Japanese Journal of Ichthyology
Vol. 25, No. 3 1978

魚類学雑誌
25巻3号 1978年

Studies on Sharks—XIV. Reproduction in the Telok Anson Shark Collected from Perak River, Malaysia

Kazuyuki Teshima, Mukhtar Ahmad and Kazuhiro Mizue

(Received March 22, 1978)

Abstract The Telok Anson shark, *Scoliodon laticaudus*, which is distributed in rivers and lakes in Indonesia and Malaysia was collected and the reproductive biology in both male and female was examined. Reproductive activity takes place throughout the year. The male *S. laticaudus* is estimated to reach maturity at about 330 mm in total length based on condition in the testis, seminal vesicle and clasper. The female *S. laticaudus* has two functional ovaries. Oocytes are lined by a single layer of follicular cells. A mature egg is small and its size at ovulation is about 1 mm in diameter. A fertilized egg is covered with a gelatinous substance, and has cilia at both sides. Yolk does not exist in the foetal placenta even in the early gestation, and capillaries are well developed in tissues inside the foetal placenta. The embryo is nourished by the placenta from the earliest stage of gestation. The umbilical stalk contains only an artery and a vein. There is no ductus vitellointestinalis. The umbilical stalk has many appendiculae, whose epithelia absorb nutrition from the uterine fluid. The size at sexual maturity in the female is estimated to be about 325～350 mm in total length.

Scoliodon laticaudus (Müller et Henle) (Fig. 1) is distributed in the Strait of Malacca and also in lakes and rivers flowing into the Strait. It is said that *S. laticaudus* occurs abundantly in Perak River and Muar River in the western part of the Malay Peninsula, and in the Barumun, Rokan, Kampar, Indragiri, Hari and Musi Rivers in the eastern part of Sumatra. This species is also found in rivers in Borneo and in the eastern part of Malay Peninsula. Of these rivers, the Perak River was chosen based on a preliminary investigation carried out in 1975 and the reproductive biology of *S. laticaudus* was studied.

Materials and Methods

The authors stayed at Telok Anson (=T. Anson), Malaysia, during the period from December 18 to 24, 1976, and collected *Scoliodon laticaudus* (Müller et Henle) specimens. T. Anson is located about 70 km upstream from the mouth of Perak River which flows from north to south in the State of Perak (Fig. 2). The number of specimens caught in Perak River and bought at markets was 70; male 31 (316～426 mm in TL), female 39 (255～498 mm in TL). Here, we call the present *S. laticaudus* the T. Anson shark.

Specimens were anatomized soon after measurement, and observations were made on the ovaries, uteri, embryos and placenta in the female, and the testes, seminal vesicles and claspers in the male. Many of the reproductive organs were preserved in formalin for histological observations.

Results

Testis. The testis of the T. Anson shark consists of many seminiferous tubules (Fig. 3A). Spermatogonia appear between the seminiferous epithelium and the basement membrane of the seminiferous tubule and develop into spermatocytes, spermatids and spermatozoa. About 50 to 60 spermatozoa gather to form a bundle, and each spermatozoon is situated with its head directed towards the basement membrane of the seminiferous tubule and with its tail towards the lumen (Fig. 3B, C). Spermatozoa produced are accumulated in the seminal vesicle after passing through the epididymis and spermiduct.

Seminal vesicle. The seminal vesicle of the T. Anson shark is divided into a number of compartments. Each comparment opens into the central duct. The internal surface has many longitudinal folds which enable the seminal vasicle to expand or contract according to the quantity of spermatozoa present (Fig. 3D).

Clasper. The dorsal and ventral views of the

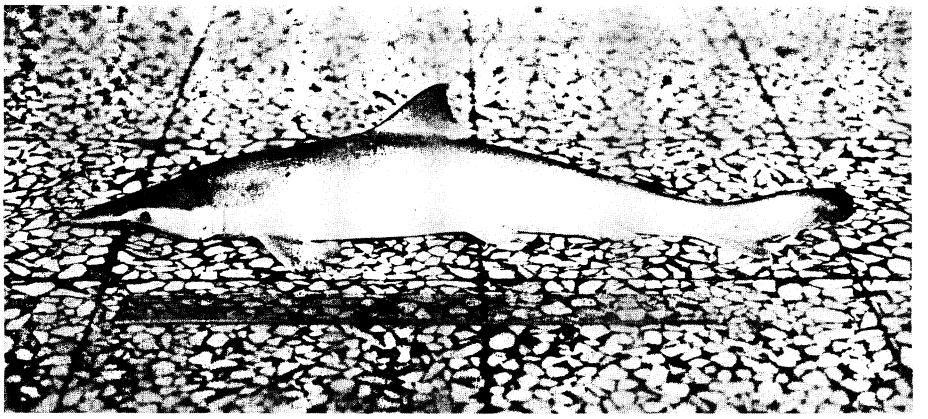

Fig. 1. T. Anson shark, *Scoliodon laticaudus*.

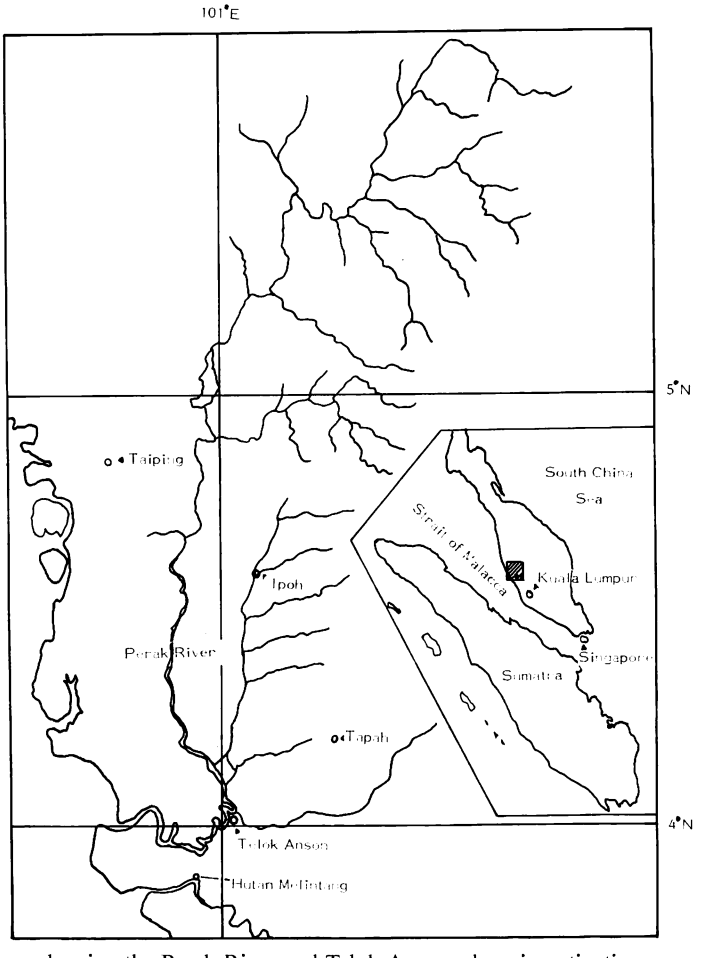

Fig. 2. A map showing the Perak River and Telok Anson where investigations were carried out.

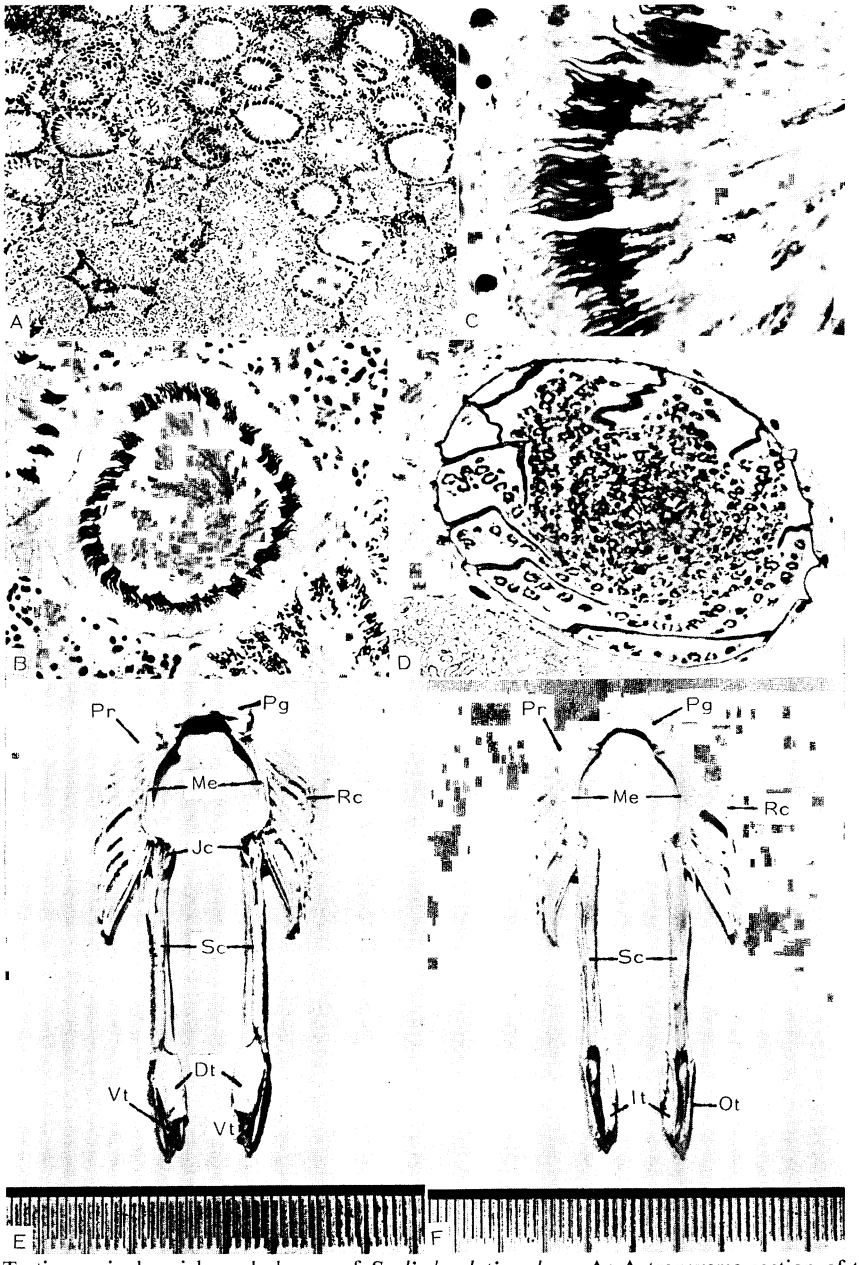

Fig. 3. Testis, seminal vesicle and clasper of *Scoliodon laticaudus*. A: A transverse section of the testis. The testis consists of many seminiferous tubules. ×20. B, C: About 50 to 60 spermatozoa gather to form a bundle. Each spermatozoon is situated with its head directed toward the basement membrane and its tail toward the lumen. B, ×200, C, ×400. D: Seminal vesicle containing spermatozoa. ×10. E: Clasper, dorsal view. F: Clasper, ventral view. Dt, dorsal terminal cartilage; It, inner terminal cartilage; Jc, joint cartilage; Me, metapterygium; Ot, outer terminal cartilage; Pg, pelvic girdle; Pr, propterygium; Rc, radial cartilage; Sc, stem cartilage; Vt, ventral terminal cartilage.

pelvic fin and clasper skeleton are shown in Fig. 3E, F. The pelvic fin consists of the propterygium, metapterygium and radial cartilages. The propterygium is attached to the distal end of the pelvic girdle, and radial cartilages are connected to the outer side of the metapterygium.

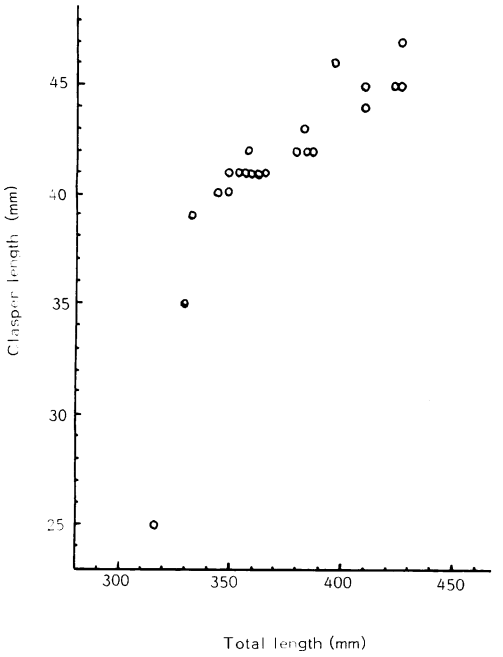

Fig. 4. Relationship between clasper length and total length.

The metapterygium is supported by the pelvic girdle. Except for the posterior six, each radial cartilage consists of two segments, a long proximal segment and a short, curved segment with a sharp end. The propterygium has a forked end.

The number of radial cartilages on each side was 14 in two specimens examined.

The clasper is connected to the metapterygium by a joint cartilage. The clasper is made up of a main stem cartilage and four terminal cartilages. The four terminal pieces located distal to the stem cartilage are the dorsal terminal cartilage, the ventral terminal cartilage, the inner terminal cartilage and the outer terminal cartilage.

The relationship between the total length and the clasper length is shown in Fig. 4. Fig. 4 reveals a rapid increase in clasper length before the shark reaches a total length of about 330 mm. Following this rapid growth period the claspers continue to grow but at a slower rate.

Ovary. Females of *Scoliodon laticaudus* have two functional ovaries. The ovaries are located at the anterior end of the epigonal organ.

Oogonia appear in the ovarian epithelium and sink into the ovary to develop into oocytes. The oocytes are lined by a single layer of follicular cells throughout their development (Fig. 5A, B). The size of a mature oocyte at ovulation is about 1 mm in diameter. The ovulated eggs are transferred through a common ostium and distributed to both oviducts.

Although many oocytes are formed in ovary, most oocytes disintegrate and are absorbed during the course of development (Fig. 5C).

Embryos and placenta. Among 39 female specimens collected 14 were pregnant. In the uteri of these pregnant females, fertilized eggs and embryos at various developmental stages were found (Fig. 6A). Fertilized eggs found in the uteri were very small, about 1 mm in maximum diameter. They have cilia at one side and a bundle of longer movable cilia at the other side, which are fixed at the uterine wall when implantation occurs (Fig. 6B). Implantation takes place at the posterior end of the uterine compartment on the ventral wall.

Placentation commences soon after implantation. The uterine wall where fertilized eggs are attached forms a protrusion which becomes the maternal placenta. At the same time, the fertilized egg is differentiated into an embryo and a foetal placenta (Fig. 6C). The embryo is connected to a foetal placenta by the umbilical stalk. The foetal placenta is globular in shape (Fig. 5F), and increases in size as the embryo grows. In late pregnancy the diameter of the foetal placenta reaches a maximum of about 15 mm.

No yolk is contained within the foetal placenta from the earliest stage of gestation. The foetal placenta is filled with blood capillaries (Fig. 5D).

At the foetal-maternal junction of the placenta, the maternal epithelium disappears and the foetal epithelium abuts against the maternal connective tissue (Fig. 5E).

Umbilical stalk. The umbilical stalk of *Scoliodon laticaudus* contains two ducts; the umbilical artery and vein (Fig. 5G). The umbilical stalk of this species has many long appendiculae (Fig. 6C). There is also an artery and a vein within an appendicula. The external epithelium of the appendicula is thin and blood capillaries are well developed in and beneath the epithelium.

Discussion

Male. A completely formed spermatozoon

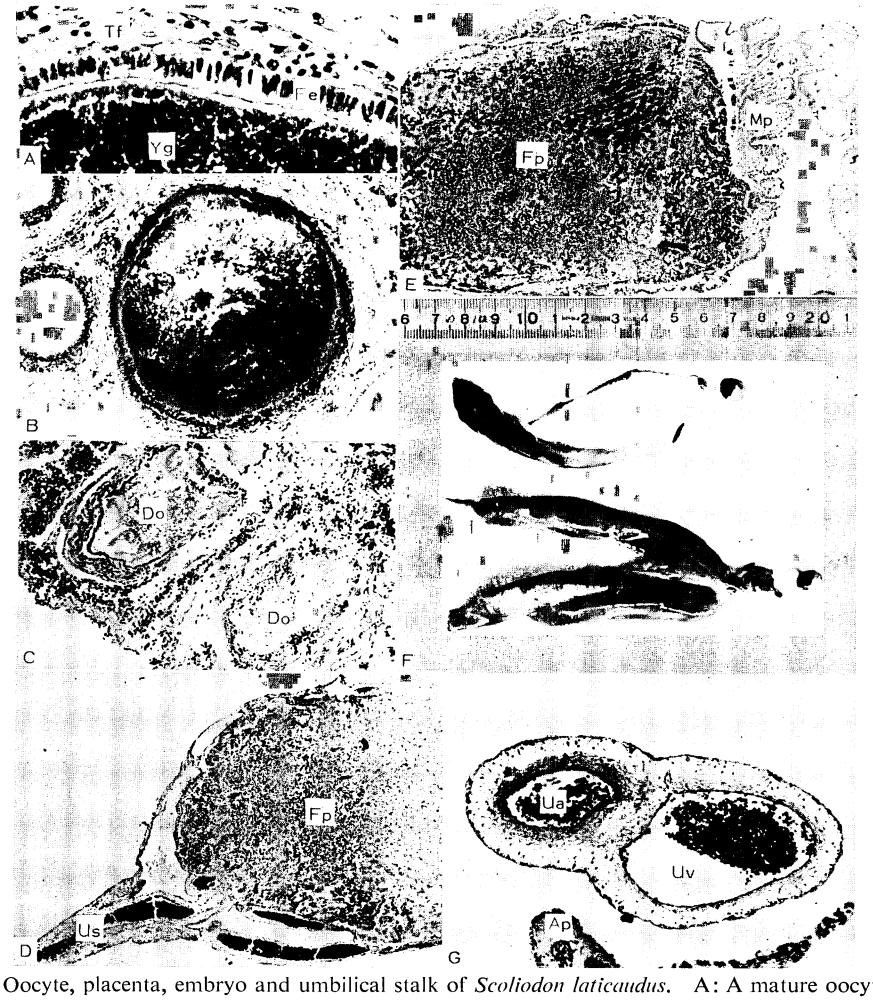

Fig. 5. Oocyte, placenta, embryo and umbilical stalk of *Scoliodon laticaudus*. A: A mature oocyte lined by a single layer of the follicular epithelium. ×200. B: A mature oocyte. Ovulation seems to occur imminently. ×50. C: Degenerating oocytes. ×50. D: Foetal portion of placenta. ×50. E: Placenta showing the junction at the foetal-maternal. ×50. F: An embryo with umbilical stalk and foetal placenta, and uterus containing the embryos. G: Umbilical stalk. There is no ductus vitellointestinalis. ×50. Ap, appendicula; Do, degenerating oocyte; Fe, follicular epithelium; Fp, foetal placenta; Mp, maternal placenta; Tf, theca folliculi; Ua, umilical artery; Us, Umbilical stalk; Uv, umbilical vein; Yg, yolk glouble.

uaually has a spiral, slender head (Chen et al., 1973). However, the head of spermatozoon of *Scoliodon laticaudus* is thicker and not as spiral compared with those of other species.

Skeletons of the pelvic fins and claspers in the present species are almost the same as those of other species in morphology. The number of terminal cartilages making up the distal end of the clasper is four, similar to those in *Squalus acanthias, Mustelus manazo* and *M. griseus* (Gilbert and Heath, 1972; Teshima, unpublished data). As Ishiyama (1958) has classified species in Rajidae using the morphological differences in clasper skeletons, the morphology of the terminal cartilage in the present species can be clearly distinguished from those in the other species described above.

A method of estimating the length at sexual maturity by the relationship between the clasper length and the total length has been used in species such as *Squalus suckleyi, S. brevirostris* and *Galeorhinus japonicus* (Yamamoto and Kibe-

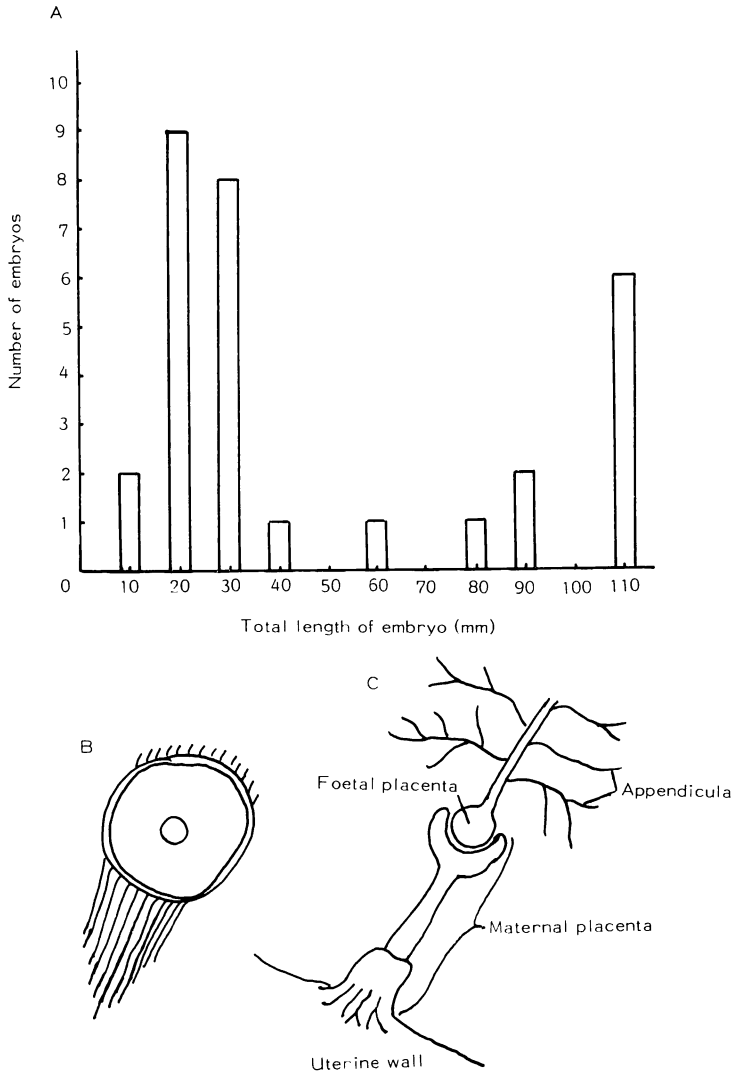

Fig. 6. A: Number of embryos at various developmental stages. B: Simplified drawing of the fertilized egg found in uterus. C: Simplified drawing of the placenta.

saki, 1949; Kibesaki, 1954; Chen and Mizue, 1973). According to those reports, clasper length increases rapidly as the shark reaches maturity, but it increases slowly after maturity. The male *Scoliodon laticaudus* is thus estimated to reach maturity when the shark is about 330 mm in total length. In addition to this, specimens having small seminal vesicles with either little quantity or no spermatozoa were less than 333 mm in total length. This fact also suggests that the male *S. laticaudus* reaches maturity at about 330 mm in length.

Mature male specimens examined had seminal vesicles which were either fully expanded and filled with spermatozoa, or partially expanded and filled with spermatozoa, or contracted and quite empty of spermatozoa. Teshima (1978), working with monthly change of the gonad index in male *Mustelus manazo* and *M. griseus* (both of which have definite reproductive season), indicated that the seminal vesicles and spermiducts of these two *Mustelus* species in the mating season were either filled with spermatozoa or quite empty. Seminal vesicles in *S. laticaudus*, how-

ever, showed considerable individual variation in condition. These suggest that male *S. laticaudus* investigated in the present study have no definite mating season.

Female. Usually many female sharks have only one functional ovary. Sharks of the genus *Scoliodon* to which the present species belongs have two functional ovaries (Mahadevan, 1940).

The follicular epithelium changes from a single layer to stratified layers as the oocyte develops and reaches maturity in species such as *Cetorhinus maximus, Galeorhinus japonicus, Mustelus manazo* and *M. griseus* (Matthews, 1950; Teshima et al., 1976; Teshima, unpublished data). However, in *Scoliodon laticaudus* the oocyte is lined by a single layer of follicular cells throughout the whole course of development.

In *Scoliodon laticaudus* the mature oocyte at ovulation is quite small (about 1 mm in diameter) compared with those in other species. Mahadevan (1940), working with reproduction of *S. sorrakowah* (Cuvier) (considered to be a synonym of *S. laticaudus* (Müller et Henle) (Matsubara, 1955)) described the ovary as very small with very inconspicuous eggs and the ova were no bigger than "those of a frog". The oocyte of *S. laticaudus* may be thus one of the smallest in size among selachians.

Most placental species establish the placenta at the middle stage of gestation, e.g., placentation commences at about three and a half months after fertilization in *Sphyrna tiburo* and at about three months after fertilization in *Mustelus griseus* (Schlernitzauer and Gilbert, 1966; Teshima et al., 1974). In *Scoliodon laticaudus* of the present investigation, however, placentation commences soon after implantation. Setna and Sarangdhar (1948), working with reproduction in *S. sorrakowah,* described the placenta in this species as forming at the 3 mm-stage of embryonic development. In most placental species the embryo is nourished mainly by yolk before the establishment of the placenta, and mainly by the mother after that. In *S. laticaudus*, however, the yolk is not contained within the yolk sac even in the earliest stage of gestation. The embryo is thus nourished by the mother throughout the whole stage of gestation. Mahadevan (1940) and Setna and Sarangdhar (1948) also indicated that in *S. sorrakowah,* unlike other elasmobranchs, the yolk sac is initially very small due to the presence of only small amounts of yolk in it. Therefore, early establishment of a placental connection becomes necessary.

In sharks where the placenta is formed at the middle stage of gestation, the foetal portion of the placenta reduces its size as the embryo grows. In *Scoliodon laticaudus,* however, the foetal placenta increases in size as the embryo grows. As has been indicated by Mahadevan (1940), growth of the external surface of the foetal placenta may make it efficient for the exchange of nutrients and excretion between the embryo and the mother.

The placenta in sharks can be separated into several types according to the mode of junction between the foetal and maternal tissues. Schlernitzauer and Gilbert (1966) refer to the placenta of *Sphyrna tiburo* as epithelio-shell-membrane-epithelial placenta, where the greatly reduced epithelia of the foetal placenta and maternal placenta are in contact with the embryonic membrane. In *Mustelus griseus* the foetal and maternal capillaries are bounded by the embryonic membrane. Teshima (1975) called the placenta of *M. griseus* endothelio-embryonic membrane-endothelial placenta. The *Scoliodon laticaudus* placenta may be expressed as syndesmo-epithelial. The placenta of *S. laticaudus* is thus similar histologically, at its foetal-maternal junction, to that of mammalians. The well developed capillaries within the foetal placenta may also increase the capacity to absorb nutrition from the maternal tissue.

In placental species, an embryonic membrane exists between the foetal and maternal junction of the placenta. Such an embryonic membrane, however, does not exist in the placenta of *Scoliodon laticaudus*. Nor is an embryonic membrane found in the placenta of *S. sorrakowah* (Mahadevan, 1940; Setna and Sarangdhar, 1948).

The protruding maternal placenta in *Scoliodon laticaudus* remains for a while even after parturition. This indicates the number of embryos which were contained within an uterus. Scars of the maternal placenta seem to disappear before the succeeding ovulation takes place.

A 110 mm-embryo found in the uterus of a female *Scoliodon laticaudus* seemed to be a near full-term embryo based on the condition of the placenta and uterus. According to Setna and Sarangdhar (1948), in *S. sorrakowah,* parturition

occurs when the embryos are 130 to 150 mm in total length. Embryos at various developmental stages (including fertilized eggs to near full-term embryos) were thus found in the uteri of the female *S. laticaudus* although the collecting period was very short. This suggests that there is no definite reproductive season in females of *S. laticaudus*. Teshima and Mizue (1972) investigated the reproduction of *Carcharhinus dussumieri* (which also has no definite reproductive season) occurring in the South China Sea. Similarly, although the collecting period was also very short, they found embryos at various developmental stages in the uteri.

The yolk stalk (which is called the umbilical stalk after establishment of the placenta) contains three ducts; artery, vein and ductus vitellointestinalis. The ductus vitellointestinalis remains after formation of the placenta (Alcock, 1890; Gilbert and Schlernitzauer, 1966; Schlernitzauer and Gilbert, 1966; Teshima and Mizue, 1972). Within an umbilical stalk of *Scoliodon laticaudus* there is only an artery and a vein. No ductus vitellointestinalis exists. The ductus vitellointestinalis functions in the transportation of yolk from the yolk sac to the embryo. In *S. laticaudus,* however, this duct is not necessary since no yolk is contained within the yolk sac. This fact suggests that the placenta should be established in the earliest stage of gestation in order to nourish the embryo. Teshima (1973), working with the umbilical stalk in *Carcharhinus dussumieri,* showed that the two blood vessels within the stalk become clearly differentiated into an artery and a vein as the placenta is established. In *S. laticaudus* two blood vessels in the stalk of the embryo at the early stage of gestation are already distinguishable as an artery and a vein. This fact also indicates that the placenta is formed during the early stages of gestation.

The epithelium of the appendicula is thin, and well developed capillaries are found in and beneath the epithelium. The epithelium of the appendicula is thus considered to absorb nutrients from the uterine fluid.

Among female specimens investigated, the smallest female whose uterus contained fertilized eggs was 324 mm in total length, and the largest female, in which ovulation seemed to occur imminently, was 351 mm in total length. Females of *Scoliodon laticaudus* are thus estimated to reach maturity at a total length between 325 and 350 mm.

Observations on the reproduction of the freshwater *Scoliodon laticaudus* collected from Perak River agree, in general, with those on the marine *S. sorrakowah* by Mahadevan (1940) and Setna and Sarangdhar (1948).

It is not yet known, due to the short period of investigation, whether the T. Anson shark, *Scoliodon laticaudus*, lives only in freshwater, or moves between freshwater and sea water as *Carcharhinus leucas* found in Lake Nicaragua does (Thorson et al., 1966, 1969; Thorson, 1971). It is also not known whether the highly developed reproductive system in *S. laticaudus* is due to this shark entering sea water from freshwater or conversely entering freshwater from sea water.

Acknowledgements

We wish to express our appreciation to the staff and scientists of the following organizations for their assistance and cooperation in conducting this study: The Philippines Center for Advanced Studied, Bureau of Fisheries and Aquatic Resources, and Naujan Fisheries Research Laboratory, Philippines, the Board of National Unity, Malaysia, the Indonesian Institute of Sciences, the National Institute of Oceanography, and College of Fisheries, Riau University, Indonesia. Thanks are also due to Dr. Tsuyoshi Muramatsu of Nagasaki University, Dr. Tetsuya Hirano and Dr. Toru Taniuchi of University of Tokyo, and Mr. Seizaburo Sonoda, Curator of Yomiuri Land Marine Aquarium for their assistance throughout the research in rivers and lakes in Southeast Asia. Dr. Daniel J. Sheehy of the Graduate School of Oceanography, University of Rhode Island, USA, was kind enough to correct the English manuscript. This study was supported by grants (No. 7531 and 7611) from the Ministry of Education of the Japanese Government.

Literature cited

Alcock, A. 1890. Observations on the gestation of some sharks and rays. J. Asiat. Soc. Bengal, 59 (2): 51～56, figs. 1～6.

Chen, C. T. and K. Mizue. 1973. Studies on sharks-VI. Reproduction of *Galeorhinus japonicus*. Bull. Fac. Fish. Nagasaki Univ., (36): 37～51,

figs. 1～8, pl. 1.
Chen, C. T., K. Teshima, and K. Mizue. 1973. Studis on sharks-IV. Testes and spermatogeneses in selachians. Bull. Fac. Fish. Nagasaki Univ., (33): 56～65, fig. 1, pls. 1～4.
Gilbert, P. W. and D. A. Schlernitzauer. 1966. The placenta and gravid uterus of *Carcharhinus falciformis*. Copeia, 1966 (3): 451～457, figs. 1～7.
Gilbert, P. W. and D. A. Heath. 1972. The clasper-siphon sac mechanism in *Squalus acanthias*. Comp. Biochem. Physiol., 42A: 97～119, figs.1～2.
Ishiyama, R. 1958. Studies on the rajid fishes (Rajidae) found in the waters around Japan. J. Shimonoseki Coll. Fish., 7 (2,3): 1～202, figs. 1～86, pls. 1～3.
Kibesaki, O. 1954. Studies on the sharks from the East and Yellow Seas. (11). Maturity of the *S. brevirostris*. Bull. Seikai Reg. Fish. Res. Lab., (5): 36～46, figs. 1～5. (In Japanese).
Mahadevan, G. 1940. Preliminary observation on the structure of uterus and the placenta of a few Indian elasmobranchs. Proc. Indian Acad. Sci. (sect. B)., 11: 2～40, figs. 1～42.
Matsubara, K. 1955. Fish morphology and hierarchy. I. Ishizaki Shoten, Tokyo, xi+789 pp., 289 figs. (In Japanese).
Matthews, L. H. 1950. Reproduction in the basking shark, *Cetorhinus maximus* (Gunner). Phil. Trans. Roy. Soc. London, ser. B., 234 (612): 247～316, figs. 1～24, pls. 10～20.
Schlernitzauer, D. A. and P. W. Gilbert. 1966. Placentation and associated aspects of gestation in the bonnethead sharks, *Sphyrna tiburo*. J. Morph., 120 (3): 219～232, figs. 1～3, pl. 1.
Setna, S. B. and P. N. Sarangdhar. 1948. Description, bionomics and development of *Scoliodon sorrakowah* (Cuvier). J. Indian Zool., 156 (1–4): 25～53, figs. 1～9.
Teshima, K. 1973. Studies on sharks-III. The stage of placentation and the umbilical stalk in *Carcharhinus dussumieri*. J. Shimonoseki Univ. Fish., 21 (3): 295～300, pls. 1～4.
Teshima, K. 1975. Studies on sharks-VIII. Placentation in *Mustelus grisues*. Japan. J. Ichthyol., 22 (1): 7～12, figs. 1～2.
Teshima, K. 1978. Studies on sharks-XII. Monthly change of the gonad index in male *Mustelus manazo* and *M. griseus*. Japan. J. Ichthyol., 24 (4): 285～289, figs. 1～2.
Teshima, K., C. T. Chen, and K. Mizue. 1976. Studies on sharks-IX. Ovary and oogenesis in selachians. J. Shimonoseki Univ. Fish., 25 (1): 41～45, fig. 1, pls. 1～2.
Teshima, K. and K. Mizue. 1972. Studies on sharks. I. Reproduction in the female sumitsuki shark *Carcharhinus dussumieri*. Mar. Biol., 14 (3): 222～231, figs. 1～11.
Teshima, K., K. Mizue, and S. Koga. 1974. Studies on sharks-VII. Reproduction in female *Mustelus griseus*. J. Shimonoseki Univ. Fish., 22 (3): 199～206, figs. 1～4, pls. 1～2.
Thorson, T. B. 1971. Movement of bull shark, *Carcharhinus leucas*, between Caribbean Sea and Lake Nicaragua demonstrated by tagging. Copeia, 1971 (2): 336～338, fig. 1.
Thorson, T. B., D. E. Watson, and C. M. Cowan. 1966. The status of the freshwater sharks of Lake Nicaragua. Copeia, 1966 (3): 385～402, figs. 1.
Thorson, T. B., G. F. Esterberg, and J. H. Johnson. 1969. Ultrasonic shark tag monitoring system. Technical Report, ONR Project No. NR-104–880, University of Nebraska, Lincoln, Nebraska, USA., 25 pp., figs. 1～8.
Yamamoto, T. and O. Kibesaki. 1949. Studies on the spiny dogfish *Squalus suckleyi*. (1) On the development and maturity of the genital glands with growth. Bull. Japan. Soc. Sci. Fish., 15 (10): 531～538, figs. 1～5. (In Japanese).

(KT: Shimonoseki University of Fisheries, Yoshimi, Shimonoseki 759–65 Japan; MA: Fakultas Perikannan, Universitas Riau, Pekanbaru, Riau, Indonesia, present address: Ocean Research Institute, University of Tokyo; KM: Ocean Research Institute, University of Tokyo, Nakano-ku, Tokyo 164, Japan)

サメ類の研究—XIV. マレーシア，ペラック河で採集された Telok Anson shark の生殖生態

手島和之・Mukhtar Ahmad・水江一弘

インドネシアおよびマレーシアの河川，湖沼およびマラッカ海峡に棲息している Telok Anson shark, *Scoliodon laticaudus* (Müller et Henle) を採集し，雌雄の生殖生態について調査を行った．本種は周年生殖を行っている．本種の雄は精巣，貯精嚢，交接器の状態より全長約 330 mm で成熟に達すると推定される．卵母細胞は単層の卵胞上皮でおおわれている．熟卵は小さく，排卵時で直径約 1 mm である．受精卵はゼラチン状の胞でおおわれ，片方に鞭毛状の動毛をもち，子宮に下降後，子宮下部腹側に動毛束で着床しそこに胎盤が形成される．胎盤胎児部には妊娠の初期より卵黄は存在していない．胎児部組織内には毛細血管が良く発達している．臍帯には動静脈のみで卵黄腸管はない．胎児は妊娠の初期から栄養を母体より供給される．また，臍帯は多くの付枝をもち，その上皮は子宮内液より栄養を吸収する．雌の成熟体長は全長 325～350 mm と推定される．

(手島: 759-65 下関市吉見水産大学校; Mukhtar: Fakultas Perikanan, Universitas Riau, Pekanbaru, Riau, Indonesia (現在: 東京大学海洋研究所); 水江: 164 東京都中野区 東京大学海洋研究所)