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SOME OBSERVATIONS ON THE REPRODUCTIVE BIOLOGY OF THE SIXGILL SHARK *HEXANCHUS GRISEUS* (BONNATERRE, 1788) FROM SOUTHERN AFRICAN WATERS

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Observations are made of the maturation status of 81 male and 88 female sixgill sharks *Hexanchus griseus* from southern African waters. Males mature at about 310 cm total length (*TL*) with the calcification of the terminal cartilage elements of the claspers. Determination of maturity for females was problematic, but most were fully mature by at least 420 cm *TL*. Newborns were captured at the same location over three consecutive summer seasons, indicating the location of a possible pupping ground.

Key words: maturity size, pupping grounds, reproduction, sixgill sharks

The sixgill shark *Hexanchus griseus* is one of the most common species of large, deep-water sharks along the outer continental shelf and upper slope off southern Africa. It is found along the West Coast from Angola around the tip of South Africa to at least Moçambique on the East Coast (Pissarro and Sanches 1973, Bass *et al*. 1975, Compagno *et al*. 1989, Ebert 1990). However, despite its abundance only taxonomic (Bass *et al*. 1975) and feeding data Ebert (1994) exist on this important deep-water predator off southern Africa. This study investigates the reproductive biology of the sixgill shark throughout most of its range around southern Africa.

MATERIAL AND METHODS

Sixgill sharks were collected by longline, rod and reel and demersal trawl along the southern African coast between Walvis Bay, Namibia, and northern KwaZulu-Natal on the east coast of South Africa during the period 1986–1991. Vessels used were the Spanish commercial trawler M.F.V. *Chicha Touza* and the South African research vessels F.R.S. *Africana* and R.V. *Meiring Naude.*

The maturation status of 81 males and 88 females was determined. Additional data were also used from 21 adolescent and adult animals collected from the Azores. Sixgills were grouped into three categories: juvenile, adolescent and adult, following the criteria of Ebert (1996) for hexanchoid sharks.

RESULTS

Male maturity and size

There was a marked increase in the total length (*TL*)/ clasper length ratio in sharks >250 cm *TL* (Fig. 1). This occurred during adolescence when the claspers become stiff and hard. Coinciding with this increase in length are several morphological features unique to the claspers of sixgills and hexanchoids in general. They include a pelvic fin scroll, a clasper sac and calcification of terminal cartilage elements of the claspers, all of which are present and fully functional in adults (Ebert 1990).

The inner free rear margin of the pelvic fin forms a scroll in which lie the claspers. In both juveniles and adolescents, the claspers remain hidden within the scroll (Fig. 2a). Only in late adolescents, when the claspers begin to elongate, can sex be easily distinguished without close examination of the pelvic fins. During maturation, the claspers lengthen, and the distal most four or five pelvic fin radials also elongated to form the scroll (Fig. 2b). At full maturity, the claspers are still partially enclosed within the scroll. Females lack a scroll and the pelvic fin radials do not lengthen (Fig. 2c).

Calcification of the terminal cartilage elements appears to be the last criterion to be met for maturity. Adolescent sharks measuring 270–308 cm *TL* had elongated claspers, but lacked calcification of the terminal cartilage elements (Fig. 2a). The claspers of juveniles <240 cm *TL* were short, soft and relatively

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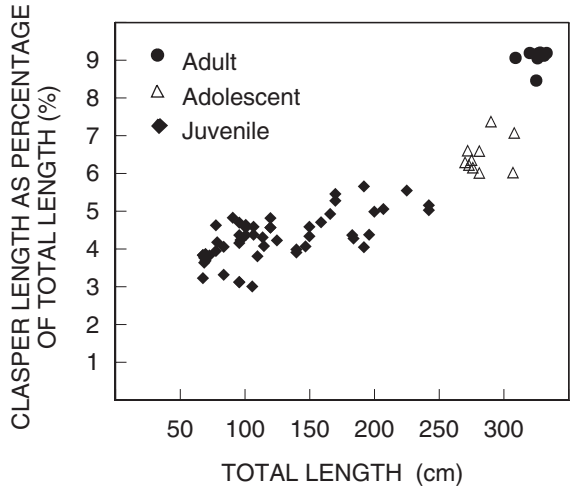

Fig. 1: Relationship between inner clasper length, as a percentage of total length, and total length of male sixgill sharks

undeveloped. Males of 310 cm *TL* and larger had calcified terminal cartilage elements and could therefore be classified as adult (Fig. 2b).

Another unique feature of sixgills is the clasper sac, which can inflate and appears to function in a manner similar to the siphon sac of other elasmobranchs. Development of the clasper sac begins in sixgills >250 cm *TL*; it is fully functional by adulthood.

The epididymis in juveniles is straight and narrow, but it transforms gradually as the shark enters adolescence. At the onset of adolescence, the anterior portion of the epididymis begins coiling loosely, and eventually this coiling extends down the entire length of the epididymis. Males in late adolescence have a highly convoluted epididymis, which contains viable sperm.

The sperm sac of late-stage adolescents (measuring >280 cm *TL*) is expanded and contains large quantities of viable sperm, which can be expelled through the genital papilla. Viable sperm was found in specimens throughout the year, but with no clear evidence of seasonality. Sharks <280 cm *TL* did not have sperm.

The length/mass (*M*) relationship for males between 67.5 and 333 cm *TL* was $M = (3.3 \times 10^{-13})TL^{4.2}$ (r^2 = 0.9, n = 61).

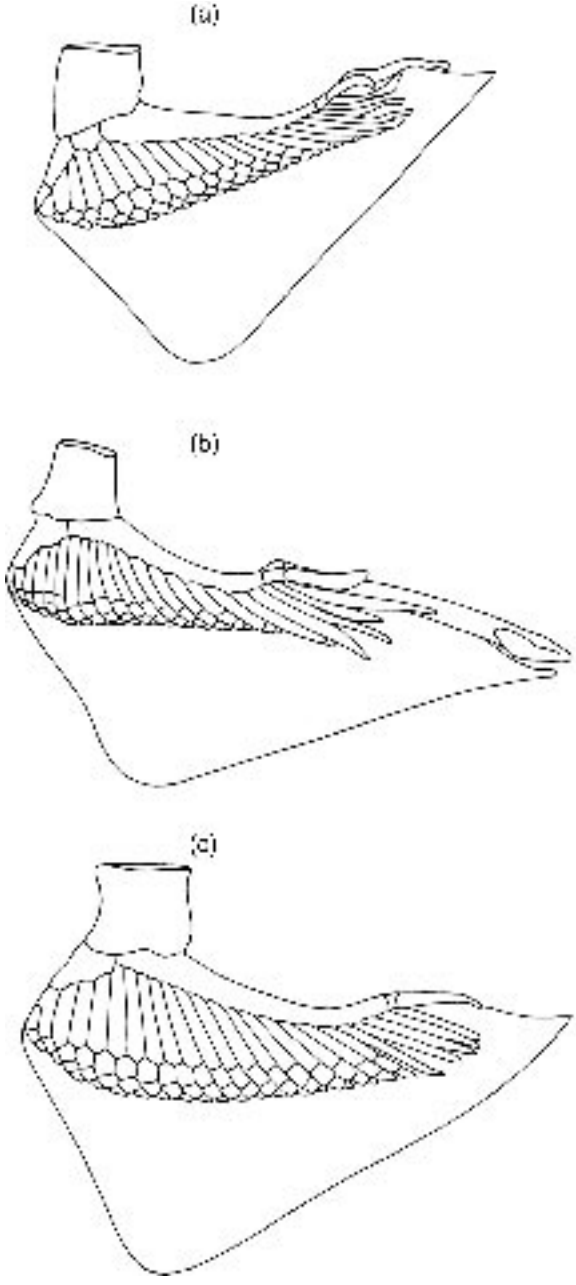

Fig. 2: Diagram of the pelvic fin skeleton of sixgill sharks – (a) adolescent male, (b) adult male and (c) adult female. Note the elongated fin radials in (a) and (b), and the terminal cartilage elements in (b)

Female maturity and size

The largest subadult female examined was 320 cm *TL*.

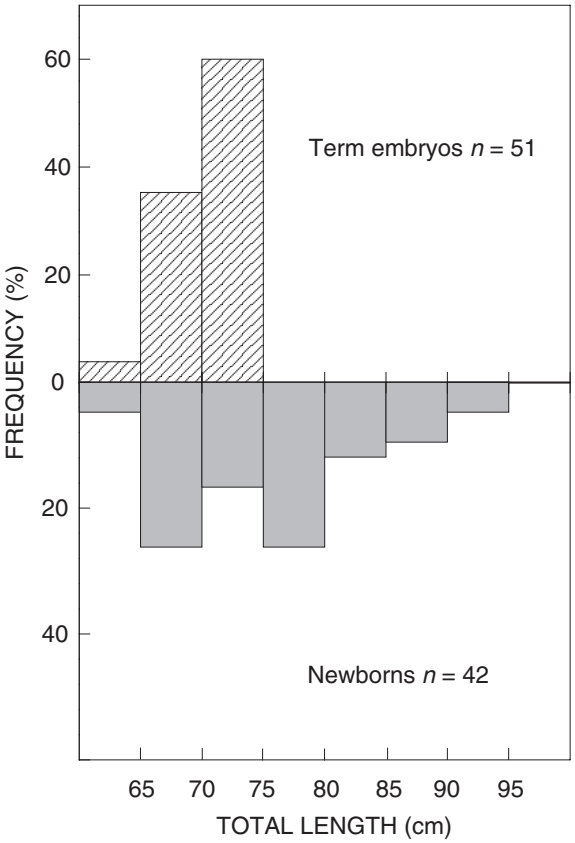

Fig. 3: Size frequency distribution of term embryos from a gravid female sixgill shark and from free-swimming newborn sixgill sharks caught off Namibia over three successive summer seasons

It had an enlarged epigonal organ and undifferentiated ovaries, and the shell gland was undeveloped. Two adult females of 405 and 422 cm *TL* had maturing ova about 50 mm in diameter; the two sharks contained 104 and 128 ovarian eggs respectively. The ovaries appeared to be functional and the shell gland was well developed. No developing embryos or uterine eggs were found. The oviducts of the larger shark were pendulous, whereas those of the smaller were undetermined.

Newborns

Newborn sixgills, defined as having open umbilical scars, were caught mostly off Lüderitz between 23°11´S, 13°17´E and 27°04´S, 14°28´E, over three consecutive summer seasons, suggesting that the region may be a pupping ground. Newborns from that region measured 61–93 cm *TL*, a similar size range to that of term embryos reported by Ebert (1986; Fig. 3).

The length/mass relationship of females 61–425 cm *TL* was $M = (1.7 \times 10^{-10})TL^{3.5}$ ($r^2 = 1.0$, $n = 72$). The mass of two specimens (405 cm *TL*; 350.5 kg and 422 cm *TL*; 466 kg) was less than a pregnant female sixgill (421 cm *TL;* 555 kg) with term embryos found off California (Ebert 1986). The size at birth of Californian sixgills was 61–74 cm *TL* (Ebert 1986). The smallest free-swimming sixgill found in this study was 61 cm *TL*.

DISCUSSION

Male maturity

The development of the clasper scroll, the clasper sac and the terminal cartilage elements began at the onset of adolescence and coincided with the internal development of the testes, epididymis and sperm sac. However, whereas most males mature internally, with respect to the production of sperm, at 280 cm *TL*, external maturity was not recorded until about 310 cm *TL*. Sixgills smaller than this did not possess intromittent organs that were developed sufficiently to transmit sperm into the female. Calcification of the terminal cartilage elements coincided with a rapid increase in clasper length. Males of at least 310 cm *TL* met all the criteria for maturity, including calcification of the terminal cartilage elements. The precise function of the terminal cartilage elements during copulation is unknown, but it may play an important role by holding the clasper inside the female during copulation. Most elasmobranch claspers have some form of terminal elements that hold the clasper inside the female during copulation (Compagno 1988).

Viable sperm was present in specimens collected year-round. However, the sample size was small and determination of any seasonal variation in the gonadosomatic index (*GSI*) would require a larger sample size. Ebert (1996) reported that the sevengill shark had viable sperm present year-round, but noted a seasonal change in its *GSI*.

Literature accounts of adult male sixgills are few. Branstetter and McEachran (1986) reported on the an adult male sixgill in the Gulf of Mexico and Crow *et al.* (1996) reported on the occurrence of seven large

male sixgills sharks from Hawaiian waters ranging between 273 and 331 cm *TL*. Although Crow *et al*. (1996) noted that four of the specimens had calcified claspers, it was unclear as to whether they were referring to the clasper rostrum or the terminal cartilage elements. However, assuming that those specimens referred to as having calcified claspers were mature, the size range 309–331 cm *TL* is comparable to the results presented in this study.

Reasons why adult male sixgills are uncommon may lie in the social behaviour of the species. As with many elasmobranchs, sixgill sharks tend to segregate by life history stage and sex (Springer 1967). All catches of adult males, including those in this study, have come from depths in excess of 300 m, whereas adult females are caught in shallower water, in one case <15 m deep (Ebert 1990 and unpublished data). Juveniles of both sexes are not uncommon on the continental shelf and often range into bays and estuaries.

Female maturity

Adult females are mature at 420 cm *TL*, but are still immature at 350 cm *TL* (Desbrosses 1938, Ebert 1986). However, a more accurate estimate of the size at maturity is wanting. Size at maturity has previously been reported as 450 cm *TL*, based primarily on gravid females measuring between 452 and 482 cm *TL* (Springer and Waller 1969). Except for females containing embryos, maturation data on large (>400 cm *TL*) specimens are few. Large female sixgills exhibit extreme variability in weight, which may reflect the animal's stage of development or reproductive condition. Until more females between 350 cm and 420 cm *TL* are examined for maturation status, maturation is assumed to take place at a minimum size of at least 420 cm *TL*.

The sixgill shark is one of the most fecund species of elasmobranch, with litter sizes of 108, 47, 70, 22 and 51 being reported (Desbrosses 1938, Springer and Waller 1969, Ebert 1986). However, the 22 embryos reported by Desbrosses (1938) were most likely from a bigeyed sixgill shark *Hexanchus nakamurai* rather than *H. griseus* (Ebert 1990). The sex ratio of 51 embryos from a specimen 421 cm long reported by Ebert (1986) was 1:1, with a size range of 64–74 cm *TL* for males and 68–72 cm *TL* for females.

Newborns

Newborn sixgills were caught off southern Namibia during mid and late summer, over three successive seasons. The depth of capture ranged between 300 and 400 m. The newborn sixgills from Namibia were similar in size to term embryos measuring between 64 and 74 cm *TL*, reported by Springer and Waller (1969) and Ebert (1986). The occurrence of gravid females carrying term embryos during spring and the presence of newborns during the summer suggests a late spring to summer pupping period. Desbrosses (1938) reported an inshore movement of sixgills during spring and autumn in the Bay of Biscay, adult females and newborns being caught between 50 and 100 m deep. Along the coast of California, juvenile sixgills are most abundant during summer and early autumn (pers. obs.). Also, fishers trawl large sixgills mainly during summer, but rarely at other times of the year.

The maximum reported size for a female sixgill shark is 482 cm *TL* (Bigelow and Schroeder 1948). Assuming that females mature by at least 420 cm *TL*, this represents 87% of their maximum *TL*. This concurs with Holden's (1974) generalization that female elasmobranchs reach maturity between 0.6 and 0.9 of their asymptotic length. Literature reports of an 800 cm *TL* specimen have been considered erroneous (Castro 1983). However, specimens in excess of 500 cm *TL* would not be unexpected in the species, making it one of the larger elasmobranchs.

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