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RESEARCH ARTICLE

Reproductive biology of the tiger shark (*Galeocerdo cuvier*) in Hawaii

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Abstract The tiger shark (*Galeocerdo cuvier*) is the largest shark in the family Carcharhinidae and the only carcharhinid with aplacental viviparous (ovoviviparous) reproduction. Despite its size and prevalence, many details of tiger shark reproductive biology are unknown. Size at maturity and litter size have been reported by several authors, but a lack of large numbers of pregnant females has made it difficult to determine gestation period, seasonality, and timing of the female reproductive cycle. Here we analyze data from shark control program fishing and incidental catches in Hawaii (n = 318) to construct the most complete picture of tiger shark reproduction to date. Males reached maturity at approximately 292 cm total length (TL) based on clasper calcification, whereas females matured between 330 and 345 cm TL based on oviducal gland and uterus widths. Litter sizes ranged from 3 to 57 with a mean of 32.6 embryos per litter. Data from 23 litters from various months of the year indicate that tiger sharks are usually 80–90 cm TL at birth, and that the gestation period is 15–16 months. Mating scars were observed in January–February and sperm is presumably stored for 4–5 months until ovulation takes place in May–July. Gestation begins in June–July and pups are born in September–October of the following year. Our data suggest that female tiger sharks in Hawaii give birth only once every three years. This could have major implications for conservation and management of this species, as it suggests that tiger shark fecundity is 33% lower than previously thought. This could greatly reduce the ability of this species to rebound from fishing pressure.

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Introduction

The tiger shark (*Galeocerdo cuvier*) is a large predator with a worldwide distribution in tropical and warm temperate seas (Castro 1983). It is the largest shark in the family Carcharhinidae and is the only carcharhinid with aplacental viviparous (ovoviviparous) reproduction (Compagno 1984). Several studies have covered aspects of tiger shark reproduction (e.g. Bigelow and Schroeder 1948; Fourmanoir 1961; Clark and von Schmidt 1965; Rivera-Lopez 1970; Branstetter et al. 1987; Simpfendorfer 1992) but complete information is lacking. Findings have been limited by small sample sizes, and details of gestation period, seasonality, and the female reproductive cycle have been particularly elusive.

Of the analyses based on relatively large (n >30) sample sizes, most have found lengths at maturity ranging from 285 to 310 cm total length (TL) for males (Kauffman 1950; Clark and von Schmidt 1965; Rivera-Lopez 1970; Stevens 1984; Branstetter et al. 1987) and from 287 to 340 cm TL for females (Fourmanoir 1961; Clark and von Schmidt 1965; Rivera-Lopez 1970;

Stevens 1984; Branstetter et al. 1987; Simpfendorfer 1992). Litter sizes ranging from 6 (Simpfendorfer 1992) to 82 (Bigelow and Schroeder 1948) have been reported, with mean values typically between 30 and 50 embryos per litter (Springer 1940; Bigelow and Schroeder 1948; Clark and von Schmidt 1965; Rivera-Lopez 1970; Simpfendorfer 1992).

Few studies have been able to examine large numbers of pregnant females, and findings based on litter information have thus been vague and incomplete. Clark and von Schmidt (1965) used data from five litters, plus four from Springer (1938, 1940), to conclude that tiger sharks have a gestation period of "slightly over a year",[1] based on the presence of both early and late embryos at the same time of year. Rivera-Lopez (1970) reported a gestation period of approximately 12 months, whereas subsequent studies have found simultaneous early- and late-term embryos (Alves 1977; Simpfendorfer 1992) but have been unable to add any precision to Clark and von Schmidt's (1965) estimate of gestation duration.

Reproductive seasonality is poorly understood, and data regarding pupping and mating times are scarce and often conflicting. Pupping season has been estimated from the capture of pregnant females carrying what were presumed to be near-term embryos in the spring and early summer in Florida (Springer 1938; Clark and von Schmidt 1965) and Puerto Rico (Rivera-Lopez 1970). Alves (1977) reported late-term embryos from May to August in northern Brazil, whereas Schwartz (1989) reported a pupping season from July to September in North Carolina. Simpfendorfer (1992) wrote that both breeding and pupping appear to occur "in summer" in northeast Australia.

Accurately determining the tiger shark pupping season is largely dependent on knowing the natural birth size. Here there are also discrepancies. Size at birth has been reported to range from 45 to 50 cm TL (Bigelow and Schroeder 1948), 60 to 70 cm (Rivera-Lopez 1970), and 51 to 76 cm (Randall 1992). Several studies have estimated birth size at approximately 70 cm (Fourmanoir 1961; Clark and von Schmidt 1965; Branstetter et al. 1987) but Sarangdhar (1945) reported embryos ranging from 75 to 80 cm, and Simpfendorfer (1992) found multiple litters with mean embryo lengths over 80 cm and concluded that tiger sharks are born at 80–90 cm TL.

[1] Several authors (Branstetter 1981; Branstetter et al. 1987; Randall 1992; Seigel et al. 1995) attribute a proposed gestation period of "13–16 months" to Clark and von Schmidt (1965). However, Clark and von Schmidt did not propose anything more specific than to say that gestation "could be slightly over a year".

Baughman and Springer (1950) claimed information that "points toward a spring breeding period" for tiger sharks in the Florida Keys, but gave no further explanation. Clark and von Schmidt (1965) reported a single male with engorged and bloody claspers from Florida in May, whereas Rivera-Lopez (1970) provided no information to support his statement that mating "probably takes place in May, June, and July" in Puerto Rico.

Few studies have included enough mature females to comment on the reproductive cycle. Branstetter et al. (1987) said that the mating season occurs before full-term females have pupped, and that the female reproductive cycle must be at least two years. Others have reported that females do not mate every year (Rivera-Lopez 1970; Simpfendorfer 1992) or that there appears to be a rest period in the female cycle (Alves 1977).

Here we analyze data from several years of shark control fishing and incidental catches from the Hawaiian Islands to shed new light on the issues described above. The number of animals examined and the year-round availability of specimens provide the most complete picture of tiger shark reproductive biology to date.

Materials and methods

Data analyzed in this study were obtained from four sources. Records for 250 sharks were taken directly from the original data sheets of the Hawaiian Cooperative Shark Research and Control Program which ran from June 1, 1967 through June 30, 1969 (Tester 1969). Fishing during this program was conducted throughout the Main Hawaiian Islands (MHI: Niihau, Kauai, Oahu, Molokai, Lanai, Maui, Kahoolawe, and Hawaii) but focused primarily on Oahu. Data for 82 sharks were obtained from the data sheets of the Billy Weaver Shark Research and Control Program, which ran from April 1, 1959 through March 31, 1960 (Ikehara 1961) and focused only on Oahu. Data from 18 animals were obtained by one of the authors (GLC) from incidental catches around Oahu between 1992 and 1996. Data for nine sharks captured off east Oahu in 2003 through 2005 were provided by R. Grubbs (personal communication). Shark Control Program data were sometimes collected haphazardly depending on sea conditions and personnel. Because of this, not all measurements were available for all sharks, and we therefore include specific (n) values for each analysis and figure in our results.

Control Program fishing was conducted primarily by longline, though handlines were also used (see Wetherbee et al. 1994 for review). Lines were baited primarily with skipjack tuna (*Katsuwonus pelamis*) and were set parallel to shore in the late afternoon at an average depth of 45 m. Lines were retrieved the following morning and sharks were killed and brought onboard the vessel for examination and measurement. The precaudal length (PCL), total length (TL), sex, and weight (occasionally) were recorded for each shark. All lengths reported in this study are TL. For animals in which no TL was recorded, the PCL was used as a basis for calculating TL from a linear regression derived from other animals in this study.

In examining reproductive condition, the length and degree of clasper calcification were noted for males, with all measurements taken from the point of insertion at the anterior margin of the cloaca to the tip of the clasper (CLI; Compagno 1984). Clasper length was plotted against total length to determine size at maturity. Males with large (>25 cm), calcified claspers were considered mature.

For females, the maximum oocyte diameter (MOD) and the width of the oviducal gland[2] and uteri were recorded, as were the number, sex, and TL of embryos from pregnant females. Pregnant sharks and those with large oviducal glands (≥60 mm width) or large uteri (≥40 mm width) were classified as mature. To analyze the duration of gestation, mean embryo lengths for each litter and TLs of the smallest neonates were plotted against time.

To investigate the presence of a resting period in the female reproductive cycle, we calculated the percent of mature females that were pregnant for each month. Since measurements of reproductive organs were not available for all females, we used a minimum length of 340 cm TL (based on the smallest pregnant female) to categorize an animal as mature for this analysis. This was considered a conservatively large estimate of length at maturity, and was used to avoid underestimating the percentage of mature females that were pregnant.

Results

Length–frequency and size at maturity

Of 359 tiger sharks (185 females, 174 males) captured, length data were recorded for 318 individuals (167 females, 151 males). The relationship between precaudal length and total length was represented by the linear regression:

$$\mathrm{TL} = 1.2191\mathrm{PCL} + 20.181 (r = 0.99, n = 187)$$

Sizes ranged from 76 to 447 cm TL. A length–frequency histogram shows that males ranging from 251 to 375 cm TL were caught in greatest abundance, and that females were caught at larger sizes than males (Fig. 1). There was no evidence of segregation by size or sex.

There was a marked increase in clasper length and calcification in males larger than 280 cm (Fig. 2). The smallest male with calcifying claspers was 260 cm, whereas the largest male with uncalcified claspers was 314 cm. There was a clear break between males with claspers measuring ≤21 cm, most of which were uncalcified, and those with claspers ≥25 cm, all but one of which were calcified (Fig. 2). The smallest male with large (>25 cm) and calcified claspers was 292 cm TL and we therefore consider this to be the approximate length at maturity.

For females, maximum oocyte diameter (MOD) was not a clear indicator of maturity, with values for immature sharks commonly overlapping those for mature and pregnant sharks (Fig. 3). Oviducal gland width was more informative, and showed a sharp increase for animals ranging from 290 to 320 cm (Fig. 4). Animals in this range were therefore considered to be maturing, but not fully mature. Most animals over 330 cm had large (>60 mm) oviducal glands and were

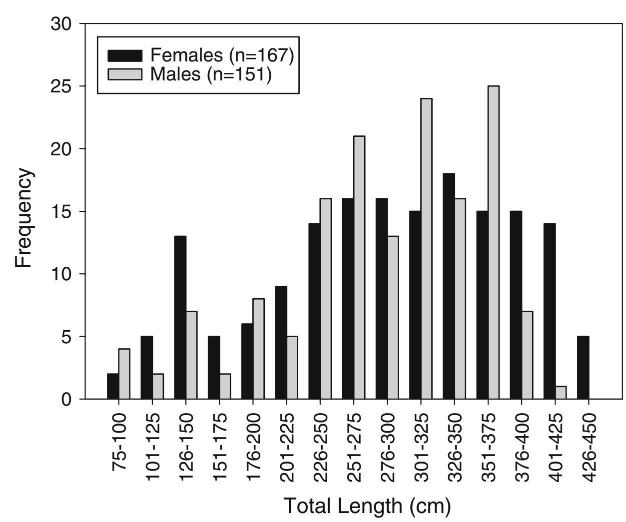

Fig. 1 Length–frequency histogram for tiger sharks. Data are pooled from the Billy Weaver Shark Research and Control Program, 1959–1960 (n = 50), the Hawaii Cooperative Shark Research and Control Program, 1967–1969 (n = 242), and incidental catches from Oahu measured by GLC (n = 18), and R. Grubbs (personal communication; n = 9)

[2] The oviducal gland has also been referred to as the ‘‘shell’’ or ‘‘nidamental’’ gland. Given that this gland produces slightly different structures in different species, and also functions as a seminal receptacle, the term ‘‘oviducal gland’’ seems to be the most inclusive (Pratt 1979; Hamlett et al. 2005).

considered mature. Uterus width increased as animals reached 300 cm, but widths were highly variable at a given TL (Fig. 5). Most sharks over 345 cm had uterus widths of 40 mm or larger. Of three females that were larger than 350 cm and had small (≤40 mm) oviducal glands, two had uterus widths of 50 mm or greater and were considered mature. The third measured 356 cm but had a small uterus (5 mm) and oviducal gland (13 mm) and was considered the largest immature. The next largest immature female was 329 cm and had oviducal gland and uterus widths of 23 and 38 mm, respectively. The smallest pregnant female was 340 cm.

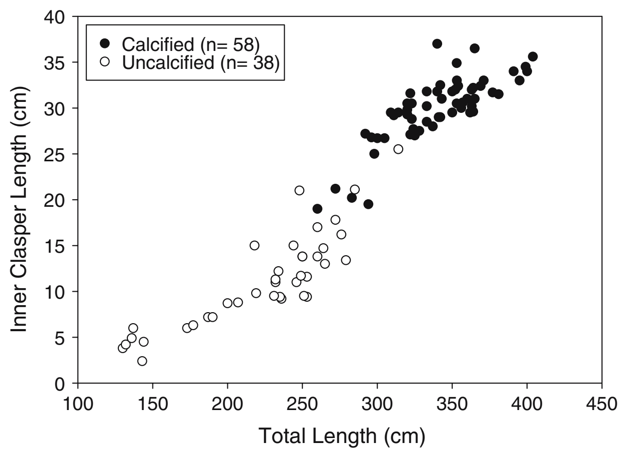

Fig. 2 Length of calcified and uncalcified claspers versus total length of male tiger sharks from the Hawaiian islands

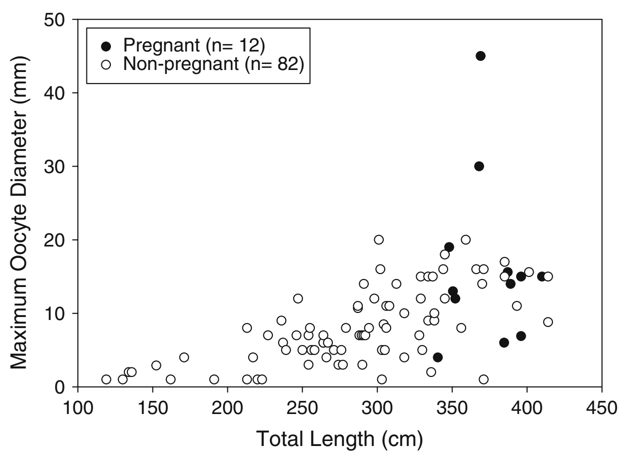

Fig. 3 Maximum oocyte diameter versus total length of female tiger sharks from the Hawaiian islands

Litter characteristics and gestation period

Twenty-three pregnant females were captured throughout the MHI. Litter sizes ranged from 3 to 57 with a mean of 32.6 embryos per litter (n = 21). Of the four smallest litter sizes (all ≤7 embryos per litter), two consisted of early- to mid-term embryos. The other two were late-term litters, and embryo number may have been artificially low as a result of females aborting embryos during landing. There was no relationship between female length and litter size. The ratio of male to female embryos was equal (253:256; n = 16 litters).

Ovaries were located on the flat surface of the epigonal organ and only the right ovary was functional. Mature oocytes were 10–11 cm in diameter and contained 50–60 ml of yolk. Uteri were compartmentalized (one embryo per compartment) with embryos increasing in size from the anterior to the posterior end of the uterus. Intracapsular fluid volume increased with increasing embryo size. Embryos over 60 cm TL had lost their external yolk sac and had an internal yolk sac. One embryo of 76.9 cm had an internal yolk sac containing 0.5 ml of yolk. Embryos ranging from 75 to 89 cm weighed 1.13–1.24 kg.

Mean embryo length within a litter ranged from 3.6 to 88.9 cm TL. One free-swimming shark captured in

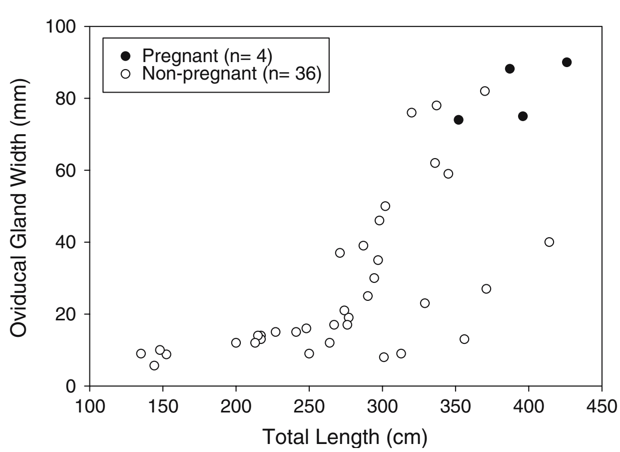

Fig. 4 Oviducal gland width versus total length of female tiger sharks from the Hawaiian islands

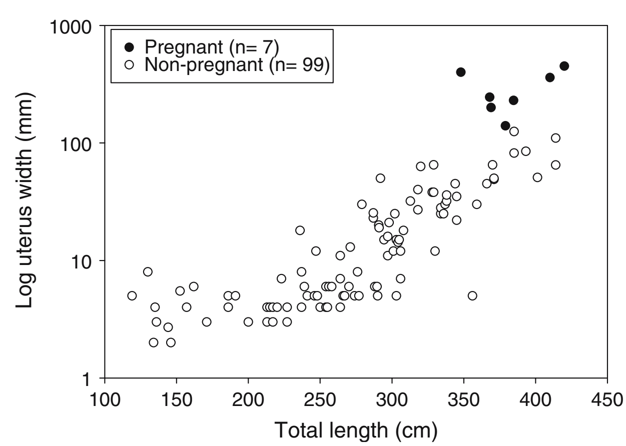

Fig. 5 Uterus width (log values) versus total length of female tiger sharks from the Hawaiian Islands

August measured 76 cm. The next five smallest neonates ranged from 86.5 to 99 cm and were all caught in October except for an 88 cm shark caught in early December. Plotting mean embryo length and neonate length versus time of the year produced two clusters of overlapping points; shifting the values of the largest embryos and neonates to the following year on the time axis produced a trend indicating a gestation period of 15–16 months (r^2 = 0.96; Fig. 6). Three adult females were caught in late September and early November with large (>100 mm), vacant uteri suggesting that they had recently pupped.

Reproductive seasonality and the female cycle

Females with mating scars (n = 3) and a spermozeugma in the anterior region of the uterus (n = 1) were recorded in late January and early- to mid-February, indicating mating behavior at this time. Nearly all mature females, including those with mating scars, had small (≤10 mm diameter) oocytes during January and February. The female bearing a spermozeugma in the anterior region of the uterus had eight small (6 mm), white eggs in the ovary. One male captured in early February released a large amount of ejaculate as it was landed. The smallest embryos were found in June and July (Fig. 6), and one female captured in June carried eggs in utero.

Assuming a 15–16 month gestation period, the percentage of mature females that were pregnant for each month was largely consistent with what would be expected under a three-year female reproductive cycle. Despite our small sample size, the percentage pregnant was 33% or less for most months, except those where consecutive year gestation periods would be expected to overlap (June through October) (Fig. 7). Even during these overlapping months, the percentage of pregnant females never exceeded 60%, and thus remained far below what would be predicted based on a biennial reproductive cycle.

Discussion

Length–frequency distribution and size at maturity

Female tiger sharks reached larger sizes, and therefore showed a broader range of total lengths than male sharks. A similar pattern has been found in previous work on this species, though large (≥350 cm) tiger sharks of both sexes were caught more frequently in Hawaii than in Australia (Stevens and McLoughlin 1991; Simpfendorfer 1992; Simpfendorfer et al. 2001) and the eastern US (Branstetter et al. 1987; Natanson et al. 1999). Fishing gear may have selected for smaller animals in the Australian studies.

Clasper size and calcification data indicate that males mature at about 292 cm, agreeing with the value of 290 cm found by Clark and von Schmidt (1965) and Bass et al. (1975). A few studies report male tiger sharks maturing at 305–310 cm (Rivera-Lopez 1970; Stevens

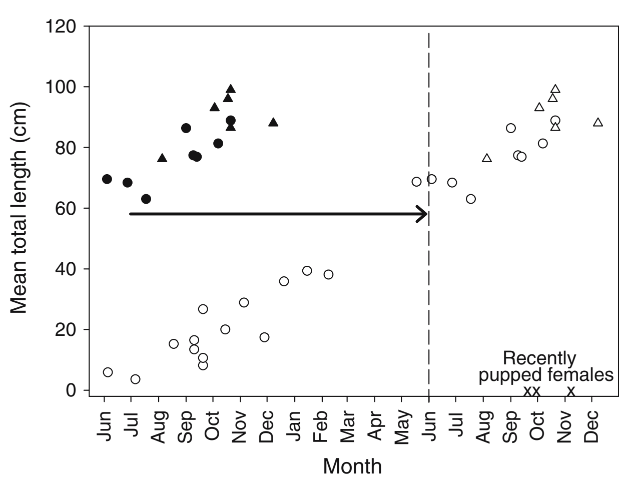

Fig. 6 Mean embryo length per litter (*circles*) and TL of free-swimming neonates (*triangles*) plotted against month of the year (n = 23 litters and six neonates). The *arrow* indicates a shift of large litters and neonates (*filled circles* and *triangles*, respectively) to the same months one year later. *X*'s indicate mature females with expanded, vacant uteri indicating they had recently given birth

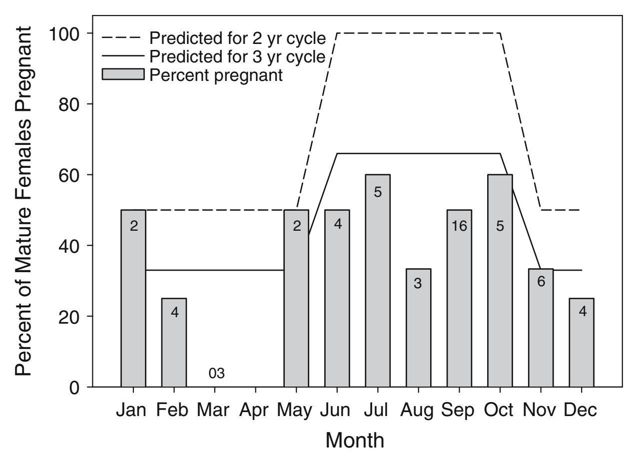

Fig. 7 Percentage of mature females (n = 54) that were pregnant for each month of the year. *Numbers* within bars represent the number of mature females that were caught during that month. *Lines* represent the percentage pregnant that would be expected for a 2-year (*dotted line*) and 3-year (*solid line*) reproductive cycle, given a 15–16 month gestation period. Since reproductive condition was not examined for all females, a minimum length at maturity of 340 cm TL was used to include females in this analysis

1984; Branstetter et al. 1987) whereas the lowest lengths at maturity appear to be 237 cm (Alves 1977) and the range of 226–290 cm given by Randall (1992). All of these studies based their determination of maturity on clasper calcification, though Branstetter et al. (1987) also incorporated the extent of siphon sac development.

Measurements of internal reproductive organs allowed us to draw general conclusions about female size at maturity. Though there was an increase in MOD with shark length, the range of mature female MODs overlapped that of small, immature females. This reflects the fact that tiger sharks do not reproduce annually and females in the resting phase carry small eggs. Oviducal gland and uterus widths begin expanding when sharks reach 290–300 cm and most are fully mature at 330–345 cm. This range is supported by the capture of a 340 cm pregnant female and agrees with sizes at maturity of 340 cm reported from Madagascar (Fourmanoir 1961) and 330 cm from Southeast Australia (Stevens 1984). Female tiger sharks in Hawaii thus appear to mature at slightly larger sizes than those in the Western North Atlantic, Gulf of Mexico, and Caribbean, which have been reported to mature at various lengths from 297 to 320 cm (Clark and von Schmidt 1965; Rivera-Lopez 1970; Dodrill 1977; Branstetter et al. 1987). Pregnant females have been reported as small as 287 cm in Northeast Australia (Simpfendorfer 1992) and 210 cm in Brazil (Alves 1977).

Litter characteristics and gestation period

Pregnant females and neonates were caught on all shores of Oahu, indicating that nursery or pupping grounds are not restricted to a single area. Litter sizes were highly variable but the mean of 32.6 pups per litter was similar to that reported in past studies (e.g. Rivera-Lopez 1970; Simpfendorfer 1992).

Embryo length data presented here from 23 pregnant females captured in ten different months of the year provide the most complete picture of tiger shark gestation to date. The capture of early- and late-term embryos within the same months indicated a gestation period of longer than one year. Shifting the largest cluster of mean embryo lengths to the following year demonstrated a clear trend in embryo growth and indicates a gestation period of 15–16 months. This extends the gestation period of "slightly over a year" proposed by both Clark and von Schmidt (1965) and Alves (1977) based on embryo lengths from 7 and 22 litters, respectively. Simpfendorfer (1992) presented embryo lengths for 25 litters covering seven months of the year, but was unable to draw any clear conclusions about gestation period.

Tiger sharks in Hawaii are born at 76–89 cm. This is consistent with a size at birth of 80–90 cm reported by Simpfendorfer (1992) and larger than the range of 51–76 cm reported by Compagno (1984) and Randall (1992). Clark and von Schmidt (1965) did not speculate on size at birth other than to say that free-swimming pups of 18–20 in. (46–51 cm) reported by Bigelow and Schroeder (1948) and Baughman and Springer (1950) seem premature. Schwartz (1994) reported late-term embryos around 80 cm and free-swimming pups as small as 85 cm from the eastern United States.

Reproductive seasonality and the female cycle

Mating appears to take place in January and February in Hawaii (based on bite marks on females, a spermozeugma in the uterus of one female, and free-flowing sperm from one male), during which time females carry very small (≤10 mm), undeveloped oocytes. Sperm is presumably stored in the oviducal gland for 4–5 months while oocytes develop and until ovulation occurs in June and July. Prasad (1944) and Pratt (1993) reported the presence of sperm in the oviducal gland of this species and Pratt (1993) noted that this was consistent with long-term storage. Embryonic uterine development begins immediately after fertilization, and gestation lasts about 15–16 months until parturition takes place in September and October of the following year. This pupping season is based on the concurrence of the largest embryos and smallest neonates during this period, and is further supported by the capture of seven neonates of 84 to 89 cm TL in the Northwestern Hawaiian Islands in late September and early October (Vatter 2003). It is possible that some females mate again after a rest period of only 3–4 months and thus show a biennial reproductive cycle. However, were this the case, then virtually all adult females in the population should be pregnant during the months of June through October. The low percentage of pregnant females suggests that most, if not all, females undergo a rest period of over a year before reproducing again, and thus follow a triennial reproductive cycle.

Whether the gestation period and female cycle described above holds true for other tiger shark populations in the Northern Hemisphere is unclear. Pooled embryo length data from the Western North Atlantic (Clark and von Schmidt 1965; Dodrill 1977), the Gulf of Mexico (Branstetter 1981; Clark and von Schmidt 1965), and the Caribbean Sea (Rivera-Lopez 1970) produce a slope that is slightly steeper than that from the Hawaii data (Fig. 8). However, a *t* test showed that this difference was not statistically significant. The inability of previous studies to draw clear conclusions about gestation period and reproductive seasonality has been largely due to small samples of pregnant females, and especially a lack of late-term females with large embryos. This latter factor has led several authors to underestimate the size at birth for tiger sharks and thereby underestimate gestation period as well. Confusion over size at birth has been compounded by the fact that tiger shark embryos absorb their external yolk sac relatively early in gestation (60 cm TL) and therefore appear fully developed several months before they are full-term. Past studies have considered embryos near-term at 70 cm TL or less based on the absence of an external yolk sac (Rivera-Lopez 1970) and the ability of an aborted embryo to survive in captivity for several weeks (Clark and von Schmidt 1965). Embryos grow much larger in utero than would be expected from the 10–11 cm egg, which has led to speculation that tiger shark embryos receive additional nourishment by ingesting periembryonic fluid (Castro 1983). This additional nutrition would allow tiger shark embryos to reach 80–90 cm TL.

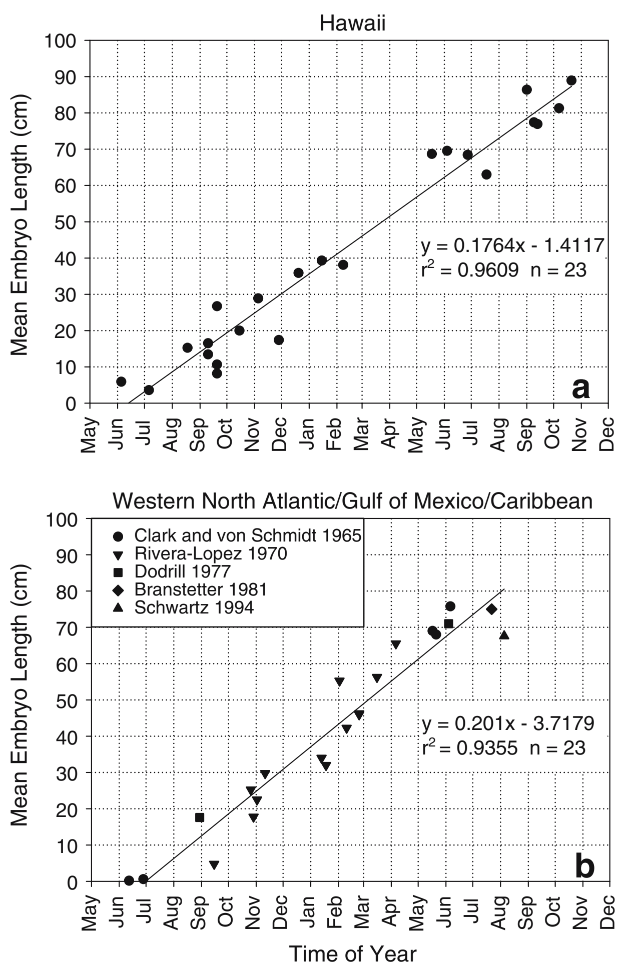

Fig. 8 Gestation period, represented by mean embryo lengths per litter, from (**a**) this study and (**b**) pooled data from the Western North Atlantic, Gulf of Mexico, and Caribbean

Though our conclusions regarding the female reproductive cycle are based on relatively few (n = 54) mature females, the only previous studies that have captured large numbers (>50) of mature females also appear to support a triennial cycle. The percentage of mature females that were pregnant in those studies was 39% in the Caribbean (Rivera-Lopez 1970), 35% in Brazil (Alves 1977), and 17% in Australia (Simpfendorfer 1992). Though a biennial reproductive cycle is typical for carcharhinids (Clark and von Schmidt 1965; Castro 1993), Musick et al. (1993) proposed a triennial cycle for the dusky shark (*Carcharhinus obscurus*) based on a 22-month gestation period and a 1 year resting phase. Triennial cycles have also been proposed for the school shark (*Galeorhinus galeus*) based on a 12-month gestation and a 24-month rest period (Peres and Vooren 1991), the spotted gully shark (*Triakis megalopterus*) with a 19–21 month gestation and 12–15 month rest period (Smale and Goosen 1999), and the shortfin mako (*Isurus oxyrinchus*) based on a 18-month gestation and 18-month resting period (Mollet et al. 2000).

A triennial reproductive cycle could have major implications for tiger shark fisheries management and conservation. For instance, in calculating intrinsic rebound potentials of various shark species, Smith et al. (1998) assumed an age at maturity of 9 years and a maximum age of 28 years for tiger sharks. Given these parameters, a biennial reproductive cycle would allow a female tiger shark to reproduce an average of 9.5 times over the course of her life whereas a triennial cycle reduces that to a maximum of 6.3 reproductive events per lifespan. Though the model used by Smith et al. (1998) emphasizes age at maturity as the most significant parameter in calculating rebound potential, decreasing fecundity by 33% could greatly reduce the ability of this species to recover from fishing pressure.

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