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Reproduction of the Bull Shark, *Carcharhinus leucas*, in the Lake Nicaragua-Rio San Juan System

NORMAN H. JENSEN

INTRODUCTION

Carcharhinus leucas, the bull shark, or cub shark, is a member of a large family, the Carcharhinidae, sometimes called requiem sharks. It is of medium size, reaching a maximum of a little more than three meters in some parts of its range, but little more than two and one-half meters in my study area. It is euryhaline, able to live for extended periods of time in both freshwater and marine environments. It is a viviparous shark, retaining the young and nourishing them by means of a yolk-sac placenta.

C. leucas occurs around the world in tropical and semi-tropical waters. Along the west coast of the Americas it is present in coastal waters from Baja California, southward to Ecuador (Kato *et al.*, 1967), and has been known there as the roundnose or pigeye shark, *C. azureus*.

In the western North Atlantic, *C. leucas* occurs from Bermuda and Chesapeake Bay to the West Indies, Gulf of Mexico and Caribbean Sea, and south along the Atlantic Coast of South America to southern Brazil (Bigelow and Schroeder, 1948; Baughman and Springer, 1950; Schwartz, 1959, 1960).

There has been controversy concerning the taxonomy of the shark long known to inhabit Lake Nicaragua. First described by Gill and Bransford (1878), the shark was regarded to be landlocked and for many years was considered (as *C. nicaraguensis*) a species distinct from its counterpart along the Caribbean coast and the mouth of the Río San Juan (*C. leucas*). Bigelow and Schroeder, in their comprehensive work of 1948, treated it as a separate species, although with some reservations. However, in 1961, the same authors wrote that, on the basis of additional evidence, they regarded *C. nicaraguensis* as a synonym of *C. leucas*. This was confirmed by Thorson *et al.* (1966), who presented evidence that the sharks throughout the length of the lake and river, to its mouth, are all the same species. They proposed that the sharks are not landlocked, but are able to move throughout the length of the river between Lake Nicaragua and the Caribbean Sea. This was later demonstrated by a tagging program (Thorson, 1971).

This leads to a number of questions. If sharks move between the sea and the lake, and there is a substantial population of *C. leucas* living in Lake Nicaragua, where do the lake sharks complete their life cycle? Do sharks in the lake stay there, mate, and bear their litters, or are they merely visitors to this habitat, reproducing in some other place?

Marden (1944) stated that "sharks and sawfishes do breed in the lake. Females have been taken who dropped their young at the moment of capture." Carr (1953) also stated that there is no doubt at all about the shark producing young in the lake because those that are caught pregnant sometimes have their pups in the boat after being

landed. McCormick *et al.* (1963) also mentioned this in their popular book, *Shadows in the Sea*.

In opposition to this view, however, are several other investigators who questioned the idea of reproduction taking place in the lake. Herre (1955), referring to sharks and sawfish that enter other fresh water regions (*e.g.*, Philippines, Ganges River, Zambezi River, Amazon River, Borneo and New Guinea), has stated that "The sharks and sawfish mentioned do not breed in fresh water but . . . return to the sea to breed." Herre (1956) again stated ". . . no one has ever presented any proof that sharks breed in Lake Nicaragua." Bigelow and Schroeder (1948), in describing *C. nicaraguensis*, stated that embryos had not been observed. Astorqui (1964, 1967) wrote that it did not appear that pregnant female sharks were captured in the lake. He believed that the young were not born in the lake, but moved there sometime after birth. Springer (1963) reported that bull sharks "regularly enter estuarine waters to give birth to their young."

Those who advocate that birth of the young sharks occurs in the lake have provided no recorded evidence. Furthermore, of those pregnant females caught in the lake, reported to have given birth to young, there is no recorded length of the young. Consequently, there is no way of knowing whether the female was in the lake to drop her full-term young or perhaps had wandered into the lake, was caught, and dropped her young prematurely.

There is little published information about the bull shark, *C. leucas*, in the Lake Nicaragua-Río San Juan System. It is the purpose of this paper to clear up some of the controversy that has prevailed about the reproduction of this shark and to provide information about the life history of *C. leucas* in general and specifically about some of its reproductive characteristics.

RESEARCH AREA

Lake Nicaragua, the largest body of fresh water between South America and the Great Lakes of North America, lies in the Nicaraguan Depression extending in a northwest-southeast axis. It is approximately 160 km long by 65 km at its widest point (Fig. 1). Its level varies normally about 65 cm between the dry and rainy seasons, but two or three m between extremes. Its physical and limnological characteristics are discussed in detail by Incer (1976) and by Cole (1976).

The Río San Juan extends from San Carlos, 190 km to its outlet at San Juan del Norte (Incer, 1976) and several km less at the Río Colorado outlet. It drops some 31 meters from the lake to the sea, mostly at a series of rapids in the upper part of the river. The turbidity of the water is high

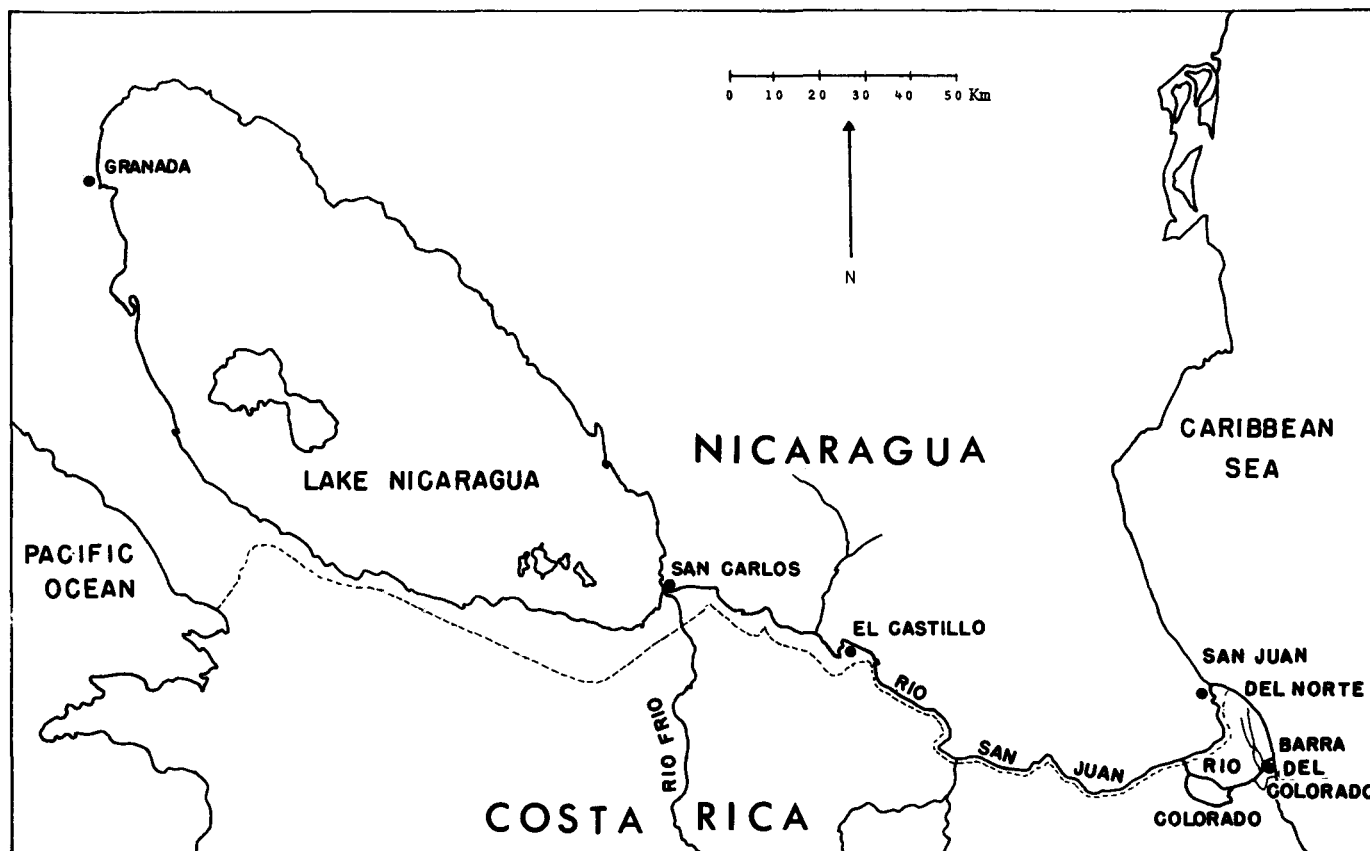


FIG. 1. Map of Lake Nicaragua-Río San Juan system.

and visibility is limited, but these vary with the amount and recency of rainfall. Temperature of the water at San Carlos in July is 25–28°C and there is 5–7 mg/l dissolved oxygen. At Barra del Colorado temperature is about 28°C and dissolved oxygen also 5–7 mg/l. At the mouth, the river water fans out to form a shelf over the clearer, denser sea water. This fan of turbid water is clearly visible from the air, extending a kilometer or more out to sea, and is carried down the coast by the prevailing current.

The main collecting site was the vicinity of Barra del Colorado, Costa Rica, a village located at the mouth of the Río Colorado. The banks and sandbars at the mouth of this river are in constant change and any description quickly becomes obsolete. Most of the fishing was done in the rivermouth or just inside. However, more limited fishing took place at many points in the system of freshwater channels near the mouth, especially Laguna Agua Dulce and Laguna Samay (Fig. 2). Limited collecting was also done at San Juan del Norte, Nicaragua, near the mouth of the Río San Juan proper. Sharks from the sea can gain access to the lake by entering any of the several outlets: Laguna Samay, Río Colorado or Río San Juan, as well as certain others during flooding.

A second major fishing site was El Castillo, Nicaragua, a village about two-thirds of the way up the river. This is the site of the strongest of the rapids, below which the sharks tend to accumulate, and the only place along the river where enough fishermen could be found to warrant fishing for the sharks.

The third major site was at San Carlos, Nicaragua, located on the Río San Juan at the point where it leaves Lake

Nicaragua. Fishing here was carried out primarily in the outlet from the lake.

MATERIAL AND METHODS

This study was carried on in conjunction with a five-year tagging program conducted on the bull shark, *Carcharhinus leucas* in the Lake Nicaragua-Río San Juan System. The data were obtained in the summers of 1967 through 1970, short periods in November, 1967, and April, 1969, and from information supplied by fishermen during one entire year of shark fishing in 1969–1970.

Fishermen of the various communities captured the sharks, for which they were paid. Fishing could not be directed, since each fisherman preferred to fish where he thought the sharks would be biting best on a particular day. The fishing pressure was, therefore, high in certain places and almost nil in others, but it varied from day to day. Occasionally, during times of calm seas, fishing was done outside the bar mouth, but still essentially in fresh water.

The type of gear used varied, but was primarily handlines. Barbed hooks, ranging from two and one-half to about eight centimeters from tip to shank were baited with fresh meat from a variety of fish, turtle, caiman and other animals (see Tuma, 1976).

Fishing was most commonly done from dugout canoes that were anchored and the baited handlines then thrown out. When a shark was caught, it was brought to shore where it was tagged or used for other studies. In some places, such as El Castillo and along the coast at San Juan del Norte, handlines were used from shore. On occasion, a

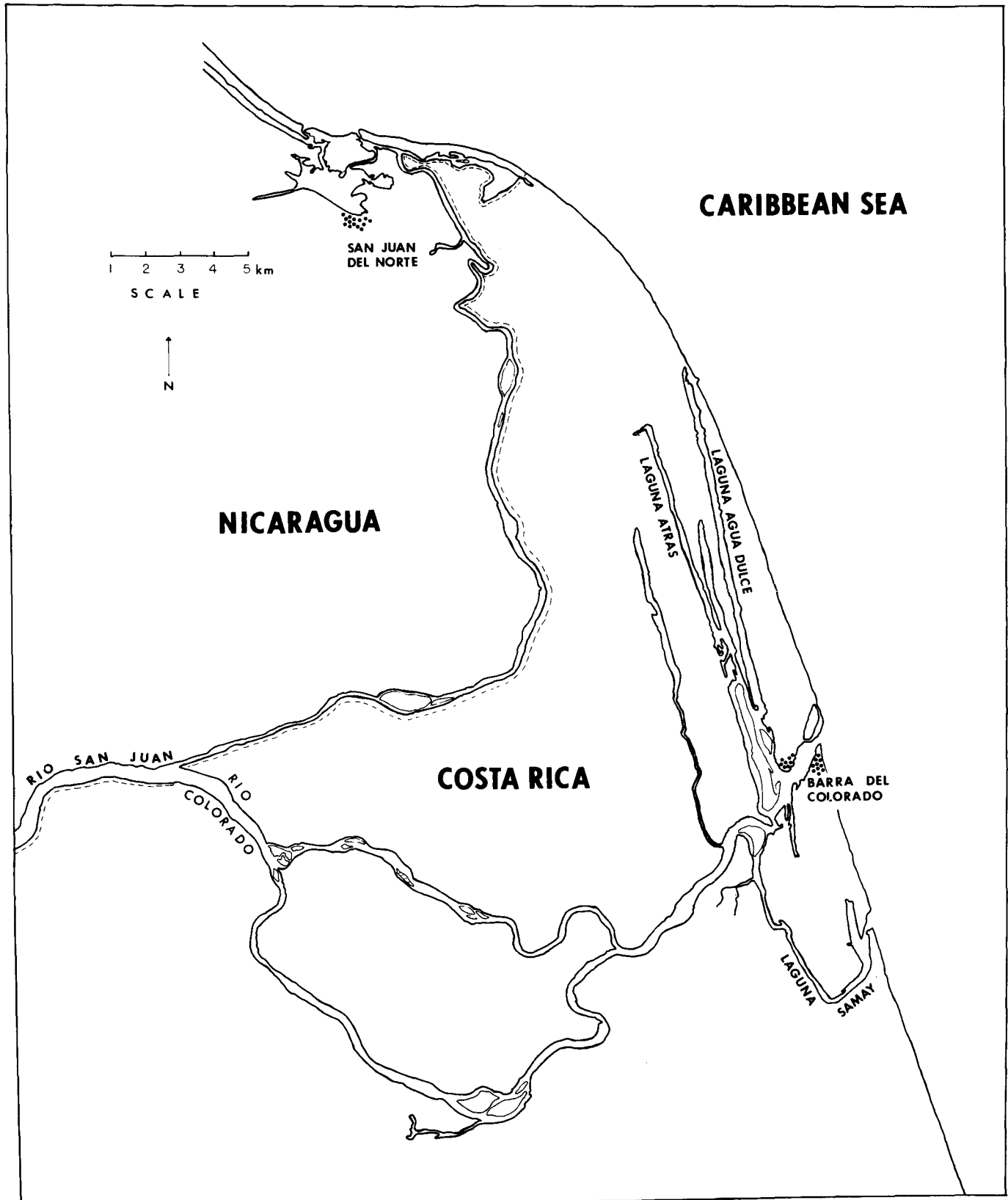


FIG. 2. Map of coastal research area.

seine was used to capture young in shallow parts of the river or other channels near Barra del Colorado, but this method did not prove very effective.

Sharks to be used in this study were selected from those brought in for possible tagging. Some of all sizes were kept for study, but primarily those that were mature or close to maturity. Females were observed for external signs of pregnancy and mating. Internally, they were examined for possible pregnancy, and condition of the ovary, nidamental gland, oviducts (uteri) and liver. Males were examined internally and externally for the condition of the testes, possible inflammation around claspers, indicating mating, and clasper lengths. Total body length was taken with a metric tape with the tail held in a "normal" position. This presented some difficulty, as was also reported by Sadowsky (1968). The weight was determined by placing the shark in a canvas sling hoisted on a 200 or 500 lb spring scale.

When pregnant females were captured, the young were removed, the total number and sex in each uterus noted, and about 45 measurements were made from each of a number of litters.

Some reproductive structures were preserved, usually in 10% formalin, but some in Bouin's solution. The preserved specimens were brought back to the University of Nebraska at Lincoln, where they could be examined in more detail.

RESULTS AND DISCUSSION

Female Reproductive System

The study of the female reproductive system is based mainly on the 66 females listed in Table 1. Some additional information is also presented in the discussion about non-pregnant sharks that are not included in this table.

Size at sexual maturity

Sexual maturity in the females was determined on the basis of size plus the state of the reproductive organs. Examination was made for developing eggs in the ovary, increase in diameter of the oviducts and increase in liver size.

This population of *C. leucas* was still definitely immature at 145 cm, having at that size no ovarian eggs developing (Fig. 3), oviducts of only several mm diameter and a liver of normal size. However, a female of 169 cm was found to have large ovarian eggs, enlarged oviducts and a large liver; and a 171 cm female taken at San Juan del Norte had three eggs that had descended to the uteri (Thorson, unpublished). Also, a female of 181 cm (No. 70-3, Table 1) was found to have placental scars, indicating previous births. The total length of the 59 pregnant females for which that measurement was made ranged from 175 to 235 cm, averaging 201 cm.

Females are approaching sexual maturity at approximately 160 to 170 cm in total length and ovulation commences at about 170 cm.

In the population of Florida *C. leucas* studied by Clark and von Schmidt (1965), the smallest female captured which was carrying young or had large ovarian eggs was 233 cm in total length. The largest was 257 cm.

Clark and von Schmidt (1965) reported that the easiest way to determine maturity in a near-adult female which had not carried young was to examine the vaginal opening and hymen. In young females the vaginal opening is small and difficult to see, lying just anterior to the urinary pore. A faint line, representing the hymen, passes anteriorly from the vaginal opening in sub-adult females. In mature virgins, the hymen was delicate and could be ruptured with a probe.

Ovaries

C. leucas has only a right functional ovary. The left ovary is either completely absent or so rudimentary as not to be seen. The right ovary is found imbedded in the anterior end of the right epigonal organ. The epigonal organs are considered hemopoietic structures by Matthews (1950) and Chieffi (1967). The right ovary extends as far forward as the base of the liver. The right epigonal organ extends forward under the ovary to form its ventral surface, and the ovary and its developing ova can only be seen from the dorsal surface. Both the ovary and the epigonal organ are suspended from the midline by a common mesentery. The left epigonal organ extends forward only to the level of the posterior end of the functional ovary. There are a large number of fibrous bands, criss-crossing in a meshwork with no apparent pattern on the dorsal surface of the ovary. Matthews (1950) noted that this pattern is also present in the basking shark, *Cetorhinus maximus*. This meshwork is noticeable in immature as well as maturing ovaries. During the development of the egg, these bands are pushed aside as the enlarging egg protrudes more and more from the dorsal surface. Stretching between the bands and covering each ovum is an encapsulating membrane which serves to maintain the ovum in the ovary until the time of ovulation.

In the center of this encapsulating membrane on a maturing ovum, a small opening of 4-5 mm was observed (Fig. 4). This opening was seen only when the membrane was moved. It was first observed on a shark that was ovulating and in which some of the eggs were already present in the uterus. It is speculated that this is the site through which the ovum escapes from the ovary at ovulation. Gudger (1940) has described a similar membrane covering a ripening egg of the frilled shark, *Chlamydoselachus*. He also concluded that the circular area in the membrane was where the follicle would rupture and release the egg into the coelomic cavity.

In a 145 cm female, the right ovary was widened at the anterior end but was still immature and contained no developing eggs (Fig. 3).

The number of eggs that enlarge prior to ovulation is approximately 15-22. Of these, 10 or fewer are ordinarily released into the coelomic cavity during ovulation. Those that are not released are retained in the ovary and undergo a slow reabsorption.

The eggs vary in size depending on the stage of the female's reproductive cycle. The smallest were seen in females just starting to mature and in females that were pregnant but very near term. The diameter of those eggs is 1-2 mm. Those that mature reach a diameter of approximately 4 to 5 cm before ovulation. During growth the eggs remain round.

Also visible on the dorsal surface of the ovary near ovulation are large numbers of small oocytes which tend to give the ovary a roughened appearance (Chieffi, 1967).

In *Cetorhinus maximus* the left ovary is also absent or so rudimentary that no trace can be found (Matthews, 1950). *Carcharhinus falciformis*, the silky shark, has only a right functional ovary (Gilbert and Schlernitzauer, 1966), as has *C. dussumieri* (Teshima and Mizue, 1972). Clark and von Schmidt (1965) found that the lemon shark, *Negaprion brevirostris*, has only a right functional ovary. However, they observed an underdeveloped left ovary that contained eggs more than 9 mm in diameter. In their observations of *C. leucas*, the largest eggs they found in the ovary were 25-32 mm in diameter. Springer (1960) found only one functional

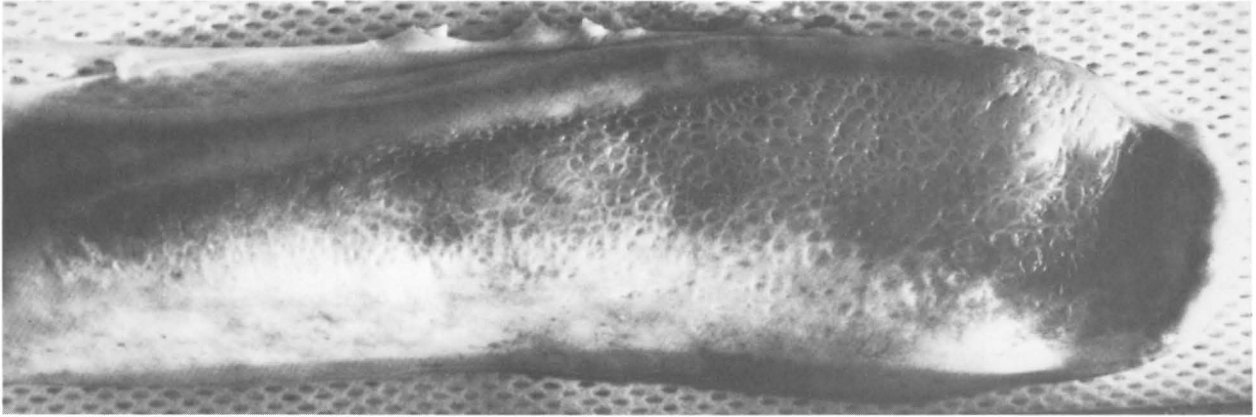


FIG. 3. Immature ovary from 145 cm female. Note meshwork of fibrous bands indicating ovary. Epigonal tissue is visible around borders of ovary.

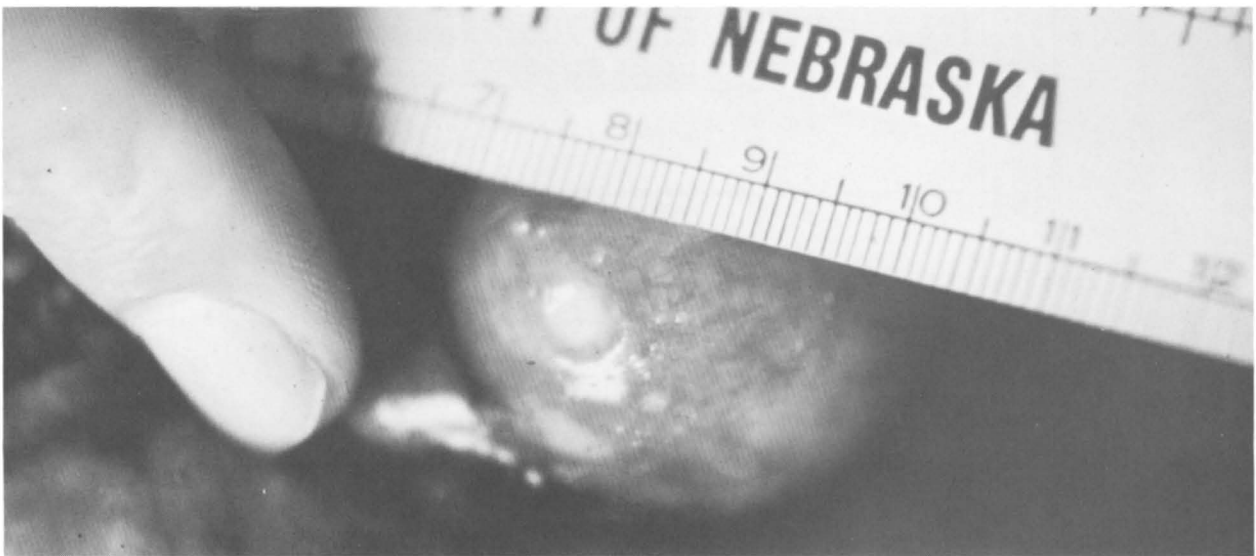


FIG. 4. Encapsulating membrane on maturing ovum. Note small opening through which the ovum will pass at ovulation.

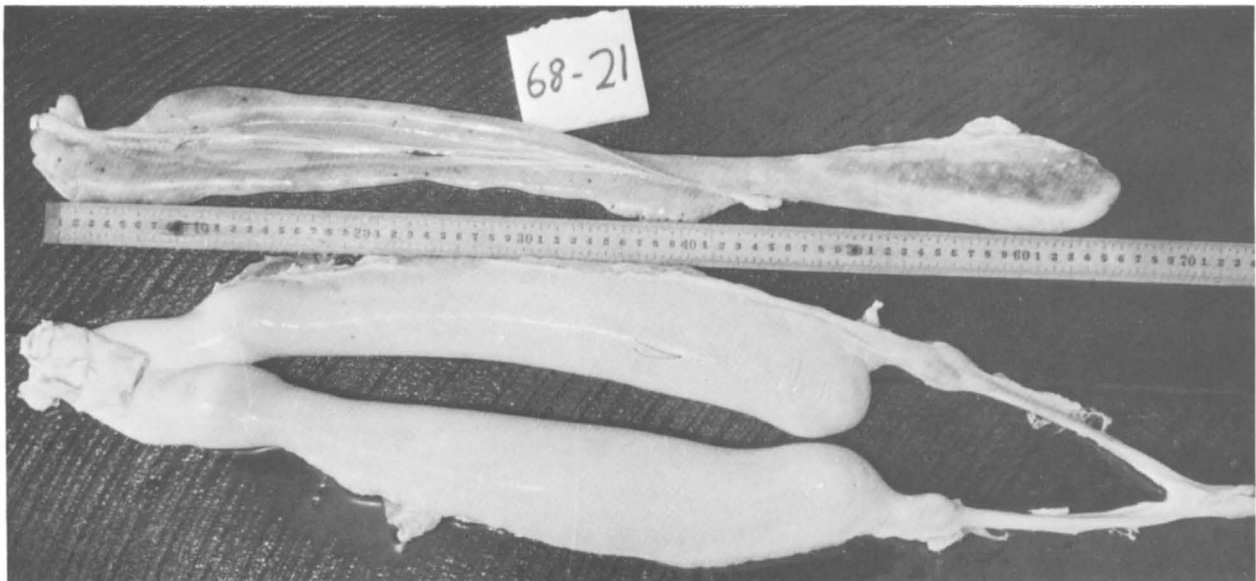


FIG. 5. Post-pregnant reproductive tract and ovary. The functional right ovary is imbedded in the anterior (right) end of the elongated right epigonal organ as seen above the meter stick. Below, the common oviduct is seen at the far right. The enlarged region of each oviduct is the uterus.

TABLE 1. Reproduction data on 66 mature females

Date caught	Shark number	Length (cm)	Number embryos in uterus		Total number embryos	Number of males	Number of females	Size range of embryos (mm)	Remarks
			left	right					
26 Nov. 67	67-46	190	3	2	5	—	—	235	One measured
27 Nov. 67	67-47	177	—	—	—	—	—	—	Ovarian eggs 2-3 cm in diam.
27 Nov. 67	67-48	193	2	4	6	4	2	—	Not measured
27 Nov. 67	67-49	199	3	4	7	5	2	401-418	
28 Nov. 67	67-51	193	3	2	5	3	2	—	Not measured
18 June 68	68-8	224	5	5	10	6	4	659-711	
24 June 68	68-24	227	4	4	8	2	6	625-745	
24 June 68	68-25	192	3	3	6	4	2	651-674	
25 June 68	68-28	—	2	2	4	1	3	651-680	
25 June 68	68-29	196	3	2	5	4	1	683-712	
26 June 68	68-30	218	4	3	7	3	4	659-699	
26 June 68	68-31	208	2	2	4	4	0	630-661	
28 June 68	68-39	182	2	2	4	3	1	217-234	
30 June 68	68-42	211	3	3	6	4	2	630-690	
1 July 68	68-43	211	4	4	8	5	3	620-60	
7 July 68	68-44	212	4	3	7	2	5	605-655	One "runt" of 460 mm
7 July 68	68-46	201	2	1	3	1	2	360-397	
8 July 68	68-50	192	3	2	5	2	3	287-309	
8 July 68	68-51	208	5	5	10	—	—	640-720	
9 July 68	68-52	222	4	5	9	8	1	630-680	
9 July 68	68-54	178	3	2	5	2	3	199-217	
9 July 68	68-55	175	2	1	3	—	—	—	
10 July 68	68-56	192	2	0	2	—	—	—	Dead in uterus
11 July 68	68-58	191	1	2	3	2	1	439-465	
11 July 68	68-59	197	1	0	1	—	—	685	Had very recently given birth to others
21 July 68	68-64	196	4	4	8	—	—	30-40	
24 July 68	68-65	190	1	1	2	—	—	—	Embryos not measured. Ovary had six 4 x 5 cm ova
3 Aug. 68	68-70	210	1	—	1	—	—	—	Only membranes, nonviable eggs and malformed embryos found
5 Aug. 68	68-72	220	4	2	6	2	4	630-665	
8 Aug. 68	68-80	201	3	3	6	4	2	645-675	
8 Aug. 68	68-87	235	4	4	8	5	3	655-710	
1 July 68	68-100	200	5	5	10	6	4	510-580	Caught at El Castillo
8 Aug. 68	68-103	180	—	—	1	—	—	215	Two unfertilized eggs also present
5 Apr. 69	69-2a	221	2	2	4	2	2	605-670	

3 Apr. 69	69-1a	207	2	2	4	-	-	-	No young, but placental scars
6 Apr. 69	69-3a	188	3	2	5	-	-	-	No young, but placental scars
6 Apr. 69	69-4a	179	1	-	1	-	-	-	Two abnormal eggs; one normal egg with blastoderm
7 Apr. 69	69-5a	207	3	3	6	3	3	540-599	
8 Apr. 69	69-6a	200	4	4	8	-	-	-	No young, but placental scars
9 Apr. 69	69-7a	219	3	3	6	5	1	619-657	
9 Apr. 69	69-8a	205	5	4	9	3	6	559-615	
10 Apr. 69	69-10a	193	2	3	5	3	2	565-596	
13 Apr. 69	69-G7	208	4	4	8	3	5	534-592	Preserved
12 Apr. 69	69-G8	182	3	2	5	3	2	567-603	Preserved
13 Apr. 69	69-G6	206	3	3	6	2	4	552-586	Preserved
12 Apr. 69	69-G5	201	2	3	5	4	1	600-614	Preserved
28 Apr. 69	69-G4	208	3	3	6	3	3	153-169	Preserved
19 June 69	69-G3	-	-	-	2	0	2	558-580	Preserved
21 June 69	69-G2	-	4	4	8	4	4	578-626	Preserved
27 June 69	69-G1	208	1	2	3	1	2	157-165	
28 June 69	69-G0	-	-	-	8	-	-	-	Not measured or preserved
28 June 69	69-1	-	2	4	6	3	3	601-644	
12 July 69	69-5	177	3	3	6	-	-	-	Eggs in blastoderm stage
28 July 69	69-6	214	2	2	4	3	1	360-400	Two abnormal embryos
								631-655	Two normal embryos
28 July 69	69-7	207	5	5	10	6	3	650-685	One abnormal (not sexed)
31 July 69	69-10	199	3	4	7	1	3	607-630	Three abnormal pups (not sexed)
8 Aug. 69	69-15	190	-	-	2	1	1	358	Female—normal
								291	Male—abnormal
15 Aug. 69	69-17	207	3	4	7	-	-	50-60	Could not be sexed
19 Aug. 69	69-19	-	3	2	5	-	-	49-54	Could not be sexed
27 June 70	70-2	198	2	2	4	-	-	-	Blastoderm stage
29 June 70	70-3	181	4	2	6	-	-	-	No young, but placental scars
29 June 70	70-5	204	2	1	3	-	-	-	Young not measured—near term
9 July 70	70-6	207	-	-	5	2	3	600-660	
3 Aug. 70	70-7	214	2	2	4	-	-	100-200	
4 Aug. 70	70-8	-	2	3	5	-	-	660-690	
4 Aug. 70	70-9	-	-	-	5	-	-	150-200	
Total			175	164	355	138	117		
N		59	60	60	66	43	43		
Mean		201	2.9	2.7	5.4	3.2	2.7		

ovary in the sandbar shark, *C. milberti*, but did not indicate right or left. He stated that the eggs attain a diameter of 1–1¼ inches (2.5–3.0 cm) and are spherical.

Mustelus canis (smooth dogfish) has only a right functional ovary. The left is represented by a strip of tissue that TeWinkel (1950) stated may be glandular. She also stated that the right ovary contained between 12 and 24 large ova that were ready for ovulation in late June.

The spiny dogfish, *Squalus acanthias*, has two functional ovaries. Hisaw and Albert (1947) indicated that the total number of eggs that reach the ovulatory stage is 8 or 9 and that they are not always divided equally between the right and left ovary. At maturity these eggs weigh approximately 50 grams each and are about 3 cm in diameter.

Babel (1967) in his study of the round stingray, *Urolophus halleri*, found that the right ovary had atrophied and the left was functional. Thorson (unpublished) has also observed that a stingray, *Dasyatis guttata*, taken near Barra del Colorado had a small and non-functional right ovary. The left ovary was larger and contained four eggs about 2.5 cm in diameter and about 20 ranging from 0.5 to 1.2 cm in diameter. We have observed that the sawfish, *Pristis perotteti*, has two functional ovaries, of approximately equal size.

Ostium and common oviduct

Ovulation from the right ovary of *C. leucas* occurs into the abdominal cavity. The ova pass through a common opening or ostium, a slit in the ventral margin of the falciform ligament. This ostium opens from the abdominal cavity to a common oviduct. This tube, from 5 to 10 cm in length, passes dorsally in the falciform ligament and divides into the right and left oviducts. (Fig. 5).

Just how the eggs reach the ostium after ovulation is not known. No eggs were found in the abdominal cavity of *C. leucas*. It has been suggested that movement of the eggs may be by ciliary action. Metten (1939) followed the movement of ovulated eggs in an anesthetized female *Scyliorhinus canicula* (lesser spotted dogfish) and found cilia on the anterior peritoneal walls, the liver, and outer surface of the oviducts. The cilia were seen to beat in the direction of the ostium, carrying the eggs toward it. It is probable that cilia are present in *C. leucas*, although none were observed.

Oviducts

Both the right and left oviducts are functional in *C. leucas*, and each receives about an equal number of eggs. From the division of the common oviduct, the right and left portions pass laterally and posteriorly in the coelomic cavity to the nidamental or shell glands. The distance from the division of the oviduct to the shell gland is about 15 cm in a mature female and the diameter of the oviduct is about 5–10 mm. The 2 oviducts then extend posteriorly to the cloacal region where each forms a vagina and the two tracts open individually into the cloaca.

The oviducts extend posteriorly alongside the vertebral column and are suspended there by the peritoneum of the abdominal cavity.

The appearance of the oviduct varies with the age of the female and the stage of her reproductive cycle. In immature females, each oviduct is very narrow and of the same diameter throughout its length. When the female reaches sexual maturity the posterior two-thirds of the oviducts are modified to form the uteri which are very elastic and undergo much change in their shape before, during and after pregnancy. Prior to sexual maturity no distinction could be

made in the diameter of the oviducts between the nidamental gland and the portion destined to become the uterus. After sexual maturity, the distance from nidamental gland to uterus was about 5 cm in ovulating and newly pregnant females with swollen reproductive tracts, and about 11 cm in pre-ovulatory and postpregnant females.

Nidamental gland

The nidamental or oviducal gland varies considerably in size depending on the reproductive stage of the female. In the immature female it is nothing more than a slight bulge in the oviduct. Maximum size is reached during the period of ovulation when the eggs are passing through the oviduct to the uterus.

Observations on an ovulating female showed both nidamental glands to be greatly enlarged and of the same size. Each gland is composed of 2 large lateral horns which branch from the posterior portion of the gland region, pass forward along the oviduct for about 6 cm and then curve dorsally and medially (Fig. 6). This gives the gland a heart-shaped appearance. The width, as well as the height, of the gland is approximately 6 cm. The length of the curved lateral horns is about 9–10 cm and their diameter about 2.5 cm. Each of the horns is divided along its lateral margin by a groove about 8 mm deep that extends for the entire length (Fig. 7). It is continuous with the lumen of the oviduct. The groove is enclosed by a membrane that is ridged along the groove and continuous around the entire horn.

The nidamental gland is reported to consist of regions which differ in function. These regions were not visually differentiated in *C. leucas* but are probably similar to those found in other elasmobranchs. Prasad (1945) in his description of the nidamental gland of the tiger shark, *Galeocerdo tigrinus* (= *cuvieri*), indicates an anterior region of the gland which secretes albumen around the yolk mass. Posterior to this is a shell-secreting region. As the egg mass passes through the gland, the albumen is first secreted around the yolk and then a thin, greenish diaphanous membrane or shell case is produced which surrounds the egg. This shell case is twisted throughout its length. TeWinkel (1950) suggested that the twisting is due to the rotation of the egg as it passes through the nidamental gland and possibly in the uterus also. The shell case is also rolled or folded upon itself and widens at one end where it surrounds the egg. It is very long, measuring about 120 cm in *C. leucas*. The shell case is able to undergo great expansion. It continues to cover the developing shark throughout the entire period of gestation, and is broken only at the time of parturition, allowing the young shark to swim free.

Price and Daiber (1967) indicated that the egg case plays a role in maintaining the necessary composition of the microenvironment of the embryo in ovoviviparous and viviparous species. Matthews (1950), who studied reproduction in the basking shark, *Cetorhinus maximus*, stated that the nidamental gland of that shark probably functions only in the secretion of albumen and that if any shell is produced, it is nothing more than a membranous sac.

Borcea (1904) believed that the stimulus normally causing secretion from the shell gland was the ovum, but he also indicated that there could be other stimuli involved. Metten (1939) has presented evidence, however, which indicates that the descending ovum is not the stimulus that causes the egg case to be formed. He found the egg case to be already more than half secreted in female *Squalus acanthias* when

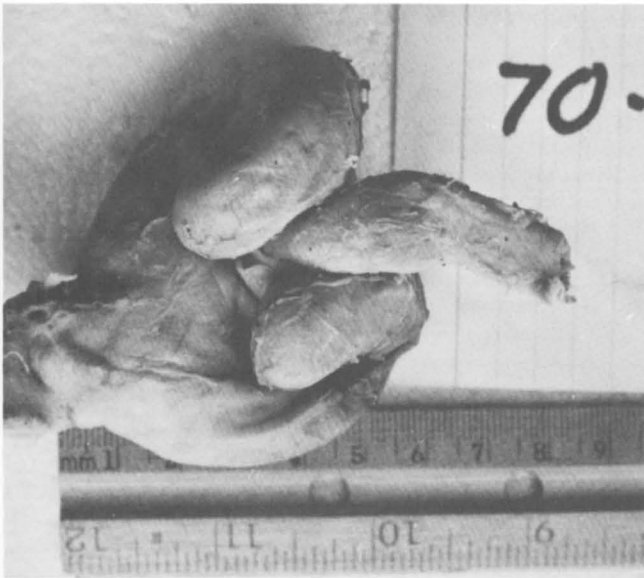


FIG. 6. Nidamental gland of an ovulating female (preserved). Note the enlarged and curved lateral horns. The cut end at the right is part of the oviduct anterior to the gland.

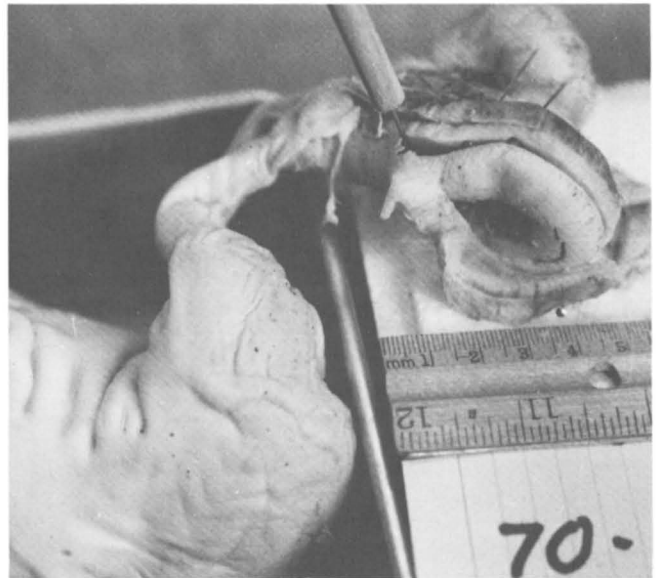


FIG. 7. Nidamental gland with outer membrane removed (preserved). Note the groove extending the length of the lateral horn which is the glandular region producing the shell membrane.



FIG. 8. Pre-pregnant uterus (preserved). Internal lining of uterus is seen with ridges running longitudinally.

the ovum was migrating in the coelom or upper oviduct. TeWinkel (1950) thought that the nidamental glands are controlled by endocrines. She stated "... that ovarian hormones, present at the time of ovulation or slightly preceding it, stimulate the secretion of a single egg-case by each oviducal gland irrespective of the number of ova discharged."

Another function of this gland may be that of a sperm receptacle. No sperm were observed in the nidamental gland of *C. leucas* but this does not rule out the possibility. Metten (1939) found that the gland served as a receptacle in *Scyliorhinus*. He found that sperm are present in the tube the year around. Some of the sperm are released with each shell formed as the egg passes down the oviduct, but the major portion of sperm is retained in the gland. Matthews (1950) could find no evidence of sperm in the region of the nidamental gland but also did not rule out the possibility. Prasad (1945) found sperm present in the gland region of the tiger shark, *Galeocerdo cuvieri*.

Gilbert and Schlernitzauer (1966) referred to the gland of *Carcharhinus falciformis* as heart-shaped and indicated that its measurements from its greatest points were 45 mm long and 43 mm wide. This shark, however, contained near-term embryos so the gland was probably much smaller than it would have been during ovulation.

Uterus

Immature state. Before the female *C. leucas* has matured, the oviducts are very slender, showing no indication of the areas of enlargement which will be the uteri. The diameter is less than 5 mm.

Prepregnant uterus. At sexual maturity, the oviducts have enlarged in the region destined to be the uteri. This includes approximately the posterior two-thirds of each oviduct but in actual length it varies with the total length of the female. A female shark at this stage, with ovarian eggs about half the size they would become at ovulation, was found to have a highly ridged internal uterine lining (Fig. 8). The ridges ran in a longitudinal direction and sent out projections that interdigitated with projections of the ridges on either side. The outside diameter of the uterus at this stage was 4 to 5 cm and the internal ridges were approximately 1 cm in height. The entire wall of the uterus was thick and spongy but not yet very vascular.

Pregnant uterus.

Pre-compartmental stage. The earliest pregnant stage seen was in a 198 cm female in the process of ovulation (Table 1, 70-2). The ovary contained 1 large egg as well as several large bloody regions which had held eggs. The left uterus was opened and examined. The wall, approximately 5 to 8 mm thick, lacked the numerous ridges seen in the previous stage. The internal surface was very vascular and smooth (Fig. 9). Two viable eggs with developing blastoderms were present in the uterus but no compartments had as yet begun to form.

Early compartmental stage. A female shark of 177 cm (Table 1, 69-5) was found to contain three eggs in each uterus. The uteri were somewhat firmer than in the previously described stage, but the uterine wall was of about the same thickness. Internally, the eggs, which were in the blastoderm stage, were separated into compartments by large flaps that had grown inward between the eggs from the dorso-lateral and ventro-medial walls (Fig. 10). The surface lining of the flaps separating the eggs was very smooth.

Each egg was surrounded by the greenish shell membrane but most of each membrane was outside of its respective egg compartment. The compartments were not completely closed as the flaps were not yet fused. The shell membrane left the egg compartment through a groove between the flaps and was found coiled up in 1 or 2 small compartments of the uterine wall. There seemed to be no pattern to the distribution of the membrane compartments other than that they were, in most cases, anterior to their respective egg compartments.

The egg in the posteriormost compartment of the uterus was separated from the posterior opening by a membrane which had grown in from the ventral and dorsal walls of the uterus but had not as yet completely closed the opening. The part of the oviduct posterior to this membrane, the vagina, was thick-walled, had a narrow lumen, and still retained the internal, longitudinal ridges.

In a second female with slightly more advanced embryos (Table 1, 68-64) the uterus was of about the same thickness as in the preceding one and its wall was very spongy. Two eggs were present, with embryos about 3 to 4 cm long, which exhibited a swimming motion on the surface of the egg. These eggs were contained in compartments almost identical in development to those previously described. The flaps had not yet fused and the long end of the greenish shell membrane left the egg compartment through the grooves between the developing flaps. The right uterus contained two shell membranes that did not surround eggs. These membranes were found bunched up in small spaces of the inner uterine wall between egg compartments (Fig. 11). A shell membrane was found in the posteriormost region of the uterus. Again, the posteriormost compartment was still incompletely closed off at the opening leading to the vagina.

Later compartmental stage. The next stage in the uterine development was seen in a 190 cm shark (Table 1, 67-46). The uterus examined contained 3 embryos and one egg which had not developed. One of the embryos was malformed and had no placental connection. The other 2 embryos were normal and one measured 23.5 cm in total length.

The undeveloped egg was in the posteriormost compartment with the flaps formed as previously described. The shell membrane was largely outside the compartment as in other stages described.

The abnormal embryo was in a compartment only slightly more advanced than those holding only eggs. No fusion of the flaps had occurred and no placental attachment had formed. No yolk was seen in the compartment. This embryo was about 10 cm in total length. The compartment was just anterior to the compartment containing the undeveloped egg.

The normally developing embryos were each contained in an almost completely closed compartment. A firmly established placenta with a well formed umbilical cord was present. A well-developed circulation had also spread out in an arborescent fashion over the placenta. There was no sign of yolk remaining. These young appeared to have their placental connections at the posterior and ventral region of their respective compartments. The shell membrane was still partially outside its embryo's compartment, but the amount outside was greatly reduced because much of it had by this time been used in covering the growing embryo. The membrane still passed from the embryo's compartment by way of a small groove that had been left during

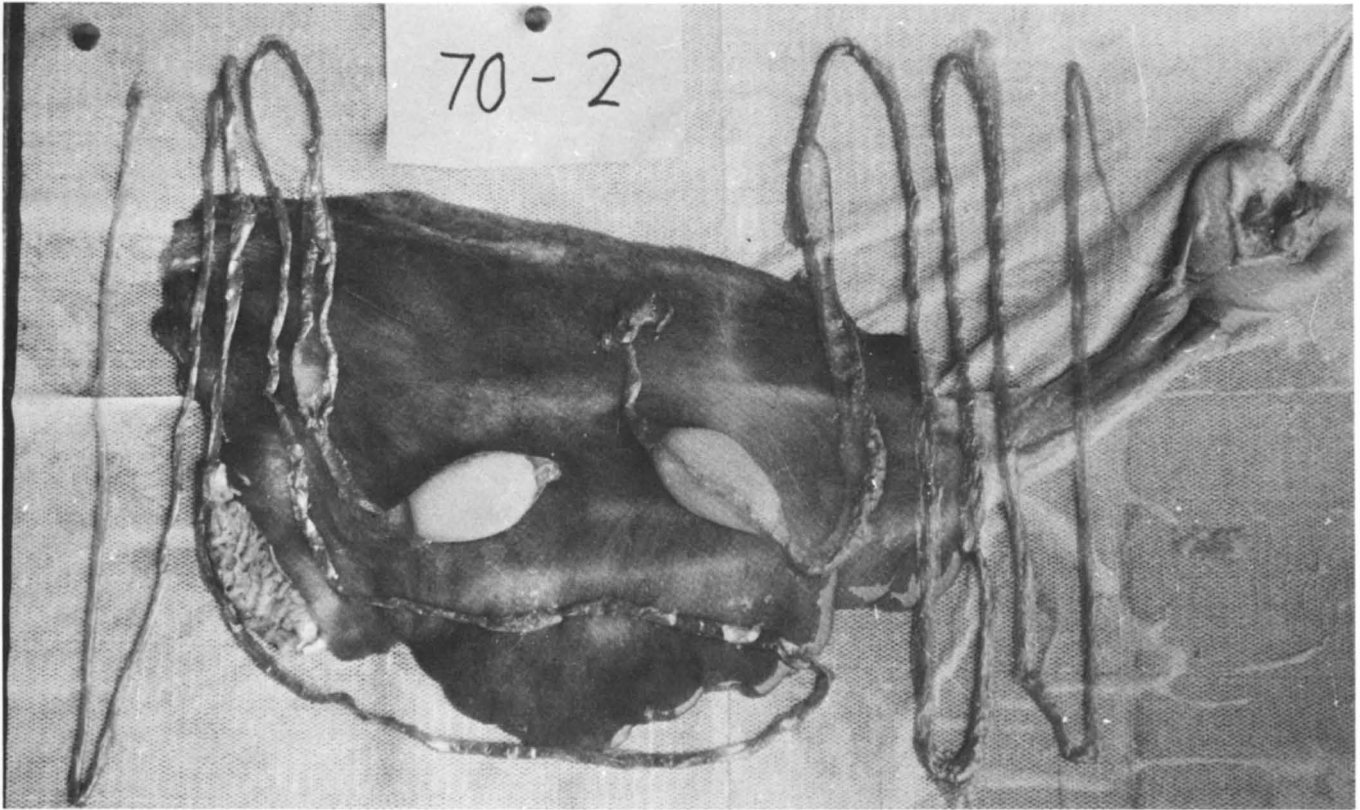


FIG. 9. Early pregnant uterus. Partitions have not yet formed. Internal lining is smooth and vascular. Two eggs were present, each surrounded by the shell membrane. Curved lateral horns of nidamental gland are at the right.



FIG. 10. Early compartmental stage (preserved). Note the partitions which have developed from the uterine wall, dividing the uterus into three compartments. Each compartment contained a viable egg.

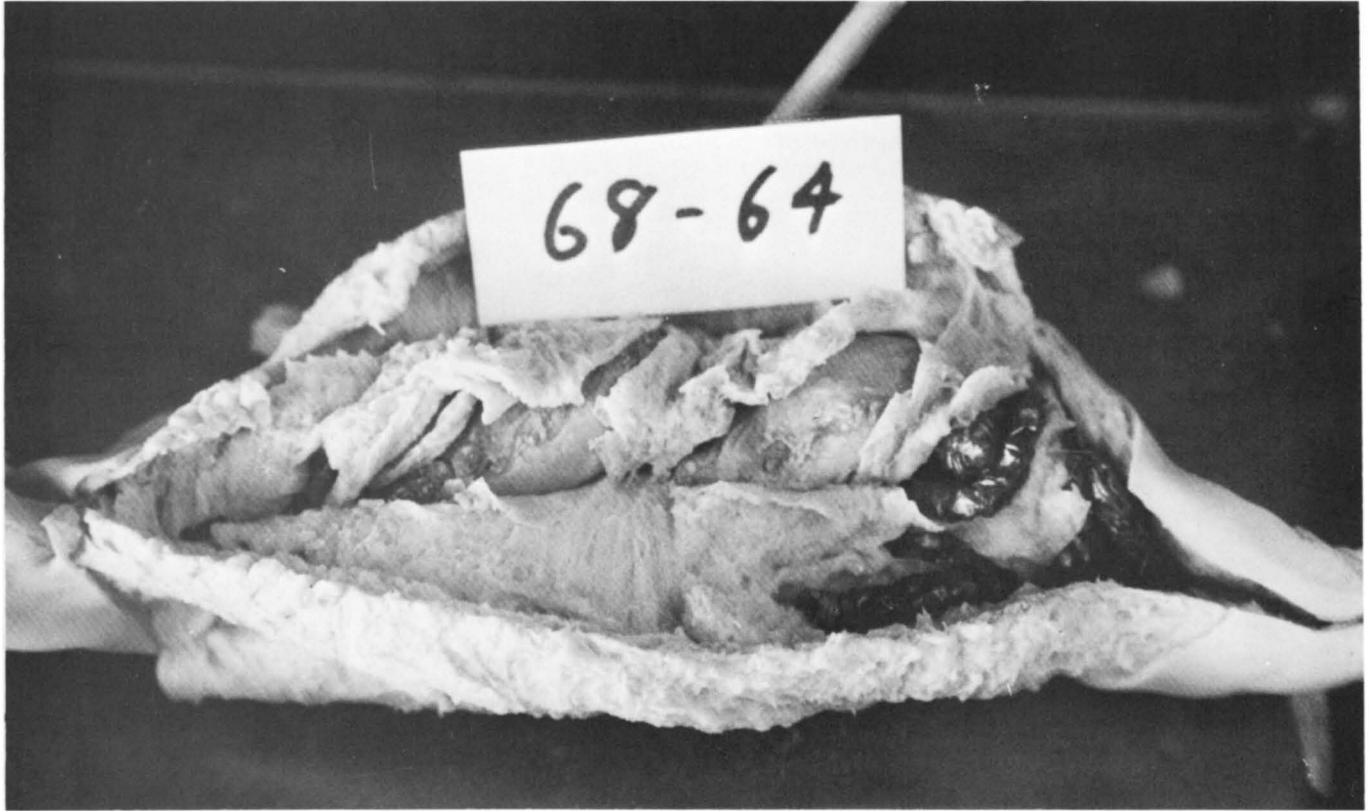


FIG. 11. Early compartmental stage, slightly more advanced than Fig. 10 (preserved). Two eggs are in compartments separated by uterine partitions. The shell membrane (dark material) at right did not enclose an egg.



FIG. 12. Post-pregnant uteri. The roughened, vascular areas indicate the sites where the placental attachments occurred. Each uterus contained four embryos.

fusion of the dorsal and ventral flaps from the uterine wall. The uterine walls were greatly stretched and, therefore, appeared much thinner than in other specimens so far discussed.

The compartments holding the normal embryos had begun to elongate in an anterior-posterior axis. Compartments previous to this stage were more transversely oriented in the uterus.

Term uterus. In most of the near-term uteri, the embryos, between 50 and 75 cm long, were arranged in longitudinal compartments. The uterus must stretch drastically to hold up to 5 or 6 embryos, and during this time its walls become very thin and translucent. It consisted of three layers: an outer, shiny layer, a middle, spongy layer which was very thin, and an inner, membranous tissue lining the compartments. This inner membranous tissue was the outer part of the flaps that had grown inward from the dorsal and ventral walls to form the uterine compartments. The placentae were located in the posteriormost region of the uterine compartments. The maternal portion of each placenta was very vascular and spread out laterally and ventrally along the uterine wall. The greenish shell membrane had been completely drawn into each embryo's compartment due to the growth of the embryos.

Post-pregnant uterus. The post-pregnant uterine condition was seen on a number of occasions. This uterus was slightly more flaccid than a pre-pregnant uterus. It was no longer stretched thin as in a near-term uterus, but had shrunk and was much thicker walled. The outer wall was rough and fibrous, and the middle layer was again very spongy and "watery", while the inner layer was relatively smooth and vascular. The inner lining also showed some very roughened and vascular areas which were the remaining evidence of the placental attachments (Fig. 12). These placental scars were seen on the ventro-lateral and ventro-medial walls of the uterus. No remains of the tissue that had formed the compartment walls could be found. With the growth of the fetuses, the compartmental walls had been stretched so thin that their attachment to the uterine wall probably disappeared before birth or very quickly after birth. Even when the near-term embryos were removed from their compartments the compartmental walls were difficult to find.

Gilbert and Schlernitzauer (1966) reported that the uteri of the silky shark, *Carcharhinus falciformis*, also form one chamber for each embryo. The anteriormost and posteriormost embryos communicate respectively, by way of a lumen, with the anterior regions of the oviduct and with the cloaca. They also reported that the placentae form on the ventral or ventro-lateral wall.

Schlernitzauer and Gilbert (1966) also found in the bonnethead shark, *Sphyrna tiburo*, development of uterine compartments during gestation. These compartments were formed from dorsal and ventral elevations of the inner uterine wall. They reported that the fusion of these does not take place until the embryos are about 125 mm in length. They stated that, preceding ovulation, the uterine wall has longitudinal ridges but that growth obliterates the ridges before the fertilized eggs descend into the uterus. The uterine wall becomes quite spongy but stretches very thin during embryonic development. They also reported that the uterine ridges or folds which separate the compartments probably do not form until the fertilized eggs reach the uterus, but they grow rapidly after this period.

This is in agreement with what we found in the early pregnant uterus of *C. leucas*.

Mahadevan (1940) has reported that in a sharp-nosed shark, *Scoliodon sorrakowah*, the early pregnant uterus was thick-walled, spongy and vascular but that it changed during pregnancy, becoming less spongy and rather semi-transparent. The compartments were formed one behind the other, but as development proceeded the compartments stretched out longitudinally and a transverse section showed several of them running side by side. In histological sections she found the partition walls composed of connective tissue surrounded on both sides by epithelium.

Carcharhinus dussumieri, the Sumitsuki or Malay shark, usually produces only one fetus in each uterus. A placenta forms in the posterior end and the excess shell membrane is stored in, and as the fetus grows, is drawn from, a storage chamber in the anterior portion of each uterus (Teshima and Mizue, 1972).

Placentation

Modified yolk-sac placenta. The embryo first obtains its nourishment from the yolk of the egg. The embryo is attached to the yolk mass by a yolk stalk through which the vitelline blood vessels pass to and from the yolk (Fig. 13). Both embryo and yolk are encased in the shell membrane which is in close contact with them. As the embryo develops, the yolk material is used up and the yolk mass which is covered by a network of vitelline vessels tends to lie in close apposition to the uterine wall. Only the shell membrane separates the yolk sac from the uterine wall, which becomes highly vascular at this location. It was not determined whether the shell membrane breaks down between the two tissues, thus placing fetal and maternal tissues into actual contact, or whether the membrane remains and separates them from direct contact with one another.

The type of placental attachment appears to be much like that described in *Carcharhinus dussumieri* by Mahadevan (1940) and Teshima and Mizue (1972) and in *C. falciformis* described by Gilbert and Schlernitzauer (1966). The latter authors noted that *C. falciformis* has a modified yolk-sac placenta in which the embryo's portion merely rests on a vascular area of the uterine wall. They mention that it could be possible that in an earlier stage, interdigitation might occur between the embryonic and maternal parts of the placenta. They examined only the right uterus of one female.

Schlernitzauer and Gilbert (1966) stated that the connection between embryo and maternal tissue in *Sphyrna tiburo* is formed by convolutions in both the yolk-sac and uterine lining which interdigitate to form the placenta. Embryos of 180 mm had developed placentae that were impossible to separate.

Mahadevan (1940) described a placental attachment present in *C. dussumieri* as "a fairly large arborescent structure . . . formed by the continued subdivision of the distal extremity of the placental cord and the remains of the yolk-sac. This is in close connection with a flat, highly vascular portion of the maternal uterine wall." In our observations of *C. leucas*, there was much the same arborescent structure resting on a highly vascularized portion of the uterine wall. No histological sections were made. Gilbert and Schlernitzauer (1966) suggested that this arrangement would allow the fetal portion to slip or move on the larger maternal portion but that physiological exchanges could continue. We doubt that this movement occurs in *C. leucas* unless it might be at an early stage of placental development.

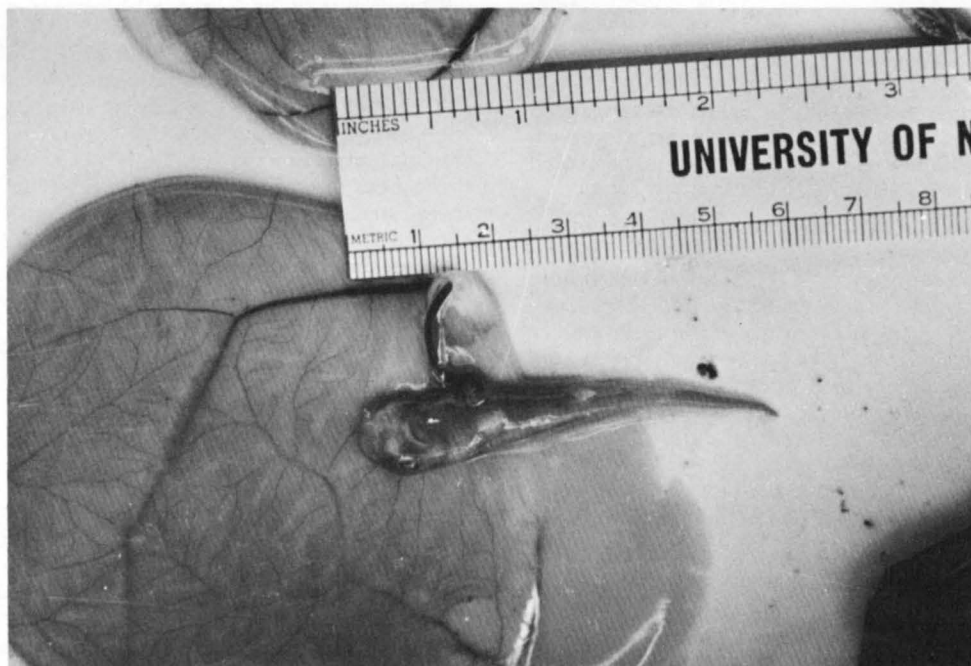


FIG. 13. Yolk-stalk of young embryo. Nourishment is derived from the yolk during the early part of gestation.

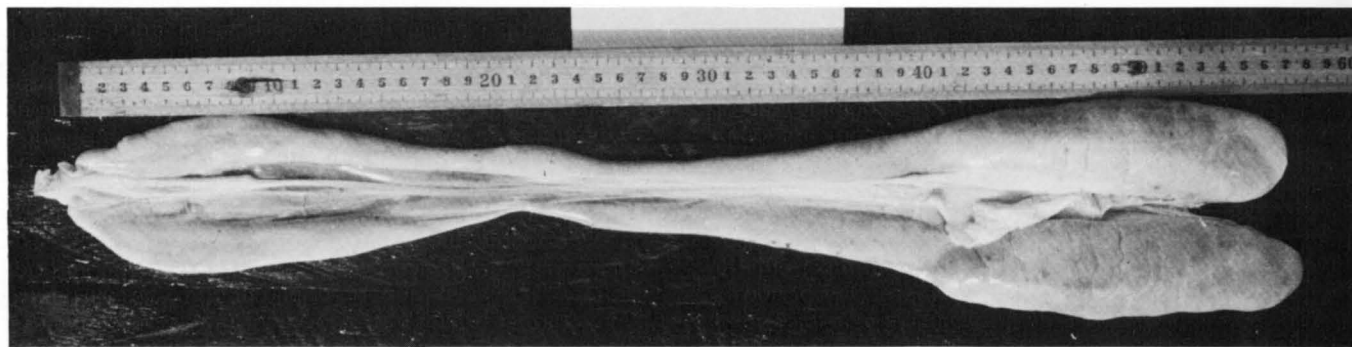


FIG. 14. Mature testes. The testes are the enlarged portions at the right. The elongated tissue connected to each testis is the epigonal organ, thought to be involved in hemopoiesis.

Umbilical cord. After the placenta has formed, the modified yolk stalk is referred to as the umbilical stalk or cord. The umbilical stalk contains 3 channels: an artery and a vein plus the *ductus vitellointestinalis* which joins the yolk-sac with the duodenum. The umbilical stalk leaves the embryo between the anteriormost portion of the pectoral fins at the mid-ventral surface.

The surface of the umbilical stalk of some sharks possesses slender, vascular projections called appendiculae. These are thought to function in absorbing nutritive secretions of the uterine wall (Alcock, 1890; Schlernitzauer and Gilbert, 1966). Such appendiculae have been reported in *Scoliodon sorrakowah*, *S. palasorrah* and *S. walbeehmi* (Mahadevan, 1940) and in *Sphyrna tiburo* (Schlernitzauer and Gilbert, 1966). The umbilical stalk of *Carcharhinus leucas* is smooth and lacks appendiculae, as has also been reported for *C. falciformis* (Gilbert and Schlernitzauer, 1966) and *C. dussumieri* (Teshima and Mizue, 1972). Teshima (1973) reported appendiculae in the umbilical stalk of a shark identified only as *Carcharhinus* sp.

Male Reproductive System

Testes

In contrast to the condition in the female, both male gonads are functional. As in the case of the ovary, the testes are situated on the dorsal surface of the anterior end of the epigonal organs (Fig. 14). They are of approximately equal size. The left and right epigonal organs are of virtually identical shape and consistency. They differ only in minor details between the sexes and have been reported by Matthews (1950) to be the center for erythrocyte formation as well as leucocyte development in *Cetorhinus* and skates of the genus *Raja*. Matthews stated that a number of authors have mistakenly considered the epigonal organ a part of the gonad.

In the immature male, the gonad appears as only a slightly enlarged anterior portion of the epigonal organ, scarcely distinguishable from the latter. With the onset of sexual maturity, it enlarges and increases in vascularity. In an immature 122 cm male, both testes measured 83 mm in



FIG. 15. Dorsal view of clasper organs (preserved). Note the distal structures which are expanded during copulation. The clasper groove lies along the medial margin of each clasper.

length, while the total epigonal length was 374 mm on the left and 381 on the right. In a 167 cm male, the right testis measured 160 mm, with a total epigonal length of 549 mm. The testes of a 172 cm male measured 182 mm long by 55 mm wide for the right and 184 mm by 53 mm for the left.

The sperm of *C. leucas* is similar to that described for other sharks, with corkscrew head and flagellum-like tail of approximately equal lengths. Sperm were taken from several mature males. In some, probably in breeding condition, the sperm were motile and remained so for some time. Fluid taken from other males was found to have sperm present, but in a non-motile state.

Clasper and siphon sacs

Internal fertilization is accomplished in all male elasmobranchs by a pair of intromittent organs which are modifications of the posterior (medial) edges of the pelvic fins, known as claspers or mixopterygia. Associated with the claspers are a pair of siphon sacs lying between the skin and musculature of the ventral body wall. The details of size and form of these organs vary among taxa and have been reported for a number of species. The history and literature concerning the anatomy and function of the clasper-siphon sac mechanism of elasmobranchs have recently been summarized and discussed by Gilbert and Heath (1972).

In their general features, claspers of *Carcharhinus leucas* are like those described for carcharhinids in general. The clasper is largest at its basal end and tapers to a smaller diameter at its tip (Fig. 15). In the sexually mature male, it is supported and given rigidity by a system of cartilaginous structures. Longitudinal folds of skin roll the clasper into a tube, the medial fold overlapping the lateral one to form a sperm duct, visible externally only as the dorso-medial clasper groove. In the erected clasper, rotated inward and forward, the groove is opened at its base, allowing the pas-



FIG. 16. Clasper organs rotated forward. Note in each clasper the groove with its opening at the base and the expanded distal end.

sage of sperm into the duct from the urogenital papilla. The skin of the clasper has no dermal denticles and thus lacks the abrasive qualities of the rest of the shark's skin. The distal end of the clasper, also supported by cartilage structures, is expandible, and on erection of the clasper, it spreads open (Fig. 16). By means of hooks, spurs and denticles this fan-shaped structure holds the oviduct open and prevents the withdrawal of the clasper during copulation. Presumably one clasper at a time is inserted in the female reproductive tract during copulation, as has been reported for several other elasmobranch species (Gilbert and Heath, 1972).

Several siphon sacs were examined in *C. leucas*. In a mature male, a small rubber tube was inserted into the clasper groove at its base and water was pumped into the opening (apophyle) of the siphon sac. In this way it was determined that the siphon sacs lie under the skin of the ventral abdominal wall and are separated from each other in the midline. The sacs extend to approximately the anterior edge of the pectoral fins. It was not determined at what stage of maturity they become capable of inflation. The same process was attempted on immature and recently born sharks but water could not be pumped in. The sacs evidently have not developed at this stage but probably do so at the time of sexual maturation, as was reported for *Squalus acanthias* and *Mustelus canis* by Gilbert and Heath (1972).

The function of the siphon sacs appears to be primarily the flushing of sperm through the clasper grooves with sea water. Presumably the sea water enters the sacs prior to copulation either by the pumping action of repeated flexing of the claspers or by swimming of the animal through the water with the claspers in the flexed position (Gilbert and Heath, 1972). The siphon sacs are lined with a glandular epithelium which secretes a substance that in the spiny dogfish is rich in serotonin and may play a part in the reproductive process (Mann, 1960).

Size at sexual maturity

Sexual maturity of males was determined largely on the basis of clasper length rather than the state of the testes, since most of the sharks caught were tagged and could not be examined internally.

A large number of clasper measurements were taken on male sharks of all available sizes. These, measured from the pelvic axil, and expressed as percent of total length, have been plotted in Fig. 17.

When the male reaches a length of approximately 140 cm, the claspers start to grow at an increased rate relative to the rest of the body. This relative increase in clasper length continues until the males reach a length of about 160 cm, when it levels off at 9.0 to 9.5% of total length. Sexual maturity thus appears to be reached at an average length of about 160 to 165 cm. There is considerable variation and a number of males between 169 and 180 cm were apparently abnormal, having small, juvenile claspers.

Lineaweaver and Backus (1970) mentioned that once maturity is reached, the growth of the claspers does not keep pace with the shark's growth in length. We found no indication of the decrease in percent of total length that would occur if this were correct. The clasper growth, in *C. leucas*, reaches its peak, levels off and then appears to keep pace with the increase in total body length.

Clark and von Schmidt (1965) indicated from their data that *C. leucas* males in the Florida region are much larger than the Nicaragua males before they mature sexually. The Florida males appear to be 220 cm or more in length before they become sexually mature, as judged by clasper length. They considered the males mature when 1) the clasper head or rhipidion (Leigh-Sharpe, 1920) is 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 can be directed anteriorly; and 4) the siphon sacs are fully elongated."

Bigelow and Schroeder (1948) have indicated that *C. leucas* matures at about seven feet in length, although they do not specify sex. They referred to sharks farther north than the population in this study.

According to Springer (1960), *C. leucas* from the region of Trinidad is considerably smaller than *C. leucas* taken from the Gulf of Mexico. The population under study is obviously closer in size to the Trinidad population than to the Florida-Gulf of Mexico populations, since our males rarely attain a length greater than two meters.

*Mating**Location*

The mating of *C. leucas* was not observed and reports of copulation are to our knowledge absent from the literature. It seems unlikely that it takes place in the fresh water of the river and its side channels or in Lake Nicaragua. Presumably it occurs in the brackish water near the river mouth or in marine water along the coast.

Time

The breeding season does not appear to be restricted to a certain time of the year. Table 1 indicates that near-term pups were found in gravid females in virtually all the months for which records are available, including June, July, and August, and to a lesser extent, April and

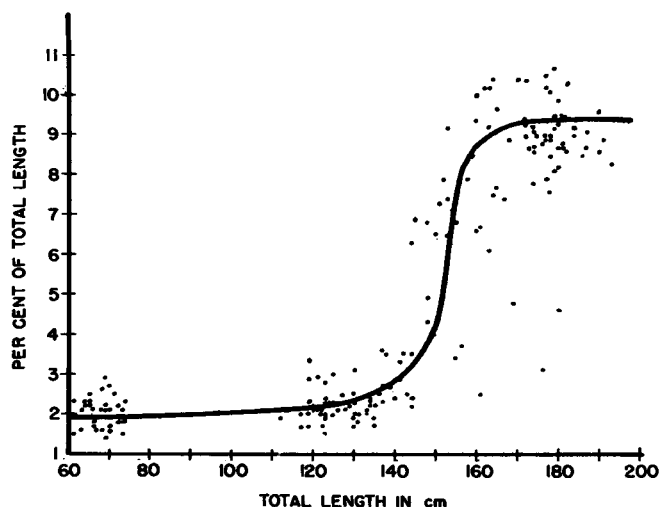


FIG. 17. Graph showing clasper growth in males of *Carcharhinus leucas*.

November. Local fishermen reported that various sized embryos are found in the uteri throughout the year. However, persistent reports suggest that the largest catch of females nearing parturition occurs in April, May and June. Apparently then, breeding occurs throughout the year but may be concentrated in certain months.

Marshall (1966) proposed that, because of the small variation in temperature in tropical seas, most species breed over a greater portion of the year than in temperate seas. The less the changes in seasons, especially in temperature, the less definite are the mating periods. The mean temperature of the research area varies only about 3°C throughout the year (Incer, 1970).

Clark and von Schmidt (1965) have indicated that the population of *C. leucas* on the west coast of Florida breeds in June and July. However, they also mentioned that in the tropics, where light and temperature changes are not so variable, the gestation periods are of a definite length but mating and birth take place throughout the year.

Baughman and Springer (1950) have indicated that the young bull sharks are apparently born in late winter or early spring in the Gulf of Mexico, but they did not mention the time of mating or the length of gestation. Bigelow and Schroeder (1948) believed that mating in *C. leucas* probably occurs shortly after birth of the preceding litter.

Springer (1960) stated that mating of the sandbar shark, *C. milberti*, probably takes place in spring or early summer around Salerno, Florida, but principally in June. This is based on observation of enlarged testes of males, and in females, some vascular congestion around the pelvic fin region and the large size of the eggs found in the ovary.

Behavior

The actual mating and courtship of elasmobranchs has only rarely been observed. It has been described in the clearnose skate, *Raja eglanteria*, by Libby and Gilbert (1960). During this mating the male seized the female by biting on a pectoral fin and then inserted a single clasper. Clark (1963)

reported the copulation of a pair of lemon sharks, *Negaprion brevirostris*, that were in captivity at Cape Haze Marine Laboratory.

Springer (1960) reported that larger carcharhinids display a pattern in which the male swims after the female and occasionally bites her on the back until she swims upside down. This is followed by copulation. Springer (1967), with indirect evidence, stated that the males probably harass the female to obtain their cooperation. This harassment may become quite violent at times. He stated that "minor cuts and scars, interpreted as courtship injuries, are common on mature females of the larger species of carcharhinid sharks, especially those having flattened, triangular teeth obviously effective for cutting . . . The location and number of these marks varies but are usually found on the dorsal surface in the pelvic region." He went on to state that, "typically, they seem to be produced by short slashes that do not show the imprint of several teeth or the crescentic pattern of the jaw."

In my study, a number of females were observed with marks of shark teeth on their bodies. Some of these strongly suggested that the sharks were attacked after being hooked, but in other cases the wounds were in various stages of healing. Although it was impossible to associate each case positively with reproductive behavior, it is reasonable to assume that some of the wounds had been acquired during mating.

Of injuries to males, Springer (1967) indicated that they are rare and are usually limited to cut-off fin tips or claspers. Springer also noted (1960) that during mating periods the bases of the claspers are congested and edematous, with subdermal hemorrhage.

In my own observations, one male was taken that might have been injured in a mating encounter, although direct evidence is lacking. A male shark of 176 cm, caught on June 20, 1968, had a large portion of the right clasper cut off. In addition, the region around the cloaca was hemorrhagic, the testes were greatly enlarged and the remaining clasper was enlarged and edematous. There were no other noticeable marks on the shark. This agrees with Springer's (1967) statement that most wounds on males are limited to dismemberment of a part during courtship and mating.

Birth of Young

My observations on actual parturition were limited to females that had been dragged onto the beach and in some cases aborted one or more of the young. The pups are extremely active when born. Some that were tagged and released, when first placed in the water, became so active in their swimming that they planed on the surface for several meters before submerging.

Orientation of young in uterus

The young face anteriorly in the uterus and birth is, therefore, tail first. This birth position is against the "grain" of the dermal denticles of the pups, but the young are still surrounded by the shell membrane which protects the mother's vaginal and cloacal surfaces. In addition to the shell membrane, a viscous substance covers the skin of the fetus, making it very slippery and allowing for an easier delivery, as well as making it difficult to handle. The pups are born in the order that the eggs entered the uterus, the posterior compartment being emptied first. No data were obtained on whether birth alternated between uteri or if one uterus first delivered all of its young and then was followed by the other uterus.

Size at birth

This population of *C. leucas* gives birth to its young at a size range of 50 to 75 cm, the majority of births occurring between 65 and 70 cm. More than 1000 sharks in the 50 to 75 cm size range were taken on baited hooks for tagging, the smallest being 50 cm long. Most of the pups taken from gravid females also fell within this range, the largest being 74 cm.

Bigelow and Schroeder (1948) gave 65 to 70 cm as the size at birth. Clark and von Schmidt (1965), however, indicated that the young of the Florida region are probably between 74 and 75 cm at birth. The size of the adults which Clark and von Schmidt studied was greater than of those we captured, so it is logical that the young might also be somewhat larger at birth. Their estimate of range of size at birth appears too restricted, because the size of the healthy young within a single litter often varies by as much as 12 cm.

Litter size

The average number of young per litter among a sample of 65 is 5.5. This number agrees with Bigelow and Schroeder's (1948) estimate of five or six. The largest litter observed included 10 young, the smallest, only one.

Sex ratio

In 43 litters, of the pups large enough to be sexed, 117 were females and 138 males, a ratio of 1:1.18. The difference tested by the Chi square method is not significant. Springer (1960) also found equal numbers of males and females in *C. milberti*. However, it is not unusual in elasmobranchs to find a significantly higher number of males than females during embryonic development. *Urolophus halleri* produces 1 female to 1.6 males (Babel, 1967) while Breder and Krumholz (1941) found 56% male embryos in the stringray, *Dasyatis sabina*, and 55.5% male embryos in *D. hastatus*.

Time of parturition

Sizes of *in utero* young, from blastoderm stage to full-term, from all females listed in Table 1, were plotted in Fig. 18, in an attempt to determine the breeding season, length of gestation and parturition time. Information is available only for the months of April, June, July, August and November. No seasonal pattern emerges from the graph. Blastoderm stages were taken in early April, June and July, and very early embryos occurred in August. Near term (50–75 cm) pups were found from early April through the first half of August and placental scars were seen in April as well as July. Young of birth size were also taken in November (size estimated), although the only measurements recorded were from about 24 to 42 cm. Local fishermen reported that young of all sizes occur throughout the year, but that females approaching parturition are somewhat more common in April, May and June.

I can only conclude that there is no definite time for parturition; that it occurs throughout the year; but it may be more common from April to June.

Gestation period

Clark and von Schmidt (1965) have suggested that *C. leucas* in Florida waters has a gestation period of 10 or 11 months. *Mustelis canis*, another viviparous species, was reported by TeWinkel (1950) also to have a 10-month gestation period. Springer (1950) estimated the gestation period of the lemon shark, *Negaprion brevirostris*, to be 10 months, while Clark and von Schmidt (1965) cited evidence that a 12-month gestation may be more accurate for that species.

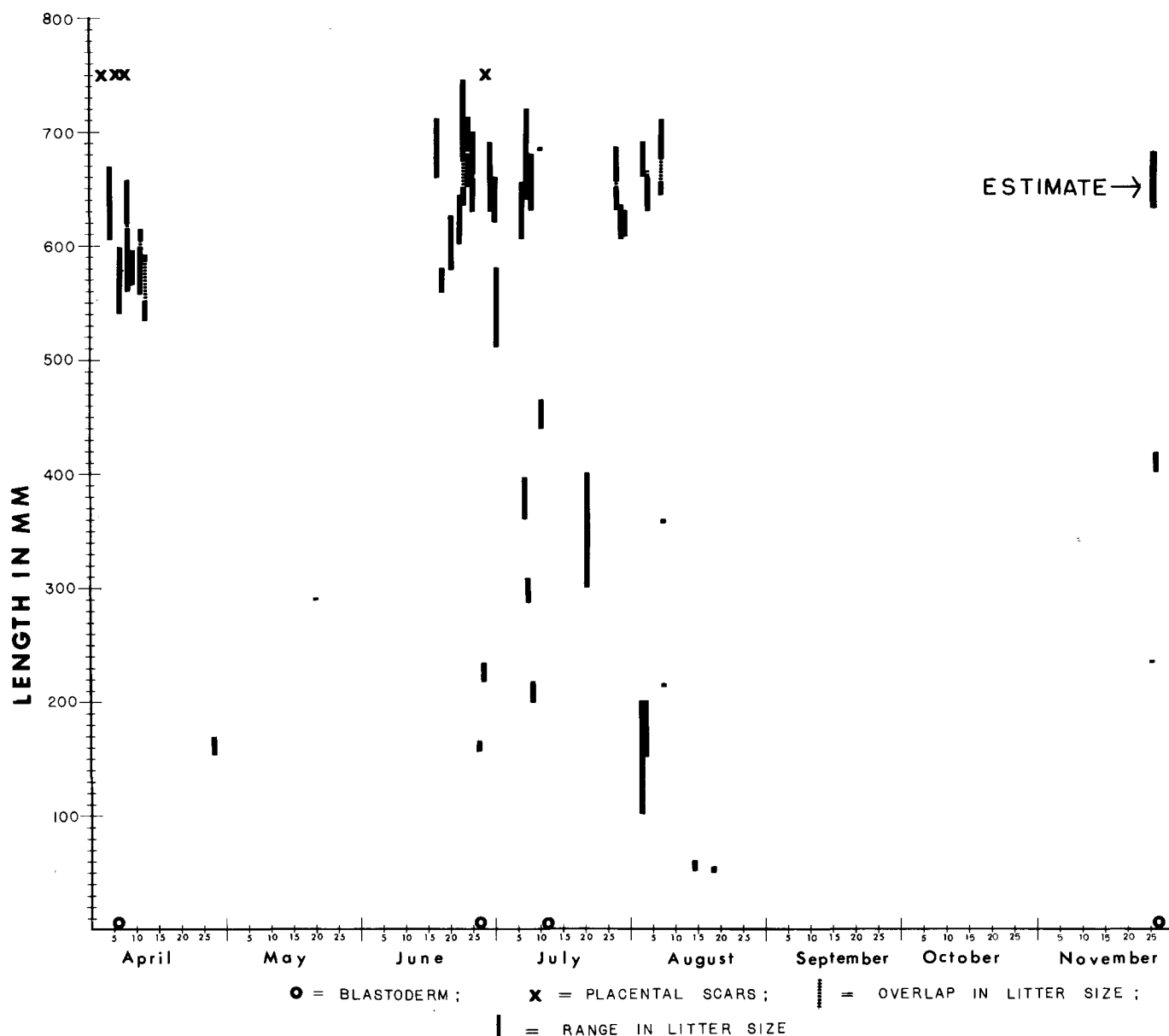


FIG. 18. Graph of size ranges of litters by time of year. Collecting periods included three two-month periods from June to August, a week in April and four days in November. Blastoderm stages are recorded along the base line (O) and placental scars at the 75 cm level (X).

Teshima and Mizue (1972), studying *Carcharhinus dussumieri* off the northwest coast of Borneo, found that the ova remaining in the ovary following ovulation of two mature eggs are gradually reabsorbed until the two resulting embryos attain a length of about 100 mm (size at birth is about 375 mm). When the embryos have attained a length of about 200 mm, the ovarian ova increase to a diameter of about 20 mm before ovulation, which occurs "immediately after parturition." If parturition were seasonal, this would indicate a 12-month gestation period. However, Teshima and Mizue found no evidence for a seasonal breeding cycle, and concluded that breeding took place throughout the year.

In the absence of observations on mating and with no seasonal pattern suggested by Fig. 18, it is impossible to

reach a conclusion concerning the gestation period of the Lake Nicaragua-Río San Juan population of bull sharks. It is probably similar to that suggested for *Carcharhinus leucas* in Florida, i.e., 10 or 11 months. It should be noted that neither females with near-term fetuses nor those showing placental scars (and therefore having recently given birth) contained a new set of ova approaching ovulation.

Place of parturition

Except for one, all pregnant females used in this study were caught at, or just inside, the mouths of the Río Colorado and Laguna Samay (Fig. 2). None were taken at the mouth of the Río San Juan, probably because very little fishing was carried on there. However, in 1963, Thorson

(unpublished) took a female there containing three uterine eggs, which had therefore presumably been fertilized.

The exception was a gravid female captured at El Castillo, about 110 km up the Río San Juan from the sea. This represents the greatest penetration of the river by any pregnant female captured during our study. Earlier accounts (Anon., 1965; Thorson, 1965) reported a pregnant female caught several miles above El Castillo and above the uppermost of the rapids (Rápidos Toro). The young of this shark were reported to be 45 to 51 cm in length, less than the size they normally reach at birth. The shark that we captured (Table 1, 68–100), carried young in the small range of birth size (51–58).

At San Carlos, where the Río San Juan leaves Lake Nicaragua, about 200 sharks were taken over a period of five years. Most of these were tagged, but a number of large females were examined, particularly when they showed any signs that they might be pregnant. None proved to be pregnant, nor did any have placental scars.

The reports of parturition in the lake have been based entirely on reports of fishermen, with no documentation by specimens, photographs or reports in the zoological literature. Even so, there is little reason to doubt that occasionally a female may drop her young in the lake. It has been definitely established by tagging that the bull sharks move up the river to the lake from the sea (Thorson, 1971) and the two reports of pregnant females at or above El Castillo indicate that the upstream migrants occasionally include pregnant females. There is no reason to doubt that now and then they go up to the lake and may on occasion give birth to their litters.

However, the overwhelming weight of evidence indicates that *C. leucas* does not use the lake for part of its normal pattern of reproduction, and birth of the sharks there is the exception rather than the rule.

My conclusion is that the lake population does not maintain itself by reproduction in the lake but by new arrivals from the sea and that reproduction normally occurs near the mouths of the river system.

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SUMMARY

Sixty-six pregnant or post-pregnant female bull sharks (*Carcharhinus leucas*) were examined for condition of reproductive organs and embryonic development.

Females have only a right functional ovary. Fifteen to 20 ova mature, of which only 10 or fewer are ovulated. Those retained in the ovary undergo reabsorption. Ova are released into the coelomic cavity, move through the ostium into a common oviduct, and then pass into either the left or right oviduct. The nidamental gland, in the anterior end of each oviduct, secretes an albumen-like substance and a diaphanous, greenish shell membrane which encloses each egg as it passes to one of the uteri.

The mature uterus has a longitudinally ridged inner lining, which becomes smooth and highly vascular in early

pregnancy. Dorsal and ventral outgrowths of the uterine wall separate the eggs into compartments. In later stages considerable stretching of uteri occurs, as the fetuses grow, with fusion of the dorsal and ventral outgrowths and complete separation of the embryonic compartments. Post-pregnant uteri have placental scars indicating recent birth of young.

Carcharhinus leucas develops a modified yolk-sac placenta. The yolk material is the first source of nutrition for the developing shark but as this is used up, a union is formed between the uterine wall and the yolk-sac, possibly separated by the shell membrane. Each fetus is attached to its placenta by an umbilical cord.

The clasper organs and associated siphon sacs of male *C. leucas* are similar to those described in other carcharhinids. The testes, both functional, are imbedded in the anterior end of the epigonal organs.

Sexual maturity is reached at lengths of approximately 160 to 170 cm in females, while males are usually mature at 160 to 165 cm.

Mating has not been observed, but is presumed to take place in brackish water near the mouths of rivers and along the coast. Breeding apparently takes place throughout the year.

The young are oriented anteriorly in the uteri and birth occurs tail first. At birth the young range from 50 to 75 cm in total length, the majority being between 65 and 70 cm. The average litter size is 5.5 and the observed ratio of females to males is 1:1.18 (not significantly different from unity). Parturition apparently takes place throughout the year, although it may occur most commonly in the months of April through June. The exact length of gestation is not known but appears to be less than a year.

Carcharhinus leucas does not appear to use the lake for its regular pattern of reproduction. Parturition normally occurs near the mouths of the river system, although occasionally a female may wander into Lake Nicaragua and give birth to her young.

RESUMEN

Se examinaron 66 tiburones (*Carcharhinus leucas*) preñadas y paridas para determinar su condición reproductora.

En las hembras sólo el ovario derecho es funcional. De quince a 20 óvulos maduran cada vez, de los cuales sólo 10 o menos son ovulados; los demás son retenidos en el ovario y reabsorbidos. Los óvulos salen a la cavidad celómica, se mueven a través del ostium a un oviducto comunal, de allí pasan al oviducto izquierdo o derecho. La glándula de la cáscara (o nidamental), situada en el extremo delantero de cada oviducto, secreta una substancia como albúmina, y una cáscara membranosa diáfana, verdosa, que envuelve el óvulo en su trayecto por uno de los úteros.

El útero maduro tiene el revestimiento interior longitudinalmente estriado, el cual se vuelve liso y altamente vascularizado al inicio de la preñez. Los óvulos van siendo separados en compartimientos formados por evaginaciones dorsales y ventrales del útero. Al ir creciendo los fetos, los úteros se estiran considerablemente, se funden las evaginaciones dorsales y ventrales y los fetos van quedando separados completamente. Los úteros paridos (post-grávidos) muestran cicatrices placentales que indican partos recientes.

Carcharhinus leucas desarrolla una placenta modificada

del saco vitelino. El vitelo (yema) es la primera fuente nutricia del embrión, pero al irse agotando se va formando una unión entre la pared uterina y el saco vitelino, posiblemente separados sólo por la cáscara membranosa. Cada uno de los fetos se adhiere a su placenta por medio del cordón umbilical.

En los machos hay órganos copuladores (claspers o mixopterigios) y sacos de sifon asociados a ellos, que son similares a los descritos de otros carcarinidos. Ambos testículos son funcionales y están incrustados en los extremos anteriores de los órganos epigonales.

La madurez sexual ocurre cuando las hembras miden unos 160 a 170 cm y los machos unos 160-165 cm.

No se ha observado la cópula, pero se asume que ocurre en aguas salobres cerca de la desembocadura de los ríos y a lo largo de las costas. La reproducción parece ocurrir durante todo el año.

Los juveniles se orientan hacia adelante en los úteros y, al nacer, la cola emerge primero. Entonces tienen una longitud total de 50 a 75 cm, la mayoría entre 65 y 70 cm. La camada promedio 5.5, y la proporción de hembras a machos es 1:1.18 (no difiere significativamente de 1:1). El parto sucede aparentemente durante todo el año, aunque es más común entre abril y junio. No se conoce exactamente cuanto dura la gestación, pero parece que es de menos de un año.

Carcharhinus leucas no parece usar el Lago en su partrón normal de reproducción. El parto ocurre normalmente cerca de la desembocadura de los ríos, aunque ocasionalmente una hembra puede entrar al Lago de Nicaragua y parir allí.

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