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Observations on the reproductive cycles of some viviparous North American sharks

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Abstract

The reproductive cycle of sharks is defined by how often a species breeds and consists of two periods: vitellogenesis and gestation. These two periods can run concurrently or consecutively, and the duration of each period is variable. Together, the periods of vitellogenesis and gestation determine the length of the reproductive cycle. The genera *Rhizoprionodon, Mustelus,* and some *Sphyrna* exhibit annual cycles with concurrent vitellogenesis and gestation, and thus, they produce one brood each year. *Carcharias taurus* females apparently have a biennial reproductive cycle with discontinuous ovulation. *Alopias* spp. exhibit an annual cycle with concurrent vitellogenesis and gestation, and have continuous ovulation. *Squalus acanthias* has a squaloid biennial cycle with concurrent vitellogenesis and gestation. Sharks of the genera *Carcharhinus*, some *Sphyrna*, and *Ginglymostoma* have a biennial cycle with consecutive vitellogenesis and gestation. *Galeocerdo cuvier* has a 12-month gestation period in the western Atlantic, its reproductive cycle may be biennial. *Carcharhinus obscurus* has an 18-month gestation period and probably a three-year reproductive cycle. The biennial cycle, with all its variations, is found in sharks of different phyletic origins such as carcharhinoid, squaloid, and orectoloboid sharks, reflecting their common physiological processes that require a long time to accumulate sufficient energy to produce a brood.

Zusammenfassung

Der Fortpflanzungszyklus der Haie definiert sich durch den Fortpflanzungsrhythmus und besteht aus zwei Abschnitten: der Vitellogenese (Dottereinlagerung) und der Trächtigkeit. Die beiden Phasen können parallel laufen oder aufeinander folgen, und die Dauer jeder Phase ist variabel. Zusammen bestimmen die beiden Abschnitte der Vitellogenese und der Trächtigkeit die Länge des Fortpflanzungszyklus'. Die Gattungen *Rhizoprionodon, Mustelus* und teilweise *Sphyrna* haben einen einjährigen Fortpflanzungszyklus mit gleichzeitiger Vitellogenese und Trächtigkeit und folglich einmal im Jahr Nachwuchs. Die Weibchen von *Carcharias taurus* haben offenbar einen zweijährigen Zyklus mit diskontinuierlicher Ovulation. Bei *Alopias* spp. ist der Zyklus einjährig bei zeitgleicher Vitellogenese und Trächtigkeit sowie kontinuierlicher Ovulation. *Squalus acanthias* zeigt den dornhai-typischen zweijährigen Fortpflanzungszyklus mit parallel laufender Vitellogenese und Trächtigkeit. Die Haie der Gattungen *Carcharhinus, Sphyrna* (teilweise) und *Ginglymostoma* bekommen alle zwei Jahre Nachwuchs, Dottereinlagerung und Trächtigkeit folgen aufeinander. Bei *Galeocerdo cuvier* im West-Atlantik dauert die Trächtigkeit 12 Monate, der Zyklus insgesamt dürfte zweijährig sein. *Carcharhinus obscurus* hat eine 18-monatige Trächtigkeitsphase und wahrscheinlich einen dreijährigen Fortpflanzungszyklus. Der zweijährige Zyklus mit den verschiedenen Varianten kommt also bei Haien unterschiedlicher stammesgeschichtlicher Herkunft vor, so bei Angehörigen von *Carcharhinus, Squalus* und *Orectolobus,* er spiegelt die physiologischen Vorgänge wider, die längere Zeit brauchen, um genügend Energie für die Produktion von Nachwuchs aufzubauen.

Résumé

Le cycle de reproduction des requins est défini par le nombre d'actes reproductifs d'une espèce et comprend deux périodes; la vitellogenèse et la gestation. Ce deux périodes peuvent être simultanées ou consécutives et la durée de chaque période est variable. Ensemble, les périodes de vitellogenèse et de gestation déterminent la longueur du cycle de reproduction. Les genres *Rhizoprionodon, Mustelus* et certains *Sphyrna* présentent des cycles annuels avec vitellogenèse et gestation simultanées et ils produisent donc une progéniture par an. Les femelles de *Carcharias taurus* semblent connaître un cycle de reproduction biennal avec ovulation discontinue. Les espèces d'*Alopias* ont un cycle annuel, avec vitellogenèse et gestation simultanées, et ont une ovulation continue. *Squalus acanthias* a un cycle biennal squaloïde, avec vitellogenèse et gestation simultanées. Le requins des genres *Carcharhinus,* certains *Sphyrna,* et *Ginglynostoma* ont un cycle biennal avec vitellogenèse et gestation consécutives. *Galeocerdo cuvier* a une période de gestation de 12 mois, dans l'Atlantique ouest, et son cycle de reproduction peut être biennal. *Carcharhinus obscurus* a une période de gestation de 18 mois et probablement un cycle de reproduction de trois ans. Le cycle biennal, avec toutes ses variations, se trouve chez des requins de diverses origines phylétiques, comme les requins carcharhinoïdés, squaloïdés et orectoloboïdés, en accord avec leurs processus physiologiques communs qui réclament un long laps de temps pour accumuler l'énergie nécessaire à la production de leur progéniture.

Sommario

Il ciclo riproduttivo degli squali è definito dalla frequenza con cui una specie dà origine a una prole e consta di due fasi: vitellogenesi e gestazione. Questi due periodi possono essere simultanei o sequenziali e la durata di ognuno è variabile. Nell'insieme, vitellogenesi e gestazione determinano la lunghezza del ciclo riproduttivo. I generi *Rhizoprionodon, Mustelus* e alcune specie di *Sphyrna* hanno cicli annuali con vitellogenesi e gestazione contemporanee e pertanto generano una prole all'anno. Le femmine di *Carcharias taurus* hanno in ciclo biennale con ovulazione discontinua. *Alopias* spp. ha un ciclo annuale con vitellogenesi e gestazione contemporanee e ha ovulazione continua. *Squalus acanthias* ha un ciclo squaloide biennale con vitellogenesi e gestazione contemporanee. Gli squali dei generi *Carcharhinus,* alcune specie di *Sphyrna* e *Ginglymostoma* hanno un ciclo biennale con vitellogenesi e gestazione sequenziali. Nell'Atlantico occidentale *Galeocerdo cuvier* ha un periodo di gestazione di 12 mesi e il ciclo riproduttivo potrebbe essere biennale. *Carcharhinus obscurus* ha una gestazione di 18 mesi e probabilmente il ciclo riproduttivo ha una durata di tre anni. Il ciclo biennale, in tutte le sue varianti, è presente negli squali di diversa origine filetica come i carcarinoidi, gli squaloidi e gli orectoloboidi e riflette la loro comune fisiologia che richiede tempi lunghi per accumulare sufficiente energia necessaria a dare origine a una prole.

INTRODUCTION

The reproductive cycle of sharks can be defined by how often a species breeds and consists of two periods. The first is the vitellogenesis period, when nutrients stored in the liver are transferred to the developing oocytes in the ovary or ovaries, and when oocytes accumulate yolk and grow rapidly. The second is the gestation period, or the time of embryonic development from fertilization to birth. Vitellogenesis and gestation can run concurrently or consecutively, and the duration of each period is variable. The duration of these periods depends on how effectively the mother can sequester energy from the environment and transfer it to the developing oocytes or embryos, and on the mode of embryonic nutrition. Together, these two periods, vitellogenesis and gestation, determine the length of the reproductive cycle.

The reproductive cycles of sharks have seldom been investigated. Several patterns of reproductive cycles are evident, and the purpose of this paper is to present some of the evidence for these cycles that I have observed in viviparous North American shark species. This paper is not a comprehensive review of the reproductive cycles of sharks; it is a sketch of the cycles of some North American sharks, as it is certain that other patterns exist. Hopefully, this paper will stimulate others to demonstrate other reproductive cycles.

In a given shark population, the females can be reproductively synchronous or asynchronous. Synchronous females are in the same stage of the reproductive cycle, while in a population of asynchronous females, all can be at different stages of the reproductive cycle. Generally, the females are synchronous in species living in temperate waters, where birth must occur at the most propitious time for the young to survive, generally in spring or summer when temperatures are well within the thermal tolerances of the species and when prey or food are abundant (Fig. 1). Females are often reproductively asynchronous in species dwelling in tropical waters, where stable environmental conditions and abundant food throughout the year permit reproduction and birth to occur year around (Fig. 2).

When dealing with populations of synchronous females, the length of the gestation period can be calculated by following the development of the embryos throughout gestation. The length of the vitellogenesis period can be estimated by following the development of oocytes. The length of the reproductive cycle depends on the duration of vitellogenesis and of gestation, and whether the two periods are concurrent or consecutive. Several patterns result from the different possible combinations. Some of these patterns have a phylogenetic basis. For example, squaloid sharks have biennial cycles with concurrent vitellogenesis and gestation (see below), while sharks of the genus *Carcharhinus* generally have biennial cycles with consecutive, year-long vitellogenesis and gestation (Castro 1993, 1996).

MATERIALS AND METHODS

Sharks were collected or examined from South Carolina to Florida, primarily in commercial fisheries from 1981 to 2007. Female sharks were examined and the reproductive tracts removed for examination and photography. Sharks, including embryos, were measured in a straight line from the tip of the nose to the tip of the upper caudal lobe

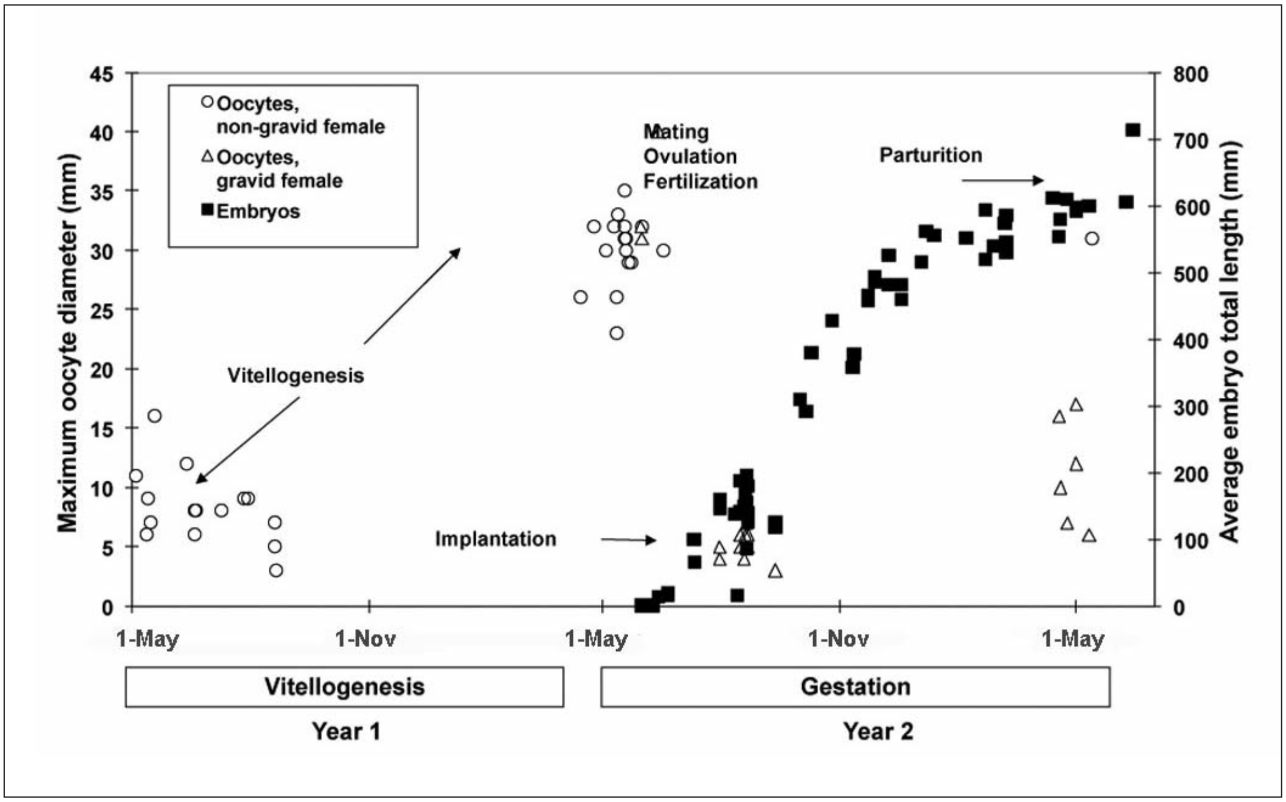

Fig. 1. *Carcharhinus limbatus*, synchronous reproduction, graph of embryo and oocyte growth.

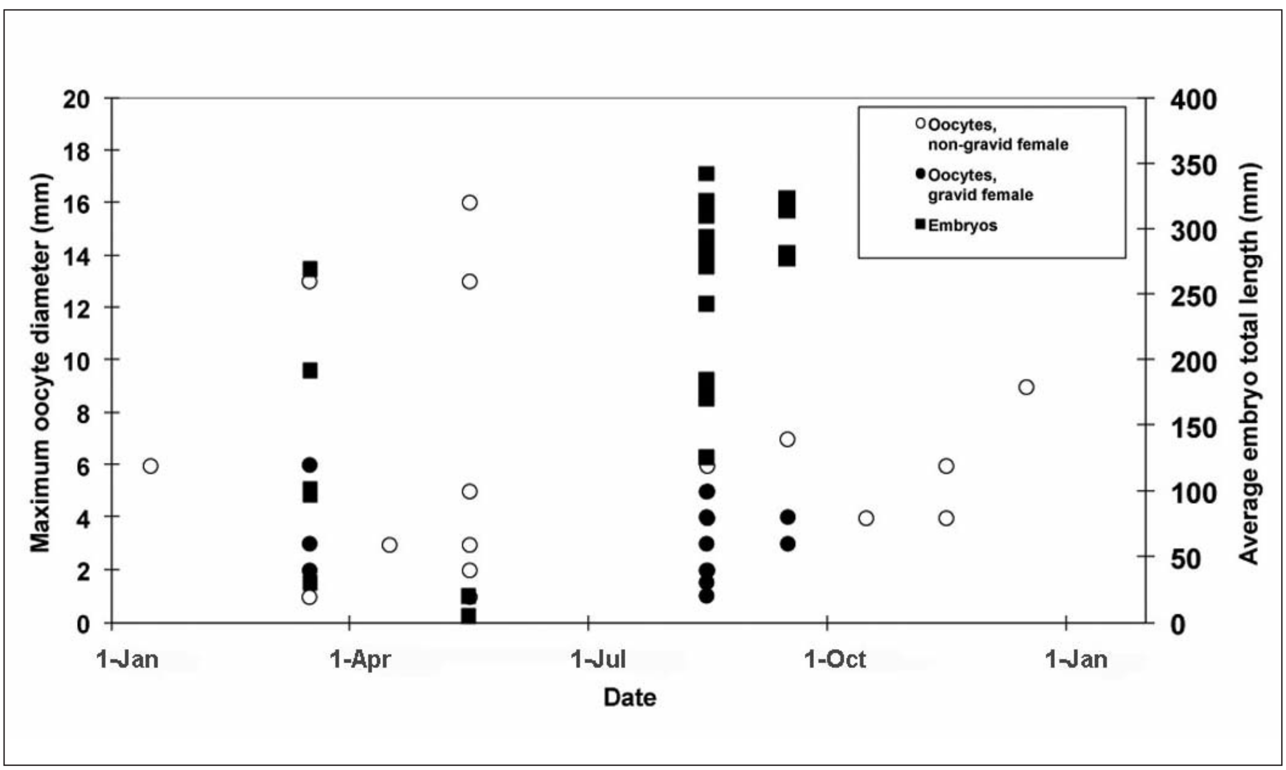

Fig. 2. *Rhizoprionodon porosus*, asynchronous reproduction, graph of embryo and oocyte growth.

of the tail, with the tail at its maximum extension. Records of the Cape Haze Marine Laboratory (1955 to 1968) were made available through the courtesy of Eugenie Clark.

OBSERVATIONS AND RESULTS.

The following six types of reproductive cycles could be discerned:

1. Carcharhinoid annual cycle with concurrent vitellogenesis and gestation

The more advanced sharks of the genera *Rhizoprionodon, Mustelus,* and some *Sphyrna* (e.g., *lewini, tudes*, and *tiburo)* are placental and exhibit annual cycles with concurrent vitellogenesis and gestation (Castro 1989, Castro & Wourms 1993). Thus, they carry developing young and oocytes at the same time (Figs 3-4). A female reaching maturity and ovulating for the first time mates and begins to gestate. It will also enter the vitellogenesis period, and at term will have fully developed

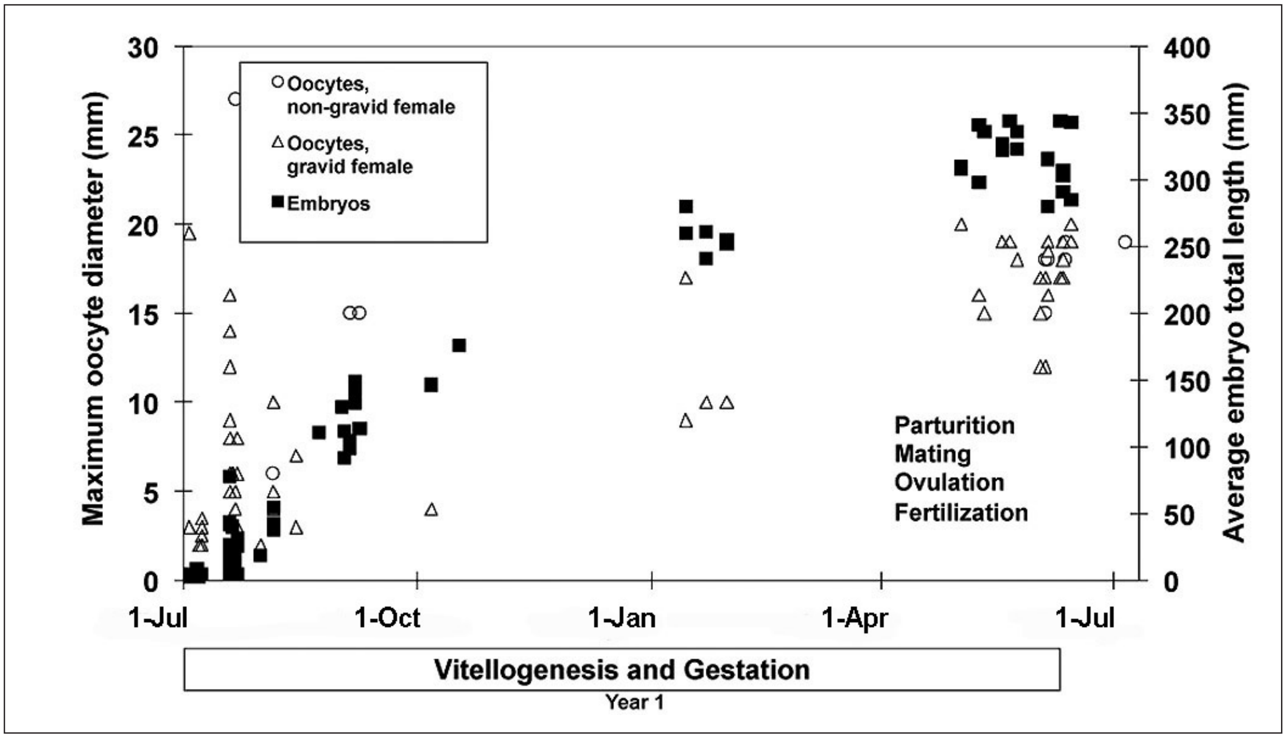

Fig. 3. *Rhizoprionodon terraenovae*, carcharhinoid annual cycle with concurrent vitellogenesis and gestation.

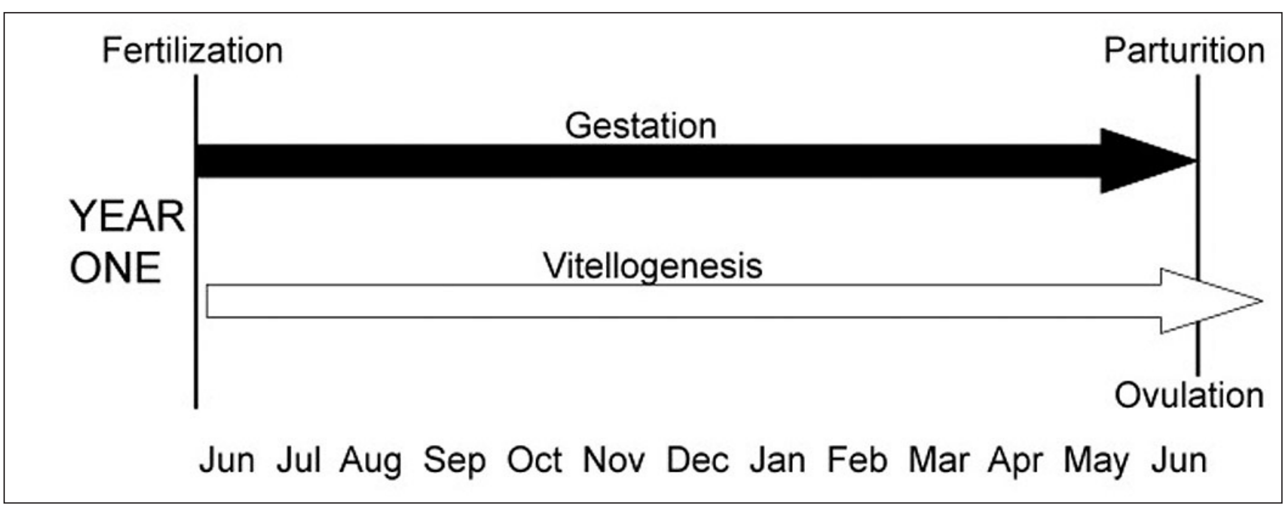

Fig. 4. Carcharhinoid annual cycle schematic.

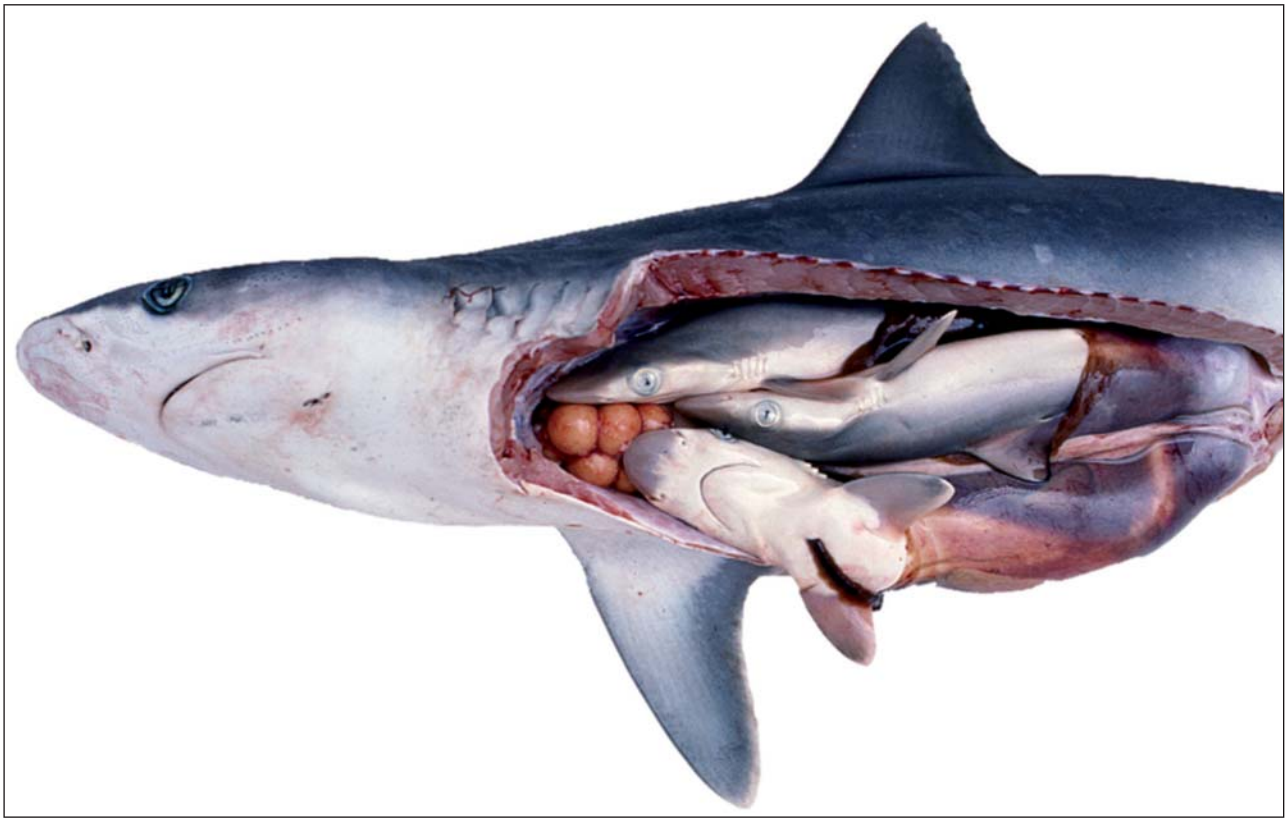

Fig. 5. *Rhizoprionodon terraenovae*, gravid female carrying term young and ripe oocytes. Photo by J. I. Castro.

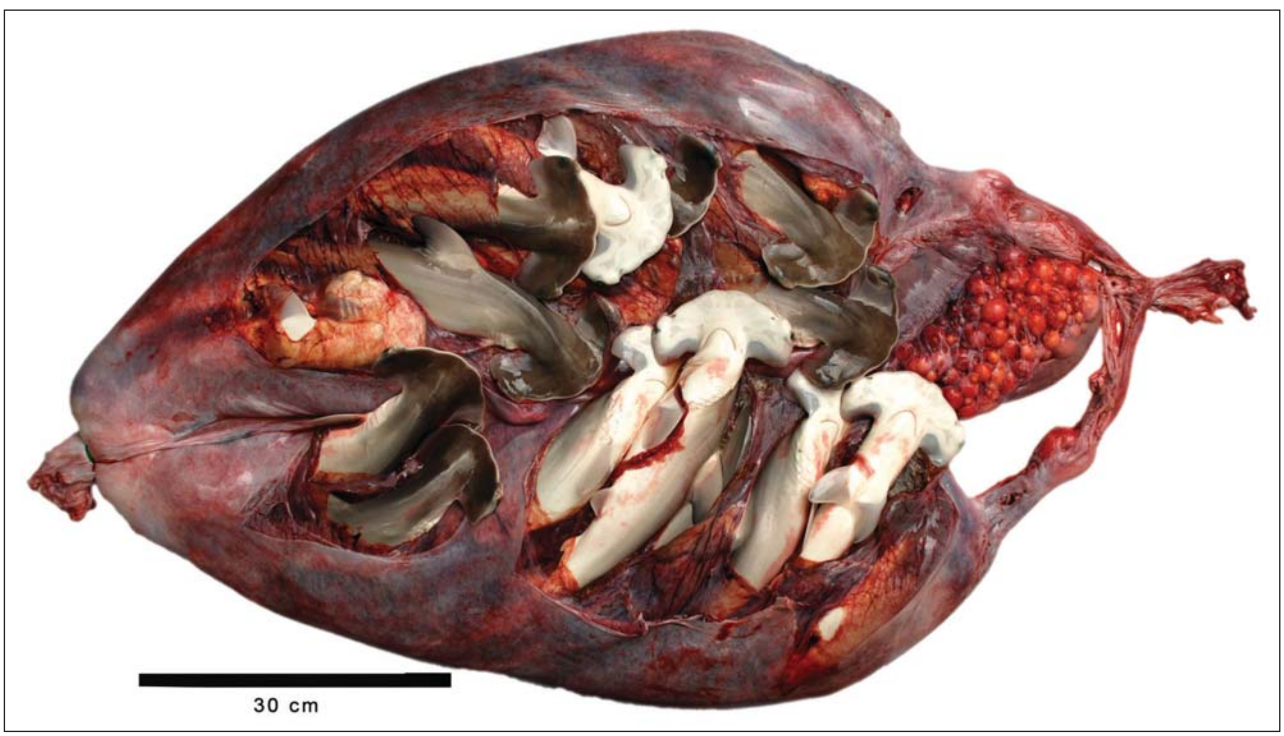

Fig. 6. *Sphyrna lewini*, gravid uterus. Note near term young and active ovary (on right side of photograph). Photo by J. I. Castro.

young and fully developed oocytes (Figs 5-6). In these sharks, all the mature females will be gravid during the season of gestation, and thus they produce one brood each year. The bonnethead (*Sphyrna tiburo* Linneus, 1758) has an interesting annual cycle, with mating occurring in October and November. However, embryonic development is delayed until March and birth occurs in August and September (Parsons 1993, Manire et al. 1995). In some of the shark species with annual reproduction, such as the genera *Rhizoprionodon* and *Sphyrna*, the umbilical cords are covered in appendiculae (Alcock 1890). The function of these structures and how they relate to the shortest reproductive cycles in sharks are still unclear.

In lamnoid sharks, the embryos feed on eggs ovulated into the uterus for their nutrition (oophagy; Springer 1948, Bass et al. 1975). Some lamnoid sharks show annual reproductive cycles, although in most cases the evidence is scanty. There are, at least, two types of reproductive cycles in these sharks:

2. Lamnoid biennial cycle with consecutive vitellogenesis and gestation and with discontinuous ovulation

Sand tiger shark *(Carcharias taurus* Rafinesque, 1810) females are synchronous (Gilmore et al. 1983, Gilmore 1993) and have a gestation period of about nine months (Fig. 7). Only a few of the ovulated eggs are fertilized at the beginning of the ovulatory period, and subsequent eggs are not fertilized. The embryos exhaust the yolk stored in their yolk sacs relatively early in their development and then start to feed on the multiple egg cases found in the uterus. In the first six months of gestation, the embryos consume large quantities of eggs in excess of their metabolic requirements and store much yolk in their highly distended yolk stomachs (Fig. 8). Ovulation continues for about five to six months until the ovary becomes flaccid and reduced in size by November (Fig. 9). At the time of birth the ovary is much reduced in size. It appears unlikely that a female could give birth in February or March and then sequester enough nutrients to start vitellogenesis and be ready to ovulate, conceive, and nourish its embryos by June, only three months later, and some authors have suggested a biennial cycle. Branstetter & Musick (1994) suggested a biennial reproductive cycle for the sand tiger shark, but provided no evidence of for the capture of mature non-gravid females taken during the breeding period of the species. It is possible that females referred to as “in a resting stage with small ovarian egg follicles” (Branstetter & Musick 1994: 248) were immature, given that the oocytes in lamnoid sharks do not differ greatly in size in ovulatory and “resting” females. Another paper by Lucifora et al. (2002) also suggested a biennial cycle for the sand tiger shark off Argentina, but the paper lacked convincing evidence (the authors had no direct evidence of mating, and

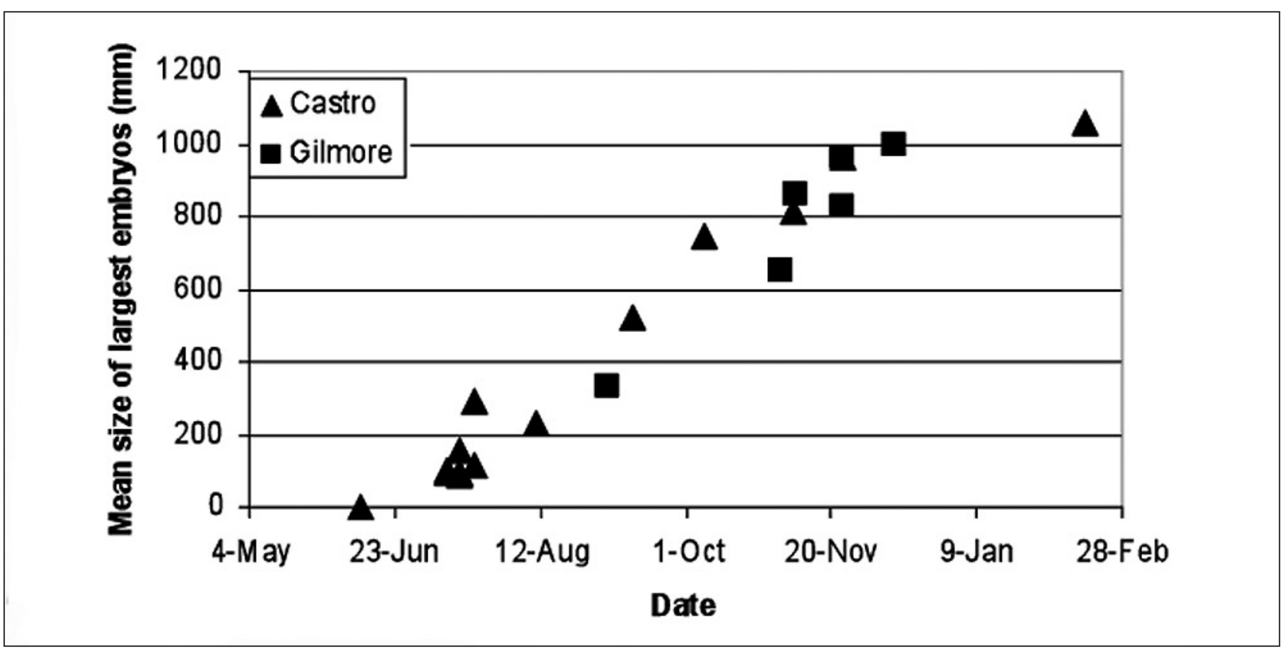

Fig. 7. *Carcharias taurus*, gestation period.

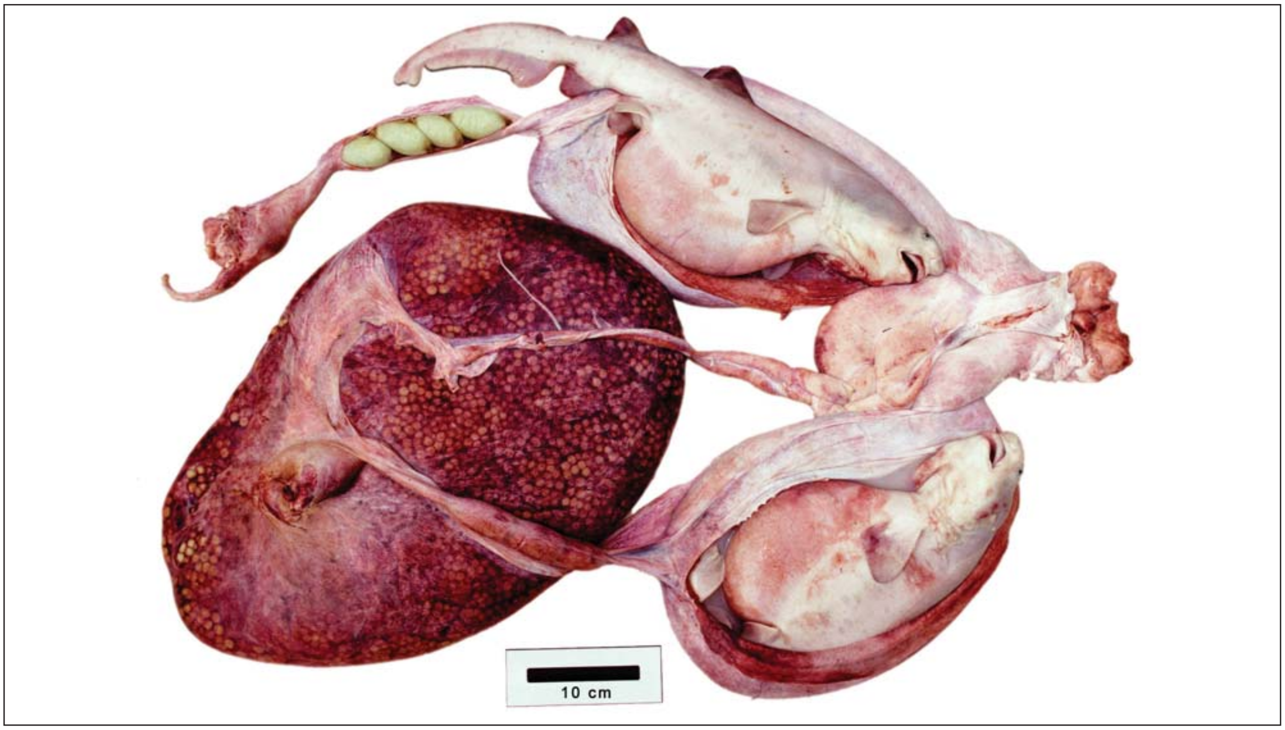

Fig. 8. *Carcharias taurus*, embryos taken in September, note egg cases in opened oviduct and large size of ovary. Photo by J. I. Castro.

Fig. 9. C*archarias taurus*, embryos and ovary from female taken in November. Note small and flaccid ovary. Photo by J. I Castro.

encountered no gravid females). Recent research by Australian workers also indicated a biennial cycle (Bansemer 2009).

In contrast to the Australian observations, all adult females, sampled by R. Grant Gilmore and me in the southeastern United States, were gravid from June to January/February (the time of gestation for the species, based on our observations). This has led Gilmore to conclude, that in the absence of non-gravid females, an annual reproductive cycle would be indicated. If sand tiger sharks had a biennial cycle, it would be necessary for all the "resting" females to leave the southeastern United States waters after parturition and spend their off year elsewhere, just to reappear the following year at mating time. However, based on the flaccid condition of the ovary of term females and the Australian evidence, I suggest that sand tiger sharks in North America are biennial and that the population of non-gravid females is probably highly localized and has not been located. If a population of non-gravid adult females could be located during the months of July to January, then this finding would support the hypothesis of a biennial cycle. Until such population is located during the months of July to January, the biennial reproductive cycle of the sand tiger shark cannot be considered demonstrated and further research is needed.

The shortfin mako *(Isurus oxyrinchus* Rafinesque, 1810) appears to have this type of lamnoid reproductive cycle, based on the ovarian cycle, but more evidence is needed. Mollet et al. (2000) suggested a 15 to 18 month gestation for the shortfin mako. However, it appears unlikely that a fast-growing lamnoid shark would have such a long gestation period. Again, more gravid specimens need to be examined before the length of the reproductive cycle can be established.

3. Lamnoid annual cycle with concurrent vitellogenesis and gestation and with continuous ovulation

Pelagic thresher *(Alopias pelagicus* Nakamura, 1935) embryos examined in September in the Gulf of California ranged from 1 mm to 1390 mm demonstrating that females are not synchronous (Fig. 10). Liu et al. (1999) reached similar conclusions based on Taiwanese specimens, stating that the species had no specific period of parturition and no resting stage in its reproductive cycle. In the thresher sharks *(A. pelagicus* and *A. superciliosus* Lowe, 1839) only the first two ovulated eggs are fertilized and each is enclosed in an egg case (Fig. 11). Thereafter, the egg cases contain several eggs and are intended to feed the young. In these sharks, vitellogenesis never ceases, and the ovary does not decrease in size during pregnancy as it does in the sand tiger shark (Fig. 12).

With a continuous food supply, thresher shark embryos feed during the entire developmental period and do not acquire the distended yolk stom-

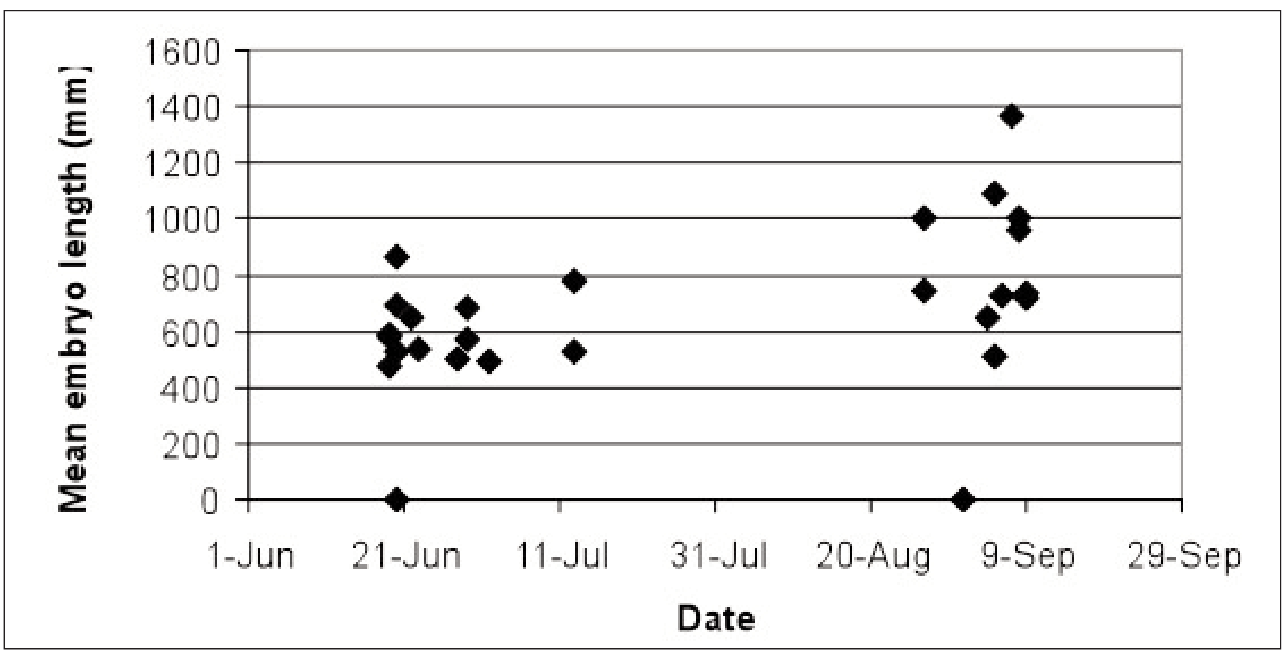

Fig. 10. *Alopias pelagicus*, embryo growth.

achs of sand tiger shark and mako embryos. Continuous vitellogenesis also insures that the ovary at term (or parturition) is as large as the ovary at the beginning of pregnancy, thus females could conceive again shortly after parturition (Fig. 13).

4. Squaloid biennial cycle with concurrent vitellogenesis and gestation

The spiny dogfish *(Squalus acanthias* Linneus, 1758) is the best-known example of this type of reproductive cycle. A female having just reached maturity, mates, ovulates for the first time, and begins to gestate. Vitellogenesis begins shortly after the beginning of gestation. Thus these females carry developing oocytes and developing embryos at the same time, and at the time of birth both embryos and oocytes have reached their maximum develop-

Fig. 11. *Alopias pelagicus*, first pair of egg cases (upper pair) each containing a single fertilized egg, and subsequent egg cases (lower pair) each containing numerous ova. Photo by J. I. Castro

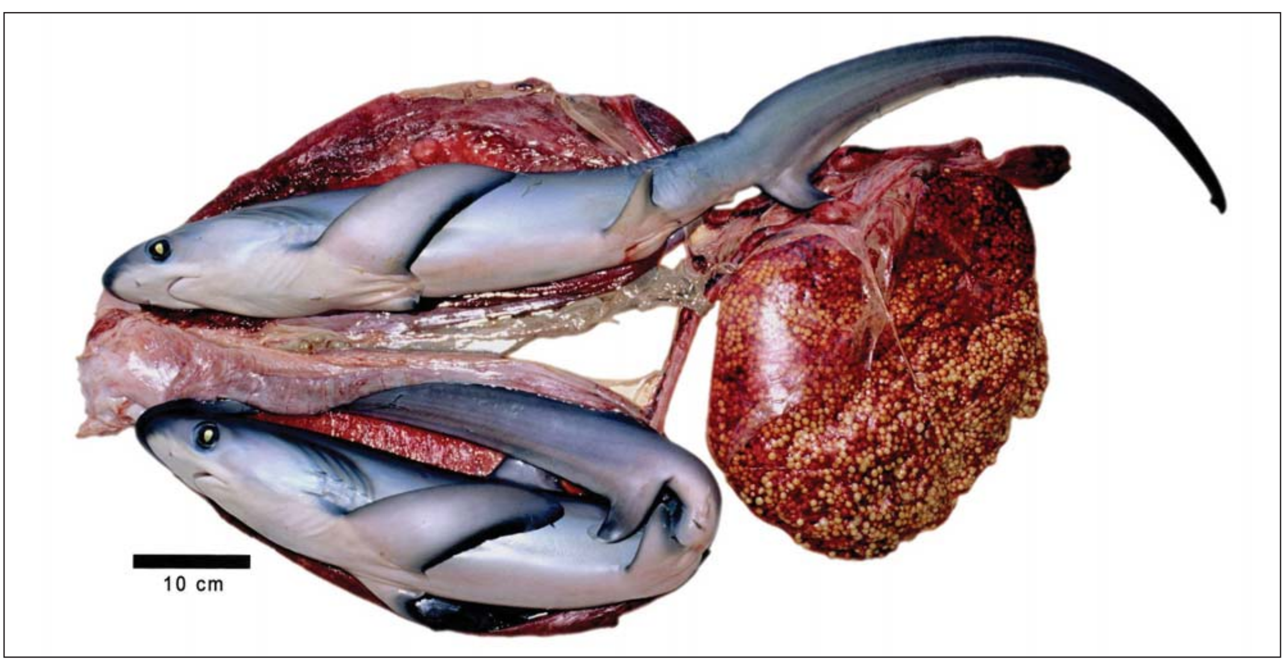

Fig. 12. *Alopias pelagicus*, 1110 and 1080-mm embryos in their second trimester, note large size of ovary. Photo by J. I. Castro

ment (Fig. 14). Gestation lasts about 23 months (Ketchen 1972, Jones & Geen 1977) and vitellogenesis appears to last slightly longer. Because of the two-year-long cycle, one can encounter two sizes of embryos most of the year, those of the females on their first year of gestation, and those of females on their second year (Fig. 15). Females mate shortly after giving birth, and the cycle begins anew, thus the cycle is said to be biennial (Fig. 16). This type of reproductive cycle has been demonstrated only for the spiny dogfish, but limited evidence (e.g. two sizes of embryos found at the same time of the year in several species of *Centrophorus)* suggests that it may be the rule in squaloid sharks.

5. Carcharhinoid and orectoloboid biennial cycle with consecutive vitellogenesis and gestation

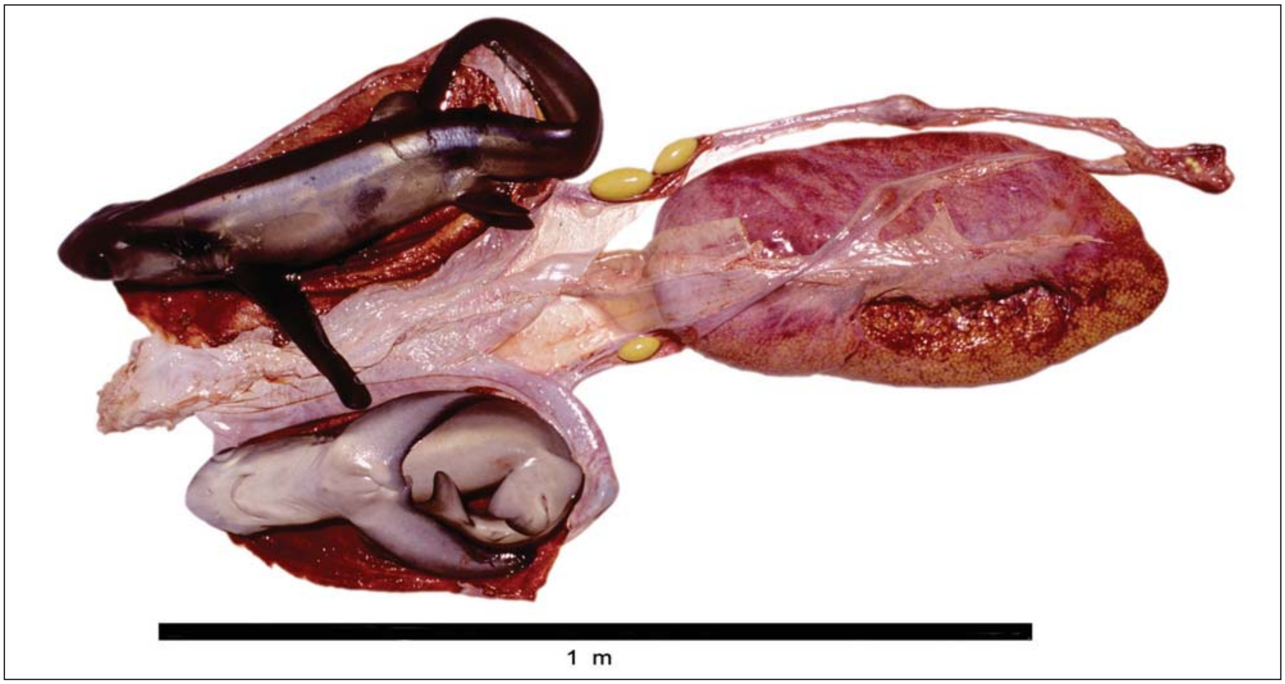

Fig. 13. *Alopias superciliosus*, term embryos. Note size of ovary, and yellow egg cases (center) in transit to embryos. Photo by J. I. Castro

Fig. 14. *Squalus acanthias*, female reproductive tract with term embryos and ripe oocytes. Photo by J. I. Castro

This is the type of reproduction found in many of the sharks of the genus *Carcharhinus*, some hammerheads *(Sphyrna mokarran* Rüppell, 1837 and *S. zygaena* Linneus, 1758), and the nurse shark *(Ginglymostoma cirratum* Bonnaterre, 1788). A female reaching maturity mates, ovulates, and begins gestation. It will gestate for about five to twelve months. After parturition, the female has an inactive ovary and enters the vitellogenesis period, which lasts from a year to 18 months. In the early stages of the vitellogenesis period, there is little visible growth of the oocytes and the female is said to be "resting". In the second half of the vitellogenesis period the oocytes grow rapidly. For example, in many of the species of *Carcharhinus*, a female conceiving in June of the first year will gestate for a year and give birth a year later in June of the following year (Fig. 17). It then enters the vitellogenesis period and its oocytes will mature a year later in June of the second year, thus having a biennial cycle (Fig. 18). In species having biennial reproductive cycles with year-long gestation periods, the population of adult females shows a 50/50 ratio of gravid to non-gravid females during most of the

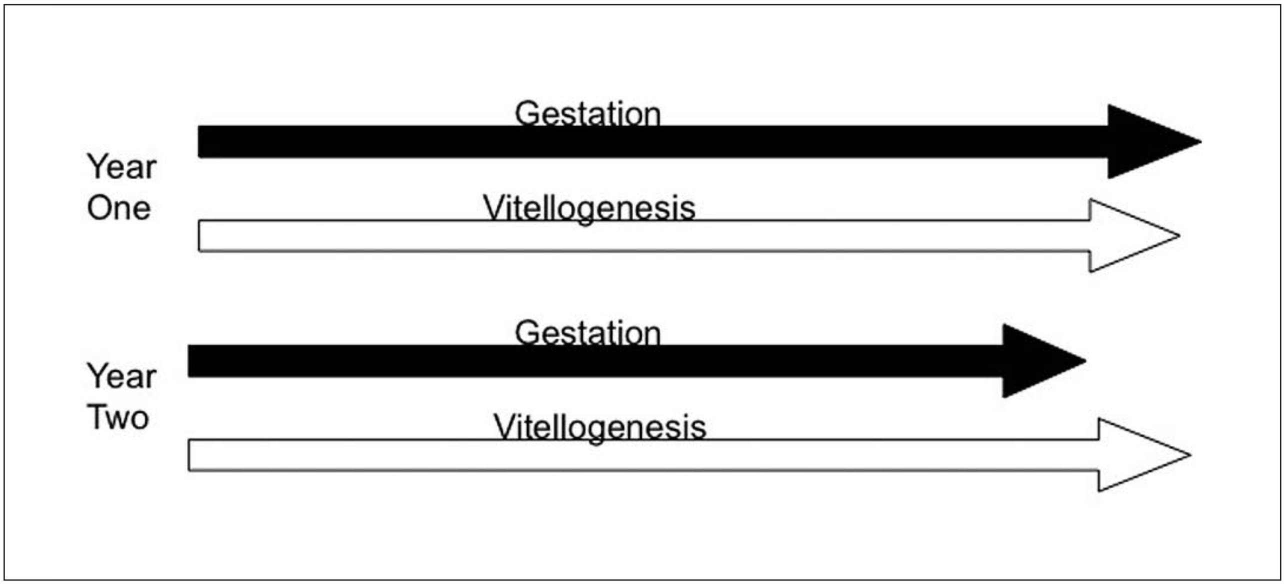

Fig. 15. Schematic of squaloid biennial reproductive cycle.

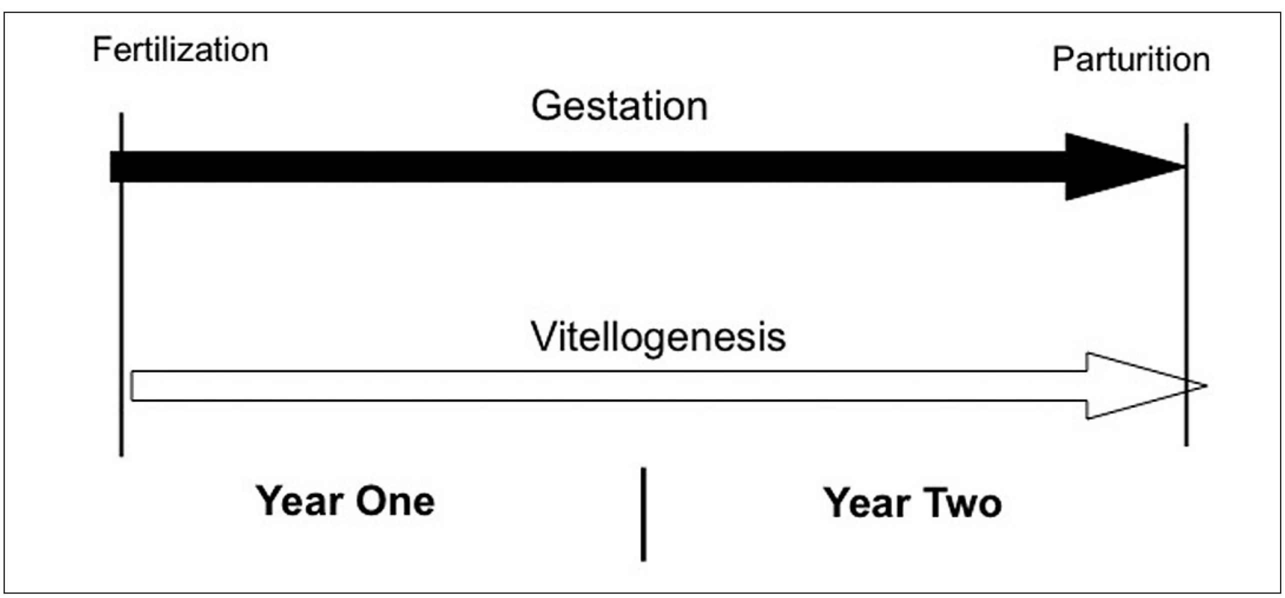

Fig. 16. Schematic of squaloid biennial reproductive cycle by year.

year. At parturition time in June, the mature females can be divided into two equal groups: one half is carrying term young and giving birth, and the other half is carrying ripe oocytes and mating. Inspection of a term female shows that it has an inactive ovary (Fig. 19). In species with shorter gestation periods, the 50/50 ratio will occur only at the time of gestation. After the time of parturition, all females (those which just gave birth and those which gave birth the previous year) will only have developing oocytes in different stages.

The nurse shark exhibits a similar biennial cycle but with a much shorter gestation period (Fig. 20). A female mating in June gestates for five to six months and gives birth in late November (Castro 2000). It then enters the vitellogenesis period, which lasts about 18 months. Consequently, it misses the mating season the following June, as it has no ripe oocytes. Its oocytes will mature in June of the following year, when it will mate, two years after the previous mating. Thus, the cycle of the nurse shark is biennial and the species produces a brood every two years (Figs 21-22). In early June the biennial cycle is confirmed by the 50/50 proportion of mature females carrying ripe oocytes to that of females carrying small, immature oocytes (those which gave birth the previous November).

It is likely that the tiger shark *(Galeocerdo cuvier* Peron & Lesueur, 1822) belongs to this group of carcharhinoid sharks with biennial reproductive cycles, although the evidence is far from clear. The tiger shark is a large carcharhinid shark widely distributed in tropical and subtropical waters. It is a migratory species whose movements cover wide areas, making it difficult for biologists to see a complete reproductive cycle at any one location. Thus, despite its abundance and wide distribution, very little is known about its reproductive processes. The tiger shark is an aplacental species, differing from most of the members of the Carcharhinidae that nourish their young through a placental connection. 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 egg envelope. The absence of any folding in their distal walls and the embryos being free inside the membranous egg envelope indicate that a placental connection does not form in the tiger shark (Sarangdhar 1943).

Whitney & Crow (2007) analyzed tiger shark data collected in research and control programs in Hawaii in the 1960s, and on nine sharks collected in 2003 to 2005. They concluded that tiger sharks had a gestation period lasting 15 to 16 months,

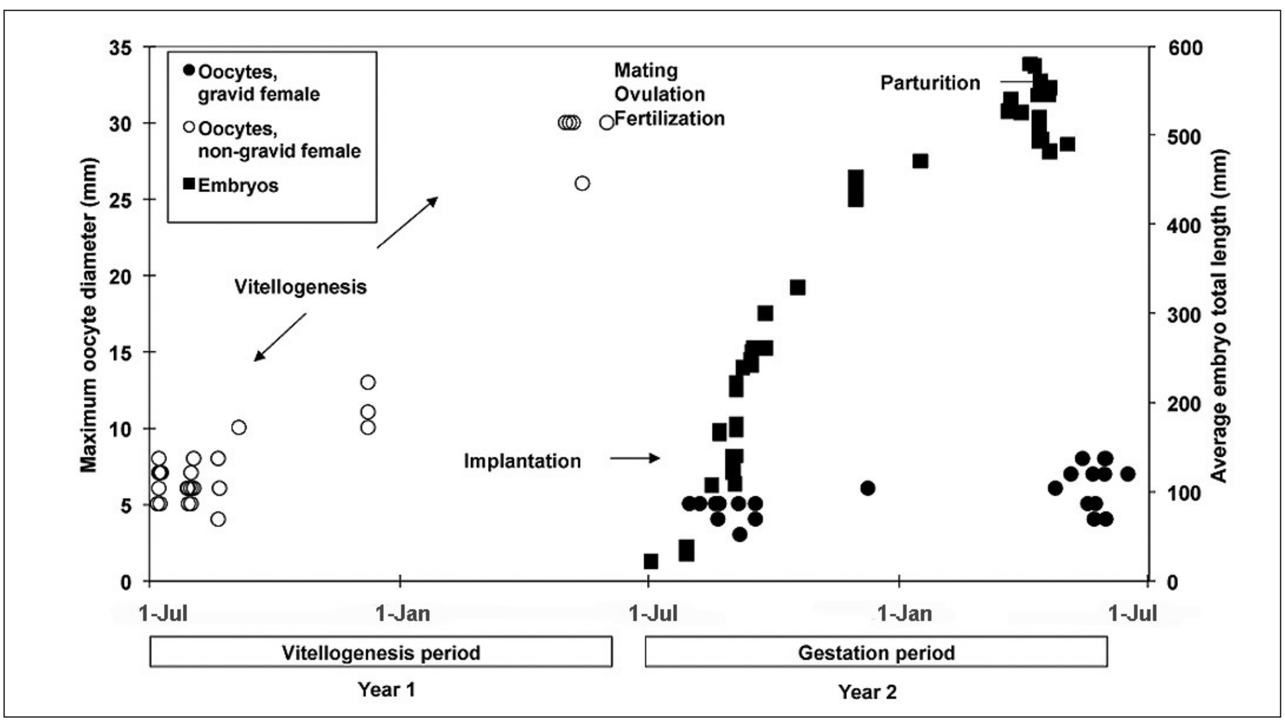

Fig. 17. *Carcharhinus isodon*, carcharhinoid biennial cycle, oocyte and embryo growth chart.

and that tiger sharks give birth only once every three years. Data on western North Atlantic (primarily Gulf of Mexico and Caribbean) tiger sharks does not support the hypothesis of a 15 to 16 month gestation advanced by Whitney & Crow (2007). Based on observations of tiger sharks carrying recently fertilized uterine eggs in mid-May (Cape Haze Marine Laboratory data) and on numerous reports of tiger sharks carrying term young in May and June, I propose that tiger sharks have a 12-month gestation period. Figure 23 also shows that the population of adult females is reproductively synchronous but that there is a two-month "window" for the entire population. Thus, one must measure the gestation period from the first time when females carrying very small embryos appear (in May) to the beginning of the birth period (the following May or when embryos reach the birth size in the graph), or from the end of the period when conception could have

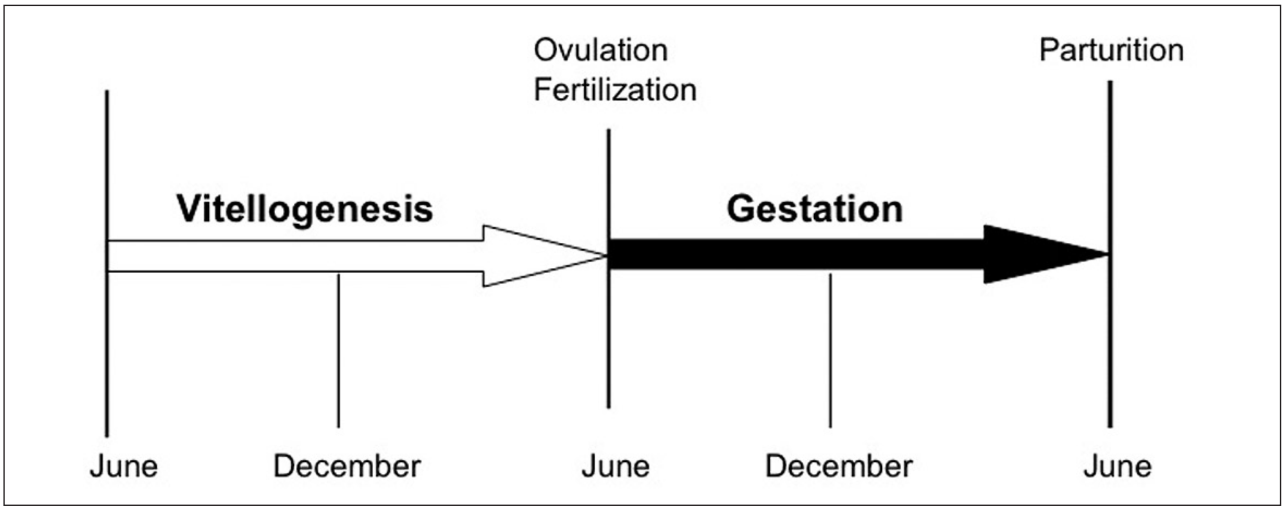

Fig. 18. Carcharhinoid biennial cycle with consecutive vitellogenesis and gestation, schematic.

Fig. 19. *Carcharhinus acronotus*, term female. Notice inactive ovary with small oocytes (on right side between oviducts). Photo by J. I. Castro.

occurred (July) to the time when the latest embryos were found (July), both measurements yielding about 12 months. This estimate agrees with Clark & von Schmidt (1965) who concluded that gestation could be slightly over a year based on the presence of both early and late embryos in spring. Because term females do not have active ovaries at the time of parturition, it is obvious that tiger sharks do not have an annual cycle.

The duration of the post partum vitellogenesis period cannot be determined at this time for the Gulf of Mexico and Caribbean population, as it must be determined from the proportion of gravid to non-gravid females. Given that the gestation period lasts 12 months, it is possible that tiger sharks may have the typical carcharhinid biennial reproductive cycle, but this remains to be demonstrated. It is also possible that differences may exist between the Pacific and Atlantic tiger sharks.

In species with biennial reproductive cycles, the

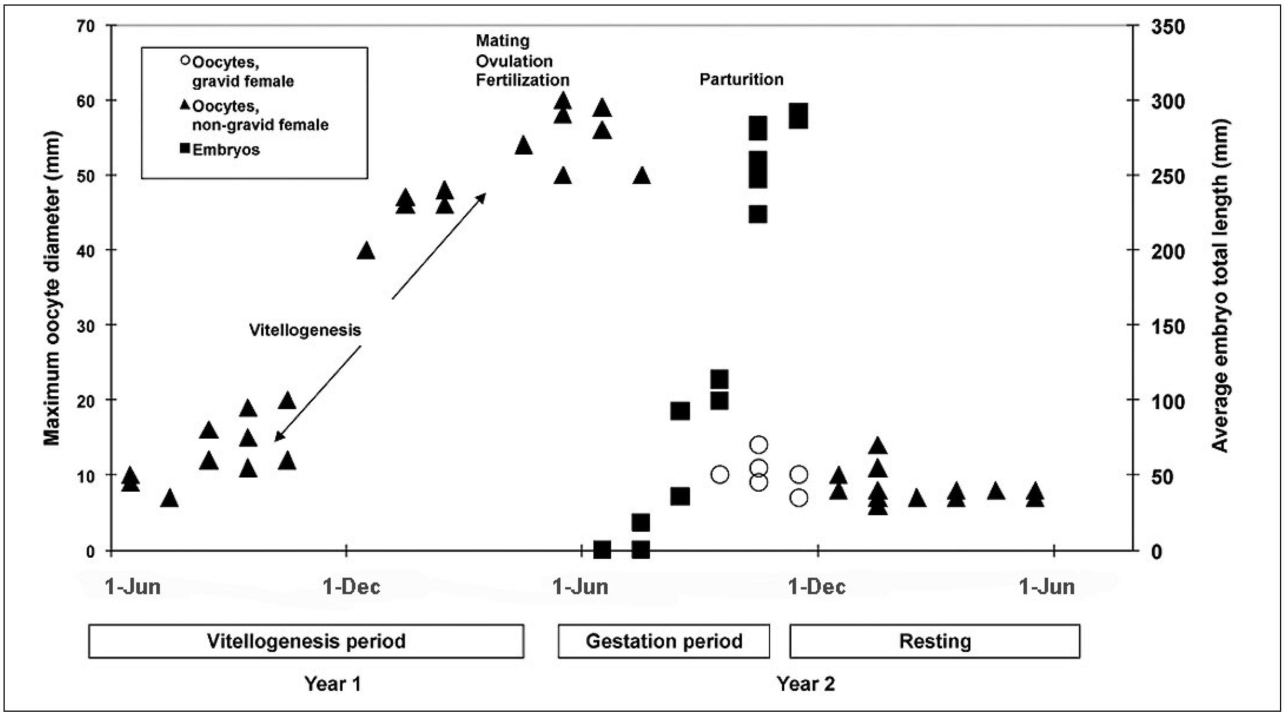

Fig. 20. *Ginglymostoma cirratum*, embryo and oocyte growth chart.

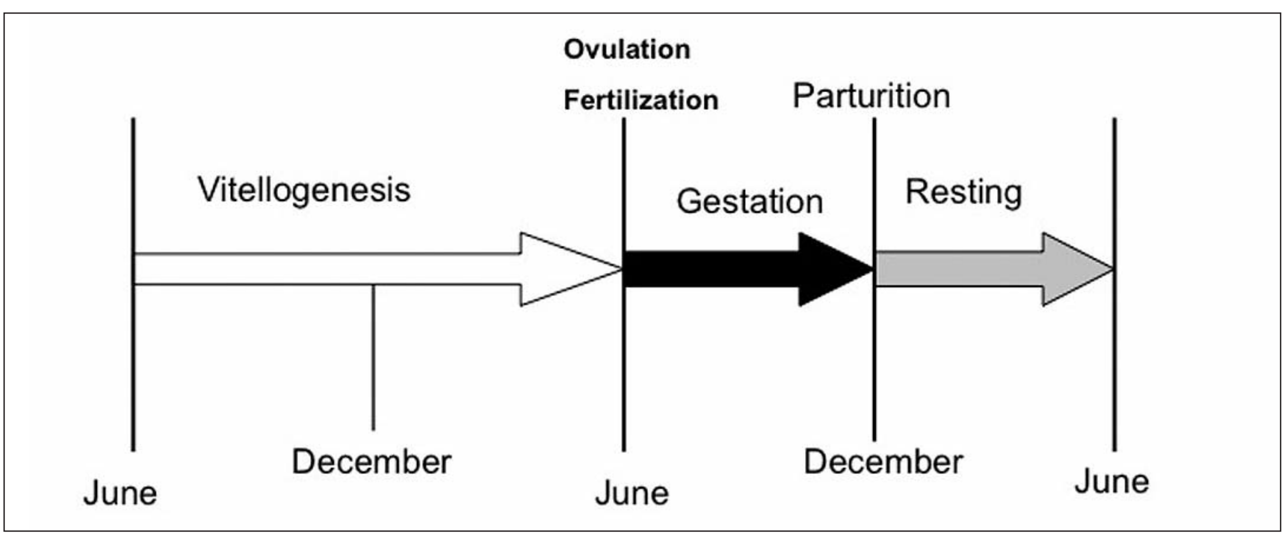

Fig. 21. *Ginglymostoma cirratum,* reproductive cycle schematic.

early stages of vitellogenesis are slow and not easily discernible, and the period after birth has often been called a "resting stage" because the female appears to be reproductively at rest. However, this concept is misleading as this is a physiologically and energetically active period, when the female actively replaces into the liver the energy spent during the previous season in producing large oocytes or in nourishing the embryos to large size. Later in the cycle, during active vitellogenesis, the nutrients are transferred to the oocytes in the form of yolk, and the oocytes grow noticeably.

6. Carcharhinoid triennial cycle with consecutive vitellogenesis and gestation

Three-year (triennial) reproductive cycles with gestation periods of 18 to 22 months have been postulated for the dusky shark *(Carcharhinus obscurus* Lesueur, 1818) by Clark & von Schmidt (1965) and Musick et al. (1993), and for the tiger shark by Whitney & Crow (2007). The case of the

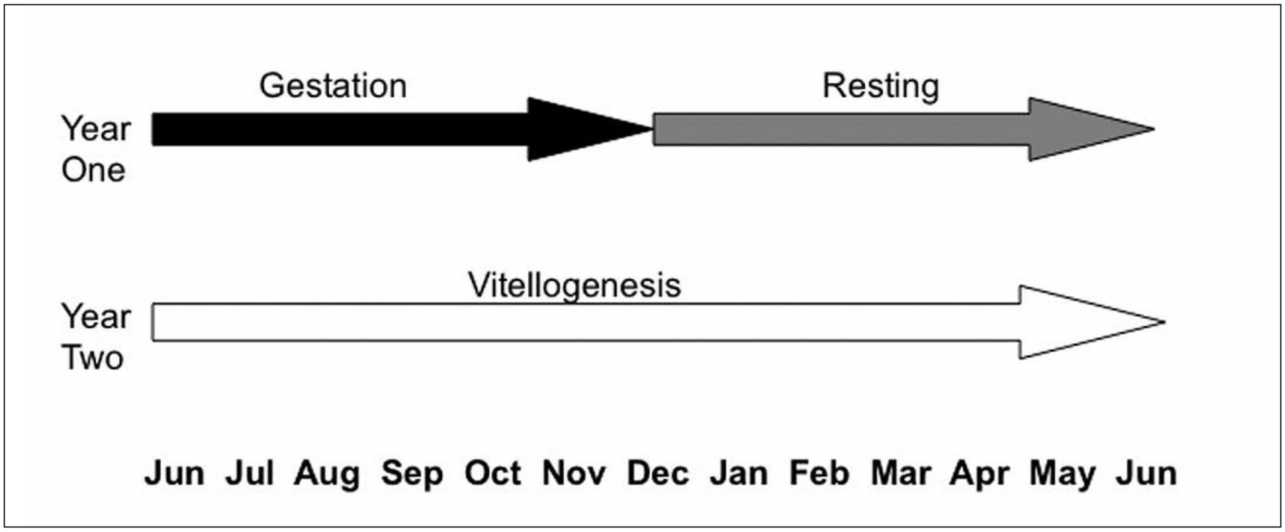

Fig. 22. *Ginglymostoma cirratum,* reproductive cycle schematic by year.

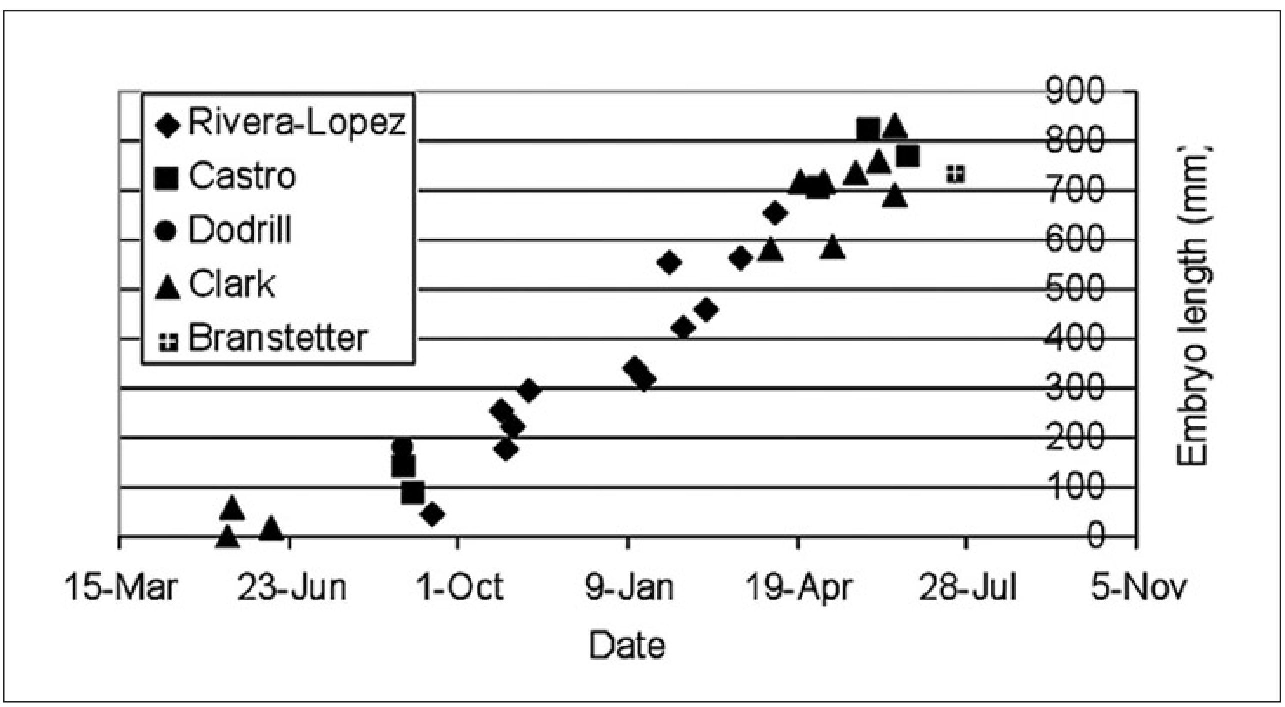

Fig. 23. *Galeocerdo cuvier*, gestation period.

dusky shark is based mainly on data collected by Clark & von Schmidt (1965) in the Gulf of Mexico. These authors reported that gravid dusky females taken off Sarasota, Florida, fell into two groups depending on the sizes of their embryos. One group, which the researchers referred to as Group A, consisted of 14 gravid females caught during the winter months and carrying embryos of 43 cm to 70 cm, and one exceptional female caught in August in offshore waters. Group B comprised four females carrying near or full-term young of 85 cm to 100 cm at the same time of the year. In addition, they showed some data from Springer (1938, 1940), which also showed the two

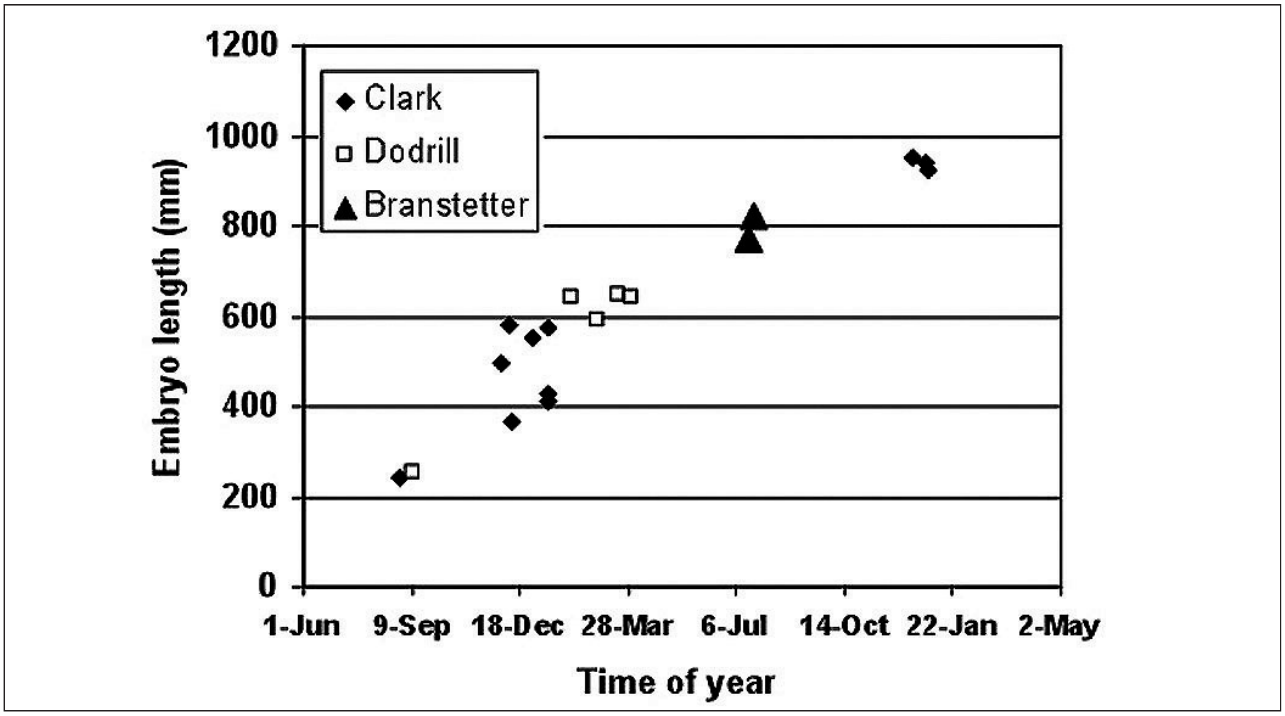

Fig. 24. *Carcharhinus obscurus*, gestation period.

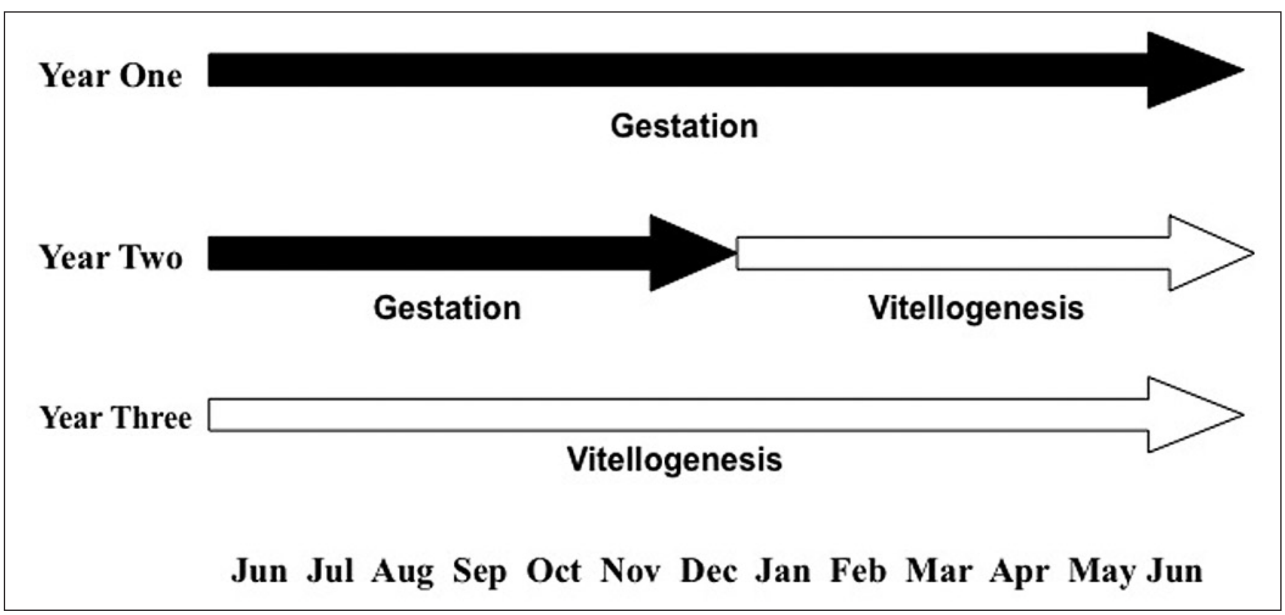

Fig. 25. *Carcharhinus obscurus*, carcharhinoid triennial cycle, schematic by year.

groups. These researchers stated that the females carrying the larger embryos possibly gave birth in the Sarasota area, but they captured no free-swimming young in that area. Based on a single ripe male caught in April, the researchers postulated that Group B would have a gestation period of eight or nine months, while Group A would have a gestation period of about 16 months. Clark & von Schmidt concluded that the evidence for the 16-month gestation was stronger, when the birth size of 97 cm suggested by Bigelow & Schroeder (1948) was considered. Figure 24 shows Clark & von Schmidt's data along with other data points obtained from Dodrill (1977), Branstetter (1981), and my own data, assuming a mating time in July as observed by both Dodrill and Branstetter. This graph indicates that dusky shark females in the Gulf of Mexico and eastern Florida are synchronous, and supports the hypothesis of an 18-month gestation period, as postulated by Clark & von Schmidt (1965) and Dodrill (1977).

Dusky shark term females carry 10-mm oocytes at the time of parturition in December while non-gravid females are carrying oocytes 25 mm to 45 mm in diameter at that time. Thus, after giving birth, the now post-partum females will not have ripe oocytes in time for the mating season in July. For them, the next mating will occur the following July, or 18 months after parturition. Thus, the limited evidence indicates that the dusky shark has a three-year reproductive cycle with an 18-month gestation. In species having such reproductive cycle, two-thirds of the adult female population would be gravid during the time when some females are carrying small embryos and some are carrying one-year old embryos, and only one third would be gravid right after the parturition season (the females on the second half of their first year of pregnancy; see Fig 25).

CONCLUSIONS

The production of large fully-formed young places severe energy strains on female sharks and their long reproductive cycles reflect the amount of time that it takes females to accumulate enough energy to be able to nurture their embryos to a relatively large size. The reproductive adaptations and cycles of sharks have a phylogenetic basis but are modified by environmental factors. The biennial cycle, with all its variations, is found in sharks of different phyletic origins such as carcharhinoid, squaloid, and orectoloboid sharks. Its presence in sharks of different phyletic origins with different ways of nourishing the embryos probably reflects that their common physiological processes require similar amounts of time to accumulate sufficient energy to produce a brood.

It is certain that other patterns of reproductive cycles exist, but it may take a while to elucidate these, given the difficulties of obtaining series of gravid shark specimens. Where commercial shark fisheries exist and large numbers of sharks are taken, it may be possible to carry out such observations. In such cases, the first necessity in determining the length of the reproductive cycle of a species is to determine whether the females are synchronous or asynchronous. If the females are synchronous, one can follow the development of oocytes and embryos in the manner illustrated previously and so determine the length of the reproductive cycle. It is necessary to determine both the length of gestation and vitellogenesis, and to correlate the two periods.

Then a model can be constructed that shows the condition of the females throughout the cycle. The model can then be tested by observing the condition of females and the proportions of gravid and non-gravid females at different times of the year. All these must then conform to the model. The difficulty lies in that large numbers of sharks must be sampled to obtain the necessary data. It is difficult to accomplish this using data collected by others a long time ago, as often some of the necessary data may not have been collected. If the females are asynchronous, as some tropical species are, other methods may have to be devised. Keeping isolated females or male/female pairs of some species in captivity may yield important observations, but it is often difficult to keep sharks alive over several reproductive cycles, and captive conditions may not reflect what occurs in nature. Recent papers (Driggers & Hoffmayer 2009, Sulikowski et al. 2007) have suggested that there may be variations in the reproductive cycle within a species, and much remains to be learned on this subject.

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REFERENCES

ALCOK, A. 1890. Observations on the gestation of some sharks and rays. *Journal of the Asiatic Society of Bengal* **59** (2, 1): 51-57.

BANSEMER, C. S. 2009. Population biology, distribution, movement patterns, and conservation requirements of the grey nurse shark *(Carcharias taurus* Rafinesque, 1810) along the east coast of Australia. Philosophy Doctor dissertation. University of Queensland. 150 pp.

BASS, A. J., D'AUBREY, J. D. & KISTNASAMY, N. 1975. *Sharks of the east coast of southern Africa. IV. The families Odontaspididae, Scapanorhynchidae, Isuridae, Cetorhinidae, Alopiidae, Orectolobidae, and Rhiniodontidae.* The Oceanographic Research Institute, Durban. 102 pp.

BIGELOW, H. B. & SCHROEDER, W. C. 1948. *Fishes of the Western North Atlantic, Lancelets, Cyclostomes, and Sharks.* Memoir No.1, Part 1. New Haven: Sears Foundation for Marine Research, Yale University. 576 pp.

BRANSTETTER, S. 1981. Biological notes on the sharks of the north central Gulf of Mexico. *Contributions in Marine Science* **24**: 13–34.

BRANSTETTER, S. & MUSICK, J. A. 1994. Age and growth estimates for the sand tiger in the northwestern Atlantic Ocean. *Transactions of the American Fisheries Society* **123**: 242-254.

CASTRO, J. I. 1989. Biology of the golden hammerhead, *Sphyrna tudes,* off Trinidad. *Environmental Biology of Fishes* **24**: 3-11.

CASTRO, J. I. 1993. The biology of the finetooth shark, *Carcharhinus isodon. Environmental Biology of Fishes* **36**: 219-232.

CASTRO, J. I. 1996. The biology of the blacktip shark, *Carcharhinus limbatus*, off the southeastern United States. *Bulletin of Marine Science* **59** (3): 508-522.

CASTRO, J. I. 2000. The biology of the nurse shark, *Ginglymostoma cirratum*, off the Florida east coast and the Bahama Islands. *Environmental Biology of Fishes* **58**: 1-22.

CASTRO, J. I. & WOURMS, J. P. 1993. Reproduction, placentation, and embryonic development of the Atlantic sharpnose shark, *Rhizoprionodon terraenovae. Journal of Morphology* **218**: 257-280.

CLARK, E. & VON SCHMIDT, K. 1965. Sharks of the central Gulf coast of Florida. *Bulletin of Marine Science* **15** (1): 13-83.

DODRILLL, J. W. 1977. *A hook and line survey of the sharks of Melbourne Beach, Brevard County, Florida.* Master of Science Thesis, Florida Institute of Technology. 304 pp.

DRIGGERS, III, W. B. & HOFFMAYER, E. R. 2009. Variability in the reproductive cycle of finetooth sharks, *Carcharhinus isodon*, in the northern Gulf of Mexico. Copeia **2009** (2): 390-393.

GILMORE, R. G. 1993. Reproductive biology of lamnoid sharks. *Environmental Biology of Fishes* **38**: 95-114.

GILMORE, R. G., DODRILL, J. W., & LINLEY, P. A. 1983. Reproduction and embryonic development of the sand tiger shark, *Odontaspis taurus* (Rafinesque). *Fishery Bulletin* **81** (2): 201-225.

JONES, B. C. & GEEN, G. H. 1977. Reproduction and embryonic development of spiny dogfish *Squalus acanthias* in the Strait of Georgia, British Columbia. *Journal of the Fisheries Research Board of Canada* **34** (9): 1286-1292.

KETCHEN, K. S. 1972. Size at maturity, fecundity, and embryonic growth of the spiny dogfish (*Squalus acanthias*) in British Columbia waters. *Journal of the Fisheries Research Board of Canada* **29** (12): 1717-1723.

LIU, K.-W., CHEN, C.-T., LIAO, T.-H. & JOUNG, S.-J. 1999. Age, growth, and reproduction of the pelagic thresher, *Alopias pelagicus* in the northwestern Pacific. *Copeia* **1999** (1): 68-74

LUCIFORA, L. O., MENNI, R. C. & ESCALANTE, A. H. 2002. Reproductive biology and abundance of the sand tiger shark, *Carcharias taurus*, for the southwestern Atlantic. *Journal of Marine Science* **59**: 553-561.

MANIRE, C. A., RASMUSSEN, L. E. L., HESS, D. L. & HUETER, R. E. 1995. Serum steroid hormones and the reproductive cycle of the female bonnethead shark, *Sphyrna tiburo. General and Comparative Endocrinology* **97**: 366-376.

MOLLET, H. F., CLIFF, G., PRATT, JR., H. L. & STEVENS, J. D. 2000. Reproductive biology of the female shortfin mako, *Isurus oxyrinchus* Rafinesque, 1810, with comments on the embryonic development of lamnoids. *Fishery Bulletin* **98** (2): 299–318.

MUSICK, J. A., BRANSTETTER, S. & COLVOCORESSES, J. A. 1993. Trends in shark abundance from 1974 to 1991 for the Chesapeake Bight region of the U.S. Mid-Atlantic coast. In *NOAA Technical Report NMFS 115, Fishery Bulletin. Conservation Biology of Elasmobranchs*, edited by S. Branstetter, pp. 1-18. United States Department of Commerce, Miami.

PARSONS, G. R. 1993. Age determination and growth of the bonnethead shark *Sphyrna tiburo*: A comparison of two populations. *Marine Biology* **112**: 23-31.

SARANGDHAR, P. N. 1943. Tiger shark – *Galeocerdo tigrinus* Muller and Henle. Feeding and breeding habits. *Journal of the Bombay Natural History Society* **44** (1): 102-110.

SPRINGER, S. 1938. Notes on the sharks of Florida. *Proceedings of the Florida Academy of Sciences* **3**: 9-41.

SPRINGER, S. 1940. The sex ratio and seasonal distribution of some Florida sharks. *Copeia* **1940** (3): 188-194.

SPRINGER, S. 1948. Oviphagous embryos of the sand shark, *Carcharias taurus. Copeia* **1948** (3): 153-157.

SULIKOWSKI, J. A., DRIGGERS, III, W. B., FORD, T. S., BOONSTRA, R. K. & CARLSON, J. K. 2007. Reproductive cycle of the blacknose shark *Carcharhinus acronotus* in the Gulf of Mexico. *Journal of Fish Biology* **70**: 1-13.

WHITNEY, N. M. & CROW, G. L. 2007. Reproductive biology of the tiger shark *(Galeocerdo cuvier)* in Hawaii. *Marine Biology* **151**: 63-70.