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The Reproductive Biology of the Frilled Shark, *Chlamydoselachus anguineus*, from Suruga Bay, Japan

Sho Tanaka[1], Yoshihisa Shiobara[2], Syozo Hioki[2], Hidenao Abe[2], Genjirou Nishi[3], Kazunari Yano[4] and Katsumi Suzuki[3]

[1] Faculty of Marine Science and Technology, Tokai University, 3-20-1 Orido, Shimizu 424, Japan
[2] Marine Science Museum, Tokai University, 2389 Miho, Shimizu 424, Japan
[3] Institute of Oceanic Research and Development, Tokai University, 3-20-1 Orido, Shimizu 424, Japan
[4] Japan Marine Fishery Resource Research Center, 3-27 Kioi-cho, Chiyoda-ku, Tokyo 102, Japan

Abstract An analysis of the reproductive biology of the frilled shark, *Chlamydoselachus anguineus*, was made on the basis of a collection of 264 specimens from Suruga Bay, Japan. This species is caught mainly from December to July. Almost all specimens were mature. The frilled shark appears to segregate by size and reproductive stage. Males mature below 1,100 mm total length (TL), while females reach sexual maturity between 1,400 and 1,500 mm TL. Males have active testes throughout the year. Females do not have a defined reproductive season. Ova emerge through each ovulation pore on the ovarian epithelium at a size of 230–250 g, and only enter the right oviduct. Ovarian eggs do not continue to develop during gestation. Egg capsules are shed when embryos reach between 60 and 80 mm TL. Young are born at a size of about 550 mm TL and 380 g body weight. Litter size ranges from 2 to 10, with a mean of 6. Late stage embryos may receive nutrients from the mother. The intervals of ovulation seem to be about two weeks. The ovulation season in each female extends over a few months. The early embryonic development is slow. The gestation period appears to last at least three and a half years. The encapsulated embryos maintained in artificial conditions grow at a rate of between 10 and 17 mm per month for a period up to 134 days.

The frilled shark, *Chlamydoselachus anguineus* Garman, is one of the most primitive species of living sharks. Since Garman (1884) first described it from Japan, several investigators have studied its anatomy and systematics (Garman, 1885; Goodey, 1910; Smith, 1937; Compagno, 1973, 1977; Masai, 1961; Masai et al., 1981; Sato et al., 1983; Ida et al., 1986). Nishikawa (1898) was the first to report on the reproduction of the frilled shark, especially the early stages of its embryos. Gudger and Smith (1933) and Gudger (1940) gave an account of the natural history and breeding habits of this species, based mainly on Dean's notes. The male reproductive system of the frilled shark was reported by Gilbert (1943). In spite of these studies, the reproductive biology of the frilled shark remains poorly understood.

In Suruga Bay, Japanese fishermen call the frilled shark "Kai-man-ryo", and consider it harmful because it tears fishing nets. The shark is mainly caught in bottom gill nets set for sea bream and scombropids, and in midwater trawl nets set for sergestid shrimp (*Sergia lucens*). We have been actively collecting the frilled shark in Suruga Bay since February 1984 in order to study its life history. In this paper, we report on the reproductive biology of this shark.

Materials and methods

We collected 139 male and 125 female sharks that were caught either with bottom gill nets, or with midwater and bottom trawl nets set at depths of 60 to 240 m in the inner part of Suruga Bay, from March 1981 to December 1988. The bottom gill net fishery is operated throughout the year, but is reduced in scale from June to December. The midwater trawl net fishery is operated over two seasons, from April to June and from October to December. The bottom trawl net fishery is operated from September to May. Since 1985, almost all sharks caught in these waters by fishermen have been retained for scientific study. Sharks collected on the same day were not always caught in the same location or with the same fishing gear.

Most specimens were immediately measured and dissected in our laboratories. Some sharks, however, were preserved in a refrigerator or 10% formalin and were then measured and dissected. Claspers were measured from their tips to the anterior margin of the cloaca. Internal reproductive organs were examined in detail and preserved in 10% formalin. Unfortunately, in some female specimens portions of the ovarian eggs, fertilized eggs, or external yolk sacs of embryos were broken before examination. The widths of the uterus and nidamental gland were measured. The testis, ovary, fertilized ovum, embryo, and liver were weighed in fresh condition. After the ovary was fixed with 10% formalin, the eggs were measured in three dimensions and weighed. The mean of the three linear measurements was used as the "diameter of ovum." A degenerating egg and an ovulation pore of an ovarian egg (Yano and Tanaka, 1987) were measured in the major and minor axes and their means were treated as the "diameter of degenerating egg" and the "diameter of ovulation pore," respectively.

After four fertilized eggs and 22 embryos with an external yolk sac were fixed with 10% formalin, they were dried in a freeze-drying apparatus (EYELA, FD-1) for a period of between 24 and 48 hours and weighed.

Ovarian eggs were classified into three categories, small, developing, and ripe. "Small" was defined as egg that is white in color and less than 15 mm in diameter, "developing" as being yolky and less than about 60 mm in diameter and 200 g in weight, and "ripe" as being heavier than 200 g in weight.

Sexual maturity of females was determined from the size of ovarian eggs and condition of the uterus. Females which had small ovarian eggs, threadlike uteri, and nidamental glands less than 15 mm in width were classed as immature (IM). The other females were classed as mature. Mature females were further classified in one of the various stages of the continuous reproductive cycle. Seven stages were recognized, as follows.

Developing ova (DO): Non-gravid females with developing ovarian eggs, a relatively expanded right uterus and a nidamental gland larger than 15 mm in width.

Ripe ova (RO): Non-gravid females holding at least one ripe ovarian egg, with an expanded right uterus, and with a nidamental gland larger than 25 mm in width.

Ovulation (Ov): Ovulating females with developing or ripe ovarian eggs, and fertilized eggs in the uterus.

Fertilized ova (FO): Post-ovulatory females with only fertilized ova in the uterus. These females had just finished ovulating.

Encapsulated embryos (EE): Gravid females carrying at least one embryo which was visible to the naked eye. These embryos were sheathed in very thin, golden brown, egg capsules, or were less than about 100 mm in total length (TL).

Free embryos (FE): Gravid females carrying embryos free in the uterus and larger than 100 mm TL.

Post-partum (PP): Non-gravid females with small ovarian eggs and flaccid uteri larger than 15 mm in width.

Sexual maturity of males was determined from the rigidity of the claspers and the presence of appreciable amounts of sperm in the seminal vesicles and sperm sac.

To examine growth of embryos, 4 encapsulated embryos taken surgically from two gravid females in May 18 and 19, 1988, were placed in two tanks containing untreated sea water; three of them were encaged and suspended near the surface in a 500 liter tank and one was placed in a 25 liter tank. Water was circulated through a filter and sometimes renewed. The water in the smaller tank was getting cold gradually. Total lengths of these embryos were measured with slide calipers. Water temperature was measured every day, and salinity and pH were also measured every week.

Embryos larger than about 100 mm TL could be sexed externally, allowing the sex ratio (male/(male + female)) to be determined. Gonadosomatic index (GSI) and hepatosomatic index (HSI) were calculated from the following formulae:

$$GSI = (GW/BW) \times 10^3$$
$$HSI = (LW/BW) \times 10^2$$

where BW is body weight (g), GW is gonad weight (g), and LW is liver weight (g).

Results

Catch condition. The total length of males collected ranged from 1,178 to 1,548 mm and that of females ranged from 1,256 to 1,852 mm. Eighty-two percent of the 264 specimens were collected between February and June (Table 1). No sharks were collected in August. In February and March, males considerably outnumbered females.

No male and only four female sharks were immature (Table 1). An immature female of 1,288 mm TL was caught singly on 19 March 1983. One of 1,503 mm TL was caught with a DO female on 7 May 1985. One of 1,559 mm TL was caught with three males and a DO female on 29 May 1986, and one of 1,256 mm TL was caught with five males, one DO, one RO and two FE females on 1 June 1986. DO or RO females were collected in every month except August and September. Ov, FO or EE females were caught from January to June. Most FE females were caught in May. Only two specimens of PP females were collected. One PP female of 1,574 mm TL was caught alone on 29 April 1984. The other of 1,560 mm TL was caught with a male on 13 October 1985.

Since 1985, 113 male and 103 female sharks have been caught on 101 days (Table 2). Twenty-two males and thirty-five females were caught singly. On 44 occasions, two or more sharks were caught on a single day. The maximum catch on a single day was 12 sharks. The maximum catch of males on a single day was nine, and that of females was seven. Multiple unisexual catches of males and females were made on ten and six days, respectively. Multiple catches of males and females together were made on 28 days. The reproductive state of females caught on

Table 1. Monthly numbers of male and female specimens of *Chlamydoselachus anguineus.* IM, immature females; DO, non-gravid females with developing ovarian eggs; RO, non-gravid females holding at least one ripe ovarian egg; Ov, ovulating females; FO, post-ovulatory females with only fertilized ova; EE, gravid females carrying at least one encapsulated embryo; FE, gravid females carrying embryos free in uterus; PP, post-partum females.

Month	Male	Reproductive stage of female								
		IM	DO	RO	Ov	FO	EE	FE	PP	Total
Jan.	5		4		1	2				7
Feb.	17		3		2					5
Mar.	27	1	3	2	2	2	3	1		14
Apr.	16		2		7	2	2		1	14
May	41	2	6	4	4	6	10	12		44
Jun.	18	1	4	1	1	3	7	4		21
Jul.	7		1	4						5
Aug.	0									0
Sep.	0							1		1
Oct.	2		1						1	2
Nov.	1			2				1		3
Dec.	5		5	2	1		1			9
Total	139	4	29	15	18	15	23	19	2	125

Table 2. Capture composition of males and females in *Chlamydoselachus anguineus* per day since 1985. Parentheses show total catches of males and females.

Number of females captured per day		Number of males captured per day										Number of days
		0	1	2	3	4	5	6	7	8	9	
	Total number of specimens		37	20	18	8	15	6			9	(113)
0			22	6	3			1				32
1	52	35	9	4	2	1					1	52
2	22	6	4		1							11
3	6		1				1					2
4												0
5	10					1	1					2
6	6		1									1
7	7						1					1
Number of days	(103)	41	37	10	6	2	3	1			1	101

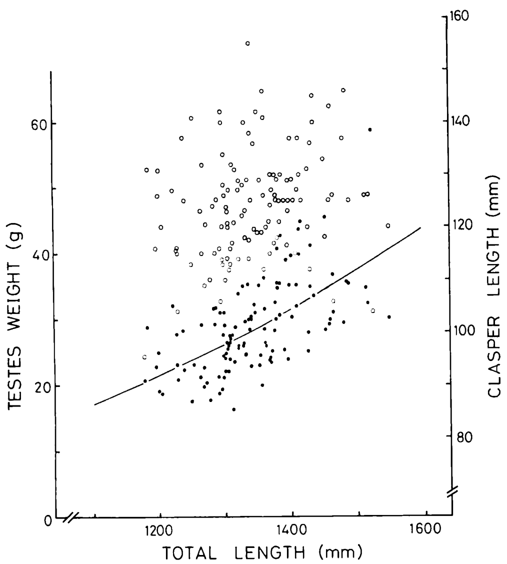

Fig. 1. Changes in testes weight and clasper length with total length in *Chlamydoselachus anguineus.* Closed and open circles indicate testes weight and clasper length, respectively. Line indicates relationship between total length and testes weight.

a single day varied.

The sex ratio (male/(male+female)) on the 23 occasions when three or more sharks were caught on a single day ranged from 0.14 to 1.00. The mean ($\bar{X}$) and standard deviation (SD) of the sex ratio on these 23 occasions were 0.62 and 0.263, respectively. Statistically, the null hypothesis that the ratio is 0.5 could be rejected at the 5% significance level, using a two-sided t-test ($t=2.13$, d.f. $=22$, $0.02<P<0.05$).

The posterior portion of the caudal fin in 12 males (8.6%) and 12 females (9.6%) had been cut off and the injury had already healed. The group of female sharks comprised four DO, five FO, two EE, and one FE females (Table 3).

Male reproductive organs. The clasper length of the smallest male was 95.3 mm and that of the largest male was 120.0 mm (Fig. 1). The 1,340 mm TL male possessed the largest (155 mm) claspers. About 70% of the male specimens had claspers that were 110–130 mm long.

The total weight of both right and left testes ranged from 16.3 to 58.6 g (Fig. 1). The testes weight of the smallest male was 20.8 g, and that of the largest male was 30.3 g. Data on total length (TL) and testes weight (TW) were transformed to natural logarithms, and a regression line was fitted by the method of least squares. The calculation produced the following equation:

$$\log TW = 2.495 \log TL - 6.352$$
$$(N=114,\ r=0.607,\ P<0.001)$$

Thus, testes weight increases with body growth.

Eighty-three of 120 specimens in which the right and left testes were weighed possessed a right testis that was heavier than the left one. The weight of the left testis ranged from 7.20 to 30.58 g with a mean of

Table 3. Size frequency of females by reproductive stage in *Chlamydoselachus anguineus.* TC, sharks with damaged caudal fin. Abbreviations of reproductive stages defined in Table 1.

Total length (mm)	Reproductive stage								
	IM	DO	RO	Ov	FO	EE	FE	PP	Total
1250–	2								2
1300–									0
1350–						1			1
1400–					1	1	2		4
1450–					1	1	1		3
1500–	1	4	3	3		5	4		20
1550–	1	5	3	5	2	3	6	2	27
1600–		8	2	5	3	1	4		23
1650–		2	5	3	1	3	1		15
1700–		1	1	1	1	6			10
1750–		4		1	1				6
1800–		1							1
1850–			1						1
TC		4			5	2	1		12
Total	4	29	15	18	15	23	19	2	125

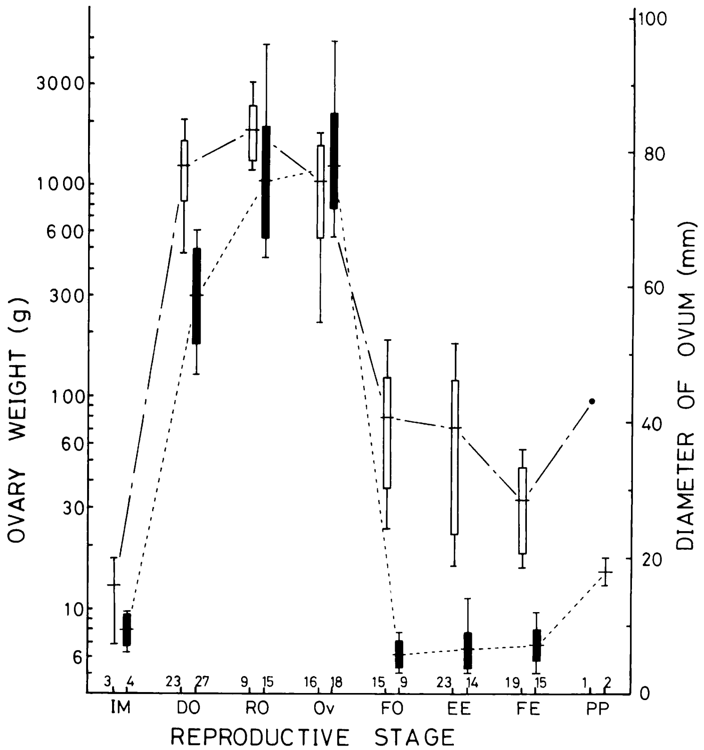

Fig. 2. Changes in ovary weight and diameter of ovum with reproductive stage in *Chlamydoselachus anguineus*. Sample numbers are shown on the horizontal axis. Broken line and open boxes indicate ovary weight. Dashed line and closed boxes indicate ovum diameter. Horizontal bars, boxes and vertical bars indicate mean, ±1 standard deviation and range, respectively. IM, immature females; DO, non-gravid females with developing ovarian eggs; RO, non-gravid females holding at least one ripe ovarian egg; Ov, ovulating females; FO, post-ovulatory females with only fertilized ova in uterus, EE, gravid females carrying at least one encapsulated embryo; FE, gravid females carrying embryos free in uterus; PP, post-partum females.

14.36 g, and that of the right testis ranged from 8.40 to 28.20 g with a mean of 15.14 g. The right testis was significantly heavier than the left one ($t=4.32$, d.f. $=119$, $P<0.001$).

Female reproductive organs: ovary. Every female that was examined possessed a functional pair of ovaries. The ovary (i.e., paired ovary) weight ranged from 6.9 to 3,048 g (Fig. 2). The ovary of immature females was less than 20 g in weight. The ovary weight in RO females was more than 1,000 g. Post-ovulatory and gravid females possessed an atrophied ovary less than 200 g in weight. FE females had the most atrophied ovary. The ovary of PP females had begun to be renascent. There is no statistical difference in the weight of the right and left ovaries in the reproductive stages at the 20% significance level ($t_{DO}=0.84$, $t_{RO}=0.23$, $t_{Ov}=1.00$, $t_{FO}=0.81$, $t_{EE}=0.03$, $t_{FE}=0.19$).

The mean diameter of developing ova in each DO female ranged from 47.0 to 68.0 mm (Fig. 2). One of the Ov females possessed the largest ripe ovum, which was 96.5 mm in diameter. Post-ovulatory and gravid females had small ova less than 15 mm. The ovarian eggs of PP females had begun to develop slightly. Thus, the ovarian eggs of the frilled shark do not develop during gestation.

Ova less than 25 mm in diameter were under 10 g in weight, and almost all ova larger than 50 mm were heavier than 80 g (Fig. 3). Ova larger than 40 mm increased in weight rapidly with an increase in diameter. The heaviest ovum in RO females was 280 g, while that in Ov females was 315 g. Log-log transformation of the diameter (D) and weight (W) data of ovarian eggs gave a straight-line relationship, and

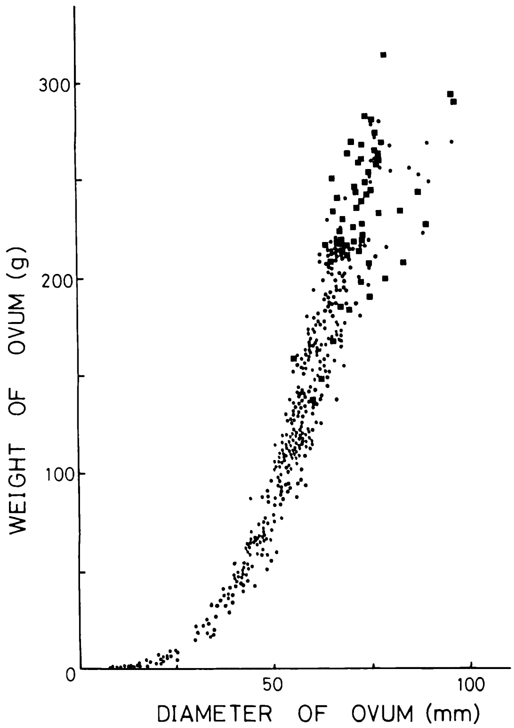

Fig. 3. Diameter and weight relationships in ovarian ova for *Chlamydoselachus anguineus.* Closed circles and squares indicate ovarian ova in DO and RO females and Ov females, respectively.

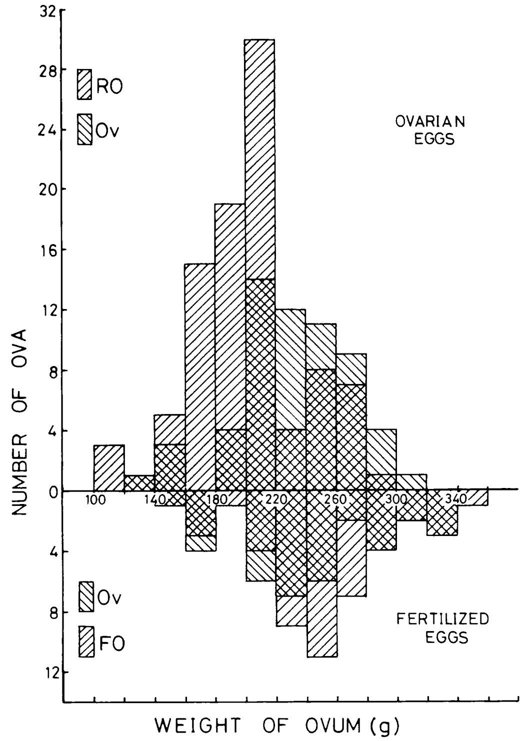

Fig. 4. Weight frequency distribution in ovarian eggs and fertilized eggs of RO, Ov and FO females for *Chlamydoselachus anguineus.* RO, non-gravid females holding at least one ripe ovarian egg; Ov, ovulating females; FO, post-ovulatory females with only fertilized ova in uterus.

is expressed in the following equation:

$$\log W = 2.644 \log D - 2.564$$
$$(N=436,\ r=0.950,\ P<0.001)$$

The diameter of eggs heavier than 200 g varied widely. Some ova larger than 80 mm had very fluid yolk.

The weight of 87 ovarian eggs in RO females ranged from 103 to 280 g (Fig. 4). Eighty percent of the eggs were less than 220 g in weight. The mode was between 200 and 220 g ($\bar{X}=199.9$ g, SD $=35.5$). On the other hand, the weight of 55 ovarian eggs in Ov females ranged from 137 to 315 g. Eighty-five percent of the eggs were heavier than 200 g. The mode was between 200 and 220 g ($\bar{X}=230.1$ g, SD $=35.5$).The mean weight of the eggs in RO females was significantly different from that in Ov females ($t=4.60$, d.f. $=140$, $P<0.001$).

The mean number of ovarian eggs decreased from 9.9 to 7.6 with progression in reproductive stage (Table 4). The number of eggs in Ov females included both ovarian and fertilized eggs. However, there was no significant difference in the mean number of eggs among DO, RO and Ov females ($F=2.527$, d.f. $=2$, 50, $0.05<P<0.10$). The number of eggs tended to decrease with the increase in mean weight of ovarian eggs in each female.

The right and left ovaries of 28 DO females had 2–13 developing eggs with a mean of 4.8, and 1–10 eggs with a mean of 5.1, respectively. The numbers of both developing and ripe eggs in the right and left ovaries of 13 RO females had a range of 1–8 with a mean of 4.3, and a range of 0–8 with a mean of 4.1, respectively. The numbers of left and right ovarian eggs in DO and RO females are not significantly different ($t_{DO}=0.429$, d.f. $=27$, $P>0.5$; $t_{RO}=0.217$, d.f. $=12$, $P>0.8$).

Each ovarian egg had an ovulation pore on the ovarian epithelium (Fig. 5A). The ovulation pore enlarged with the development of the ovum (Fig. 6). Data on the diameters of egg (E) and ovulation pore (OP) were transformed to natural logarithms, and a regression line was fitted by the method of least squares. The equation was as follows:

$$\log OP = 1.092 \log E - 0.877$$
$$(N=421,\ r=0.830,\ P<0.001)$$

The diameter of the ovulation pore in eggs larger than 40 mm varied widely. Eggs heavier than 200 g had the most variation in size of the ovulation pore. Eggs with an ovulation pore over 25.5 mm were very soft and ovulation appeared imminent.

Post-ovulatory follicles (corpora lutea) were found in the ovary of Ov, FO and EE females. Recently ovulated follicles were located under ovulation pores and contained a little liquid. This liquid was observed in the abdominal cavity and uteri of Ov females. These follicles subsequently degenerated with progression in reproductive stage.

Large degenerating eggs (corpora atretica) of more than 30 mm in diameter were found in the ovaries of 61 females representing all of the mature reproductive stages (Table 5). Degenerating eggs were whitish yellow in color and pseudomorphous (Fig. 5B). One EE female had a degenerating egg of 125×75 mm maximum size. Retention rates were over 50% except in FE females. The number of degenerating eggs was much higher in the ovaries of DO females. These observations suggest that the ovarian eggs in gravid females develop to some degree, but not fully.

Female reproductive organs: nidamental gland and uterus. Although the right and left nidamental glands are both oval-shaped, the right one was larger than the left in every specimen (Fig. 7). Nidamental glands enlarged with the development of ovarian eggs and shrank with the growth of embryos. RO females had the largest nidamental glands. Fertilized eggs and embryos were found only in the right

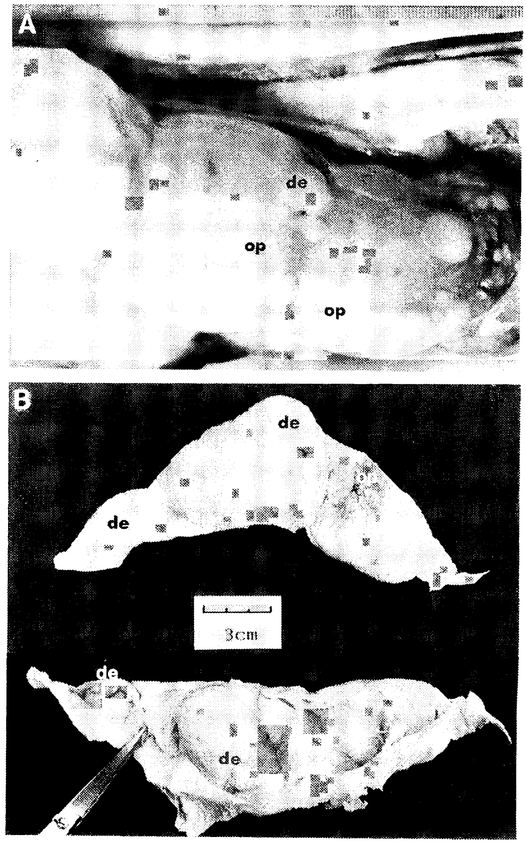

Fig. 5. Ovaries of *Chlamydoselachus anguineus*. A, ovulation pore on the ovarian epithelium of DO female; B, the outside (above) and inside (below) of the ovary in post-ovulatory female. de, degenerating egg; op, ovulation pore.

uterus. Some RO females had a whitish, viscous fluid, possibly semen, in their uteri. No villi were macroscopically found on the internal surface of the uterus of gravid females. The right uterus expanded during the growth of ovarian eggs and development

Table 4. Numbers of ovarian ova, fertilized ova and embryos by reproductive stage in *Chlamydoselachus anguineus*. Ov stage shows total number of both ovarian and fertilized ova. Abbreviations of reproductive stages defined in Table 1.

Reproductive stage	Number	Mean	Standard deviation	Minimum	Maximum
DO	27	9.9	3.47	6	23
RO	14	8.3	2.52	6	16
Ov	14	7.6	2.47	5	14
FO	11	6.1	2.07	2	9
EE	20	6.3	2.61	2	10
FE	19	6.0	1.56	2	8

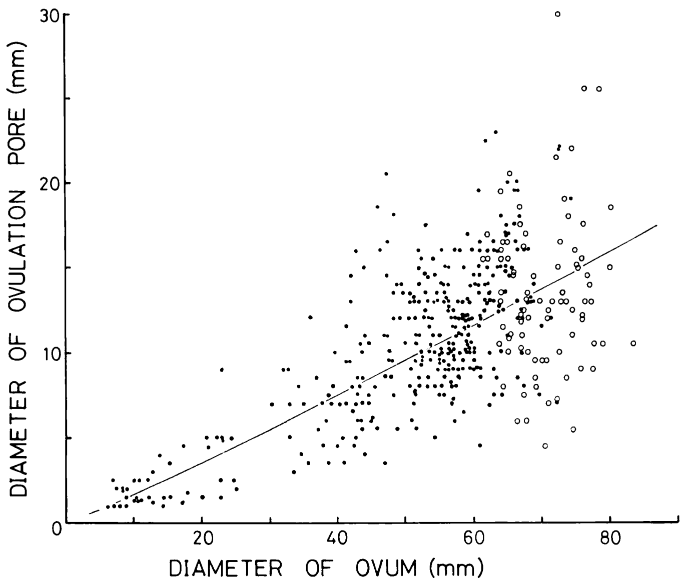

Fig. 6. Relationship between diameters of ovum and ovulation pore for *Chlamydoselachus anguineus*. Closed and open circles indicate ova under and over 200 g in weight, respectively.

of the embryos (Fig. 7). The left uterus also expanded with the growth of ovarian eggs, attaining its largest width during ovulation, and shrinking with the growth of embryos after ovulation.

A single egg capsule without a fertilized ovum was observed in the right uterus of one female and the left uterus of two others among the 17 Ov females, and in the right uterus of five females and the left uterus of one other among the 15 FO females. One FO female had two egg capsules without eggs in the right uterus. Egg capsules containing transparent mucus were 64–105 mm in length, 22–25 mm in width, and 15–20 g in weight. They had a light to dark golden color. These observations indicated that the left nidamental gland was functional and had not atrophied.

Fertilized egg and embryo. Fertilized eggs and embryos less than about 60 mm TL with an external yolk sac were enclosed in an egg capsule, while embryos larger than 80 mm TL were not enclosed. The egg capsule seemed to be sloughed off when the embryo grew to 60–80 mm TL. The discarded egg capsules collected at the posterior end of the uterus. The uterus of FE females did not contain discarded egg capsules. Therefore, the egg capsules appear to be discharged through the vagina.

The wet weight of 34 fertilized eggs in Ov females ranged from 158.7 to 329.0 g (Fig. 4). The mode was 220–240 g ($\bar{X}=239.3$ g, SD=46.6). The wet weight of 46 fertilized eggs in FO females ranged from 157.0 to 341.0 g. The mode of 240–260 g ($\bar{X}=249.3$ g, SD=44.7) was larger than that in Ov fe-

Table 5. Occurrence frequency of degenerating ova over 30 mm in diameter by reproductive stage in *Chlamydoselachus anguineus*. Abbreviations of reproductive stages defined in Table 1.

Reproductive stage	Number of degenerating ova								
	0	1	2	3	4	5	6	7	Mean
DO	6	4	5	6	1	1	1	1	2.2
RO	4	5	3		1				1.2
Ov	2	5	3	3	1				1.7
FO	5	4	3						0.8
EE	5	9	1	4		1			1.4
FE	9	5	1	1					0.6
PP		2							1.0

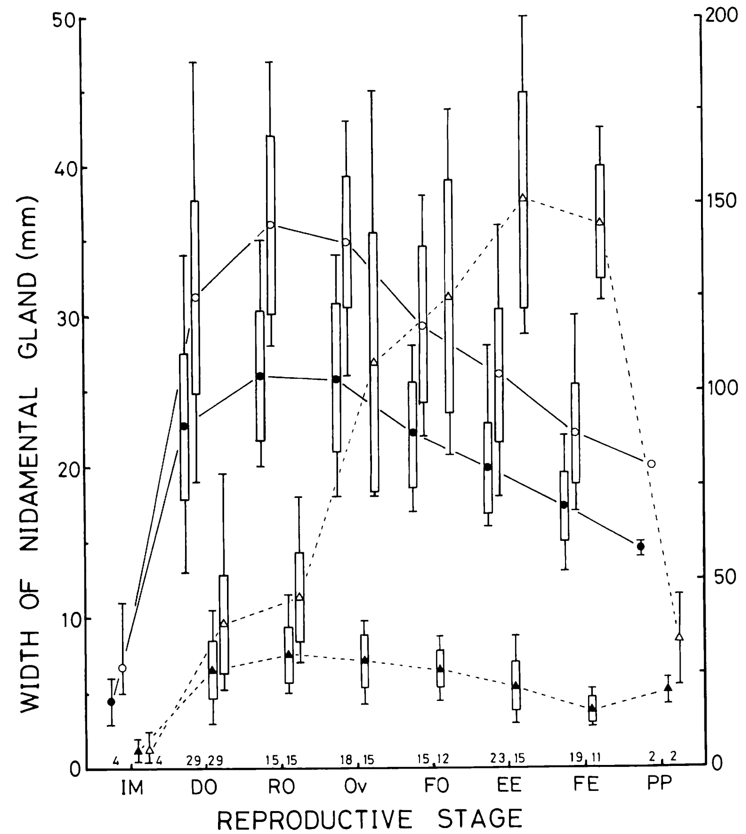

Fig. 7. Changes in width of nidamental gland and uterus with reproductive stage for *Chlamydoselachus anguineus.* Closed and open circles indicate the mean width of left and right nidamental glands, respectively. Closed and open triangles indicate the mean width of left and right uteri, respectively. Boxes indicate ± 1 standard deviation. Vertical bars indicate range. Abbreviations defined in Fig. 2. Sample numbers are shown on the horizontal axis.

males. The mean weight of fertilized eggs in Ov females is not significantly different from that in FO females ($t = 0.960$, d.f. $= 78$, $0.2 < P < 0.5$). Furthermore, there is no significant difference in mean weight between the ovarian eggs and fertilized eggs of Ov females ($t = 1.050$, d.f. $= 87$, $0.2 < P < 0.5$). Ovarian eggs appear to be mainly ovulated at a wet weight of 230 to 250 g.

All of the fertilized eggs of the 13 Ov and 12 FO females, except one Ov and two FO females, weighed more than 200 g. The exceptional Ov female possessed fertilized eggs of 158–175 g, and ovarian eggs of 137–208 g. The two FO females had fertilized eggs of 157–176 g and 185–209 g. The greatest difference between maximum and minimum wet weights of fertilized eggs within a litter was 26.1 g in an Ov female with 6 eggs and 46.0 g in a FO female with 7 eggs.

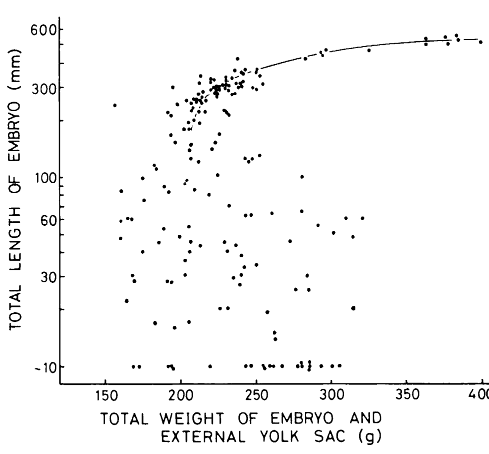

Fig. 8. Relationship between total wet weight of embryo and external yolk sac and total length of embryo for *Chlamydoselachus anguineus.*

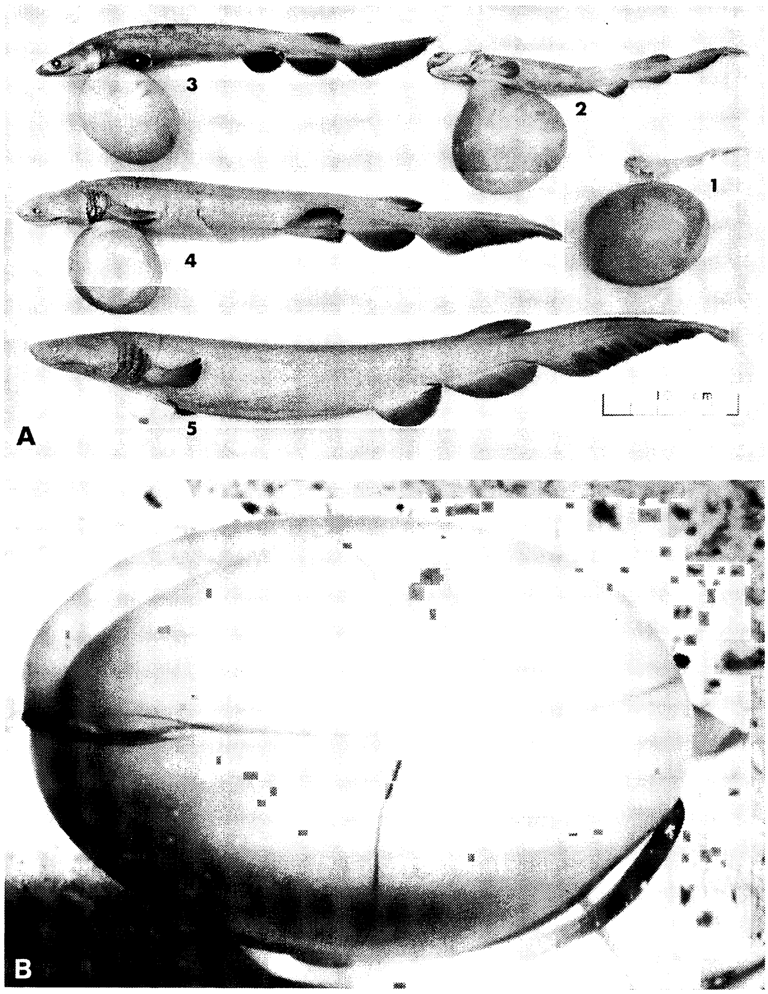

Fig. 9. Embryos of *Chlamydoselachus anguineus*. A, free embryos. 1, male, 98 mm TL; 2, female, 244 mm TL; 3, male, 305 mm TL; 4, male, 418 mm TL; 5, female, 535 mm TL. B, living encapsulated embryo (40 mm TL) maintained in artificial conditions.

The wet weight of embryos with an external yolk sac ranged from 157.0 to 398.5 g (Fig. 8). The largest embryo was 549 mm TL (382.2 g BW). The wet weight of the 80 embryos smaller than 100 mm TL varied in a way similar to that of the fertilized eggs. The weight ranged from 160.0 to 320.9 g ($\bar{X}$= 231.7 g, SD=46.7). There is no significant difference in the mean weight between these embryos and the fertilized eggs of Ov and FO females ($t=1.827$, d.f.$=158$, $0.05<P<0.10$). The correlation coefficient ($r=0.306$) between the total length of FO and EE females and the mean weight of fertilized eggs and encapsulated embryos in a litter is not significant ($t=1.575$, d.f.$=24$, $0.1<P<0.2$). The wet weight of embryos between 100 and 400 mm TL ranged from 157 to 260 g, while that of 12 embryos larger than 400 mm TL was over 286 g, except for one embryo of 238 g. Embryos larger than 200 mm TL became heavier with increasing length. The size of the external yolk sac in embryos below 400 mm TL hardly changed. Embryos larger than 500 mm TL either possessed a small external yolk sac or lacked one (Fig. 9A). The greatest difference between maximum and minimum wet weights of embryos within a litter was 60.3 g in an EE female with 6 embryos and 69.0 g in a FE female with 6 embryos.

The dry weight of four fertilized eggs ranged from 73.2 to 131.6 g with a mean of 101.6 g, and that of 22

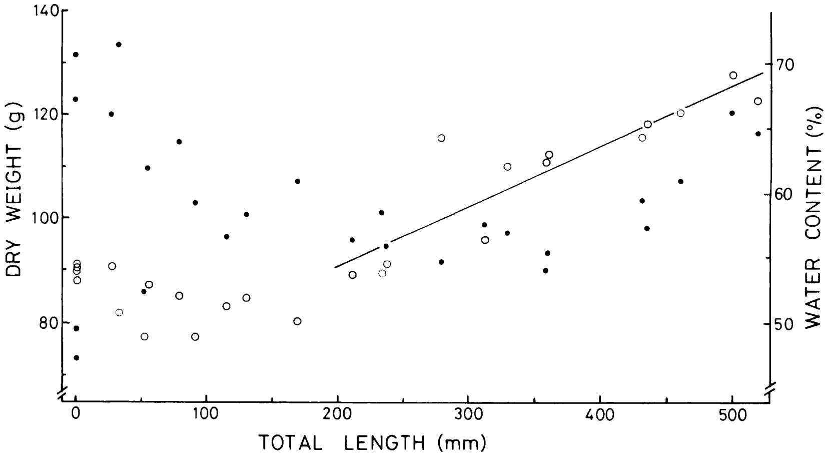

Fig. 10. Changes in dry weight and water content with total length of embryo in *Chlamydoselachus anguineus*. Closed and open circles indicate dry weight and water content, respectively. Line indicates relationship between total length and water content.

embryos between 27.4 and 518 mm TL ranged from 86.1 to 133.5 g (Fig. 10). The dry weight of the fertilized eggs and embryos smaller than 100 mm TL varied in a way similar to their wet weight. The weight of the 11 embryos between 100 and 400 mm TL hardly changed with increasing length, while the five embryos larger than 400 mm TL tended to become heavier with growth. The latter embryos ($\bar{X}=109.0$ g) were significantly heavier than the former embryos ($\bar{X}=97.0$ g) ($t=3.47$, d.f.$=14$, $P<0.005$).

The water content in wet weight of fertilized eggs averaged 54.0% and had little variance despite differences in weight (Fig. 10). The water content of the nine embryos smaller than 200 mm TL was slightly lower than that of the fertilized eggs, while that of the 13 embryos larger than 200 mm TL increased linearly with growth to about 70%. A regression line between the total length (TL) and water content (WC) of embryos over 200 mm TL was fitted by the method of least squares. The calculation produced the following equation:

$$WC=0.046TL+45.09$$
$$(N=13,\ r=0.896,\ P<0.001)$$

Three EE females possessed both fertilized eggs and encapsulated embryos. The maximum size of the embryos in the three females was 19, 30 and 40 mm TL. The greatest difference between the maximum and minimum sizes of embryos in a litter was 66 mm in an EE female with 10 embryos and 99 mm in an FE female with 8 embryos. Embryos in the posterior part of the uterus of EE females were more developed than those in the anterior part.

The number of fertilized ova in FO females averaged 6.1 (Table 4). EE females carried a mean of 6.3 embryos and FE females carried 6.0 embryos. There is no significant difference among these three means ($F=0.013$, d.f.$=2, 45$, $P>0.5$). The number of the eggs in Ov females tended to be greater than that in FO females. This observation suggests that some of the ovarian eggs degenerate just before or during ovulation, and that fertilized eggs usually develop without miscarriage.

There is no significance in the correlation coefficient ($r=-0.235$) between the mean wet weight of fertilized eggs and encapsulated embryos in a litter of FO and EE females and their number ($t=-1.157$, d.f.$=23$, $0.2<P<0.5$). The correlation coefficient ($r=0.252$) between the total length of the gravid females and the number of fertilized eggs and embryos in the uterus is not significant ($t=1.816$, d.f.$=39$, $0.05<P<0.1$), either.

The sex ratio of free embryos in the litters of 17 mothers had a range of 0–0.95 and a mean of 0.44. The mean of the sex ratio is not significantly different from the expected 0.5 sex ratio ($t=0.989$, d.f.$=16$, $0.2<P<0.5$). Five gravid females carried more male than female embryos. In nine other females, the female embryos outnumbered males. The total numbers of male and female embryos were 49 and 56, respectively.

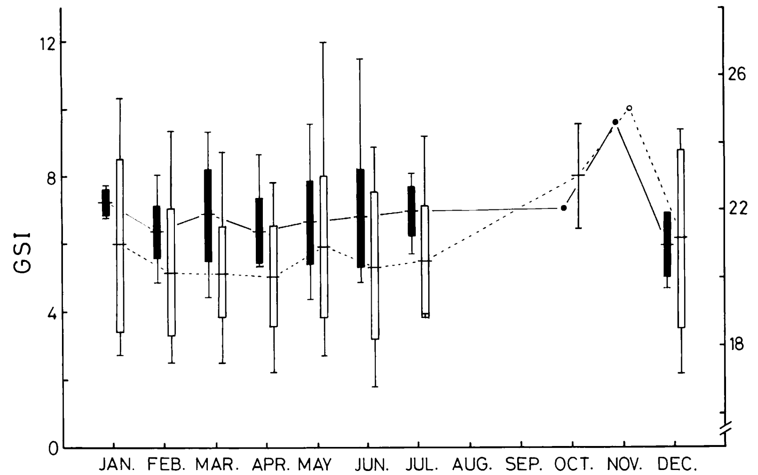

Fig. 11. Monthly changes in gonadosomatic (GSI) and hepatosomatic (HSI) indices in males of *Chlamydoselachus anguineus*. Solid line and closed boxes indicate GSI. Dashed line and open boxes indicate HSI. Horizontal bars, boxes and vertical bars indicate mean, ±1 SD and range, respectively.

Growth of embryos in artificial conditions. Four encapsulated embryos could be maintained in sea water tanks for a period from 43 to 134 days (Table 6). The embryos were moving actively in a space between the egg capsule and the yolk sac (Fig. 9B). When congestion in the membrane of the yolk sac, a whitish, muddy area in the yolk, or a yolk seepage was observed, the embryos were dull of moving. Then the blood stopped flowing gradually and the embryos died.

The growth rate per month of each embryo ranged from 10.2 to 16.7 mm. The growth rates of three similarly-sized embryos (Nos. 1–3) in the period between June 3 and June 30 were almost the same, while those of No. 4 embryo in the same period and of No. 3 embryo in the period between June 30 and October 1 were lower. The temperature, salinity and pH in the larger tank including Nos. 1, 2, and 4 embryos varied from 12.5 to 15.0℃, from 32.55 to 33.45‰, and from 7.3 to 7.6, respectively, during the experiment, while those in the smaller tank containing No. 3 embryo were from 8.3 to 15.5℃, from 27.60 to 34.58‰, and from 7.8 to 8.1, respectively. The large variance in salinity of the smaller tank resulted from cooling of the water.

Size at maturity. All male specimens, measuring 1,178 to 1,548 mm TL, had a pair of elongate and hard claspers, and appreciable amounts of sperm in the seminal vesicles and sperm sac. The skin of the claspers in some sharks was congested and swollen. The amount of sperm varied in each male. Onset of sexual maturity in males appears to occur at about 1,100 mm TL.

Ten of 109 females were smaller than 1,500 mm (Table 3), two being immature and eight being gravid. The largest immature female was 1,559 mm TL. The smallest gravid female was 1,376 mm TL. Females seemed to mature at 1,400–1,500 mm TL. Females became mature at a larger size than males. Both male and female sharks appear to grow after

Table 6. Growth of encapsulated embryos of *Chlamydoselachus anguineus* in artificial conditions. No. 3 embryo was maintained in a small tank. *Measured on June 6.

Embryo No.	Total length of embryos (mm)					
	Date of measurement					
	June 3	June 17	June 30	July 18	Aug. 22	Oct. 1
1	29	37	44			
2	35*	40	48			
3	29	37	43	47	60	70
4	15	20	25	33		

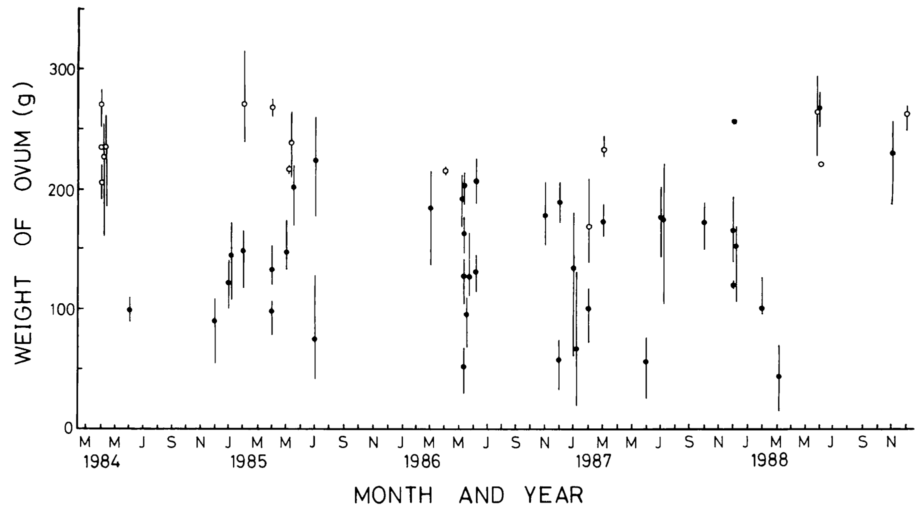

Fig. 12. Weight of ovarian ova in each shark per month since 1984 for *Chlamydoselachus anguineus.* Open and closed circles indicate the mean weight of ova in ovulating and non-gravid females, respectively. Vertical bars indicate range.

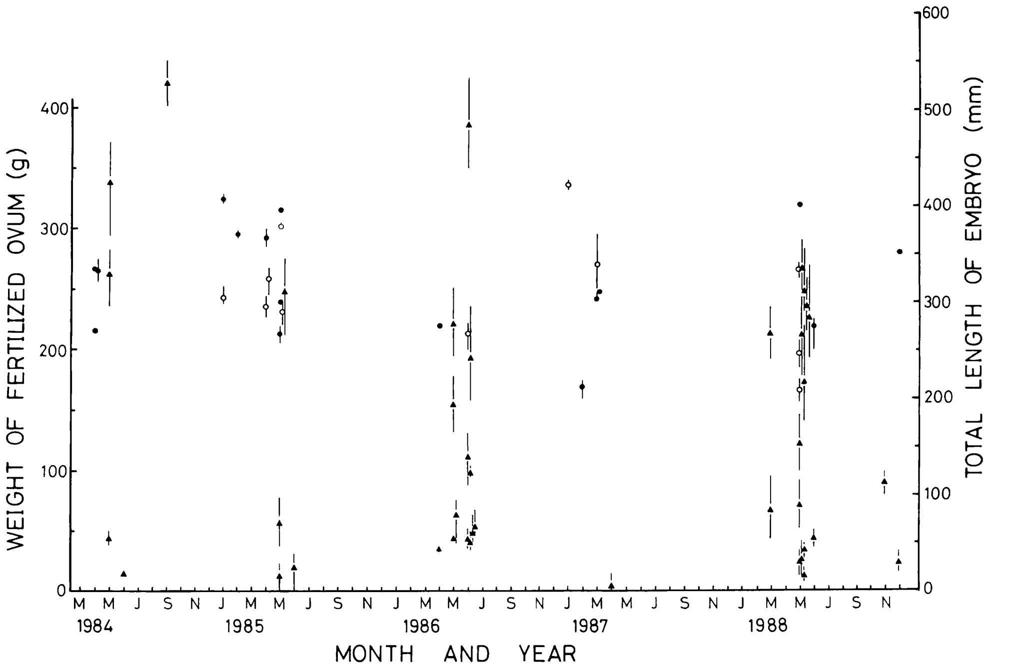

Fig. 13. Weight of fertilized ova and total length of embryos in each shark by month since 1984 for *Chlamydoselachus anguineus.* Closed and open circles indicate the mean weight of ova in ovulating and post-ovalatory females. Triangles indicate the mean length of embryos. Vertical bars indicate range.

the onset of maturity.

Seasonal reproductive activity. The mean of the monthly GSI for males between December and July ranged from 6.3 to 7.5, and did not show any periodicity (Fig. 11). The GSI in November when only one male was caught was 9.6. All male specimens had an appreciable amount of sperm in the seminal vesicles and sperm sac. Thus, male frilled sharks

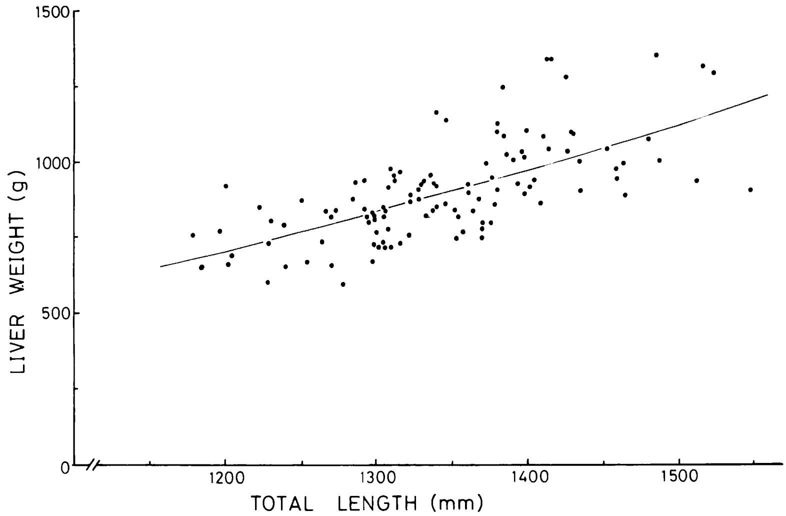

Fig. 14. Relationship between total length and liver weight in male of *Chlamydoselachus anguineus.*

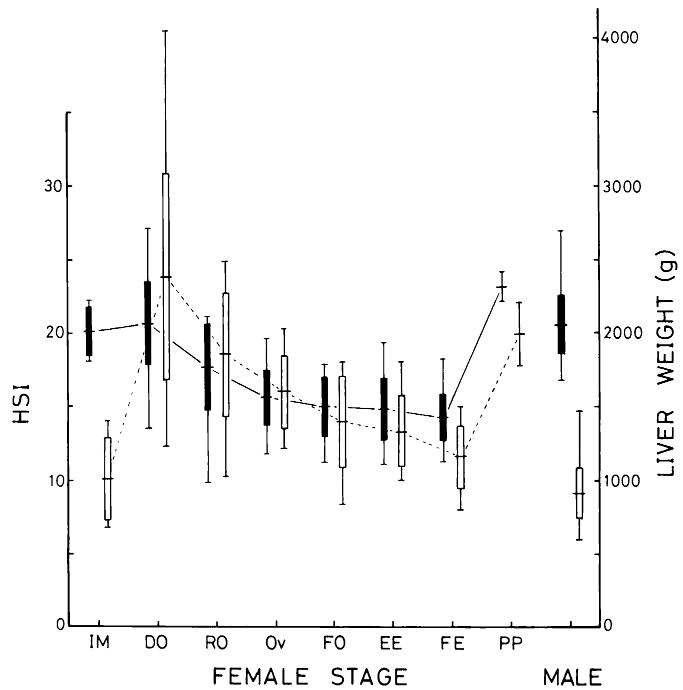

Fig. 15. Changes in hepatosomatic index (HSI) and liver weight for females by reproductive stage, and for males of *Chlamydoselachus anguineus.* Solid line and closed boxes indicate HSI. Dashed line and open boxes indicate liver weight. Horizontal bars, boxes and vertical bars indicate mean, ±1 SD and range, respectively. Abbreviations defined in Fig. 2.

seem to have no defined reproductive cycle, i.e. they are reproductively active throughout the year.

Ovarian eggs did not show any periodicity in their development (Fig. 12). Ripe ova were recognized between November and July. Females in the Ov stage were collected during the first half of the year. Fertilized eggs were found in January and from March to June (Fig. 13). Though the mean weight of fertilized eggs in Ov and FO females varied, a correlation between mean weight and occurrence time was not discerned. The period of ovulation extends at least from December through June.

Thirty-nine of the 42 gravid females were caught between March and June (Table 1). The size of the embryos varied (Fig. 13). Embryos larger than 500 mm TL were found in June and September. Two post-partum females were caught in April and October. Thus, female sharks seem to have no special pupping season.

Liver. The monthly HSI of males did not display any periodicity (Fig. 11). The liver weight in males increased with an increase in body length (Fig. 14). Log-log transformation of total length (TL) and liver weight (LW) data gave a straight-line relationship, that is expressed in the following equation:

$$\log LW = 2.108 \log TL - 3.642$$
$$(N = 114,\ r = 0.687,\ P < 0.001)$$

HSI and liver weight of mature females decreased during the successive stages of reproduction, and increased after parturition (Fig. 15). The HSI in Ov, FO, EE and FE females was almost the same. The mean HSI of PP females was highest compared with that of other females and males. The HSI of males and immature females was higher than that of any mature females except for the DO and PP females, though in the former liver weight was light. The liver weight of DO females was very variable. These observations suggest that a major aspect of liver function in females is closely related to vitellogenesis and the growth of embryos.

Discussion

Few frilled sharks were caught between August and November. During this season, the water temperature of the 100 m deep layer in Suruga Bay rises above 15℃ and the difference in temperature between the 50 and 200 m deep layers ranges from 7 to 12℃ (Nakamura, 1982). The rise in temperature appears to prevent the sharks from moving upward. As a result, during this season sharks may migrate either to deeper areas or to colder latitudes.

The sharks caught in Suruga Bay were mostly mature. However, gravid females with full-term embryos and post-partum females numbered only four (3.3% of the mature females). Although Yasuhara et al. (1983) and Kubota (pers. comm.) reported small juvenile sharks, possibly young-of-the-year, of 535 mm and 573 mm TL from this area, adolescent sharks under 1,100 mm TL were not collected. These data suggest that frilled sharks segregate by size and reproductive stage. Segregation by size, sex and reproductive stage has been reported in deep sea sharks (Bullis, 1967, Muñoz-Chápuli, 1984; Kobayashi, 1986; Baba et al., 1987; Yano and Tanaka, 1988). Segregation of deep sea sharks is considered to be a general adaptive pattern similar to that described in pelagic sharks by Springer (1967).

Twenty-four sharks (9.1% of the total specimens) possessed an injured caudal fin. The specimen first described by Garman (1884) had also lost the posterior end of the caudal fin. Male and female sharks are known to bite each other during copulation in order to maintain position (Wourms, 1977). However, the loss of the posterior end of the caudal fin in the frilled shark was probably due to predatory attack by other shark species, because the frilled sharks in copulatory condition (males with swollen and congested clasper sacs and females with whitish semen in the uteri) had no fresh injuries. Furthermore, the form and arrangement of the teeth of the frilled shark do not appear capable of inflicting such damage.

During ovulation, the frilled shark releases an ovum through an ovulation pore on the wall of the ovary as do deep-sea squaloid sharks (*Centroscymnus* spp.) (Yano and Tanaka, 1987). As the size of the ovulation pore is much smaller than that of the ripe ovum, the ovum which becomes very flexible is probably forced out by the pressure of the follicular liquid. The ovum is assumed to enter the common ostium with the follicular liquid, because ovulating females contained this liquid in the abdominal cavity and uterus. The details of the ovulation system needs to be studied still more in future.

Hisaw and Albert (1947) divided sexually mature females of the spiny dogfish, *Squalus acanthias*, into four groups depending on the stage of development of their embryos. Stages A, B, C, and D in their study correspond to FO, EE, FE, and late FE or PP in this study, respectively. The females in stages C and D had developing or ripe eggs in their ovaries. On the contrary, ovarian eggs in the frilled shark do not continue to enlarge during gestation. This may be related to the large volume of the ovum and embryo. The abdominal cavity of gravid females is occupied mostly by the liver and the embryos in the uterus. Therefore, we suggest that ovarian eggs cease to grow because there is no room to develop. The liver in elasmobranchs is also known to take part in vitellogenesis (Craik, 1978; Rossouw, 1987). However, the liver in FE females is smaller than that in DO females. Moreover, lipids may not be available for storage in the liver because feeding is probably inhibited at that time. Consequently, vitellogenesis would not be carried out actively during gestation. The sharpnose sevengill shark, *Heptranchias perlo*, and deep-sea squaloid sharks, *Centroscymnus* spp., which have large livers, also do not develop ovarian eggs during gestation (Tanaka and Mizue, 1977; Yano and Tanaka, 1988).

The frilled shark maintains its embryos only in the right uterus, whereas in many other sharks both the right and left uteri are functional. The left nidamental gland seemed to be functional because egg capusules without ova were found in the left uterus. No differences in structure between the right and left oviducts were recognized in macroscopic dissection. Babel (1967) reported that the right uterus in some rays is nonfunctional. The cause of asymmetric uterine function during gestation is obscure.

There was a marked variation in the weights of fertilized eggs and encapsulated embryos among individuals. However, the mean weight of fertilized eggs and encapsulated embryos in a litter did not correlate with the total length of the mother or their numbers. The greatest difference between the maximum and minimum weights of fertilized eggs and encapsulated embryos in a litter was 46.0 g and 60.3 g, respectively. These variations among individuals and in a litter may relate to the length at birth. Ketchen (1972) reported that the length at birth in the spiny dogfish ranged from 23 to 30 cm. The variation in the length at birth is recognized in other sharks (Tanaka, 1984). Therefore, the length at birth in the frilled shark may vary considerably.

The reproductive pattern of the frilled shark was tentatively classified as lecithotrophic by Wourms et al. (1988). In this pattern, the embryo is mainly nourished by yolk. In the frilled shark embryos over 200 mm TL, the wet weight of the embryo with an external yolk sac increased with growth and full-term embryos attained a wet weight of about 375 g. This value is about 1.6 times as heavy as the wet weight of ripe ovarian eggs or fertilized eggs. These phenomena are related to the change of water content in the ovum and embryo as stated by Ranzi (1932). The water content of fertilized ova and full-term embryos in the frilled shark was 54% and 70%, respectively, as in other sharks (Ranzi, 1932; Ōya et al., 1940; Hisaw and Albert, 1947; Suyama, 1959).

Wourms et al. (1988) stated that during embryonic development the total loss of organic weight from ova by metabolic energy ranged from 25 to 35%. If the total loss in the frilled shark is 25%, a fertilized egg of 102 g dry weight becomes a full-term embryo of 76.5 g. However, the observed dry weight of embryos over 400 mm TL tended to become heavier and that of two full-term embryos was 120 g and 116 g. Thus, the dry weight hardly changes in the early and middle embryonic stages and increases at the late stage. These facts mean that the embryos receive a nutrient from the mother, though the system of nutrition is unknown. A histological study of the reproductive organ and embryo will be published on another occasion.

Ov females accounted for 14% of all female specimens. The maximum difference between the largest and smallest encapsulated embryos in a litter was 66 mm TL. Furthermore, the growth rate of the encapsulated embryos in artificial conditions ranged from 10.2 to 16.7 mm per month. These may mean that the period between the first and last ovulation of the season in each female is fairly long. If encapsulated embryos grow 14 mm per month in the uterus, the shark with the above-mentioned embryos with the maximum size difference of 66 mm has the ovulation season of about five months. The shark contained 10 embryos. Therefore, the shark had ovulated every two weeks. The interval of egg-laying in the oviparous Japanese bullhead shark, *Heterodontus japonicus*, kept in the Shimoda Floating Aquarium ranged from 11 to 15 days at a water temperature of 17.0℃, 15 to 19 days at 16.2℃ and 21 to 24 days at 14.3℃ (Hagiwara, pers. comm.). Mellinger (1983) reported that the interval of egg-laying in the dogfish, *Scyliorhinus canicula*, ranged from 9 to 16 days. Therefore, the long interval in the frilled shark is not strange judging from the formation of large egg capsules. Nishikawa (1898), Gudger and Smith (1933) and Gudger (1940) reported that the reproductive season, most probably the ovulation season, extended over a long period between early spring and summer. In this study, ovulation seemed to continue throughout the year. Sharpnose sevengill sharks and deep-sea squaloid sharks do not have a defined reproductive season (Tanaka and Mizue, 1977; Yano and Tanaka, 1988). Since these sharks mainly inhabit water deeper than

200 m where hydrographic conditions hardly change, the absence of a distinct reproductive season is not surprising.

The largest embryo in this study was 549 mm TL, while the smallest free living shark reported from Suruga Bay was 535 mm TL (Yasuhara et al., 1983). This indicates that the length at birth is about 550 mm TL. However, the length of the gestation period could not be made clear. Gudger (1940) noted that gestation probably lasted at least two years owing to the large yolk and the low temperature of the habitat. The spiny dogfish inhabiting cold waters bears young ranging from 230 to 310 mm around November, after about two years gestation (Ketchen, 1972; Jones and Geen, 1977). Jones and Geen (1977) reported that the fertilized eggs of the spiny dogfish are in the "candle" stage for about four months. Small embryos could be recognized in the uteri around April. Thus, the early embryonic development of the spiny dogfish is slow and the growth rate of the embryos averages 14 mm per month. In the frilled shark, the formation of embryos was hardly recognizable macroscopically in fertilized eggs of Ov and FO females. If the early embryonic development was fast, the embryo would be often found in Ov females and FO females would not be collected so frequently. This indicates that the early embryonic development is as slow as that of the spiny dogfish. The encapsulated embryos maintained in tanks grew at a mean rate of 14 mm per month which is almost the same as that of the spiny dogfish embryos in uteri. If the embryos continued to grow at a rate of 14 mm per month till birth, the gestation would therefore extend over 39 months. Though the growth rate of late stage embryos is unknown, the gestation period seems to last at least three and a half years (including early embryonic development).

The minimum sizes of mature male and female sharks in our collections were 1,178 mm and 1,256 mm, respectively. However, the minimum size of maturity in males could not be determined, because all male specimens were mature. Bass et al. (1975) reported that males were mature at about 970 mm and females at 1,350 mm. The largest size reported for the frilled shark reported is 1,650 mm for males and 1,960 mm for females (Gudger and Smith, 1933). Therefore, this shark probably continues to grow after the onset of maturity.

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駿河湾産ラブカの生殖

田中 彰・塩原美敞・日置勝三・阿部秀直・
西 源二郎・矢野和成・鈴木克美

駿河湾で採集した 264 個体のラブカ *Chlamydoselachus anguineus* をもとに，その生殖について調査した．本種は 12 月から 7 月の間に主に採集され，成長段階および成熟・繁殖段階で棲息域を異にしていると考えられた．雄は全長 1,100 mm ですでに成熟しており，雌は全長 1,400–1,500 mm の間で成熟に達した．卵巣卵は重さ 230–250 g になると卵巣壁にある排卵孔から排卵され，右輸卵管のみに入り，卵殻腺で卵殻に包まれ，子宮内に保持される．排卵は約 2 週間ごとに行われ，排卵期間は数カ月におよぶと考えられる．初期の胚発生は非常におそく，妊娠期間はすくなくとも 3 年半におよぶと考えられる．妊娠期間中，卵巣卵は発達しない．胎仔が全長 60–80 mm に成長すると，卵殻はそれからはがれ，膣を通り排出される．胎仔は子宮内で主に卵黄によって全長約 550 mm，体重 380 g まで成長し産まれる．全長 400 mm 以上の胎仔は母体から栄養分を受けとっていると考えられる．1 腹の胎仔数は 2–10 個体で平均 6 個体であった．雄の生殖腺指数は一年中ほとんど変化しなかった．雌は卵巣と子宮の状態から明瞭な繁殖時期がないと考えられる．卵殻に包まれた胎仔が最長 134 日海水中で生存し，その成長率は 1 月当り 10–17 mm であった．

（田中：424 清水市折戸 3–20–1 東海大学海洋学部；塩原・日置・阿部：424 清水市三保 2389 東海大学海洋科学博物館；西・鈴木：424 清水市折戸 3–20–1 東海大学海洋研究所；矢野：102 東京都千代田区紀尾井町 3–27 海洋水産資源開発センター）