A primer on shark reproduction for aquarists

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Introduction

Aquariums are one of the most popular and profitable public entertainment enterprises, and sharks are invariably one of their most popular and prized exhibits. Unfortunately, due to a variety or reasons, sharks are among the most difficult species to maintain in captivity. Only a few species can be maintained for long periods and even fewer reproduce in captivity. Some small catsharks have been maintained in aquaria for many successive generations, and a few large species, such as the sand tiger shark and the nurse shark can survive in captivity for decades. The larger species are generally difficult to maintain in captivity, and most survive in present day aquariums only for short periods of days or weeks, or at best a few months.

The goal of most aquarists, and the final test of successful aquarium husbandry, is to provide a captive environment where a species can attain its full life span and reproduce successfully, engendering successive captive generations. The purpose of this paper is to provide a primer on shark reproduction for aquarists, to help in understanding the reproductive processes of the sharks they keep and to provide a framework for aquarists to make observations that will contribute to our understanding of the reproductive biology of sharks. Because of the difficulties of studying and observing sharks in the natural environment, much can be learned in the aquarium, and aquarists can contribute significantly to our knowledge of sharks when their observations are systematically recorded and subsequently published.

In the course of their long evolution, sharks evolved different reproductive adaptations that enhance the survival of their offspring. The first of these adaptations is internal fertilization.

In animals with internal fertilization, the male transfers its sperm to the female, and fertilization occurs inside the female's body, so it is said to be internal. In male sharks, the pelvic fins are modified into stout, tube-like copulatory organs known as claspers, which are inserted into the female during copulation to transfer sperm. The clasper tip is armed with hooks or claws and it expands when inserted into the female, effectively attaching the male, hence the name "claspers". All sharks have internal fertilization, and their embryos spend their most vulnerable stages protected inside their mother’s womb, and thus their survival is enhanced. By contrast, fishes with external fertilization cast hundreds of thousand of gametes into the waters where they suffer heavy mortality.

In addition to internal fertilization, sharks evolved diverse reproductive modes of nourishing their young to relatively large size. Most sharks produce small numbers of relatively large young that hatch or are born fully developed, looking like miniature copies of the adults. These young may reach as much as 25-30 % of the length of the mother. By being born at a relatively large size, the young sharks encounter fewer predators and have more available prey, thus enhancing their chances of survival. The production large young requires that large amounts of nutrients be available to nurture the embryo to large size, and sharks have evolved various modes of transferring nutrients to the young. These will be discussed below.

Another adaptation of sharks which enhances the survival of their young is the use of nursery areas. These are specific areas of high productivity where the females travel to give birth and where the young encounter few predators and an abundance of small prey (Castro, 1993).

The reproductive modes of sharks have been traditionally grouped into two major categories: oviparity (egg laying) and viviparity (giving birth to live young). In turn, viviparous sharks can be divided into several groups, depending on their mode of nourishing their embryos to large size. The different forms of viviparity have been the subject of various classifications (For reviews see Wourms, 1977; Hamlett and Koob, 1999; Conrath and Musick, 2012). None of these is completely satisfactory because there are so many adaptations and because we know so little about the maternal-embryonic processes of sharks. It is not the author’s purpose here to propose a new classification of the modes of reproduction in sharks, nor is it to demonstrate all the variations of viviparity in sharks. The purpose of this paper is to provide a simple primer to be used by aquarists and others to understand some of the reproductive processes of some the sharks they encounter in their work or investigations. Much remains to be learned about the reproductive processes of sharks and aquarists can contribute much to that endeavor.

Oviparity

The most primitive mode of reproduction in sharks is oviparity or egg laying. This is a modified oviparity, different to that of bony fishes. Oviparous sharks lay large eggs that contain sufficient yolk to nourish the embryo through development, and allow it to emerge as a fully developed miniature shark. By contrast, the eggs of most bony fishes are relatively minute and contain only a small amount of yolk. The small amount of nutrients in the egg can only support the developing embryo for a short time, and thus the embryo hatches out as a larva that usually bears little resemblance to the adult. Both eggs and larvae are highly vulnerable to biotic factors and predators for prolonged periods of time and consequently suffer heavy mortality. Oviparity in sharks is primarily confined to three families: the Scyliorhinidae, the Orectolobidae, and the Heterodontidae.

The evolution of shark oviparity and the production of a small young that hatch at a relatively large size has contributed to the evolutionary success of sharks. The eggs of oviparous sharks are enclosed in leathery cases that are deposited on the bottom without any further contact with the parent. These egg cases are usually rectangular of conical and have adhesive tendrils used for attachment to bottom structures (Figure 1). The embryos hatch out after some months or a year, depending on water temperature. The hatchlings of oviparous sharks are very small in comparison to the mother's size, because the embryos have only that amount of yolk in the egg case to nurture them through development. The chain dogfish (*Scyliorhinus retifer*), a species common in the continental slope of eastern North America, is an example of an oviparous shark that has been studied in the aquarium (Castro et al., 1988), and its reproductive biology will be briefly summarized here.

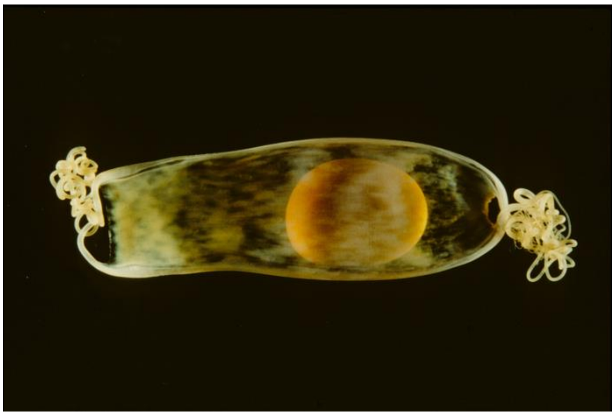

Figure 1. Chain dogfish egg case. Note adhesive tendrils on each corner of the egg case.

Courtship begins as male and a female swim together almost constantly, often in slow, tight circles near the bottom, with the male often biting the female. When the sharks are ready to mate, the male bites the female near the tail and proceeds to move it bite forward. The female may struggle at first but soon becomes listless. The male moves its bite anteriorly along the flanks and eventually grabs the pectoral fin or the axilla. When firmly attached to the pectoral fin or area, the male then curls it body around the female, inserts a clasper and copulation is accomplished. After a short while the two sharks swim apart. In the natural environment as well as in the aquarium, chain dogfish females use vertical bottom structures to attach their eggs. When a female is ready to lay her eggs, the long adhesive tendrils at each corner of the egg case protrude through the cloaca and trail behind the shark. The female then locates a vertical structure (a coral, a sponge, or any solid structure) and begins to swim tight circles around the structure, causing the trailing tendrils to adhere to the structure (Figure 2). Once the tendrils are firmly attached to the structure,

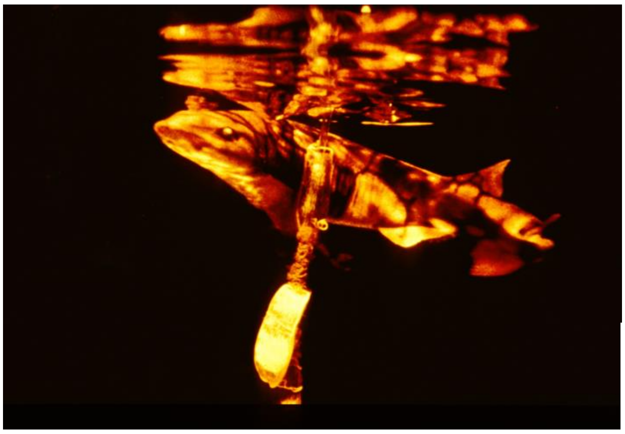

Figure 2. Chain dogfish females attaching egg cases to upright structure.

the female speeds up her circling, and this causes the egg case to be physically pulled from the cloaca. Females usually ovulate their oocytes in pairs. The interval between successive pairs is about two weeks. The interval between the deposition of the first egg case of a pair and the second ranges from a few minutes to a few days, with the longest interval observed being 8 days. Each female produces egg cases of consistent size and coloration, thus an aquarist can usually determine which female may have produce a given egg cases in a tank of several females. In the wild, structures suitable for egg attachment may be scarce, and many females in one area may use the same structure, creating large masses of egg cases with embryos in many different stages. Whether this is done because of the scarcity of suitable structures or whether the eggs derive some protection from the clustering is unknown. The egg cases have small slits that open enzymatically after the embryo reaches a given size (Figure 3). These slits serve to aerate the egg case, and the embryo constantly fans its tail for this purpose. Embryo development is temperature dependent and in the case of the chain dogfish average development time was 256 days at water temperatures of 11.7–12.8ºC, and hatching occurred when embryos reached 10–11 cm. These patterns outlined above may only apply to the genus Scyliorhinus. Other genera of oviparous sharks may be quite different. Because so many species of catsharks and other small oviparous sharks are maintained in aquaria, aquarists may make useful observations concerning their reproductive biology.

Figure 3. Chain dogfish egg case with embryo. Egg case slits are open just anterior to embryo's head.

Viviparity

Viviparity is the retention of the fertilized eggs within the body of the female for a prolonged period of development and often for the duration of gestation, so that the young can be born fully developed. In the animal kingdom, viviparity has evolved separately over the eons in diverse phyla ranging from insects to elasmobranchs and mammals. Viviparity is a common solution to the problems of embryo survival, and it has been achieved through diverse adaptations in different phyla. In sharks, viviparity has evolved in different lineages and it occurs in most families of sharks (or in 26 out of 29 families, depending on how families are defined). The advantages of viviparity over oviparity are many. In viviparous animals, the embryos spend their most vulnerable developmental stages inside the body of the female and their vulnerability to predators is reduced. The embryos can be nourished to a large birth size with the concomitant advantages of being born large mentioned above, and the females can select the most propitious environment for their young to be born (nursery areas) further enhancing their survival.

Viviparity in sharks has been traditionally divided into two categories: aplacental viviparity and placental viviparity. Aplacental viviparity is a heterogeneous category that includes sharks of different lineages and includes all the reproductive variations of viviparity except for placental viviparity. By contrast, the term placental viviparity is very specific and confined to those cases where a placental connection was formed between mother and offspring, as in sharks of the genera *Carcharhinus* and *Sphyrna*.

The term 'ovoviviparity" was used in the past to describe viviparous animals where the female retained the fertilized eggs until hatching and birth, but passed no further nutrients to the embryo. The problem with the term or concept is that it is too ambiguous or imprecise, and today we know enough about the maternal-embryonic processes of sharks to use more accurate terms. Many of the sharks that were once called ovoviviparous at one time now are known to be oophagous (see below) or are nourished in some other way.

Yolk sac viviparity

This group includes sharks of different lineages where the young are solely nourished by yolk stored in the egg or yolk sac (Figure 4). The spiny dogfish (*Squalus acanthias*) is an example of this mode of reproduction, and it is likely that most of the squaloid sharks share this type of nutrition and reproductive cycle. Gilbert (1959) demonstrated that the embryos of the spiny dogfish can be surgically removed from the mother long before term and, if placed in bacteria-free environments (aquariums, finger bowls, or plastic tubes) and provided flowing filtered sea water, they will develop normally to term. This experiment demonstrates that all the nutrients necessary for embryonic development are present in the fertilized egg and that the mother does not contribute additional nutrients during gestation.

Figure 4. Spiny dogfish embryo near mid-term.

When compared to oophagous or placental species, species nourishing their embryos by yolk-sac viviparity produce relatively large eggs, while their new-born are relatively small (Figure 5). Their eggs are large because they must contain all the nutrients necessary to bring the embryo to term; the embryos are small because the amount of nutrients available is small, being limited to what can be stored in the egg. The reproductive cycle of the spiny dogfish is biennial and involves a gestation lasting about 22 months (Ketchen 1972, Jones and Geen, 1977) concurrent with vitellogenesis (Castro, 2009)

Figure 5. Spiny dogfish reproductive tract near mid-term. Note the embryos ready for birth and large oocytes ready for ovulation.

Serial yolk sac viviparity

Two species, the nurse shark (*Ginglymostoma cirratum*) and the whale shark (*Rhincodon typus*) exhibit a type of yolk sac viviparity where the embryos are in considerably different stages of development for most of gestation. Both of these species produce large broods. Nurse shark broods can reach 52 young (Castro, 2000), while those of the whale shark may exceed 300 young (Joung et al., 1996). Because of the large broods and because usually oocytes are ovulated in pairs at discrete intervals, ovulation is a prolonged process probably lasting at least 2–3 weeks in the nurse shark and much longer in the whale shark. Thus the first pairs of oocytes to be ovulated and fertilized may be developmentally several weeks more advanced than the last pairs to be fertilized. In these species one can find that females in mid-gestation carry embryos still inside the egg cases, while other older embryos have consumed their yolk sac and appear ready for birth. Thus, I have chosen to call this mode of reproduction 'serial yolk sac viviparity'

Figure 6. Nurse shark embryo at hatching.

The nurse shark is one of the most commonly displayed sharks in aquariums of the tropical Americas. Although it is a hardy shark that survives in captivity for many years, it seldom reproduces in captivity, probably due to inadequate or too small aquariums. The embryos feed solely on nutrients stored in the yolk-sac (Castro, 2000). For the first 12–14 weeks of gestation, the embryos are enclosed in their horny egg cases, hatching when they reach a length of 218–233 mm (Figure 6). Because of their different ages,

Figure 7. Nurse shark reproductive tract at midterm. Note embryo still inside egg case while others have already absorbed their yolk sacs.

Figure 8. Nurse shark egg case just about to be expelled from uterus.

embryos in a brood are at different developmental stages through the first months of gestation (Figure 7). Empty egg cases somehow find their way to the cloaca, become folded lengthwise, and are expelled (Figure 8). By the end of October all embryos have hatched and the egg cases have been expelled. The presence of empty egg cases on the bottom of the aquarium is usually t female is pregnant. By mid-November, the embryos have generally absorbed their yolk-sacs (Figure 9). Embryos are born at 280–305 mm in late November and early December, after a gestation period of 5–6 months. Parturition is spread out over a few weeks (Castro, 2000), because the embryos are not ready for the first indication to aquarists that their “fat” nurse shark birth at the same time. Embryos are released singly or a few at a time as they become fully developed (Figure 10). The reproductive cycle of the female nurse shark is biennial with consecutive vitellogenesis and gestation, with female nurse sharks producing broods every two years (Castro, 2000). After parturition, a female enters a resting period for about six months before it starts to develop its next batch of oocytes. It mates some 18 months after the last parturition, and the cycle begins again.

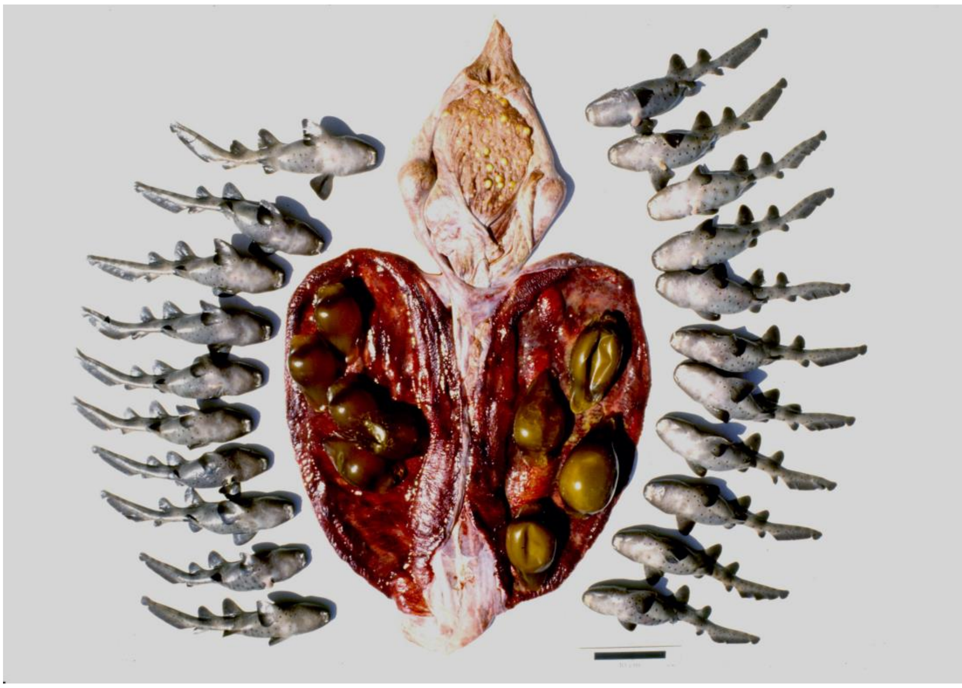

Figure 9. Nurse shark reproductive tract near term

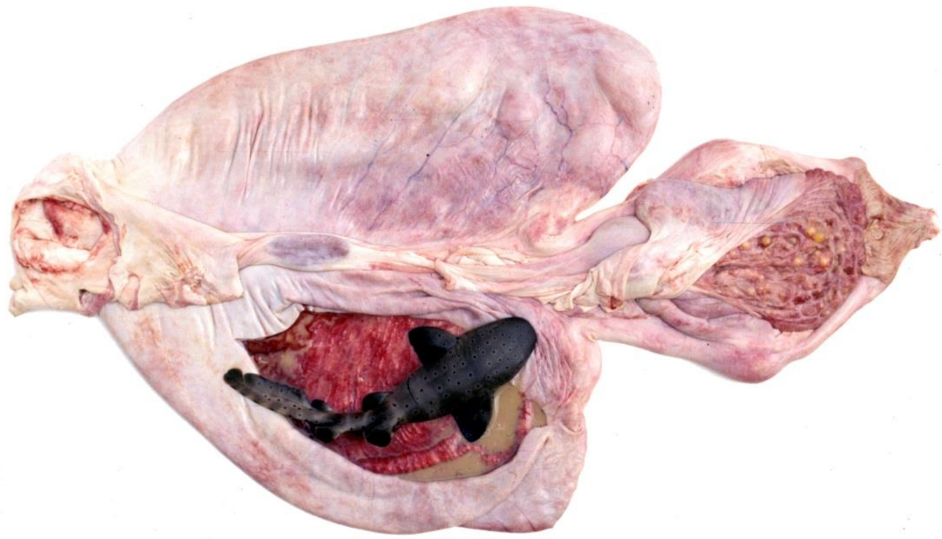

Figure 10. Nurse shark reproductive tract at term when embryos are being released.

Oophagy

Oophagy or “egg eating” is a type of aplacental viviparity where the embryos are initially nourished from a minute yolk sac, but later the embryos ingest eggs ovulated into the uterus for their nutrition. Oophagy is primarily found in the lamnoid sharks, although some orectolobid sharks and the false catshark exhibit it also. Usually, only the first eggs ovulated by the female are fertilized, and these are each encapsulated in individual egg cases. The number of fertilized eggs going into each uterus is variable, depending on the species, and can range from one to a dozen. Subsequent eggs are usually unfertilized and are used solely to feed the embryos, each egg case containing many eggs. Apparently, oophagy is a very efficient way of quickly nourishing embryos to large size. There are numerous patterns of oophagy in sharks, and a few examples will follow.

Figure 11. Sand tiger shark 5-cm embryo with precocious dentition.

Figure 12. Sand tiger shark uterus with 10-cm embryo that has killed smaller embryos. The embryos swim in a sea of egg cases.

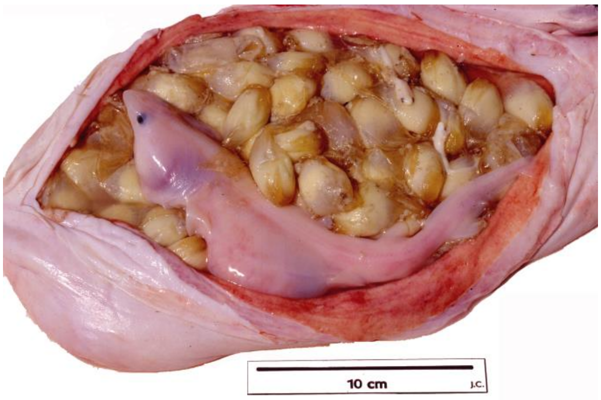

Figure 13. Sand tiger shark 30-cm embryo and smaller dead embryos.

The sand tiger shark (*Carcharias taurus*) is a popular aquarium sharks because it survives for decades in captivity, where its fierce appearance and large size make it a favorite with the public The sand tiger shark has a peculiar type of oophagy that has been termed adelphophagy (Wourms, 1977) or sibling cannibalism.

Springer (1948) was the first to note sand tiger oophagy, and the process was described by Gilmore and Dodrill (1983). In this species, when the largest embryo reaches 5–7 cm, its head is greatly developed and it develops a precocious dentition (Figure 11). The largest embryo then seeks and kills all the smaller embryos in the uterus (Figures 12 & 13). Later it will consume them along the large supply of egg cases that has accumulated in the uterus. Like in the shortfin mako, most of the yolky oocytes in the huge ovary are ovulated early in gestation and for a few weeks the embryo swims in a sea of egg cases. By the time the embryo reaches 50 cm it will have ingested all the egg cases and has developed a huge yolk stomach. The ovary will have released most of its ripe oocytes in the first half of gestation (Figure 14). The embryos will have consumed their expanded yolk stomachs by the time of birth.

Figure 14. Sand tiger shark embryos at about two thirds of development. Note that the ovary has released all the ripe oocytes and the egg cases have been ingested by the embryos.

In the shortfin mako (*Isurus oxyrinchus*) multiple embryos (sometimes a dozen on more) coexist in the uterus. In the shortfin mako, the ovary ovulates most of its ripe oocytes in the first few months of gestation. The embryos ingest a large number of egg cases in early gestation and acquire huge distended yolk stomachs (Figure 15). Normally up to ten embryos coexist in each uterus (Figure 16). However, in certain occasions, when there are runts or dead embryos, the larger and normal embryos may turn cannibalistic and consume other embryos. (Joung and Hsu, 2005).

Figure 15. Shortfin mako 30-cm embryo with large yolk stomach.

In the pelagic thresher (*Alopias pelagicus*) only the first two eggs are fertilized (Figure 17) and each is enclosed in its own egg case. Subsequent eggs are not fertilized (Castro 2009). These fertilized eggs, one cm in diameter, are larger than subsequent eggs. One egg case containing a fertilized egg goes to each

Figure 16. Shortfin mako brood at midterm.

Figure 17. Pelagic thresher egg cases. The upper two egg cases are the first to be ovulated and each contains one fertilized egg. The following egg cases (lower two cases) are just feeding egg cases.

uterus. Subsequent eggs are smaller and 10–20 are packed into each egg case (Figure 18). In this species, the ovary ovulates eggs continuously throughout gestation. Thus the embryos have a continuous supply of yolk and do not acquire the distended yolk stomachs of other oophagous species (Figure 19). The bigeye thresher (*Alopias superciliosus*) has a similar pattern of oophagy (Figure 20).

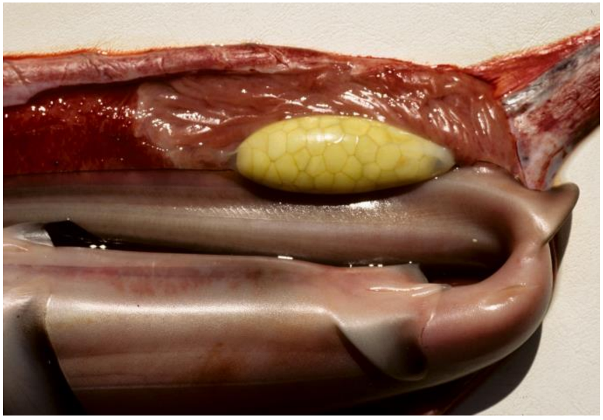

Figure 18. Pelagic thresher egg cases packed with eggs.

The tawny nurse shark, *Nebrius ferrugineus* (= concolor), is a common shark of the Pacific Ocean. It has been displayed in the Okinawa Churaumi Aquarium and other aquariums throughout the Pacific area. Despite its abundance and being kept in captivity, little is known of its reproductive processes. Teshima et al. (1995) demonstrated that the embryos of this orectoloboid shark are oophagous. Its birth size is not known with certainty. Much could be learned about this interesting shark in captivity.

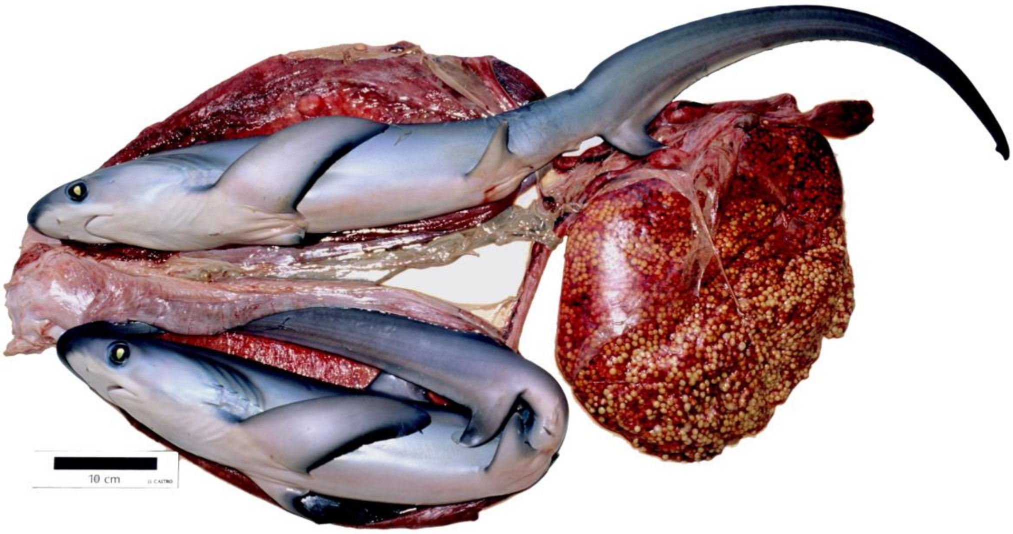

Figure 19. Pelagic thresher embryos at about two months of gestation. Note that the embryos do not acquire distended yolk stomachs and the ovary continues to ovulate eggs during gestation.

Figure 20. Bigeye thresher, panoramic view of reproductive tract with two embryos and ovulated egg cases.

Histotrophic viviparity

Another aplacental viviparous shark, the tiger shark (*Galeocerdo cuvier*), produces large young reaching 85 cm at birth (Castro, 2011) that are apparently nourished primarily by histotrophe (uterine milk). There is little published information on the reproductive processes and development of the tiger shark. Sarangdhar (1943) described 52-cm embryos removed from a female caught off Sassoon Dock, India in 1942. These embryos had large yolk-sacs with a considerable amount of yolk left in them, and were enclosed in 'water-filled' sacs formed in the shell membrane (Figure 21). The absence of any folding in their distal walls and the embryos being free inside the membranous egg case indicate that a placental connection does not form in the tiger shark (Sarangdhar, 1943). Castro (1983: 23) wrote that term embryos had everted stomachs protruding slightly from the mouth, and that it was possible that the abundant fluid may have nutritive properties ("uterine milk") and may be imbibed by the embryos through their everted stomachs. Current work by the author, A. B. Bodine, and Keiichi Sato of the Okinawa Churaumi Aquarium has revealed that the embryos gain considerable weight during development. The uterine fluid is currently being analyzed to investigate its nutritive properties. The reproductive cycle of the tiger shark is the subject of debate. Whitney and Crow 2007 proposed a 16-month development for tiger sharks off Hawaii, while Castro (2009) proposed a 12-month gestation period for North American tiger sharks.

Figure 21. Tiger shark embryo in fluid-filled egg case.

Placental viviparity.

Placental viviparity is the most advanced mode of reproduction in sharks. The embryos of viviparous sharks are initially dependent on yolk stored in the yolk sac (Figure 22), just like other sharks, but they are later nourished by the mother through a placental connection. Because the embryos spend their entire developmental time inside their mother's body, the egg case of placental sharks is thin and diaphanous. In

Figure 22. Atlantic sharpnose shark, 12-mm embryo inside egg case, during yolk-dependent stage.

Figure 23. 80-mm Atlantic sharpnose embryo has consumed all the contents of the yolk sac.stage.

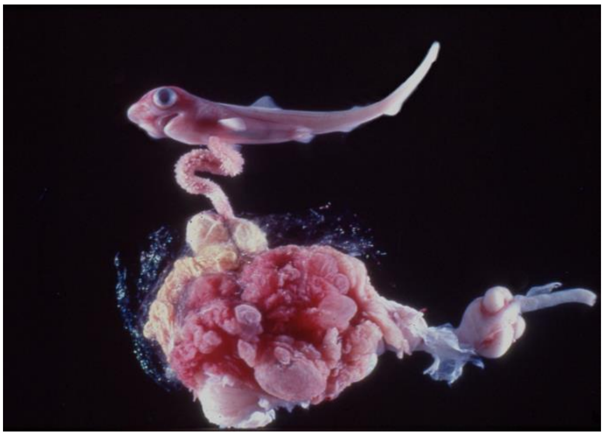

Figure 24. Atlantic sharpnose shark with flaccid yolk sac implanting on uterine wall.

Figure 25. Atlantic sharpnose shark. Where the yolk sac comes in contact with the uterine wall, the placenta is formed.

placental sharks, the contents of the yolk sac are usually consumed in the first few weeks of gestation (Figure 23). In these sharks the yolk sac enlarges as it contents are consumed, and develops as a long yolk stalk that bears a reduced, flaccid yolk sac at its end (Figure 24). Where the yolk sac comes in contact with the uterine wall, it becomes modified into the yolk sac placenta (Figure 25). In the placenta, the tissues of mother and offspring come into intimate contact, and nutrients are passed on to the embryo. Thus the embryo has an almost unlimited supply of nutrients that are shunted to it directly from the mother’s blood stream. Placental viviparity is confined to the most advanced groups of sharks: the smoothhounds, the requiem sharks and the hammerhead sharks. In some viviparous sharks, such as the sharpnose sharks and most of the hammerheads (Figure 26), the umbilical cords are covered with thread or finger-like structures known as "appendiculae." The function of these structures is not clear but it has been postulated that they may serve to absorb histotrophe (uterine milk) produced by the uterine lining.

Figure 26. Scalloped hammerhead embryo. Note the umbilical cord covered with appendiculae.

The patterns described above are only a few of the ones studied. It is certain that many more types exist in this group of ancient fishes, and that there are transitional forms as well. These modes of reproduction are modified by complex biennial or longer reproductive cycles. See Castro (2009) for descriptions of some of these cycles.

In the past, the aquarium community in general contributed little to the knowledge of sharks because few observations were published. Often valuable and interesting observations were forgotten or lost when personnel retired or died. The pattern of neglect is slowly changing, with better education of aquarium personnel, more enlightened leaders, better record keeping, the availability of PIT tags, etc. In 2004 the aquarium community made its first attempt at collecting and publishing observations on elasmobranchs with the publication of the 589-page The Elasmobranch Husbandry Manual (Smith et al., 2004). This fine publication may serve as a guide for future contributions from the aquarium community.

The following topics are suggested for observation and recording:

Oviparous sharks

1. Record any reproductive behavior (courtship, mating, etc). Few species of sharks have been seen mating, so these observations are often valuable and publishable.
2. A description of temperature and light regimes. A temperature log will be necessary to accompany the determination of incubation time.
3. Egg laying behavior, type of substrate used for egg case attachment.
4. In many cases, the egg cases of a given female may bear distinctive markings and it may be possible to attribute egg cases to a given female. Egg cases should be labeled and kept in separate tanks during their developmental period.
5. Record the egg laying rate or periodicity of egg case laying.
6. Record the length of development the time to hatching.
7. Little is known about the length of the reproductive cycle and its periodicity in oviparous sharks and much could be learned by keeping track of egg laying patterns over several years. Because many sharks have biennial reproductive cycles, a female could lay eggs only every other year. Such observations would be most interesting. Whether the constant light and temperature regimes affect the endogenous reproductive cycles of the animals, or whether the endogenous cycles are maintained despite the constant conditions will have to be determined empirically or by comparison to wild-caught specimens.

Viviparous sharks

Obviously, observations on the development of viviparous sharks are difficult to carry out in aquariums, as normally they can only be made by dissection of dead specimens. Observations using methods such as ultrasound usually lack the necessary precision to be useful. Ultrasound has been used to confirm that a shark is pregnant, in most cases a foreknown fact. Sampling of reproductive hormone titers may be feasible under some conditions. Little is known about this subject and much could be learned from aquarium sharks. Injecting newborn sharks with tetracycline may reveal growth rates at a later time, although these growth rates may differ significantly from growth rates in the wild.

Records of aquarist's observations should be permanently maintained at the aquarium. Whenever possible individual sharks should be marked with unobtrusive PIT tags, so that their identity and date of arrival at the aquarium can be determined years later, if it is questionable at later times. The record should be part of the aquarist's duties and should be the property of the aquarium, so that it will remain available even after aquarists leave. However, aquarists should copy their observations so that a second copy of the record is available for future publication if the aquarium loses or does not publish the observations.

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