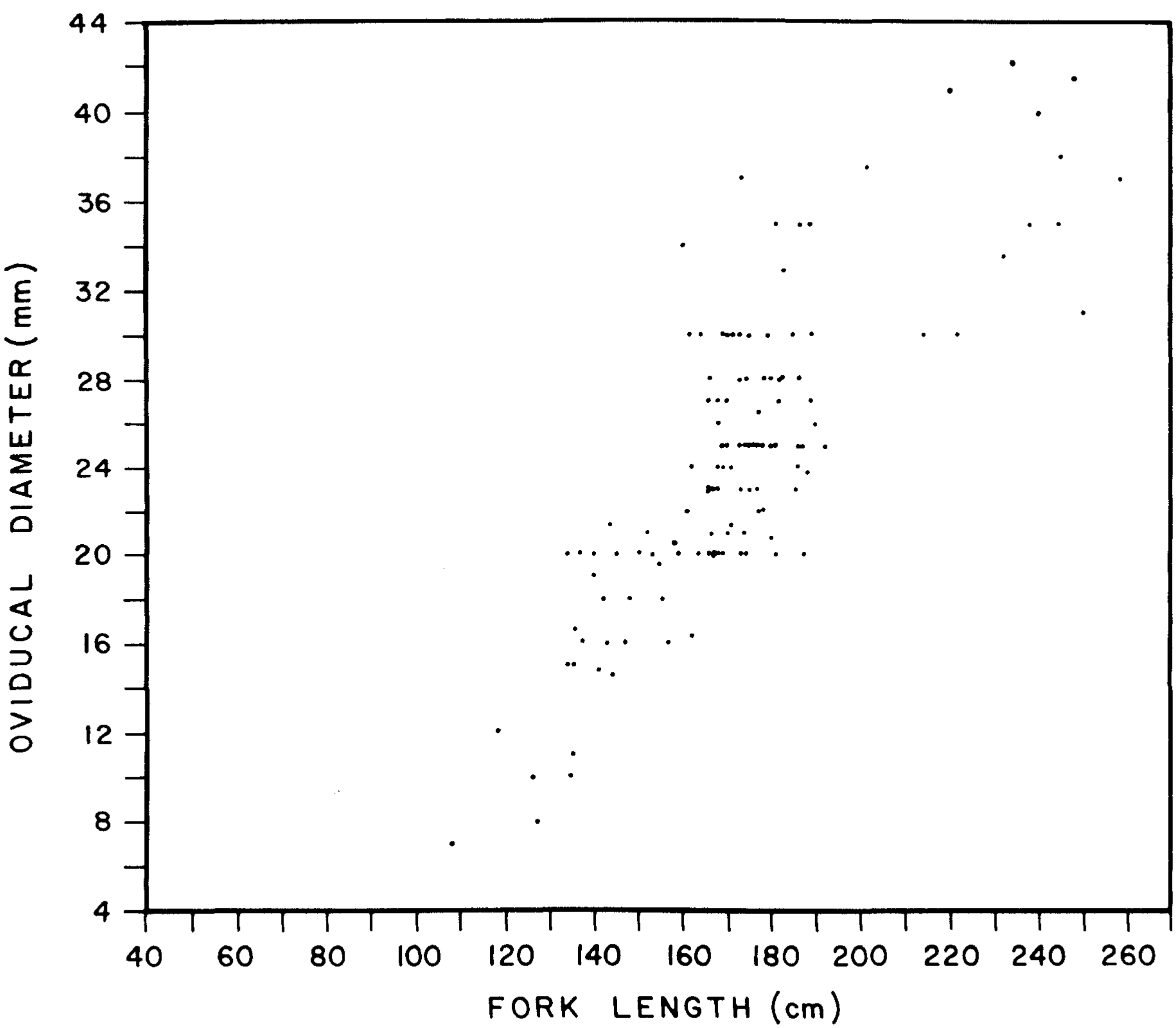

FIGURE 18.—Oviducal outside diameter-body fork length relationship in the blue shark.

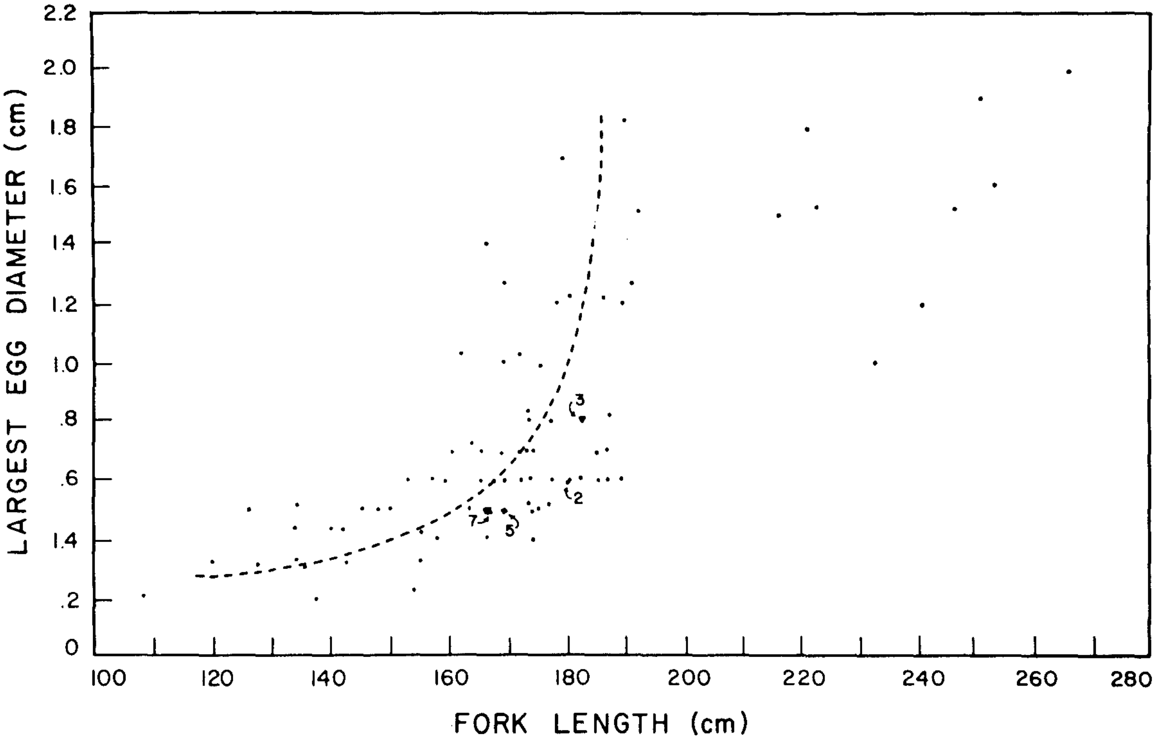

FIGURE 19.—Largest egg diameter-fork length relationship in the blue shark. Hand fit curve follows the first generation of eggs in the subadult population. Egg diameters accompanying lengths >200 cm are from mature or gravid females that have released or absorbed one or more generations of eggs and are producing subsequent generations.

maturity is reached at 180-190 cm body length by this criterion. Egg diameters accompanying body lengths >200 cm are from mature or gravid females that have released or absorbed one or more generations of eggs and are producing subsequent generations.

Gravid Females

The smallest recorded gravid females should be slightly longer, due to elapsed gestation time, than females carrying their first generation of ripe ovarian eggs (Figure 19). Gravid blue sharks with the smallest fork lengths reported in the literature from the Atlantic are as follows: 166 cm (Tucker and Newnham 1957), 193.3 cm (Aasen 1966), and 177-203 cm (Bigelow and Schroeder 1948); from the Pacific: 168 cm (Suda 1953) and 173.3 cm (Strasburg 1958).

Blue sharks carrying embryos are encountered infrequently in the world ocean. Suda (1953) examined 115 Pacific blue shark females bearing embryos and concluded that gestation lasts 9 mo and birth occurs between December and April. At this time the embryos have attained a maximum length of 39 cm. Strasburg (1958) examined 18 large females from the Pacific of which at least 10 were pregnant. The largest embryos were also 39 cm and occurred in March and May.

Francis Williams[6] caught eight pregnant female blue sharks while longlining in the eastern Pacific. His sample was unique because the size range of gravid females was small (153.3-171.6 cm). The embryos also were in a narrow size range (21.9-34.7 cm).

Gubanov and Grigor'yev (1975) reported small embryos (3.2-28 cm) from February to July in the equatorial Indian Ocean. They speculated that birth of young blue sharks occurs outside of this area.

[6]Williams, F. 1977. Notes on the biology and ecology of the blue shark (*Prionace glauca* L.) in the eastern Pacific Ocean and a review of data from the World Ocean (unpubl. manuscr.). Pers. commun. via John Casey, Northeast Fisheries Center Narragansett Laboratory, National Marine Fisheries Service, NOAA, Narragansett, RI 02882, 1977.

There are few published accounts of gravid female blue sharks in the North Atlantic. Aasen (1966) examined 48 caught by longline primarily around the Canary Islands. He reported lengths of 11 individuals and embryo lengths from only 2 specimens with means of 28.1 and 40.0 cm. The largest embryo length he measured was 43.0 cm. From these lengths he concluded that birth occurred between February and April.

Beebe (1932) reported a gravid female taken off Nonsuch Island, Bermuda, in September of 1931. She carried 50 embryos averaging 8.3 cm long. Tucker and Newnham (1957) reported a small (166 cm) gravid female caught in the sport fishery off Looe, England. They summarized the eastern Atlantic and Mediterranean observations of gravid females with embryos.

From 1967 to 1975, I examined 19 gravid female blue sharks from the western Atlantic. These specimens include a blue shark taken in January approximately 300 mi northeast of the Windward Islands (lat. 21°20′ N, long. 58°52′ W); 2 caught in the Gulf Stream south of Sable Island in May; and 16 obtained from off the coast of Long Island, N.Y. These fish were caught within 50 mi of shore during June and July. The embryos from 13 fish were examined, the remainder having been lost or aborted during capture. In addition, Richard Backus[7] has supplied information on 19 gravid females.

Embryos

Growth of the placentally viviparous embryos appears to be linear, gestation taking 9-12 mo. Figure 20 combines all available North Atlantic and Mediterranean data for a summary of embryo length and season. The trend line seems to indicate a gestation of 12 mo, 3 mo longer than reported by Suda (1953). A 12-mo gestation also agrees with my proposed sexual cycle. However, since the left-hand data points are from offshore observations and the right-hand points are from inshore fish, it is quite possible that the offshore embryos may be born in March while embryos from inshore females could have been conceived in September and born in June, 9 mo later. These data cannot therefore resolve gestation time.

On 23 July 1978, a female blue shark in the first stages of pregnancy was examined at Montauk. It contained two embryos 11 and 13 mm long attached to 22 mm yolks with 38 less-developed eggs arranged in a dorsoventral series in both uteri.

[7]Original data from Richard H. Backus of Woods Hole Oceanographic Institute. Pers. commun. via John Casey.

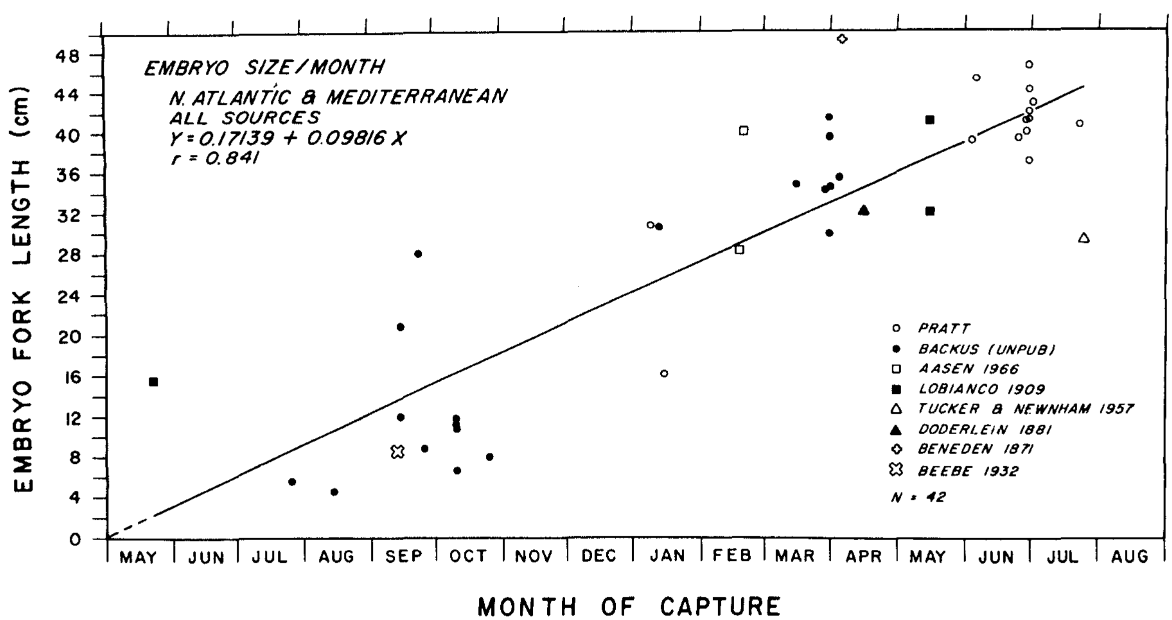

FIGURE 20.—Embryo length-month relationship for North Atlantic and Mediterranean blue sharks.

The embryos taken during June and July were full term (mean lengths 37.1-46.6 cm). Some were larger than any reported in the literature (42-46.6 cm) except for one 49 cm embryo reported by Beneden (1871) and cited by Tucker and Newnham (1957).

The range of smaller embryo sizes reported by other authors as "full term" may result from examination of young "in utero" or aborted on deck. Judging from my January sample, after only 4-5 mo gestation embryo blue sharks have lost branchial gills and yolk sacs, and appear to be full-term replicas of the adults. When returned to the ocean they are active and quickly swim away. Premature embryos (up to 30 cm) have a proportionally thin body for the size of the head giving them a tadpolelike appearance. Full-term embryos (Figure 21) have a girth that equals or exceeds the head circumference. The pregnant female sampled in January carried 82 embryos averaging 13 cm long. Suda (1953) indicates this 264 cm female could be between 4 and 5 mo pregnant. Only the report of Gubanov and Grigor'yev (1975) of 135 young exceeds this observation. Minimum number of young could not be determined due to reports of premature parturition while the fish were being boated.

Gubanov and Grigor'yev (1975) agreed with a proposition of Lübbert and Ehrenbaum (1936) that embryo blue sharks develop and are born in stages. No evidence was found in the Atlantic to support this hypothesis. Embryos occurred in the same relative stage of development in each female. This is apparent in Figure 22. The 37 cm ($\bar{x}$) embryos ventral to the 232 cm pregnant female appear slightly smaller due to camera parallax. Nearly every litter contains one stunted or decomposing embryo. The explanation may be failure to attain placentation, dislodgement, or tangling of the umbilical cords. A stunted embryo is 10th from the left in the ventral row of embryos (Figure 22).

The smallest free-swimming young have been observed in the Pacific by Francis Williams (see footnote 6) at 35 cm and Strasburg (1958) at about 38 cm. The smallest Atlantic specimen is Bigleow and Schroeder's (1948) report of 44 cm. These lengths resemble lengths of the largest embryo sizes, and available evidence suggests that size at birth for the blue shark is between 35 and 44 cm. The pupping season can be interpolated from Figure 20 to occur from March to July. The apparent lack of "young-of-the-year" blue sharks suggests an offshore pupping. The blue shark is the most prolific of the large oceanic sharks (Bigelow and Schroeder 1948), yet I have seen only one free-swimming fish that was <1 m FL. Blue sharks in the first and second year of life must, therefore, inhabit an unknown niche.

Structure and Function of the Oviducal Gland

The oviducal gland (Figure 23) as defined by Metten (1941) has also been referred to as the

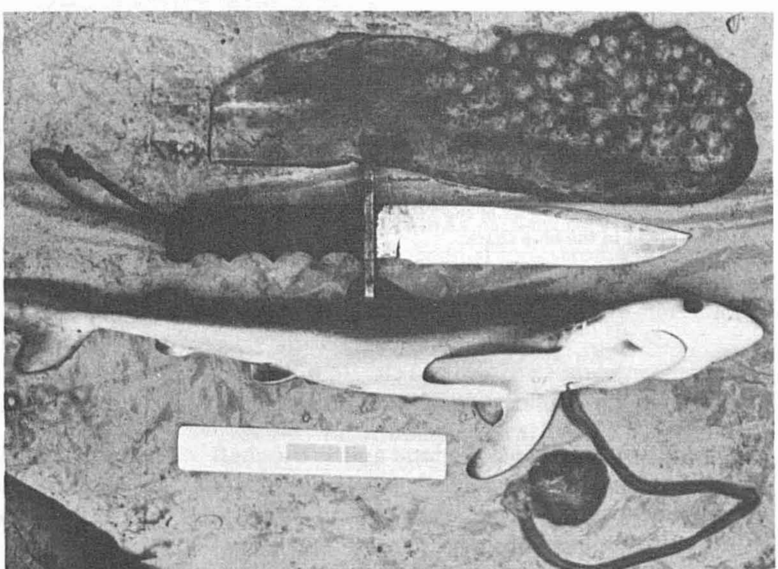

FIGURE 21.—Ovary and 43 cm FL full-term embryo from 220 cm FL gravid blue shark.

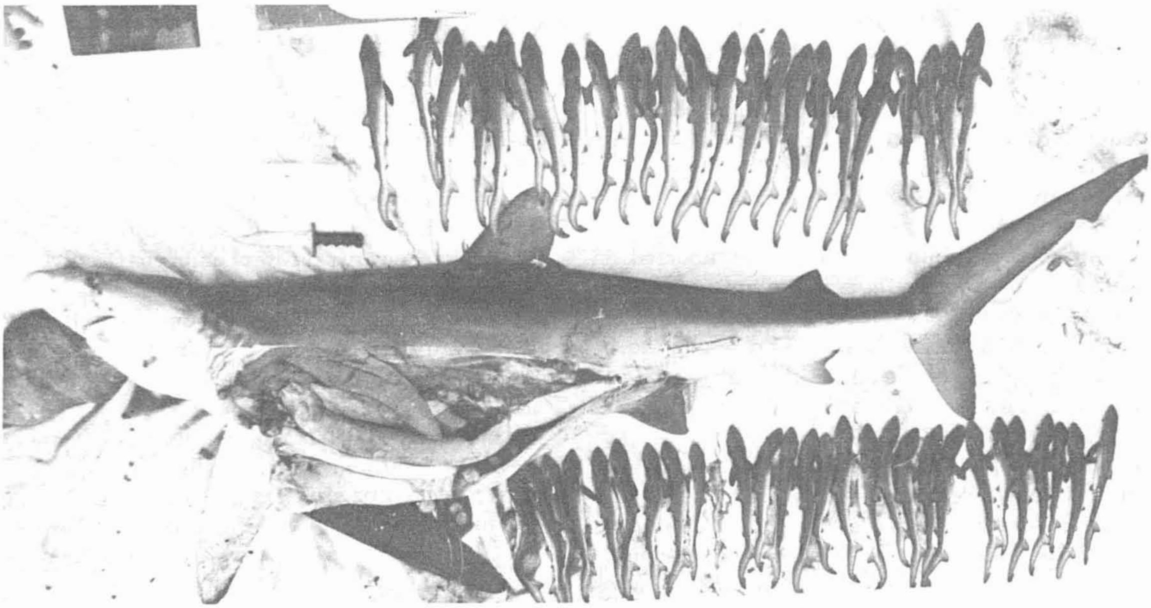

FIGURE 22.—Gravid female blue shark.

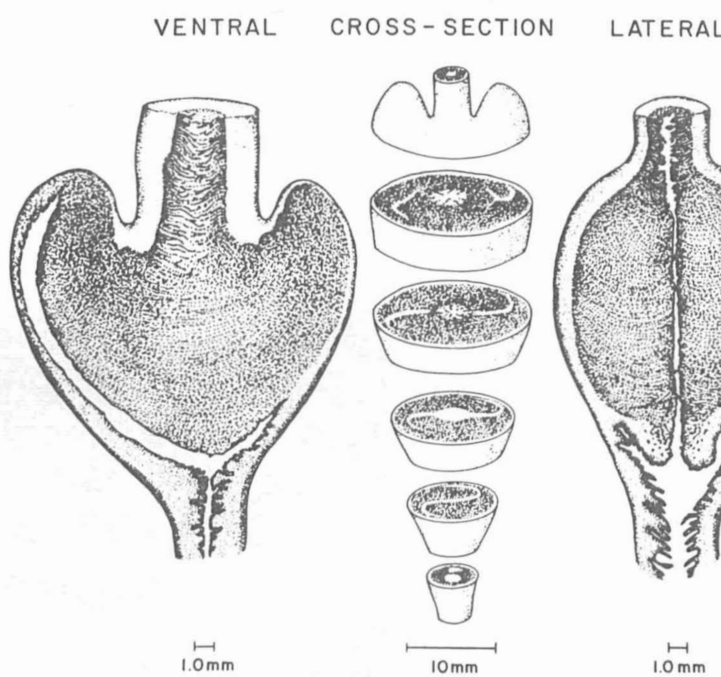

FIGURE 23.—Schematic views of the oviducal gland in the blue shark.

nidamental or nidamentary gland and as the shell gland. The term "nidamental" is inappropriate since it is derived from the Latin "to nest" which is not a trait of elasmobranchs. Since a functional shell is produced in only a few species of shark, oviducal is a more accurate term for this specialization of the oviduct.

A sagittal section of the oviducal gland reveals the two major tissues (Figure 24), an anterior albumen-secreting zone and a posterior shell-

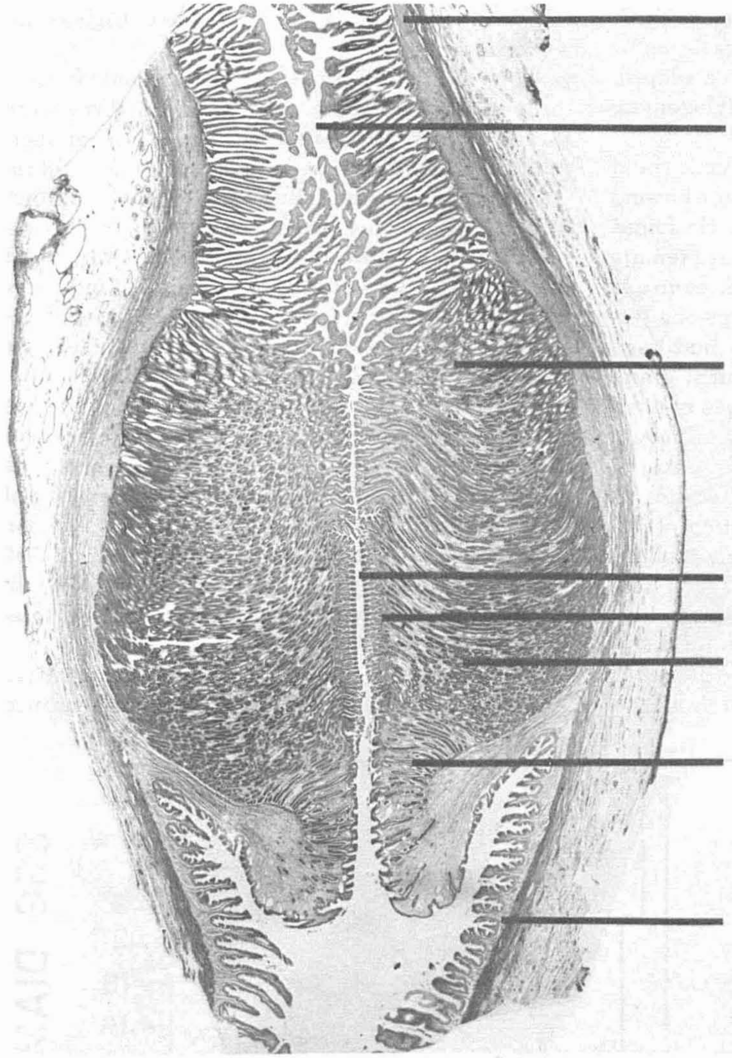

FIGURE 24.—Sagittal section of the oviducal gland in the blue shark (×5 cross section).

secreting zone. The mucus-secreting zone found in some elasmobranchs is reduced or absent in the blue shark, perhaps because of the limited shell that is produced. Secretory tubules originate blindly around the circumference of the gland and extend inward, parallel to one another. In the course of their travel they bow posteriorly for several millimeters, then return to the latitude of their origin where they communicate with the central lumen.

The albumen-conducting tubules enter the lumen as a series of 13-15 evenly spaced lamellae with irregularly flattened ends. The shell-secreting tubules terminate in tufted pockets bordering the central lumen.

The posterior half of the shell-secreting section communicates with the lumen through paired caudal protuberances of secretory tissue (Figure 24). They are embedded in a stroma of connective tissue and run a shorter, more irregular course to the lower central lumen where they end in larger and less uniform lamellae.

As the gland matures the lumen branches into two diverticula, which extend around its circumference and into each lateral horn in a medial cross section. These two diverticula give the lumen a symmetrical S-shaped appearance (Figure 13).

Of those sharks studied by Prasad (1944, 1945, 1948), the oviducal gland of the blue shark most closely resembles that of *Carcharhinus dus-*

sumieri. This is to be expected because both *C. dussumieri* and *P. glauca* are viviparous forms in which a yolk-sac placenta has been developed. (See Prasad 1944, for a discussion of phylogenetic significance.)

Metten (1941) observed that the oviducal gland of *Scyliorhinus canicula* has a function beyond that of albumen and shell production. He found active male spermatozoa in every mature female oviducal gland that he dissected. In *S. canicula* this gland is a seminal receptacle. Eggs are fertilized, not in the anterior oviduct as had been previously suggested, but in the oviducal gland itself. It is not known how many species of elasmobranchs share this trait. Matthews (1950) could not find sperm in the oviducal gland of the basking shark. Prasad (1944) observed the presence of spermatozoa in the oviducal glands of four viviparous species from the Indian Ocean: *Carcharhinus dussumieri*, *Hemigaleus balfouri*, *Scoliodon palasorrah*, and *S. sorrakowah*. He also gives an excellent account of the search for a "receptaculum seminis" and its existence in other animals. Prasad (1945) observed spermatozoa in the oviducal gland of the tiger shark, *Galeocerdo cuvieri*.

Stevens (1974) found that 16% of female British blue sharks had tooth cuts. Of these, three were dissected and oviducal glands examined for spermatozoa. His failure to find spermatozoa could result from technique, sample size, or the dynamics of the British blue shark population which contains very few males (Stevens 1974). Only 4% of the males in his sample reached sexual maturity as defined by my criteria based on the spermatophore development of western Atlantic blue sharks.

I have found spermatozoa in the oviducal glands of 79 of 160 female blue sharks collected over a 3-yr period (Figure 25). In all cases sperm was detected in a cross section of the posterior third of the oviducal gland using light microscopy. Fifteen micrometer sections were examined at 120-500 diameters magnification and the presence of brightly stained sperm confirmed at 1,250 diameters (Figure 26).

In the last year of field collections, comparative tests were conducted to determine if the presence

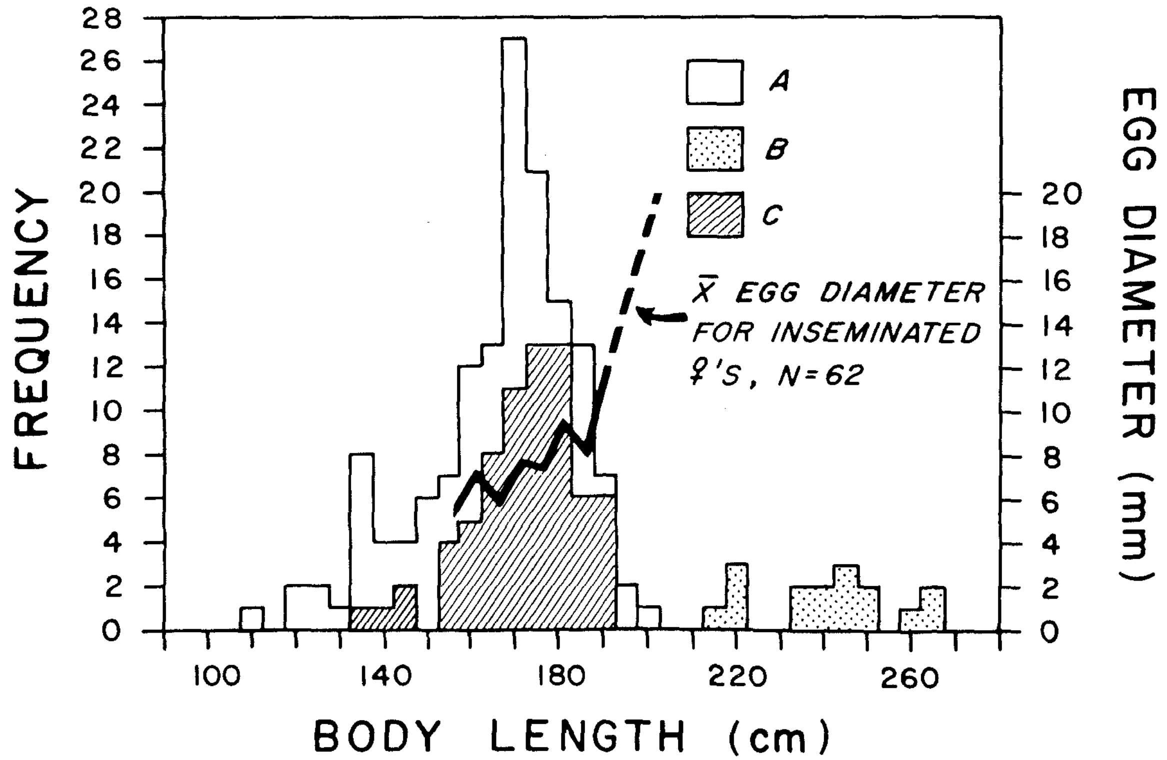

FIGURE 25.—Frequency of occurrence of female blue sharks off Bay Shore, N.Y., with data on insemination, egg diameter, and body length relationship: A) uninseminated females, B) adult females, C) inseminated females.

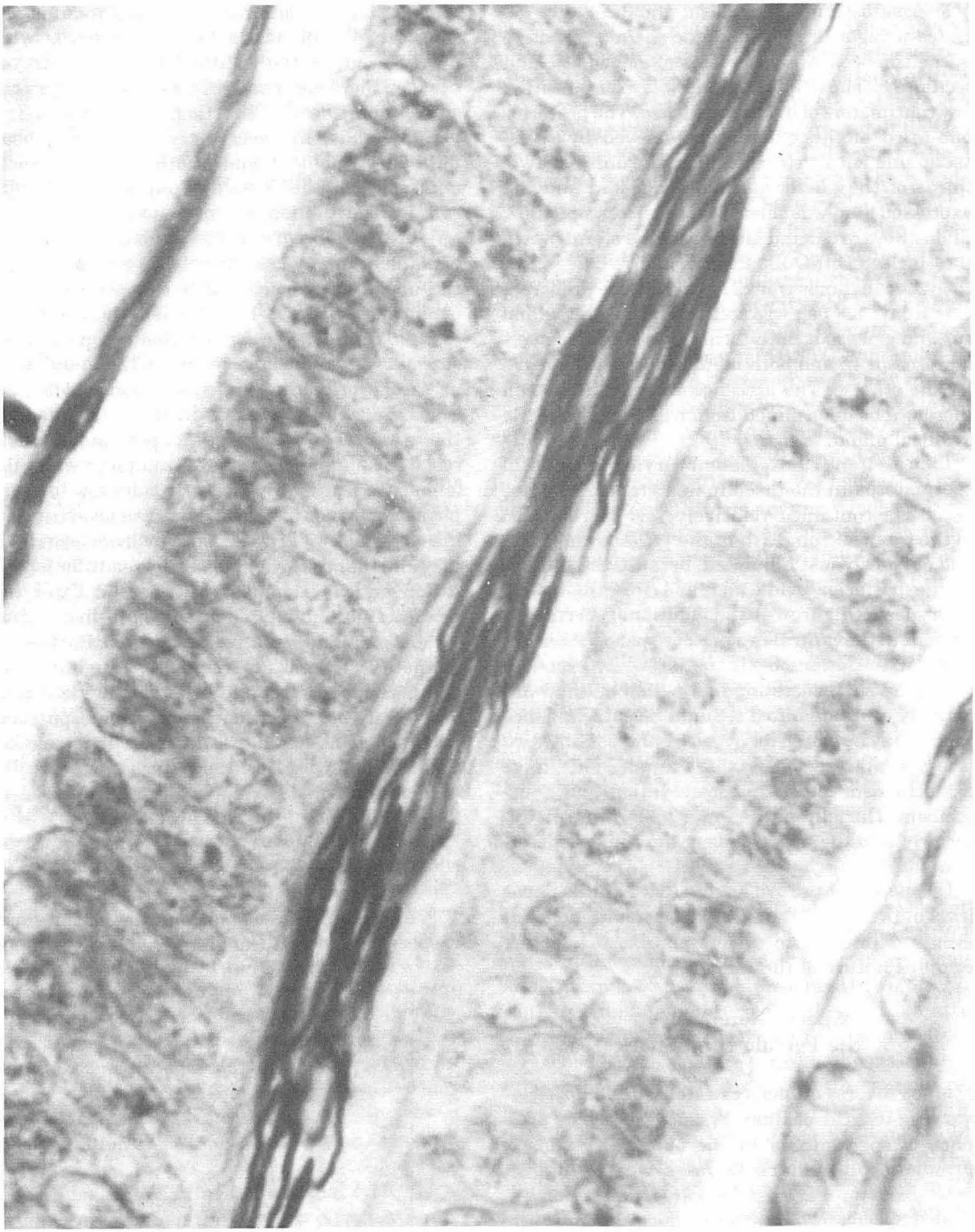

FIGURE 26.—Spermatozoa in tubules of oviducal gland in the blue shark (×2,500).

of spermatozoa in the oviducal gland could be detected using a smear technique as an alternative to the time-consuming process of embedding and sectioning. The oviducal gland was excised with a few centimeters of oviduct attached. The posterior one-third of the gland was removed by cross-sectioning with a clean scalpel. The anterior two-thirds of the gland was then squeezed and the expressed fluid was smeared on a microscope slide. Slides were dried and later fixed and stained with the Harleco Diff-Quik stain system.

Oviducal glands from 21 sharks were prepared. One from each fish was sectioned; the other gland cut and smeared. Both techniques revealed spermatozoa in 15 and both methods proved negative for the other 6. The presence of spermatozoa can therefore be determined from fresh smears of the oviducal gland.

Like Metten (1941), I found varying amounts of spermatozoa in the inseminated glands. Females >200 cm contained relatively few spermatozoa in the tubules. Some fish in the 160-180 cm group had obviously just copulated, because the tubules of the posterior oviducal gland were distended with sperm (Figure 14) and additional sperm was present in the central lumen. The spermatozoa are stored in the lower lobes of tubules which probably once were shell-secreting in function but now are actively evolving into a seminal receptacle. Since sperm may be stored for over 1 yr and possibly two (see Sexual Cycle below) these tubules must have a mechanism for sperm preservation and nourishment. Ducts from the lower lobes also run anteriorly into the upper ends of the lumen's diverticula.

I suspect that the ova are fertilized at this upper level of the oviducal gland. The exact sequence of events is difficult to understand because of the complex nature of the lumen.

Sperm Retention in the Female Blue Shark

Many diverse animals can store spermatozoa for varying lengths of time (Prasad 1944). The presence of spermatozoa in the oviducal glands of pregnant blue shark females would suggest extended storage. Histological examination revealed spermatozoa in the oviducal gland of the Sargasso Sea specimen. The other gravid females examined histologically are from northern waters caught in May, June, and July. A total of nine gravid females contained spermatozoa. Two females did not contain spermatozoa and it is possible that the glands lacking spermatozoa were poorly fixed, or the spermatozoa was destroyed because these sport-caught fish often hang in the sun for hours before dissection. Alternatively, it is possible that the reservoir of sperm has been naturally depleted and another copulation is necessary. If the female could physiologically sense this depletion, the presence in coastal waters of 225-240 cm nongravid females would be explained. In any case, it may be concluded from the above that spermatozoa can persist in the oviducal gland for at least the length of gestation (9-12 mo). If delayed fertilization is a part of the sexual cycle, then storage for 18-22 mo would be necessary for sperm to be found in a gravid female. Since the oviducal gland is at the anterior end of the uterus it is doubtful that spermatozoa could reach the gland if copulation took place while the female was carrying young. In addition to these physical obstacles to the transfer of spermatozoa, the presence of 110-120 ripe ovarian eggs also suggests that the gravid female is ready for fertilization and development of a second litter immediately after pupping. The offshore distribution of most pregnant females (Aasen 1966; Backus see footnote 7) in areas not frequented by adult males and perhaps unreceptive behavior in the female very likely act to prevent males from copulating with pregnant females. Therefore, it is possible that the quantities of spermatozoa found in the nine gravid female oviducal glands are sufficient for fertilization of the ripe ovarian eggs.

Sexual Cycle

The high incidence of mating scars and presence of sperm in the oviducal gland indicate a summer

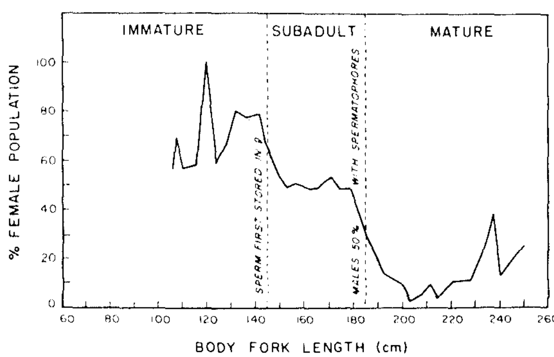

FIGURE 27.—Blue shark sex ratio in June off Bay Shore, Long Island, N.Y., 1965-72, n = 2,174.

breeding season for the blue shark on the continental shelf off southern New England. The length-frequency histogram of these inseminated females approximates a curve of normal distribution with a peak at 175 cm (Figure 25). The phenomenon of carrying spermatozoa seems to separate an age-class from the combined length frequency of the female population. If this is an age-class, then Stevens' (1975) age curve for the blue shark indicates that the inseminated females are 5 yr olds and the uninseminated fish are primarily fours and fives. Since most of my samples were taken in June and July, it is possible that the unfertilized 5 yr olds would be inseminated later in the season. Since all nongravid females on the continental shelf bear tooth cuts and many have vaginal scars, it would appear that only females >4 yr have organ systems developed enough to retain spermatozoa. The growth curve of ovarian eggs in inseminated females (Figure 25) shows the eggs as half-mature in 5 yr olds. Five-yr-old inseminated females that I sampled as late as October in continental shelf waters off southern New England do not contain mature ova or embryos. Due to immature egg size and the lack of developing embryos, I conclude that this age class is not ready to bear young during the summer of insemination. If fertilization occurred during the winter, the 9-mo gestation proposed by Suda (1953) and Aasen (1966) would produce full-term embryos in gravid females through the following summer and into the fall. This is not the case. Full-term females occur most frequently during the spring and early summer (Figure 20).

The age-6 female length-frequency mode (190 cm; Stevens 1975) is conspicuously absent from the shelf waters in the summer months (Figure 27), while males of this size are numerous. Backus (see footnote 7) caught two females offshore that could be 6 or 7 yr old by Stevens' (1975) criteria (197.4 and 209.5 cm); each carried 11.0 cm embryos in September and October, respectively. I examined one gravid female in July with two embryos 11 and 13 mm. The uterine eggs were otherwise undeveloped. Typically, gravid females in this population are of lengths indicating 7 yr of age and older.

Based on these findings, the sexual cycle of the female blue shark in the western North Atlantic would start as 4- and 5-yr-old fish arrive on the feeding/mating grounds of the continental shelf in late May and early June. Here they interact with males receiving dermal punctures and lacerations (tooth cuts). The 5-yr-old females and some 4 yr olds, copulate with the males of 180 cm and larger judging from the size of the tooth interspace reflected in bite marks and male sexual maturity. This process is known to continue as late as November and may continue year round in Bahamian waters (Stephen Connett[8]). The following spring, the 6-yr-old females remain offshore and fertilize their eggs (May, June). Embryos reach full term in 9-12 mo. Pupping is from April to July. At this time the female is 7 yr old. This is the probable trend for most female blue sharks. There are many exceptional bits of data such as reliable reports of small (165 cm) gravid females (Suda 1953; Tucker and Newnham 1957) and embryo sizes that depart from the trend, especially in the eastern North Atlantic (Figure 20). These are to be expected in a wide ranging, abundant species with a long breeding season. A small number of females in the inshore population have very advanced organs and egg development for their length. It is possible that these precocious individuals bear young a year earlier than their siblings or shift completely out of phase by bearing young at random seasons.

Stray gravid females occur regularly in southern New England shelf waters. Their diminuitive numbers are an insignificant part of the spawning population. Too little is known of the early life history and feeding habits of the blue shark to determine whether the young would fare better in the rich waters of the continental shelf or offshore along the margins of the Gulf Stream.

Sex Ratio

Suda (1953) reported the blue shark sex ratio at birth to be 1:1. Data from a population of 2,174 males and females sampled at Bay Shore, Long Island, from 1965 to 1972 is presented in Figure 27. In this sample immature females consistantly outnumber the males until a fork length of 150 cm is reached because unlike females, the males only move inshore when the sex organs start to mature. The sex ratio then becomes equal in the subadult sizes when a large number of mating wounds and inseminated oviducal glands are prevalent. In the adult size group (180-250 cm) the sex ratio shifts rapidly to a preponderance of males. The inflexion point at 180 cm coincides with the size at which

[8]Stephen Connett, instructor, summer oceanography program St. George's School, Newport, R.I., pers. commun. April 1977.

ovarian eggs are reaching maturity (Figure 18) and the greatest number of females are becoming inseminated (Figure 27). Larger females are caught in decreasing numbers on the mating grounds on the shelf. Their absence probably indicates a successful insemination and offshore migration. Since courtship and copulation are not without peril to the female, it is reasonable that they should move offshore at this time. The sex ratio remains between 5 and 10% female, from 200 to 230 cm where a second peak occurs. These are mostly postpartum and gravid females in their first pregnancy. They have probably followed the main population inshore for its summer feeding migration. It is possible that since their eggs are ripe they may also need to supplement the amount of spermatozoa in the oviducal gland.

CONCLUSION

The blue shark's success as a species is partly dependent on a highly evolved system for reproduction. The blue shark differs from other carcharhinids in having a steady growth rate for the sexual organs, a lack of seasonality in the generation of sex products, and a distinct female subadult stage. A different approach has been necessary to discern the size at sexual maturity for both sexes: an analysis of spermatophore development for the male, and an examination of the seminal receptacle present in the female oviducal gland.

There are many stages between the generation of sexual products (sperm, eggs, embryos) and the time of their delivery. Elaborate capabilities have been developed by both sexes for lengthy storage and nourishment of spermatozoa, first in the epididymis, then as spermatophores in the ductus deferens, and finally in the oviducal gland of the female where they are retained for months and possibly years.

Sexual maturity occurs for both sexes at a similar body length when they are together on the continental shelf for the summer season.

While the details of mating and copulation are obscure, it is highly successful since not a single female of age was observed without evidence of mating activity and 49% were inseminated.

With the exception of the strays examined opportunistically during this study gravid females occupy a niche that is different from the continental shelf population. The release of young and their early development apparently occur in oceanic areas. Little is known of this important period in their life history.

SUMMARY

Males

The internal anatomy of the male blue shark is similar to other carcharhinids. The vas deferens is enlarged and convoluted for the storage of sperm and spermatophores. The clasper lacks a spur and resembles that of the basking shark and tope. Juvenile and small mature males 4 and 5 yr old (153-180 cm) are the most commonly encountered size group on the continental shelf off southern New England from June to October. Male blue sharks reach maturity at 180 cm and probably copulate frequently through the summer. Only about 2% of all males caught have claspers swollen and discolored by mating.

Females

The internal anatomy of the female blue shark is similar to other species of placentally viviparous carcharhinids. The single right ovary delivers ova up to 20 mm in diameter to paired oviducts. They are fertilized as they pass through the oviducal gland by stored spermatozoa and develop in paired uteri.

Female blue sharks can be grouped into immature, subadult, and adult categories based on size, behavior, and development.

1. Immature females range from 46 cm (birth) to a maximum of 145 cm long. The ovary is small with many undeveloped follicles. The oviducal gland and uterus are undifferentiated from the oviduct. The vagina is sealed by a membrane which may persist to a fork length of 135 cm.
2. Subadult females range from 145 to 185 cm long and possess differentiated though not completely functional reproductive organs. The ovary contains follicles between 2 and 6 mm. Externally, the oviducal gland is heart shaped and roughly twice the diameter of the oviduct. The uterus is differentiated from the oviduct but not >2 cm in diameter and never contains embryos. The skin begins to thicken to receive the courtship wounds of the males. There are several reasons for considering these females as a separate group. Fish in this condition are the most common group of females on the continental shelf from Hudson

Canyon to Georges Bank. They are sexually active with obvious external mating wounds on every individual in shelf waters. The presence of male spermatozoa in the oviducal gland indicates that a large proportion have successfully copulated. Subadults were found inseminated at a minimum size of 135 cm. They bear abrasive scarring on the lateral walls of the vagina in fish as small as 158 cm.

3. Mature females range from 185 to >300 cm long. They possess fully differentiated organ systems that are actively developing eggs, embryos, or both. The ovary is robust with over 100 ova from 16 to 21 mm in diameter and hundreds of smaller follicles. The oviducal gland is large and heart-shaped with the anterior horns slightly coiled. The uterus when empty is long and flaccid. Skin thickness is increased to over twice that of similar-sized males. Recent internal and external mating wounds are usually not present on mature females. Old healed scars are often present on fins and body.

Spermatozoa Storage

Both sexes store spermatozoa. It is first stored in the epididymis of the male in a matrix of supportive tissue, then as spermatophores in the lower ductus deferens. After copulation, spermatozoa is stored as clusters of individuals in tubes of the oviducal gland of the female. Histological sections of oviducal glands from a full size range of 160 females revealed spermatozoa stored in 79.

Sexual Cycle

Four- and five-year-old female blue sharks arrive on the continental shelf off southern New England in late May and early June. Here they sexually interact with males, receiving tooth cuts. The 5 yr olds and some 4 yr olds copulate with males of 180 cm (6 yr olds) and larger. The 4-yr-old females are too undeveloped to store spermatozoa. Five-year-old females actively mate and retain copious amounts of spermatozoa. The following spring, this age-group, now 6 yr old, remain offshore and fertilize their eggs in May or June. Embryos reach full term in 9-12 mo. Pupping is from April to July with up to 82 young being born. It is probable that the 7-yr-old female again copulates as the oviducal glands of gravid females contain a relatively small amount of spermatozoa. The full complement of ripe ovarian eggs present in every gravid female that I have examined suggests that another fertilization is imminent.

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