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Reproductive Cycle of a Viviparous Fish, the White-edged Rockfish, *Sebastes taczanowskii**

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Abstract

Oogenesis and annual rhythm of oocyte development were observed histologically to clarify the reproductive cycle of a viviparous fish, *Sebastes taczanowskii*. The morphological changes in developing oocytes were described in seven stages. Major components of an oocyte were yolk globules and oil droplets, and development of yolk vesicles were invariably poor. Oocytes at the chromatin-nucleolus and peri-nucleolus stages were observed in the ovary throughout the year. Oocytes at the oil droplet and primary yolk stages first appeared in July and September, respectively. During the long period of vitellogenesis from September to March, ovarian oocytes could be divided into two groups: the peri-nucleolus stage and the tertiary yolk or the more advanced stages. The stage composition in oocytes showed that type of oocyte development was group synchronous, and that these features were distinctly reflected in the mode of single brood production in the subsequent gestation. During the gestation period (April-May), all of the intra-ovarian embryos developed at the same rate, and GSI value became increasingly greater until just before parturition. Females released their brood all at once until the middle of June. Spent ovaries contained only oocytes at the chromatin-nucleolus and peri-nucleolus stages. From the results obtained, the annual reproductive cycle of *S. taczanowskii* was divided into four periods: the recovery period (July-August), the vitellogenic period (September-March), the gestation period (April-May), and the parturition period (June).

Introduction

In bony fishes, it is known that the family Scorpaenidae is the greatest group next to the Poeciliidae including intensively about 110 species of viviparous fishes (Wourms, 1981). Generally scorpaenid fishes do not show a particular modification of a nutrient transfer structure, and are a trophically primitive group with regard to the modes of fetal-maternal relationships.

Reproduction in Japanese scorpaenid fishes has been studied intensively (Mizue, 1957, 1958, 1959a, b; Tateishi et al., 1958; Mio, 1960a, b; Shiokawa and Tsukahara, 1961; Shiokawa, 1962a, b; Igarashi, 1968; Sasaki and Igarashi, 1974; Suzuki et al., 1978). However, detailed histological studies of seasonal changes in the gonad have been made for only a limited number of species: *Sebastiscus marmoratus* and *Sebastes inermis* (Mizue, 1959a) in females, and *Sebastiscus marmoratus* (Mizue, 1958), *Sebastes inermis* (Mizue, 1959b), *Sebastes taczanowskii* (Igarashi,

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1968) and *Sebastes vulpes* (Sasaki and Igarashi, 1974) in males.

The white-edged rockfish, *Sebastes taczanowskii* (Steindachner) used in this study is commonly distributed in shallow depths along the shores of northern Japan. Information is not available on the annual reproductive cycle of females, though Igarashi (1968) reported the seasonal changes of the testis in this species. This study deals with seasonal histological changes in the ovary, and, in particular, with the process of oogenesis in this species.

Material and methods

The white-edged rockfish used in this study were collected by angling or gill nets along the shores of Usujiri in the suburbs of Hakodate, southern Hokkaido. Two to ten fish were sampled at intervals of about one month from July 1980 to June 1983. During the winter season from November to April, samples were obtained from stocks of fish which had been reared in indoor circular tanks (1-ton capacity) flushed with seawater under natural daylight conditions. After anesthetizing in ethyl 4-aminobenzoate, body length, body weight and gonad weight of each fish were recorded. The ovaries were fixed *in toto* or after cutting into small pieces in Bouin's solution. Serial sections of 8 μm were prepared by the usual paraffin method and stained with Delafield's hematoxylin-eosin. The periodic acid Schiff (PAS) method was used to test the presence of polysaccharides in yolk vesicles. In addition, small pieces of the ovary were fixed in Karnovsky's glutaraldehyde-paraformaldehyde mixture in 0.2 M cacodylate buffer (pH 7.4) for about 3 hours at room temperature, and postfixed in 1% osmium tetroxide in the same buffer for about 2 hours at 4°C. After dehydration and embedding in Epon, tissues were sectioned at about 1 μm thick for light microscopic observations.

Results

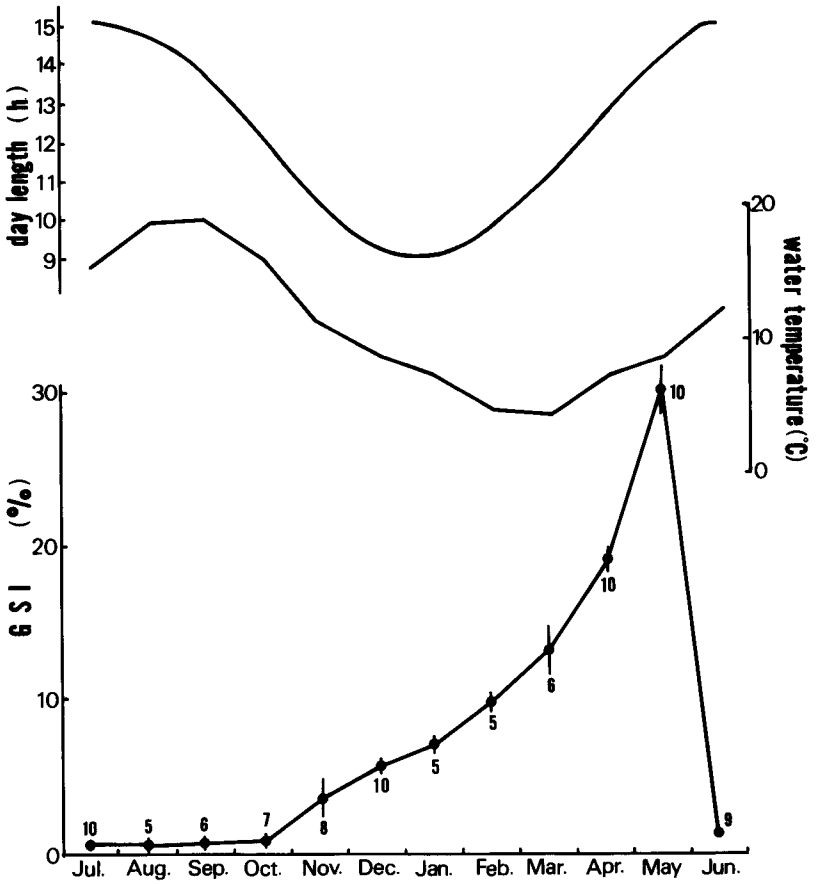
Seasonal changes in GSI

In Text-fig. 1, changes in the gonadosomatic index (GSI: gonad weight/body weight $\times 100$) are shown together with changes in natural day length and water temperature. The GSI values remained very low from June through October. Subsequently, GSI increased gradually from 0.4 ± 0.05 in October to 13.7 ± 1.4 in March, coinciding with the development of ovarian oocytes. Then a rapid increase in GSI eve was observed from a mean of 19.3 ± 0.5 during early gestation in April to a peak value of 30.9 ± 1.2 during late gestation in March. After parturition in June, the GSI level rapidly decreased and exhibited the lowest value for the year.

Morphological changes of oocytes

The process of egg formation was divided into seven stages to facilitate observation of dynamic aspects of egg recruitment in an annual cycle.

The smallest oocytes, about 20 μm in diameter, are found lying just beneath the surface of ovigerous lamellae throughout the year. They have a thin cytoplasm and a large nucleus occupying the greater part of the oocyte. In the nucleus, chromatin-reticulum spreads accompanied with chromatin-nucleoli. In this stage of oocyte development, pre-synaptic, synaptic, and post-synaptic oocytes are observed as



Text-fig. 1. Seasonal changes in GSI, water temperature and natural day-length.

described in the flounder, *Liopsetta obscura* (Yamamoto, 1956) (chromatin-nucleolus stage, Fig. 1).

As the oocyte grows, the cytoplasm gradually increases in volume and shows a strong affinity to hematoxylin. A relatively large spherical nucleus contains many chromatin-threads and a few nucleoli, varying in size (Fig. 2). As the oocyte develops further, the affinity of the cytoplasm to basic dye gradually decreases. The nucleoli are distributed around the inner margin of the nuclear membrane. The thin follicle layer surrounding the oocyte is observed, though the vitelline envelope is not clear at this stage (Fig. 3). Some oocytes exhibit the zoning phenomenon in stainability of the cytoplasm (Fig. 4). The size of the oocytes in this stage ranges from 30 to 130 μm in diameter (peri-nucleolus stage).

Following this stage, oil droplets appear in the peri-nuclear cytoplasm and increase rapidly in number and volume. These oil droplets are almost vacuolar in the preparation made in the routine manner (Fig. 5), though they stain black with osmium tetroxide (Fig. 6). PAS-positive granules corresponding to the yolk vesicles which have been universally found in the oocytes of oviparous fishes, are

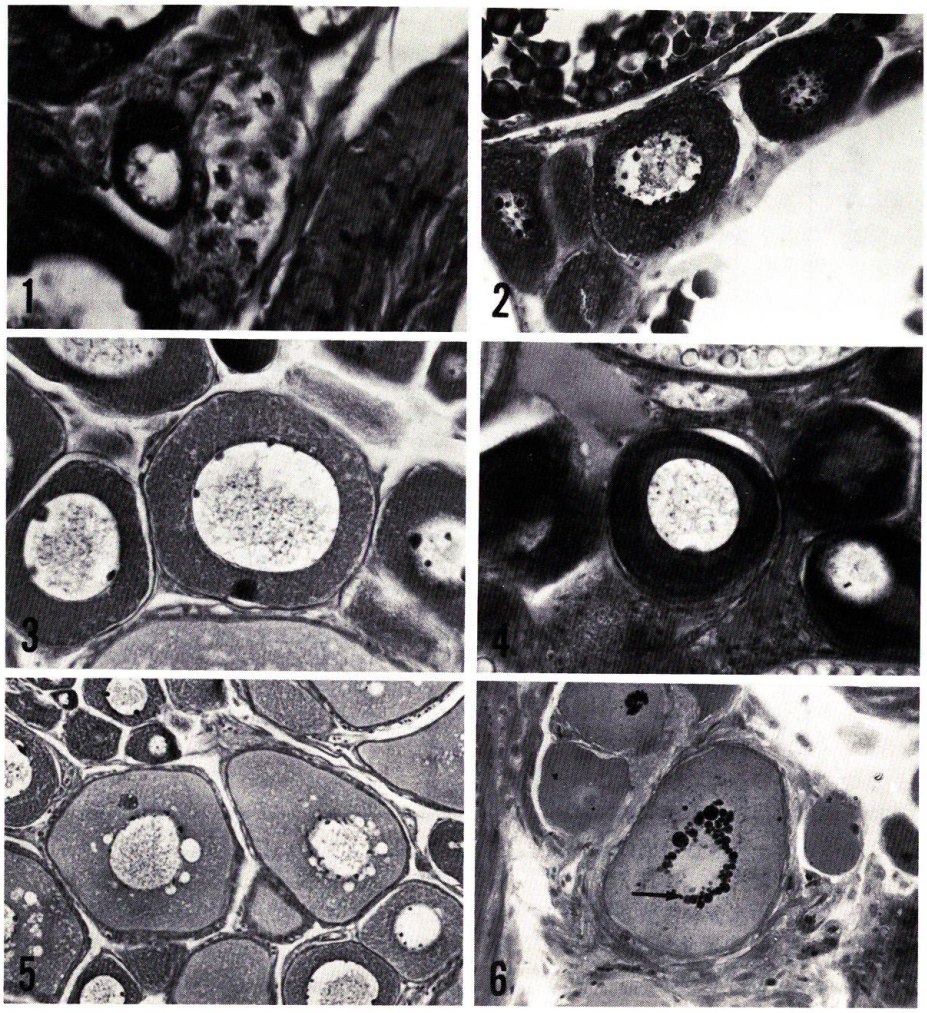


Fig. 1. Oocytes at the chromatin-nucleolus stage. ×880.
Fig. 2. Oocytes in the early phase of peri-nucleolus stage. ×290.
Fig. 3. Oocytes in the late phase of peri-nucleolus stage. ×360.
Fig. 4. Oocytes showing phenomenon of cytoplasm zoning at the peri-nucleolus stage. ×400.
Fig. 5. Oocytes at the oil droplet stage. ×470.
Fig. 6. Epon section (1 μm) of oocyte at the same stage as above. Arrow indicates oil droplets. ×280.

scarcely observable in the oocytes at this stage. The follicle layer is thicker than that in the previous stage, but no vitelline envelope can be detected at this point. The oocytes at this stage range from 130 to 190 μm (oil droplet stage).

When oil droplets, variable in size, form a circular zone around the nucleus, yolk globules begin to appear as minute granules in the peripheral cytoplasm. The yolk globules are less than 2 μm in diameter and gradually increase in number and size as the oocyte grows (Fig. 7). In the oocytes fixed with osmium tetroxide, small

vacuoles corresponding to the yolk vesicles, are barely observable in the peripheral cytoplasm between the yolk globules (Fig. 8). Vitelline envelope is observed as a very thin membrane between the cytoplasm and the follicle layer. The size of oocytes at this stage ranges from 140 to 260 μm in diameter (primary yolk stage).

As the oocyte grows further, the cytoplasm is filled with many small yolk globules. A circular zone consisting of oil droplets of various sizes is located in the

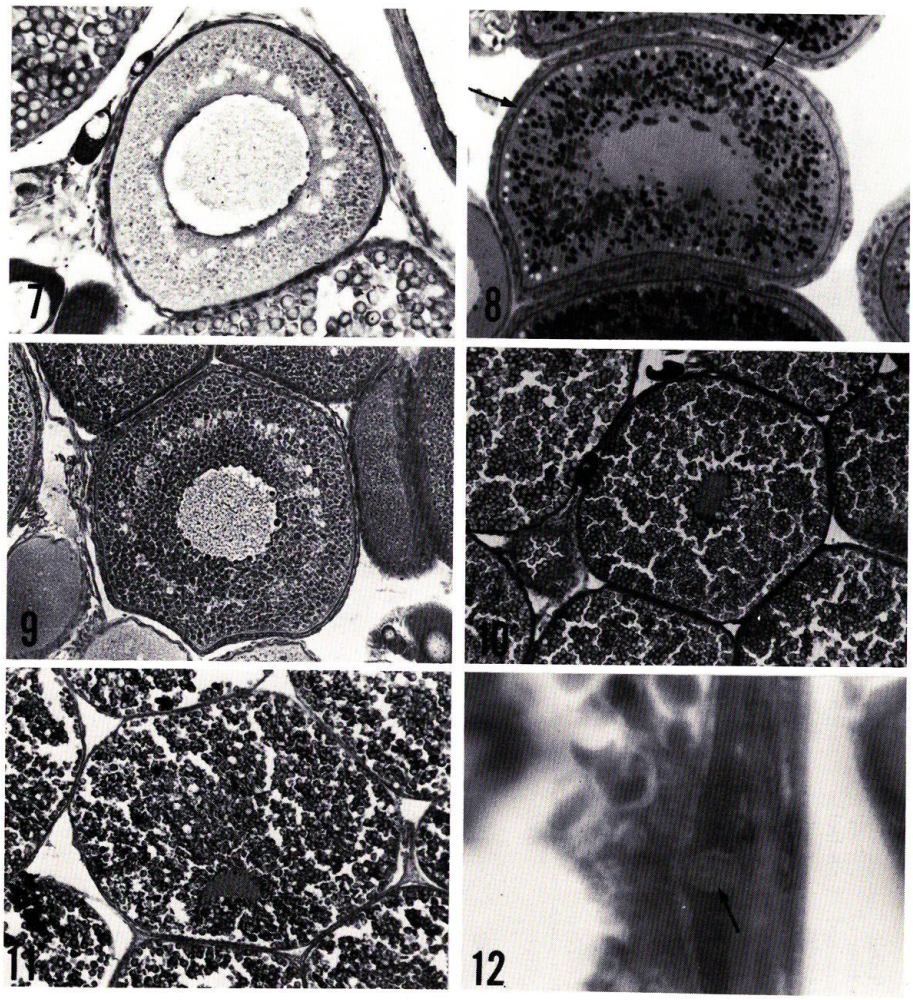


Fig. 7. Oocyte at the primary yolk stage showing a circular zone of oil droplets and numerous minute yolk globules in peripherial cytoplasm. ×200.
Fig. 8. Epon section (1 μm) of oocytes at the same stage as above. Arrows show yolk vesicles. ×390.
Fig. 9. Oocyte at the secondary yolk stage. ×100.
Fig. 10. Oocyte at the tertiary yolk stage. ×160.
Fig. 11. Oocyte at the migratory nucleus stage. ×160.
Fig. 12. Micropyle of an oocyte at the same stage as above. ×1000.

Table 1. Seasonal changes of stage composition in oocytes.

Month	Total number of examined oocytes	Percentage of oocytes at each stage						Gestation stage	Atretic * oocytes	Remarks
		Peri-nucleolus stage	Oil droplet stage	Yolk stage			Migratory nucleus stage			
				Primary	Secondary	Tertiary				
	1150	100								
Jul	947	100								
	479	92.3	7.3							
	2576	98.6	1.4							
	2114	81.1	18.9							
Aug	1150	84.4	15.6							
	577	92.0	8.0							
	3841	83.8	16.2							
	1999	70.9	29.1							
Sep	1947	86.3	13.7							
	1256	79.5	12.7	7.7						
	5202	78.7	19.4	1.9						
	3351	66.4	18.6	15.0						
Oct	2322	70.2	2.6	7.4	19.8					
	1222	78.6	1.7	8.5	8.3	2.9				
	6895	69.8	10.2	11.3	8.1	0.5				
	2449	64.1	5.1	3.9	1.9	25.0			+	After copulation
Nov	1355	65.4	1.5	1.3	1.5	30.3				After copulation
	1784	68.3	1.7	1.1	0.6	28.4				After copulation
	5288	65.8	3.0	2.3	1.3	28.1				
	1257	61.1	0.6	0.9	1.2	36.2			++	
Dec	1066	62.1	1.8	2.2	2.4	31.5			++	
	635	56.4	0.3	0.5	0.5	42.4			++	

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	2958	60.4	1.1	1.3	1.5	85.8			
	891	62.7	0.7	1.7	0.9	34.0			
Jan	734	65.3	0.4	1.1	0.3	33.0			
	630	81.0				19.0		+++	
	2255	68.6	0.4	1.0	0.4	29.5			
	729	80.2				19.8			
Feb	293	69.6				19.8	10.6		
	237	72.2				8.4	19.4		
	1259	76.3				17.6	6.1		
	412	70.1				7.0	22.8		
Mar	670	69.3				4.9	25.8	+	
	430	80.9				2.6	16.5	+	
	1512	72.8				4.8	22.4		
	1047	100						+	
Apr	644	100						+	
	626	100						+	
	2317	100							
	766	100						+	
May	484	100						+	
	414	100						+	
	1664	100							
	403	100							After parturition
Jun	526	100							After parturition
	568	100							After parturition
	1497	100							

* Relative amounts of atretic oocytes are indicated by marks, + to +++.

middle layer of the cytoplasm. At this stage, the oocyte diameter is 230 to 300 μm (secondary yolk stage, Fig. 9)

The oocytes continue to grow larger and the largest size reaches to about 550 μm in diameter. The entire cytoplasm is filled with a large bulk of yolk globules which have grown larger, when compared to the previous stage, the largest of which measuring about 10 μm. They exhibit a strong positive PAS reaction. The nucleus situated at the center of the oocyte is spherical in form, and the nucleoli are distributed within the nucleoplasm free from its membrane. The vitelline envelope is very thin, measuring about 2 μm thick (tertiary yolk stage, Fig. 10).

In the oocytes at the most advanced stage observed in this study, the nucleus is seen moving towards the animal pole (Fig. 11). At times, a small micropyle can be seen in the thin vitelline envelope of the animal pole (Fig. 12). The nucleus is elliptic in form and contains many nucleoli situated in the inner part of the nucleoplasm and on its periphery. Oocytes are of the same size as those at the previous stage, with many yolk globules occupying the entire cytoplasm (migratory nucleus stage).

Seasonal changes in stage composition in oocytes

The stage composition was determined by counting oocytes at each stage using serial sections of ovaries. Table 1 shows the monthly percentage composition of different oocyte stages. Oocytes at the chromatin-nucleolus stage were not counted because they were too numerous to be compared with the number of oocytes at the more advanced stages.

Oocytes at the peri-nucleolus stage were observed throughout the year. In July, two out of three fish had oocytes belonging to the peri-nucleolus stage while the other already had a small number (7.3%) of oocytes at the oil droplet stage in the ovary. In August, oocytes at the oil droplet stage remarkably increased to an average of 16.2% of all oocytes counted, and those of the peri-nucleolus stage decreased to 83.8% (Fig. 13). Although oocytes of ovaries sampled in September were similar in appearance to those in August, the number of oocytes in the oil droplet stage increased to 19.4%. One out of three sampled fish had 7.7% of its oocytes at the primary yolk stage in which yolk globules had just appeared for the first time (Fig. 14).

In October, the percentage of the primary yolk stage oocytes was an average of 11.3% in all the ovaries sampled. Yolk-laden oocytes at the secondary and tertiary yolk stages gradually increased to 8.1% and 0.5%, respectively. On the contrary, the oocytes of the peri-nucleolus and oil droplet stages were found to have decreased when compared with those of the previous month.

By November, 28.1% of all the oocytes had developed into the tertiary yolk stage. During this month, the number of oocytes at the secondary yolk, primary yolk and oil droplet stages markedly decreased and reached to 6.6% of the total (Fig. 15). A similar tendency was also observed in the ovaries fixed in December and January. One out of three fish sampled in January had only two groups of oocytes, namely those of the tertiary yolk stage and of the peri-nucleolus stage. Degenerating oocytes laden with yolk were observed in the ovaries obtained in November through January, but were most abundant in December. Many of the yolkless oocytes, especially at the peri-nucleolus stage, showed the zoning phenomenon at

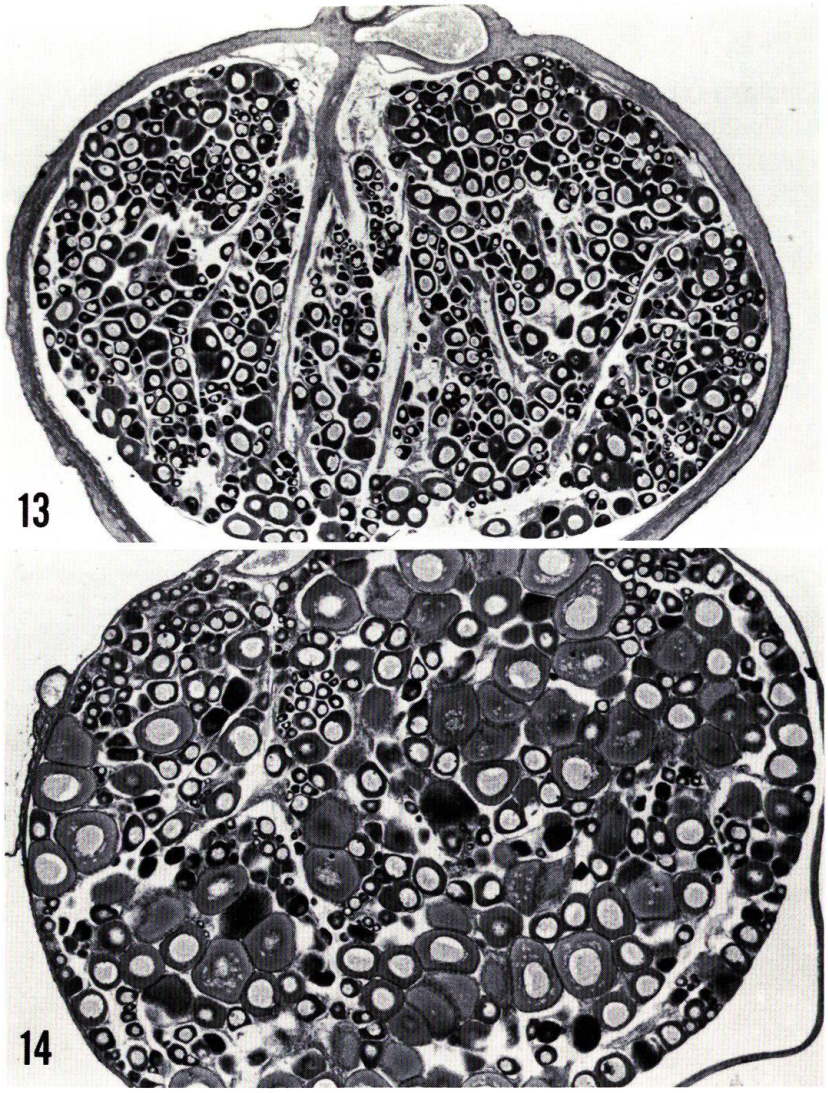


Fig. 13. Cross section of an ovary in the recovery period (August). ×35.
Fig. 14. Cross section of an ovary in the early phase of the vitellogenic period (September). ×50.

that time.

In the ovaries of fish collected in February, the most developed oocytes were at the migratory nucleus stage with value of 6.1%, while oocytes at the tertiary yolk stage decreased to 17.6%. Oocytes at the secondary yolk, primary yolk and oil droplet stages disappeared from the ovaries during this month. Although the condition of ovaries in March was almost similar to that in February, oocytes at the migratory nucleus stage further increased to 22.4% and oocytes at the tertiary yolk stage decreased to 4.8% (Fig. 16).

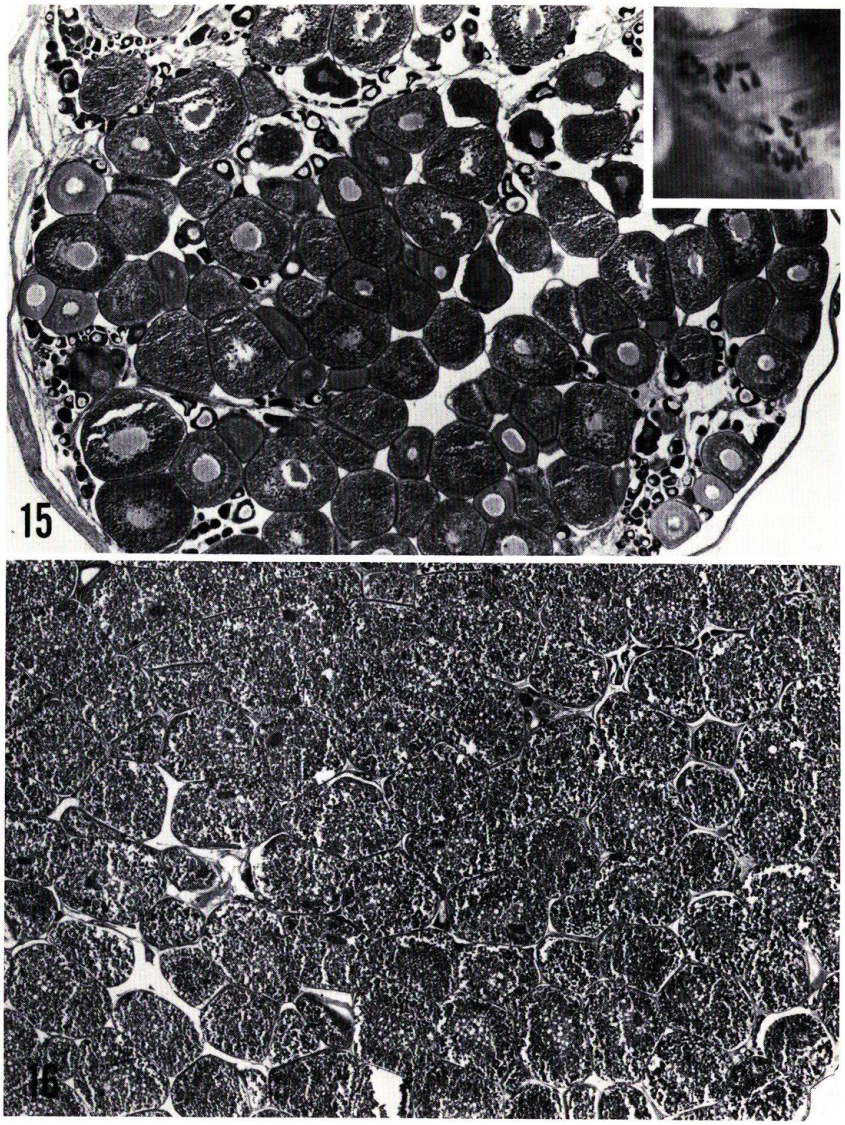


Fig. 15. Cross section of an ovary in the middle phase of the vitellogenic period (November). ×50. Inserted photograph shows spermatozoa located in the ovarian cavity during this period. ×850.

Fig. 16. Cross section of a part of an ovary in the early phase of the vitellogenic period (March). ×30.

In April, the ovary consisted of two groups; oocytes younger than the perinucleolus stage and embryos at the early developing stage. The embryos lying in the ovarian cavity developed synchronously (Fig. 17). The same case was observed in May, but the brood of embryos was at the more advanced stage of embryogenesis

(Fig. 18).

Extrusion of the brood of embryos was completed by the middle of June. Only oocytes younger than the peri-nucleolus stage remained in the spent ovary.

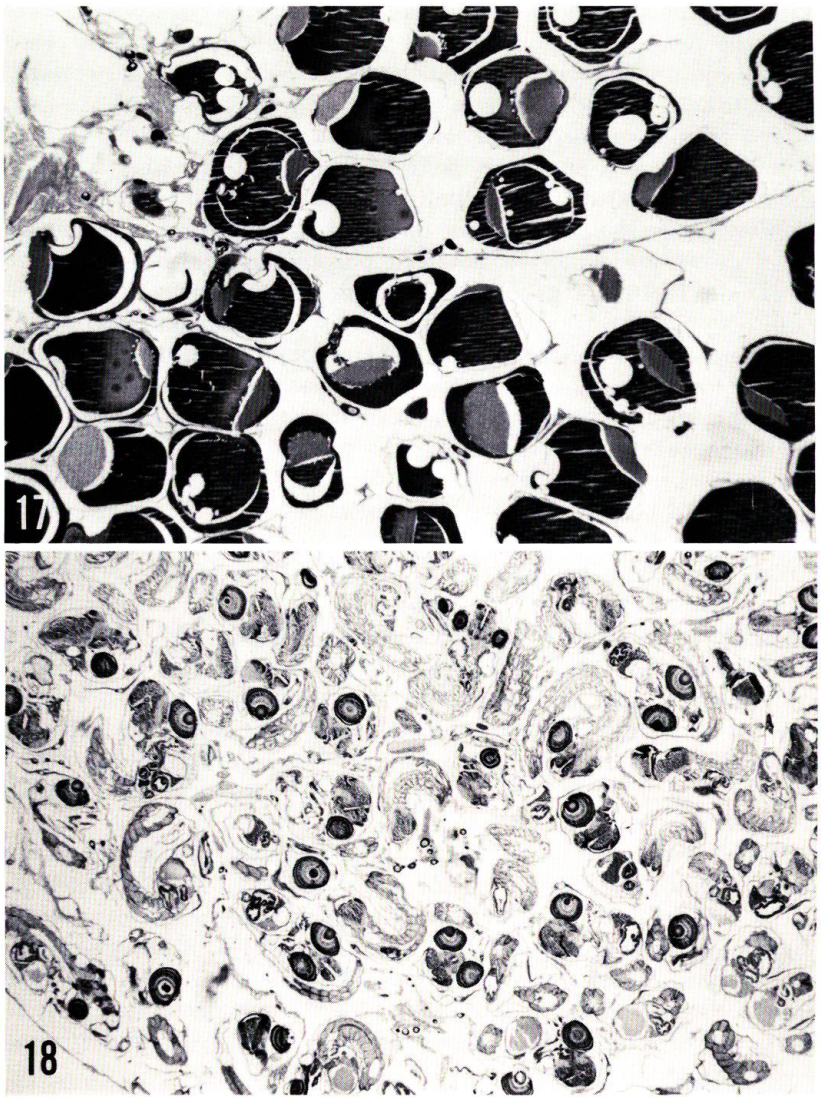


Fig. 17. Cross section of a part of an ovary in the early phase of the gestation period (April). ×30.

Fig. 18. Cross section of a part of an ovary in the late phase of the gestation period (May). ×10.

Discussion

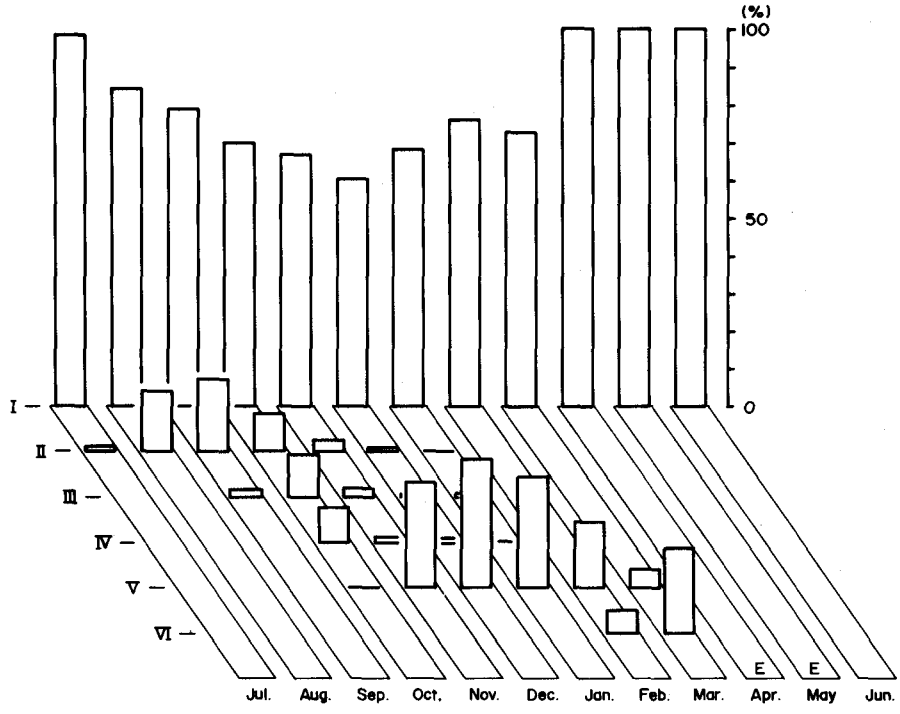
In the present study, the process of oocyte formation was divided into seven stages based on the histological observations. A marked feature in egg formation compared with that of oviparous fishes is the scanty appearance of a so-called "yolk vesicle" in this species. Yolk vesicles were hardly observed in the preparations made for the routine method and also in the results of PAS reaction. In the oocytes of rockfish, the presence of yolk vesicles was not noted in detailed observations (Moser, 1967), and was not demonstrated clearly for *Sebastiscus marmoratus* (Takano et al., unpublished). Furthermore, a paucity of yolk vesicles in the oocyte was reported for a viviparous poeciliid, *Lebistes reticulatus* (Takano, 1964). It is known that the yolk vesicle is a precursory form of the cortical alveolus, which plays an important role in formation of perivitelline space at the time of activation of fish eggs. In bony fishes, the peri vitelline fluid and its containing membranes provide a number of protective, nutritive, flotative, polyspermy preventive and regulative functions (Laale, 1980). A paucity of yolk vesicles together with a thin vitelline envelope of oocytes may be modified characteristics associated with viviparity in fish. Its physiological implications will remain unknown until further information is obtained. Oocytes developed beyond the migratory nucleus stage could not be observed in this species during the period of investigation. In scorpaenid fishes, morphological events in oocytes during the process of final maturation are not mentioned in the literature (Mizue, 1959a; Moser, 1967). The pre-maturation and maturation stage of oocytes in scorpaenid fishes including *S. taczanowskii*, if they occur, may be of a very short duration as Mizue (1957) pointed out in his study. The *in vitro* incubation technique may be useful to clarify the morphological changes associated with oocyte maturation.

Changes in composition of oocytes at various stages clearly exhibit the seasonal reproductive cycle of viviparous *S. taczanowskii* (Text-fig. 2).

From June to August, ovaries contained only pre-vitellogenic oocytes. In the early phase of this period, residual oocytes at the chromatin-nucleolus and peri-nucleolus stages were distributed at random in deformed ovigerous lamellae. In the late phase, they gradually increased in number, and oocytes at the oil droplet stage began to appear in reconstructed lamellae in dendriform.

Vitellogenesis began in September though GSI was still at a low level, and proceeded slowly throughout the autumn and winter in agreement with a gradual elevation of GSI values. The long duration of vitellogenesis, over a six-month period, in this northern species presents a striking contrast to the short duration in a southern species, *Sebastes inermis* (Mizue, 1959a). In the latter, vitellogenesis begins in late November and is shortened to only about one month. A still more prolonged period of vitellogenesis of over seven to nine months was ascertained for *Sebastes marinus* of the north Atlantic (Sorokin, 1961).

In November, when the most advanced oocytes attained the tertiary yolk stage, spermatozoa were first observed to be scattered in the ovarian cavity adjacent to the ovigerous lamellae. This condition was maintained until the time of fertilization which might have taken place in late March or early April. In sebastines, the male gametogenic cycle more or less precedes that of the female. Although copulation occurs when the females contain mature or nearly mature ova in *Sebastodes*



Text-fig. 2. Scheme of the developing pattern of oocytes in an annual cycle. I : Peri-nucleolus stage, II : Oil droplet stage, III : Primary yolk stage, IV : Secondary yolk stage, V : Tertiary yolk stage, VI : Migratory nucleus stage, E : Embryonic stage.

paucispinis inhabiting the coastal waters of California (Moser, 1967b), spermatozoa are introduced into the ovaries at the active vitellogenic phase about five months before fertilization in *Sebastes marinus* (Sorokin, 1961). In *S. taczanowskii*, the time of appearance of spermatozoa in the ovaries agrees with the discharging period of spermatozoa described in the male of the same species (Igarashi, 1968), and spermatozoa may have been reserved in the ovary for over four months before fertilization. It would be interesting to clarify the physiological mechanisms of copulation and sperm reservation in scorpaenid fishes.

In the late phase of vitellogenesis, oocytes came to divide into two distinct groups, the peri-nucleolus stage and the tertiary yolk or more advanced stages. These profiles of changes in composition of oocytes at different stages show that the type of oocyte development in this species is of group synchronous out of three basic types represented in oviparous fishes (Wallace, 1981 ; de Vlaming, 1983). The dynamic aspect of oocyte growth was also distinctly reflected in the mode of single brood production in the subsequent gestation. Female released their brood all at once until the middle of June.

On the basis of observation on the ovarian histology and changes of stage composition in developing oocytes, the annual reproductive cycle of *S. taczanowskii* can be divided into four periods : the recovery period (July-August), the vitellogenic period (September-March), the gestation period (April-May), and the parturi-

tion period (June).

The members of viviparous scorpaenid fishes differ in the number of broods produced each year, so they divided into two groups, the single spawner and the multiple spawner. From this point of view, viviparous scorpenid fishes found in Japanese coastal waters are listed up as follows: single spawners, *Sebastes inermis* (Mizue, 1959a; Mio, 1960), *Sebastes pachycephalus pachycephalus* (Mizue, 1959a; Shiokawa and Tsukahara, 1961; Shiokawa, 1962b), *Sebastes schlegeli* (Kusakari, 1977), and *Sebastes taczanowskii* (this study); multiple spawners, *Sebastiscus marmoratus* (Mizue, 1959a; Mio, 1960; Shiokawa, 1962a), and *Sebastiscus albofasciatus* (Mizue, 1959a).

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