Copeia, 1995(3), pp. 659–665

Reproduction in the Sandbar Shark, *Carcharhinus plumbeus,* in the Waters off Northeastern Taiwan

Shoou-Jeng Joung and Che-Tsung Chen

The purpose of this study was to investigate the reproductive biology of sandbar sharks, *Carcharhinus plumbeus* from northeastern Taiwan waters. A total of 885 sandbar sharks was examined. The size of 50% maturity in sandbar shark is taken to be 170–175 cm and 175 cm for females and males, respectively. The number of embryos per litter ranged from four to 12, with a mean of 7.54. Pregnant individuals containing six, seven, or eight embryos constituted 59 (80%) of the 74 females examined. Of 558 embryos in 74 litters examined, 274 were female and 284 were male. The null hypothesis of a 1:1 sex ratio is not rejected at the 0.05 level. Pups are born from Feb. to April. We estimate the gestation period to be 10–12 months. Most embryos had attained a total length of about 60–65 cm after 10–12 months of development, at which size they could be readily separated from the placenta, suggesting that they were full term and ready to be born. The relationship between the total number of uterine embryos and the total length of mother is roughly described by the regression equation (n = −7.544 + 0.075 TL; n = 74; r = 0.41). Although it is clear from this regression that fecundity is related to the size of the mother, the relationship is not particularly strong. We find that fertilization occurs during April and May, two months prior to the estimate reported by Taniuchi for *C. plumbeus* in Japanese waters.

SANDBAR sharks, *Carcharhinus plumbeus,* are found in tropical and subtropical regions worldwide (Tester, 1969; Bass et al., 1973; Bigelow and Schroeder, 1948). Springer (1960), Garrick (1982), and Compagno (1984) provide details of the taxonomy and distribution of this species in their respective revisions of the genus *Carcharhinus.*

Carcharhinus plumbeus is common in the waters off northeastern Taiwan (Fig. 1) and comprises a large component of the species taken by the commercial shark fishery in northeastern Taiwan. According to catch statistics from the Nan Fan Ao fish market near Suao City, sandbar sharks make up more than 170 tons or 10% of the total annual shark catch in the region. Most are caught between Nov. and March when waters are cooler.

Like other elasmobranchs, sandbar sharks have a complex reproductive cycle. Springer (1960), Taniuchi (1971), Bass et al. (1973), and Baranes and Wendling (1981) all have studied sandbar shark reproduction. Springer (1960) reviewed the natural history of the sandbar shark. His observations focused on the external morphology of the eggs and the embryos at different stages of development. Most of Springer's (1960) observations were later confirmed by Wass (1973) in the course of his work on sandbar sharks from Hawaiian waters. The mating season of sandbar sharks in Hawaii (Wass, 1973) and the East China Sea, near southern Japan (Taniuchi, 1971), occurs in the summer months (July and Aug.). In the northern Red Sea, mating occurs earlier in the summer (Gohar and Mazhar, 1964; Baranes and Wendling, 1981). By contrast, Bass et al. (1973) found that young are born in South African waters between Dec. and Feb. after a gestation period of 10–12 months, corresponding to the southern hemisphere's summer season. The sex ratio of litters is usually 1:1 (Springer, 1960; Wass, 1973; Baranes and Wendling, 1981). Wass (1973) reported that the average litter size for the population he examined was 5.5 embryos per litter, which he noted was smaller than for that seen in other areas. Bass et al. (1973) reported a range of between six and 11 pups per litter, which is similar to the observations of Baranes and Wendling (1981).

The present study provides the first detailed information concerning aspects of reproduction for the sandbar shark population found off northeastern Taiwan. Data collected for this survey are compared and contrasted with surveys from other regions.

Materials and Methods

A total of 885 sandbar sharks was examined for this study (Table 1). All of the specimens examined were caught by the commercial longline fishery off northeastern Taiwan between Nov. 1989 and March 1992.

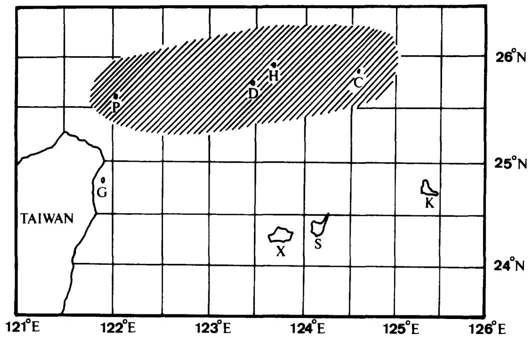

Fig. 1. Sampling area of *Carcharhinus plumbeus* off northeastern Taiwan. C: Chih Wei Yeu; D: Diaw Yu Tair; G: Guei Shan Island; H: Huang Wei Yeu; K: Kung Ku Island; P: Peng Jia Yeu; S: Shih Yuan Island; X: Xi Biao Island.

Measurements (in cm) were taken of total length (TL), fork length (FL), and precaudal length (PCL). Methods follow Branstetter and McEachran (1986) and Branstetter and Stiles (1987). Total length is used throughout this report. Fork length and precaudal length were estimated from these measurements to facilitate comparison with literature reports using the following formulae:

Female:

$$FL = 0.657 + 0.810\ TL \quad (n = 197;\ r^2 = 0.940)$$
$$PCL = -5.055 + 0.786\ TL \quad (n = 189;\ r^2 = 0.950)$$

Male:

$$FL = 2.641 + 0.823\ TL \quad (n = 166;\ r^2 = 0.937)$$
$$PCL = -0.491 + 0.739\ TL \quad (n = 210;\ r^2 = 0.943)$$

Body weight, reproductive status, clasper length (CL) measured from cloaca to the tip of claspers, condition of the uterus, ovarian egg diameter, and number also were recorded. In addition, when pregnant females were examined, embryos were counted, sexed, and measured for total length.

Sexual maturity for males was assessed using the following criteria: (1) the abrupt change in the relationship between clasper length to TL (Aasen, 1966; Holden and Raitt, 1974; Pratt, 1979); (2) the clasper and rhipidion fully formed and spread open on a fresh specimen (Clark and von Schmidt, 1965; Pratt, 1979); (3) the base of the clasper rotates easily such that the clasper can be directed anteriorly (Clark and von Schmidt, 1965); (4) stem cartilages becoming hardened or calcified when mature (Springer, 1960); and (5) presence of male sexual products (Kauffman, 1950). Sexual maturity for females was assessed using the following criteria, based on the examination of numerous females: (1) immature—ovaries thin and of homogenous cellular appearance throughout the gonad; uteri threadlike, flaccid and relatively indistinct from the oviducts; (2) premature—ovary showing differentiation of the ova; ova approximately 5–20 mm in diameter; uteri with thickened walls distinct form oviducts; and (3) mature—ovary with large yolked eggs greater than 20 mm in diameter; uteri well developed.

Table 1. Number of Specimens Examined in This Study.

Month	Female n	Female Range of TL	Male n	Male Range of TL
Nov. 1989	28	158–219	2	180–198
Dec. 1989	101	126–220	57	133–204
Feb. 1990	34	169–205	76	160–209
Mar. 1990	42	161–215	32	150–196
Jul. 1990	—	—	8	179–197
Aug. 1990	14	173–212	5	172–190
Sep. 1990	1	167	5	169–193
Oct. 1990	—	—	7	188–198
Nov. 1990	43	157–221	17	150–196
Dec. 1990	13	144–217	63	133–205
Jan. 1991	57	143–213	30	86–199
Feb. 1991	1	126	15	121–169
Mar. 1991	25	142–216	13	132–194
Apr. 1991	5	175–207	6	167–181
May 1991	8	138–207	21	173–199
Jun. 1991	2	193–195	4	178–190
Jul. 1991	1	182	—	—
Aug. 1991	1	191	—	—
Nov. 1991	16	180–210	13	171–186
Dec. 1991	3	161–200	—	—
Jan. 1992	61	146–215	39	127–201
Mar. 1992	—	—	16	172–200
Total	456	126–221	429	86–209

TL: total length (cm).

Results

The onset of sexual maturity in male sandbar sharks appears to occur about 160–165 cm TL (Table 2). Of the 406 males examined, 83 of the 86 specimens < 165 cm TL had soft claspers and straight vasa deferentia and were considered immature. Eighteen of the 101 males between 165 and 180 cm TL were categorized as premature, based on a moderate coiling of the vasa deferentia and hardness of the claspers. Two hundred seventeen of the 219 specimens > 180 cm TL had rigid claspers and tightly coiled vasa deferentia and, thus, were consid-

TABLE 2. NUMBER OF SPECIMEN IN THE MATURING STAGES OF *Carcharhinus plumbeus.*

TL of specimen (cm)	Female			Male		
	I	P	M	I	P	M
120–125				2		
125–130	4			2		
130–135	2			5		
135–140	3			5		
140–145	8			7		
145–150	6			7		
151–155	14			5		
155–160	18			18		
160–165	17			32	2	1
165–170	17	5		18	7	8
170–175	14	10	7	10	7	10
175–180	3	7	19	1	4	36
180–185		6	21		2	43
185–190		1	37			76
190–195			54			62
195–200			41			27
200–205			50			6
205–210			36			3
210–215			27			
215–220			9			
220–225			1			

ered mature. The ratio of clasper length to TL increased noticeably at a TL of about 165 cm (Fig. 2). Size of 50% maturity for male sandbar sharks is taken to be 170–175 cm TL (Table 2).

The onset of sexual maturity in female sandbar sharks appears to occur at a TL of about 165–170 cm (Table 2). Of the 437 females examined, 89 of the 94 specimens < 170 cm TL had thin ovaries, threadlike uteri, and flaccid oviducts and were considered immature. Twenty-three of the 87 females between 170 and 185 cm TL were categorized as premature, based on differentiated ova, ova approximately 5–20 mm in diameter, and uteri with thickened walls distinct from the oviducts. Two hundred fifty-five of the 256 specimens > 185 cm TL had eggs greater than 20 cm in diameter and well-developed uteri and, thus, were considered mature. The size of 50% maturity for female sandbar sharks is taken to be about 175 cm TL (Table 2).

Size at sexual maturity of female sandbar sharks as determined in this study are in keeping with Holden and Raitt's (1974) suggestion that the mean length at maturity for female elasmobranchs approximates 60–90% of the asymptotic length. Our data show that 50% maturity in female sandbar sharks is attained at a TL of about 175 cm (Table 2), which represents 81% of the asymptotic TL of 216 cm. The smallest of the 74 pregnant females we examined was 180 cm TL. In the females we examined, only the right ovary became developed, whereas both uteri appeared functional.

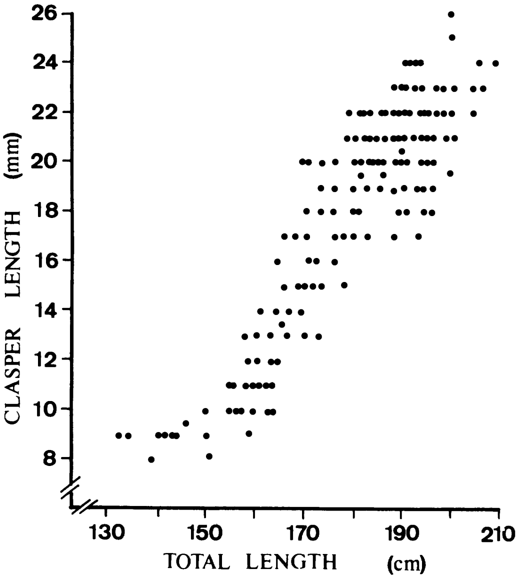

Fig. 2. Clasper-body length relationship of *Carcharhinus plumbeus.*

The number of embryos per litter ranged from 4–12 (Table 3), with a mean of 7.54. Pregnant females containing six, seven, or eight embryos constituted 59 (80%) of the 74 examined. We did not find a marked difference in the number of embryos between the right and left uteri (Table 4). Of the 42 litters examined, 28 had equal numbers of embryos in each uterus, 10 had one more embryo on one side or the other, whereas only four had a difference of two or more between sides. Of 558 embryos in 74 litters examined, 274 were female and 284 were male. The null hypothesis of a 1:1 sex ratio is not rejected at the 0.05 level.

In *C. plumbeus,* the uterine compartments form as the embryo develops. Each embryo, enclosed by its embryonic membrane, is contained within its own individual uterine compartment. These compartments arise as ridges on the internal surface of the uterine wall. The ridges form on both sides of the embryo as soon as the eggs are first fertilized. As the embryos grow, the ridges increase in height until they overlap completely, encapsulating the embryo in a chamber. However, the ridges do not fuse together in the regions of overlap. The entire encapsulation process is generally completed before the embryos attain a TL of 15 cm. At this stage, the chambers are positioned obliquely. As the embryos reach full term the overlap-

TABLE 3. FREQUENCY DISTRIBUTION OF THE NUMBER OF EMBRYOS PER LITTER IN *Carcharhinus plumbeus* taken from northeastern Taiwan.

No. of embryo:	4	5	6	7	8	9	10	12	Total
Male	2 3	1 2 3	2 3 4	2 3 4 6	2 3 4 5 6 7	4 5	4 5 6	9	284
Female	2 1	4 3 2	4 3 2	5 4 3 1	6 5 4 3 2 1	5 4	6 5 4	3	274
No. of litters:	1 2	1 1 1	4 2 2	2 7 6 2	8 6 8 5 6 1	1 1	1 2 2	2	74
Subtotal	3	3	8	17	34	2	5	2	74

ping portions of the compartments become increasingly narrow until they finally separate, at which point parturition occurs.

Pups are born from Feb. to April. We estimate the gestation period to be roughly 10–12 months (Fig. 3). No embryos were found in May, June, or July, although some mature sharks had fertilized eggs in their uteri during April and May. After 10–12 months of development, most embryos had attained a total length of around 60–65 cm, at which size they could be readily separated from the placenta, suggesting that they were full term and ready to be born.

Counts were made of the number of uterine embryos and eggs in 74 pregnant females (180–219 cm TL). These counts ranged between four and 12 with a mean of 7.54. The relationship between the total number of uterine embryos and the total length of the mother is roughly described by the regression equation (Fig. 4):

$$n = -7.544 + 0.075TL \qquad n = 74$$

where n is litter size and TL is the total length of the mother in cm. Although it is clear from these data that fecundity is related to the size of the mother, the relationship is not particularly strong ($r = 0.41$).

Some females were found to have fertilized eggs in their uteri in April and May. In Aug., pregnant females contained embryos that ranged in size from 12–15 cm TL. (Fig. 3). In his study of sandbar sharks from the western Atlantic, Springer (1960) noted that it took at least three months following fertilization for embryos to attain a TL of 30 cm. Based on this information, Taniuchi (1971) speculated that the embryos of *C. plumbeus* that he examined in the East China Sea at the end of Oct. must have been fertilized between June and July. (He came to this same conclusion even after accounting for a possible difference in growth rate between the two regions.) In the present study, we find, as did Taniuchi (1971), that 30-cm TL embryos occur during Oct. However, we find that fertilization occurs during April and May, two months prior to the estimate reported by Taniuchi (1971) for *C. plumbeus* in Japanese waters.

DISCUSSION

The simplest method to assess maturity is to contrast secondary sexual characteristics in large individuals with those same characteristics as they appear in less developed individuals, as outlined in the methods section. In the present investigation, we found the most immediate way to assess maturity in males was clasper morphology and hardness. Pratt (1979) has also noted the utility of these features in assessing male sexual maturity. Springer (1960) pointed out that clasper calcification in *C. plumbeus* occurred at about the same time as the testis become enlarged, suggesting that clasper morphology is both a practical and accurate means by which to assess sexual maturity. We found that, when claspers are less than 15 cm in length, they could not be easily rotated anteriorly, whereas when claspers exceed 18 cm in length, they could be readily rotated to an anterior position.

Deep sea squaloid sharks, such as *Centroscymnus* spp. and the frilled shark (*Chlamydoselachus anguineus*), release an ovum through an ovulation pore on the wall of the ovary (Yano and Tanaka, 1987; Tanaka et al., 1990). We speculate that sharks in the genus *Carcharhinus* do

TABLE 4. FREQUENCY DISTRIBUTION OF THE NUMBER OF EMBRYOS IN THE LEFT AND RIGHT UTERI.

	Number of embryos										Total
Left uterus	3	3	3	5	3	4	4	5	4	5	5	
Right uterus	1	2	3	1	4	3	4	3	5	4	5	
Frequency	1	1	10	1	1	6	16	2	1	1	2	42

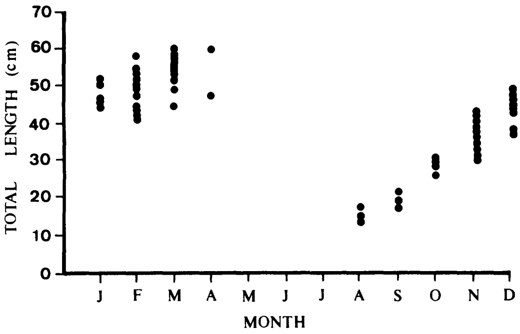

Fig. 3. Embryo length-month relationship for Taiwan sandbar shark.

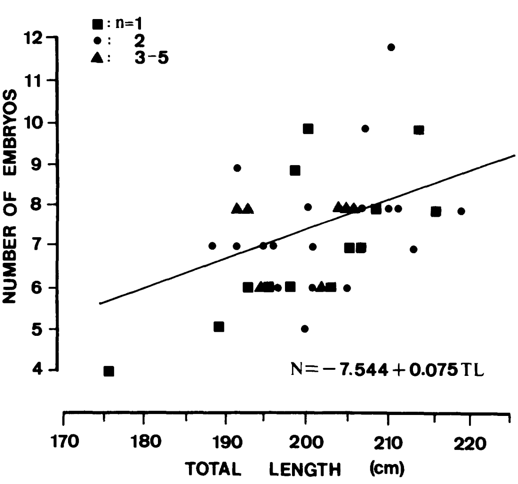

Fig. 4. The relationship between the number of embryos and maternal TL.

the same. Because the diameter of the ovulation pore is much smaller than that of the ripe ovum, we assume that the ovum, which becomes very flexible, must be forced out by the pressure of the follicular liquid. The fact that we find follicular liquid in the abdominal cavity and the uterus in female *C. plumbeus* lends some support to this supposition.

Ovarian eggs in *C. plumbeus* do not continue to enlarge during gestation. Tanaka et al. (1990) have made the same observation for the frilled shark, *C. anguineus*. They suggested that, in the case of the frilled shark, this was probably due to a space constraint in the body cavity. They suggested that there was simply no room for ovarian eggs to develop, when all of the available space was taken up by the liver and the developing embryos. Although this argument may hold for the frilled shark, we do not think that it applies to the sandbar shark because the size of fully developed ovarian eggs in sandbar sharks are considerably smaller (35–40 mm) than are those of the frilled shark (100 mm). In general, egg size reflects the reproductive strategy of the species. For example, in *Scoliodon* and *Gymnura*, where in the egg is much reduced in size, the developing embryos receive almost all of their nutrients from the mother via a placenta or trophonemata (Ranzi, 1934). In *C. plumbeus*, the developing embryos receive almost all of their nutrients from the mother via the placenta.

Wourms (1977) categorized three basic types of reproductive cycles: (1) reproduction throughout the year; (2) a partially defined annual cycle with one or two peaks during the year; and (3) a well-defined annual or biennial cycle. The first category consists of those species that are either reproductively active throughout the year or for the major part of the year. An example of this kind of reproductive strategy is reported by Liao (1992) for *Galeus sauteri* from northeastern Taiwan, which appears to breed throughout the year. The frilled shark *C. anguineus* also seems to have year-round reproductive activity Tanaka et al. (1990).

The sandbar shark would appear to be an example of the third type of reproductive cycle, showing a distinct biennial cycle. As mentioned earlier, the gestation period of the sanbar shark is estimated to vary between eight to 12 months, commonly nine months off Florida, 11–12 months off South Africa and the South China Sea (Compagno, 1984), 8–12 months off Australia, and 10–12 months in the East China Sea (Taniuchi, 1971). In the current survey, we estimate the gestation period to be 10–12 months. During the breeding season in northwestern Taiwanese waters, we find that approximately 50% of mature females are pregnant. In other words, we find that two distinct reproductive groups are apparent, the first has full-term embryos in the uterus and undeveloped ovaries, whereas the second has large ova with empty but expanded and flaccid uteri. Although this biennial reproductive strategy might seem to have an adverse effect on recruitment for the species, it is possible that the alternating "year of rest" may be essential to the survival of the adult females.

Sandbar sharks are abundant in the coastal seas around northeastern Taiwan, especially between Nov. and March in the winter and spring seasons. The longlining industry rarely captures individuals smaller than 120 cm TL, possibly because the smaller individuals keep to shallower waters nearer the shore. The sex ratio of the captured specimens is 1:1, although it varies from month to month. Springer (1960) noted that sexes are often segregated, except during courtship and mating. This type of sexual segregation might account for deviations in the sex ratio during the course of the year. It is interesting to note that, in the western Atlantic off the US southeastern seaboard, adult females far outnumber males by five or six to one. Furthermore, only 17–27% of the females captured in these western Atlantic waters were pregnant (Springer, 1960). Compagno (1984) has suggested that the low incidence of pregnant females might be attributable to the apparent scarcity of males in the area. Such imbalances in sex ratio apparently do not occur in waters off the Hawaiian Islands, nor is there an underrepresentation of pregnant females. Wass (1973) reported that 42% of the adult females he examined from Hawaiian waters were pregnant. This finding is comparable to our own where we find that approximately 40–50% of adult females are pregnant.

According to fishermen, pupping grounds occur in the shallow waters off northeastern Taiwan, into which pregnant females come to drop their young in spring (Feb. to March). Females are thought to be inhibited away from feeding grounds when they give birth and for a short period afterward (Springer, 1960). This is thought to be a mechanism to protect the young from cannibalism. The females leave the pupping grounds soon after giving birth, whereas the young remain in the shallow coastal waters. Thus, these "nursery" grounds are separated from the normal ranges of adults except, of course, when females arrive to drop their young.

Taniuchi (1971) reported the length at birth of the sandbar shark in the East China Sea to be between 65–75 cm. Springer (1960) reported a mean TL at birth of 61 cm for sandbar sharks from the western North Atlantic. The largest uterine embryos in this study measured 60–65 cm TL. Taniuchi (1971) reported that the number of pups per litter ranged from 2–10 with a mean of six in the East China Sea; Springer (1960) reported a range of 1–14 with a mean of nine for the western north Atlantic; whereas we report a range of 4–12 with a mean of 7.5 for the northeastern Taiwanese population. It would seem that the size and number of pups produced is a consequence of the available space in the uterus, more pups can be produced if they are dropped at a smaller size.

Acknowledgments

We thank G. Naylor, for reading the manuscript critically. We acknowledge L. F. Chen, Nan Fan Ao Fish Market, for his assistance in collecting samples. Financial support was received from National Science Council (contract: NSC 81-0209-B019-01 and NSC 82-0409-B019-012).

Literature Cited

Aasen, O. 1966. Blahaien, *Prionace glauca* (Linnaeus) 1958. Fisken. Havet. 1:1–16.

Baranes, A., and J. Wendling. 1981. The early stages of development in *Carcharhinus plumbeus*. J. Fish Biol. 18:159–175.

Bass, A. J., J. D. D'Aubrey, and N. Kitnassamy. 1973. Sharks of east coast of southern Africa. I. The genus *Carcharhinus* (Carcharhinidae). Oceanogr. Res. Inst. (Durban) Invest. Rep. 33:3–168.

Bigelow, H. B., and W. C. Schroeder. 1948. Sharks, p. 59–546. *In:* Fishes of the western North Atlantic, Part One. A. E. Parr and Y. H. Olsen (eds.). Sears. Found. Mar. Res., Yale Univ. Mem. 1, New Haven, CT.

Branstetter, S., and J. D. McEachran. 1986. Age and growth of four carcharhinid sharks common to the Gulf of Mexico: a summary paper, p. 361–371. *In:* Indo-Pacific fish biology: Proceedings of the Second International Conference on Indo-Pacific. T. Uyeno, R. Arai, T. Taniuchi, and K. Matsuurs (eds.). Ichthyol. Soc. Jap., Tokyo.

———, and R. Stiles. 1987. Age and growth estimates of the bull shark, *Carcharhinus leucas*, from the northern Gulf of Mexico. Environ. Biol. Fish. 20:169–181.

Clark, E., and K. von Schmidt. 1965. Sharks of the central Gulf coast of Florida. Bull. Mar. Sci. 15: 13–83.

Compagno, L. J. V. 1984. FAO species catalogue. Vol. 4. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. FAO Fish. Synop. 125:251–655.

Garrick, J. A. F. 1982. Shark of the genus *Carcharhinus*. U.S. Dept. Comm. NOAA Tech. Rep. NMFS Circ. 445:1–194.

Gohar, H. A. F., and F. M. Mazhar. 1964. The elasmobranches of the Northwestern Red Sea. Publ. Mar. Biol. Stn. Ghardaqa. 13:1–144.

Holden, M. J., and D. F. S. Raitt. 1974. Manual of fisheries science Part 2—methods of resource investigation and their application. FAO Fish. Tech. Paper 115, rev. 1. United Nations Development Program, Food and Agriculture Organization of the United Nations, Rome.

Kauffman, D. E. 1950. Notes on the biology of tiger shark (*Galeocerdo articus*) from Philippine waters. U.S. Fish. Wildl. Ser. Res. Rep. 16:1–10.

Liao, I. Y. 1992. Reproductive biology of blacktip sawtail catshark, *Galeus sauteri* around the Guei Shan island of Taiwan water. Unpubl. master's diss., Nat. Taiwan Ocean Univ., Keelung:1–87.

Pratt, H. L. Jr. 1979. Reproduction in the blue shark, *Prionace glauca*. Fish. Bull. NOAA Tech. NMFS 77:445–470.

Ranzi, H. 1934. Le basi fisiomorfologische dello sviluppo embrionale dei Selaci-Part II et III. Pubb. Staz. Zool. 13:331–437.

SPRINGER, S. 1960. Natural history of the sandbar shark, *Eulamia milberti.* U.S. Fish Wildl. Serv. Fish., Bull. 61:1–38.

TANAKA, S., Y. SHIOBARA, S. HIOKI, H. ABE, G. NISHI, K. YANO, AND K. SUZUKI. 1990. The reproductive biology of the frilled shark, *Chlamydoselachus anguineus,* from Suruga Bay, Japan. Jap. J. Ichthyol. 37:273–291.

TANIUCHI, T. 1971. Reproduction of the sandbar shark, *Carcharhinus milberti,* in the East China Sea. *Ibid.* 18:94–98.

TESTER, A. L. 1969. Co-operative shark research and control program. Univ. Hawaii Final Rept. 1967–69:1–47.

WASS, R. C. 1973. Size, growth, and reproduction of the sandbar shark, *Carcharhinus milberti,* in Hawaii. Pac. Sci. 27:305–318.

WOURMS, J. P. 1977. Reproduction and development in chondrichthyan fishes. Am. Zool. 21:473–515.

YANO, K., AND S. TANAKA. 1987. Reproductive organs of deep sea sharks, *Centroscymnus owstoni* and *C. coelolepis.* J. Fac. Mar. Sci. Tech. Tokai Univ. 25: 57–67.

GRADUATE SCHOOL OF FISHERY SCIENCE, NATIONAL TAIWAN OCEAN UNIVERSITY, 2 PEI-NING ROAD, KEELUNG 20224, TAIWAN, REPUBLIC OF CHINA. Send reprint requests to C-TC. Submitted: 8 Aug. 1994. Accepted: 9 Dec. 1994. Section editor: R. Winterbottom.

Copeia, 1995(3), pp. 665–675

Allozyme Variation and Expression in Lizards of the *Tropidurus nanuzae* Species Group (Iguania: Tropiduridae)

JOSÉ MANOEL MARTINS

The tropidurid lizards of the genus *Tropidurus nanuzae* species group comprise three species (*T. nanuzae, T. amathites,* and *T. divaricatus*) that occur along or close to the Serra do Espinhaço in eastern Brazil. *Tropidurus nanuzae* is saxicolous and is considered the earliest derived species of the group. The other two species are psammophilous, occurring on the continental dunes of the Rio São Francisco (Bahia, Brazil). An allopatric model affords an explanation of the speciation mechanism in these psammophilous lizards. A protein electrophoresis study corroborates the monophyly of the group. The molecular and morphological evolutionary rates for *T. amathites* and *T. divaricatus* are conspicuously different. The study also shows genetic divergence between saxicolous and psammophilous populations of *T. nanuzae.*

Os lagartos iguanídeos do gênero *Tropidurus,* incluídos no grupo *nanuzae,* englobam três espécies (*T. nanuzae, T. amathites* e *T. divaricatus*), que ocorrem ao longo ou nas adjacências da Serra do Espinhaço. *Tropidurus nanuzae* é considerada a espécie morfologicamente mais primitiva do grupo e predominantemente saxícola. As outras espécies do grupo são psamófilas, ocorrendo na região de dunas interiores do rio São Francisco (Bahia, Brasil). Existe um modelo alopátrico que permite explicar a especiação deste par de espécies. Foi realizado um estudo de eletroforese de proteínas que apoiou a monofilia do grupo. Constatou-se que existe uma discrepância flagrante entre as taxas de evolução molecular e morfológica para *T. amathites* e *T. divaricatus.* O estudo também apóia a existência de diferenciação genética entre as populações saxícolas e psamófilas de *T. nanuzae.*

THE *Tropidurus nanuzae* group comprises three species that occur near or along the Serra do Espinhaço, Brazil: *T. nanuzae, T. amathites,* and *T. divaricatus* (Rodrigues, 1986, 1988; Kasahara et al., 1987). *Tropidurus nanuzae* is predominantly saxicolous and occurs in several localities in the southernmost and middle portions of the Espinhaço range at altitudes around or above 900 m. Only one population of this species is known from sandy areas near Pedra Menina, in the state of Minas Gerais. Nevertheless, despite the habitat differences,