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Gonadogenesis and Sex Succession in the Protogynous Wrasse, *Cirrhilabrus temmincki*, in Suruga Bay, Central Japan

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Abstract The present paper deals with gonadal formation and sex succession based on histological observations in the wrasse, *Cirrhilabrus temmincki* Bleeker, from Suruga Bay. Gonads of the present species are in the undifferentiated stage in young fish ranging from 11.4 to 19.5 mm TL. In fish ranging from 21.1 to 40.4 mm TL, gonads begin to differentiate initially into ovaries, forming an early ovarian cavity of the parovarian type and no evidence is found for the existence of any primary male. Reproduction takes place from June to September. The minimal size of sexual maturation is thought to be about 50 mm TL for females and about 88 mm TL for males. The androgenic transformation generally starts after the completion of female's reproductive function and these females thus change sex rather slowly. Several intersexual gonads are found both before and after the reproductive season. Although the intersexual form which shows the normal course of protogynous sex succession is found after the reproductive season, a few fish change sex previous to the reproductive season from female to male but their gonads seem to function only as female during this season. On the other hand, a group which is formed only of young or small transitionals and secondary males is obtained in April. The role and significance of this occurrence in hermaphroditism are discussed. *C. temmincki* is established as a monandric and dimorphic species. All the fish which show the terminal phase are secondary males, but the others which show the initial phase form a complex consisting of females, transitionals, and secondary males. A marked elongation of the second ventral ray is seen only in males as the result of a positive correlation with body growth.

The occurrence of protogynous hermaphroditism is better known in the family Labridae than in other fish families, and several authors have recently reported on a complex phenomenon related to intersexuality among this family, i.e., some species are diandric, having both primary and secondary males, while some others are monandric, having only secondary male (Warner and Robertson, 1978). Both dichromatism and monochromatism are seen commonly among the two different andric groups. In the dichromatic wrasses, the body colors generally change from a somber initial phase into a gorgeous terminal phase accompanying sex succession from female to male. In certain species, however, the dichromatism shows a more obscure composition, or a complex combination with the appearance of hermaphroditism, or a process of normal sex succession from female to male. In the Labridae, the role or significance of hermaphroditism has hitherto been investigated from ecological points of view, focusing on the relations between gonadal sex change and body color, by several investigators (Kinoshita, 1934; Atz, 1964; Reinboth, 1970; Choat and Robertson, 1975; Robertson and Warner, 1978; Nakazono, 1979). However, very little is known about the process of gonadal sex differentiation in early life stages and the seasonal occurrence of sex changes in the family Labridae. The present paper deals with gonadogenesis in juvenile fish and sex succession in older ones based on many histological and macroscopic observations in *Cirrhilabrus temmincki* Bleeker, which inhabits Suruga Bay. This is contribution No. 111 from the Marine Science Museum, Tokai University.

Materials and methods

All 329 fish specimens (11.4–104.5 mm TL) were collected by SCUBA diving with an encircling net (5×2 m) and a small scoop net at depths up to 25 m off the coast of Enashi, Numazu City, Suruga Bay. The live or fresh specimens were examined for color patterns by naked eye immediately after they were caught. Their gonads were then fixed in 10% formalin or Bouin's solution. The fixed gonads were sectioned by the routine paraffin method at 6 to 8 μm.

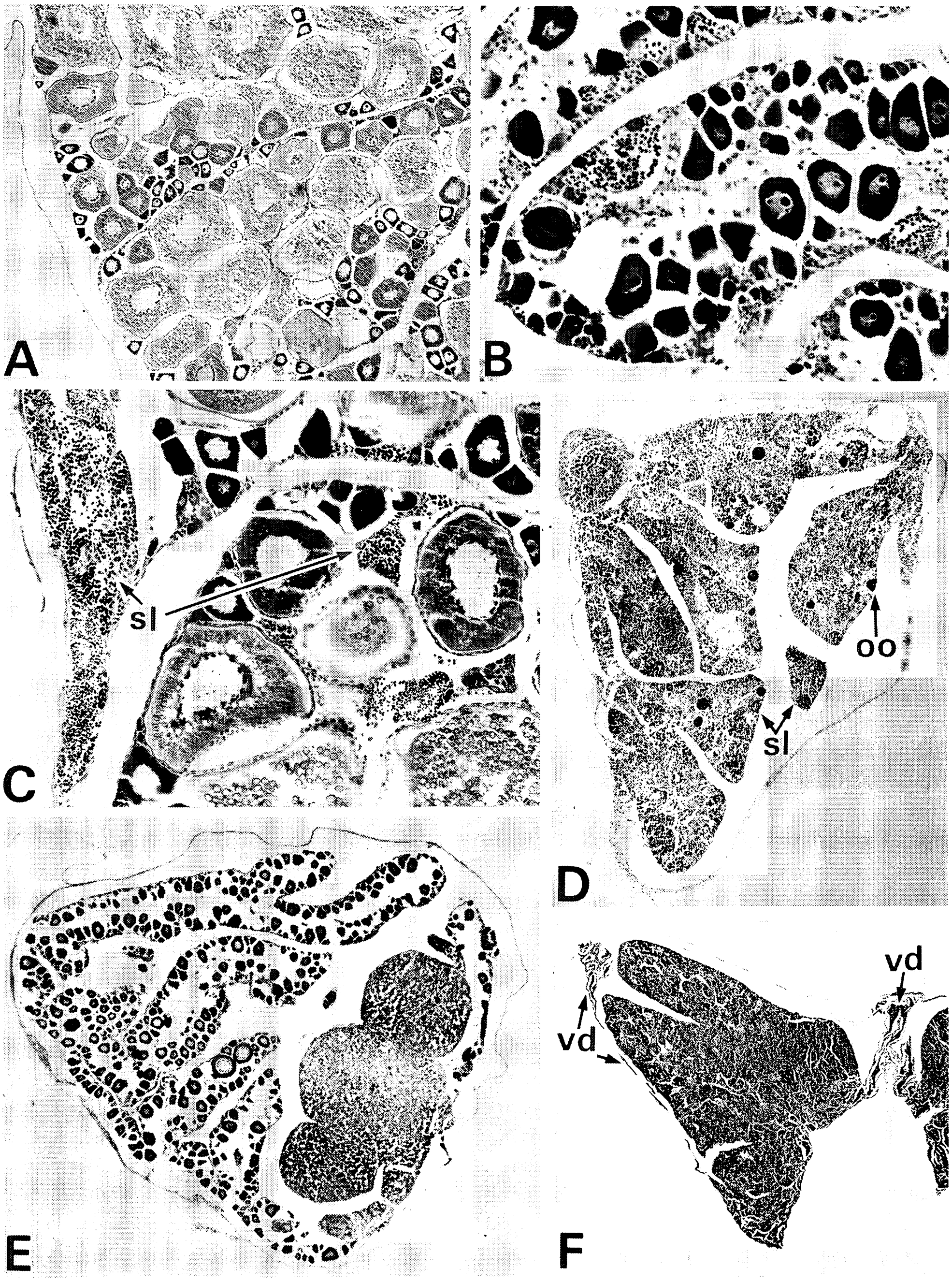

Fig. 1. Various sexual stages in the gonads of *Cirrhilabrus temmincki*. A: Mature ovary of a fish of 72.0 mm TL collected in June, ×45. B: Formation of spermatogenic cysts with many degenerating oocytes in a transitional gonad, 81.2 mm TL, September, ×150. C: Appearance of developing seminal lobules (sl) in a mature ovary, 91.0 mm TL, July, ×121. D: Expansion of seminal lobules (sl) with degenerating oocytes (oo) in the ovigerous lamellae of a transitional gonad, 73.8 mm TL, October, ×61. E: Occurrence of two opposite sexual zones in a single gonad, 76.5 mm TL, May, ×33. F: Mature testis, 99.5 mm TL, July, ×20. vd, vas deferens.

Mayer's acid-hemalaum or Delafield's hematoxylin-eosin methods were used to stain the gonadal materials submitted to histological examination.

Results

General appearance of gonadal structure. The gonads of the present species were distinctly fork-tailed bisymmetrically. The ovaries and testes were easily distinguished macroscopically in fish larger than about 50 mm TL, but several intersexual gonads were found histologically among both apparent ovaries and testes. The gonads of young or juvenile fish less than about 50 mm TL were thread-like in shape and minute in size; they were therefore difficult to remove and identify positively even in macroscopic observations.

Composition of gonad. The gonadal structures in 262 fish (45.7–104.5 mm TL) collected from May 1975 to April 1976 could be separated into three groups as follows: 128 fish (45.7–91.0 mm TL) had true ovaries (Fig. 1A), 45 fish (51.0–94.0 mm TL) had transitional gonads (Fig. 1B–E), and 89 fish (73.8–104.5 mm TL) had secondary testes (Fig. 1F). In the transitional gonads, both oocytes and seminal lobules were found abundantly in the ovigerous lamellae. These seminal lobules usually contained numerous spermatogenic cysts in various stages from the spermatogonium to the spermatid. These transitional gonads were at various stages of sex succession: 1) many spermatogenic cysts formed small clusters close to the marginal part of the ovigerous lamellae (Fig. 1B); 2) some of the ovigerous lamellae were partially occupied by many seminal lobules containing a great number of testicular cells at various stages (Fig. 1C); and 3) almost all parts of the ovigerous lamellae were fully occupied by numerous seminal lobules, and a small number of oocytes remained (Fig. 1D). In these secondary testes (Fig. 1F) the vas deferens ran dorsally or ventrally along the gonad, but in a few specimens a small number of oocytes remained. In *C. temmincki*, in general, the intersexual gonads gradually changed from ovaries into testes through transitional stages with a mixed composition of ovarian and testicular elements in a single gonad. In one exceptional case (76.5 mm TL), however, a single gonad was clearly separated into two opposite sexual zones (Fig. 1E).

Ovarian differentiation in juvenile gonads. Among 24 fish (11.4–40.4 mm TL) collected in October 1977, the seven smallest fish (11.4–18.5 mm TL) had a sexually undifferentiated gonad in which no inner cavity could yet be found, while only a few gonial germ cells encircled by numerous somatic cells were observed (Fig. 2A), and in a gonad in one fish (16.8 mm TL) among them, mitosis was seen in the gonial germ cells. In five larger fish (18.7–19.5 mm TL), mitosis was observed more commonly in the gonial germ cells, and in one fish (18.7 mm TL) the gonial germ cells reached the pre-meiotic stage and the mesentery extended downward (Fig. 2B). In seven still larger fish (21.1–29.6 mm TL), the germ cells increased remarkably in number and reached the chromatin-nucleolus oocytic stage, and the upper gonadal region extended and curved towards the basal part of the mesentery at the frontal-middle section of the gonad (Fig. 2C). The upper margin of this region of the gonad eventually became confined with in the bottom of the mesentery and formed an early ovarian cavity (Fig. 2D) which enclosed a narrow lateral duct at the rear section. Thus the process of ovarian differentiation was shown to be of the parovarian type. In the five largest fish (31.0–40.4 mm TL), the ovigerous lamellae were seen to be developing into those of a true ovary (Fig. 2E). It was established that all the early gonads in the present species initially differentiated into ovaries at a juvenile stage of 11.4–40.4 mm TL, and there was no sign of the existence of a primary testis among *C. temmincki*.

Sexual maturation and reproduction. Sexually functional gonads were found among the specimens collected from June to September. In July and August, almost all the ovaries and testes were fully ripened. It was therefore ascertained that the reproduction of *C. temmincki* in Suruga Bay took place from June to September and reached a climax in July and August. According to histological observations of the gonads, the smallest female and male whose gonads were fully ripened or already functioned were collected in June, and measured 50.4 mm TL and 88.2 mm TL, respectively. It therefore seems that, in Suruga Bay, the present species reaches sexual maturity at a minimal size of about 50 mm TL as a female and about 90 mm TL as a male. The ovarian structures of *C. temmincki* clearly showed a type believed to belong to the metaclone which spawned repeatedly in one reproductive season.

Occurrence of transitional fish and secondary males at a young stage. In April 1977, 43 young fish (37.0–77.5 mm TL) were collected separately from

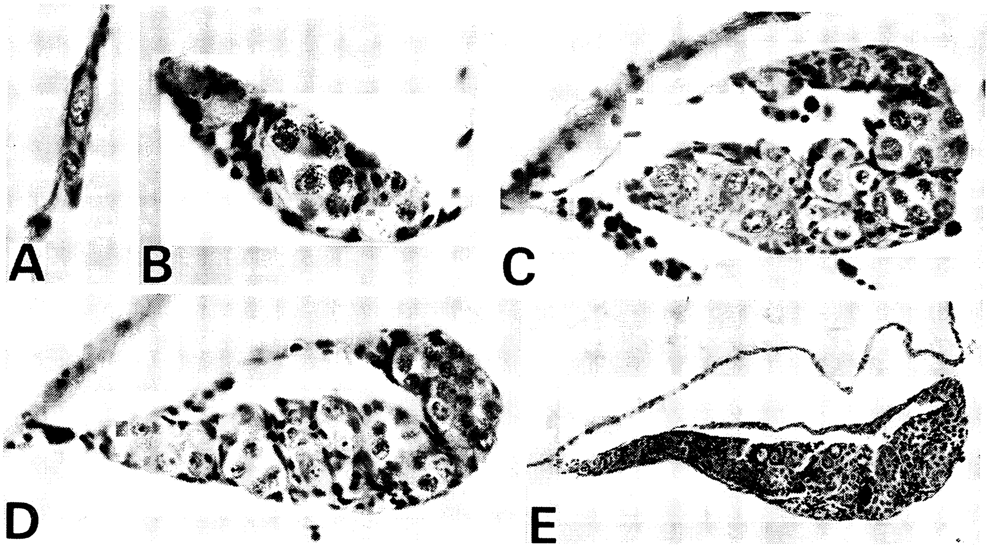

Fig. 2. Processes of ovarian differentiation in the early gonads of *Cirrhilabrus temmincki* collected in April. A: Sexually undifferentiated gonad of a fish of 11.4 mm TL, ×420. B: Starting of ovarian differentiation, several germ cells are reaching the pre-meiotic stage, 18.7 mm TL, ×500. C: Extending and curving of the upper gonadal region at the frontal-middle part of gonad, the oocytes are reaching the chromatin-nucleolus stage, 26.6 mm TL, ×330. D: Rear zone of an ovary, the ovarian cavity runs along the dorsal margin of the gonad, 26.6 mm TL (identical to the specimen of C), ×358. E: Young ovary, 31.0 mm TL, ×123.

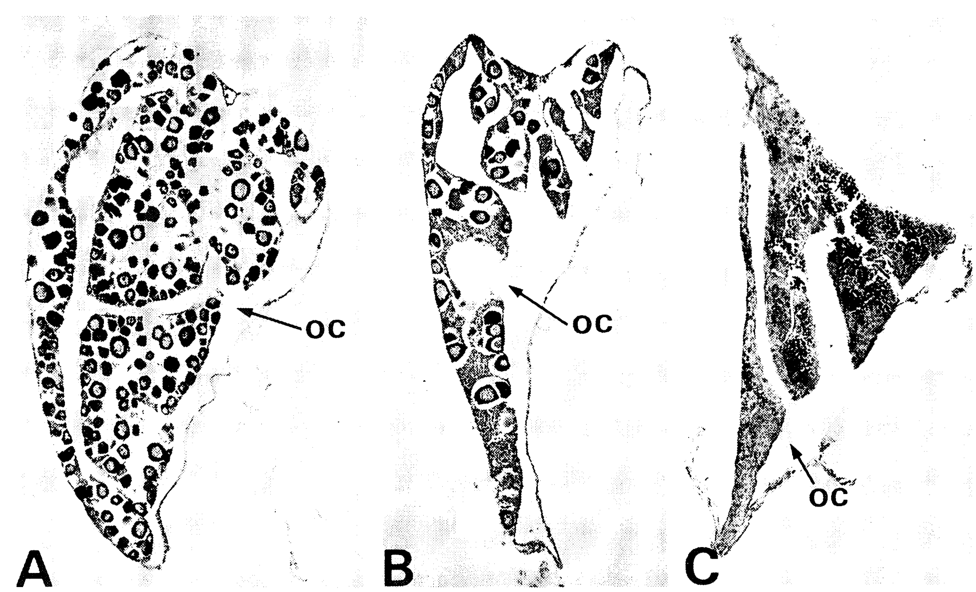

Fig. 3. Sex successional gonads from ovary to testis of young fish of *Cirrhilabrus temmincki* collected in April at about two months previously to the reproductive season. A: Yolkless immature ovary of a fish of 37.0 mm TL, ×56. B: Transitional gonad, 62.5 mm TL, ×44. C: Immature secondary testis, 58.3 mm TL, ×130. oc, ovarian cavity.

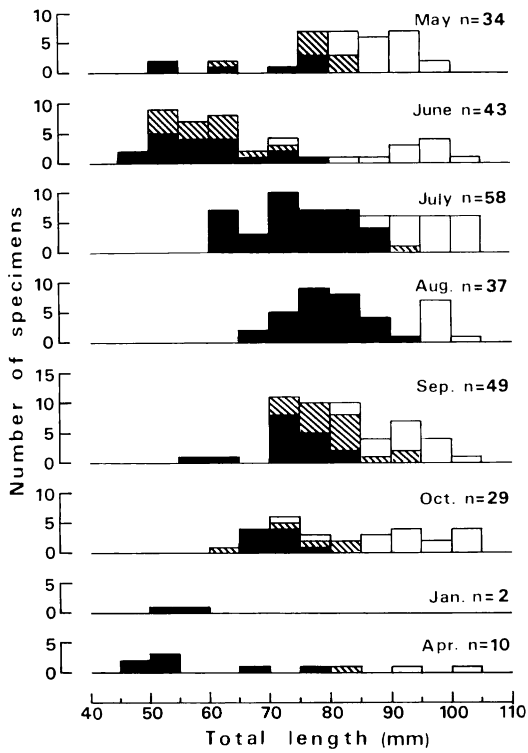

Fig. 4. Seasonal change of size frequency with gonadal sex distribution against total length in *Cirrhilabrus temmincki*. Solid bars, ovary; shaded bars, transitional gonad; open bars, secondary testis.

the other specimens. They formed only a school in which no adult-size males were contained prior to the reproductive season. Twenty-two (37.0–64.8 mm TL) of the fish had true ovaries whose oocytes had reached the perinucleolus stage in the ovigerous lamellae (Fig. 3A); the gonads of another 13 fish (38.2–67.7 mm TL) clearly showed an ovarian structure at various transitional stages from ovary to secondary testis, the ovigerous lamellae containing many small seminal lobules and a few oocytes (Fig. 3B); 8 other fish (58.3–77.5 mm TL) had a secondary testis which was occupied by numerous seminal lobules with a remaining ovarian cavity (Fig. 3C). Relationship between size distribution in total lengths of fish and gonadal structures in whole 329 specimens were as is shown in Table 1.

Protogynous sex succession. Among 262 fish specimens (45.7–104.5 mm TL) collected monthly, a number of intersexual gonads were present. These 45 intersexual specimens could be divided seasonally into two groups; 22 fish (51.0–83.2 mm TL) collected in May, June and April (prior to the reproductive season), and 23 fish (64.0–94.0 mm TL) collected in July, September and October (during or after the reproductive season). The former group showed no development of seminal lobules nor degeneration of oocytes. It therefore seemed doubtful whether further progress would occur in sex changing from female to male (Fig. 4). The latter was to be concentrated at the end of the reproductive season, and among them, for example, was a specimen (84.0 mm TL), collected in September, whose gonads contained both several testicular cells in various stages from the spermatogonium to the sperm and degenerating oocytes among the vitellogenic stages in ovarian lamellae. It clearly showed to be in a process of sex changing from functional female to functional male in the next reproductive season (Fig. 5). Ovaries and secondary testes were found commonly through all the months when the fish were collected, whereas intersexual gonads were found irregularly or rather concentratedly from April to July, and from September to October. These individuals might function as females in the reproductive season that followed in this year. One large adult male (99.5 mm TL), collected in July,

Table 1. Relationship between size distribution in total length and gonadal structure in *Cirrhilabrus temmincki* from Suruga Bay. A, sexually indifferentiated gonad; B, under sexual differentiation; C, ovary; D, sexually transitive gonad; E, secondary testis.

Group	Total length (mm)	Gonadal structure				
		A	B	C	D	E
I	10.0–19.9	12				
(Oct. 1977)	20.0–29.9		7			
	30.0–39.9			4		
	40.0–49.9			1		
II	30.0–39.9			4	3	
(Apr. 1977)	40.0–49.9			9	1	
	50.0–59.9			7	4	1
	60.0–69.9			2	5	5
	70.0–79.9					2
III	40.0–49.9			4		
(May 1975–Apr. 1976)	50.0–59.9			17	7	
	60.0–69.9			24	7	
	70.0–79.9			57	15	3
	80.0–89.9			25	13	22
	90.0–99.9			1	3	50
	100.0–109.9					14

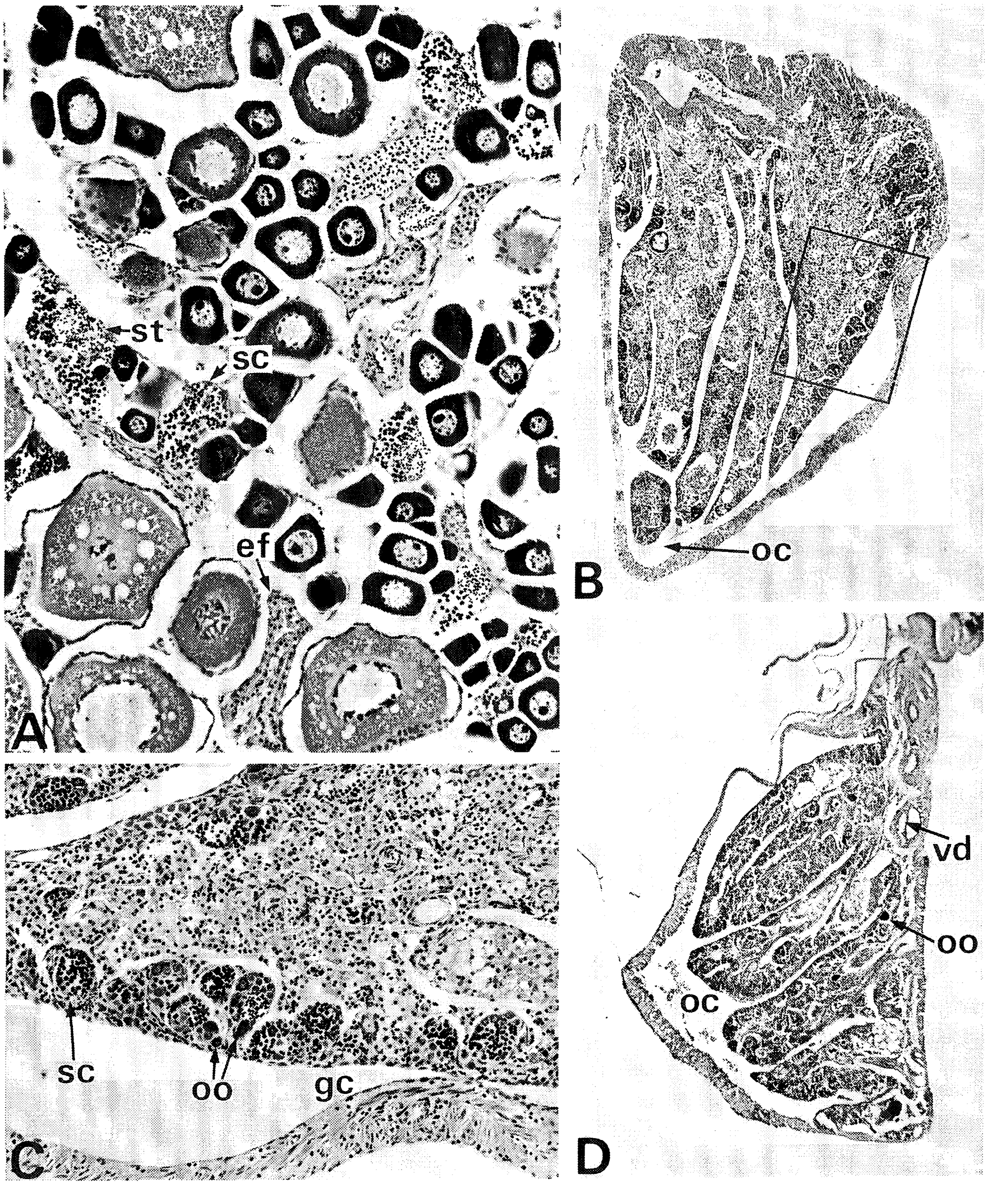

Fig. 5. Transitional gonads in protogynous sex succession in *Cirrhilabrus temmincki*. A: Formation of seminal lobules in the ovigerous lamellae of mature ovary of a fish of 84.0 mm TL collected in September, ×150. ef, empty follicle; sc, spermatocyte; st, spermatid. B: Developing somatic cells and degenerating oocytes with their residues in the ovigerous lamellae, 94.0 mm TL, September, ×43. oc, ovarian cavity. Framework is enlarged in C. C: Magnified aspect of the framework in B, ×153. gc, gonial germ cells; oo, oocytes. D: Early secondary testis, 90.0 mm TL, September, ×43. vd, vas deferens.

clearly had a developed secondary vas deferens with a degenerated oviduct in its testis. This vas deferens spread along the gonadal wall and it was mostly occupied by a great number of active sperms, and the oviduct was seen at the inner side of the vas deferens in the rear zone of the gonad (Fig. 6).

Correlation between sexual dimorphism and gonadal sex.

1) Dichromatism: Sexual dichromatism in *C. temmincki* has hitherto been described by Moyer and

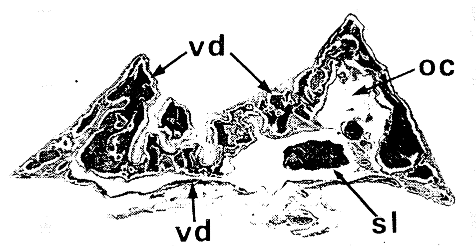

Fig. 6. Cross section close to rear end of a functional secondary testis being filled with numerous active sperms in *Cirrhilabrus temmincki*, 99.5 mm TL, July, ×20. oc, ovarian cavity; sl, seminal lobules; vd, vas deferens.

Shepard (1975), Randall and Shen (1978) and Bell (1983), but no one has mentioned its sexual dimorphism. Under the sea, as reported previously, live individuals of *C. temmincki* could be easily sparated into two types by body color and size. Fish smaller than about 80 mm TL showed a somber brownish body color (type A), while those larger than about 80 mm TL were of a conspicuous, brilliant blue-green color which took on an increasingly beautiful gloss during the reproductive season (type B). On the other hand, immediately after landing, they could be divided into three types by body color, i.e., brownish fish smaller than about 50 mm TL (type C), the middle-sized scarlet fish between about 50 and 80 mm TL (type D), and the largest fish, beyond about 80 mm TL, whose bodies had a beautiful deep red color with a glossy blue caudal fin (type E). Comparison of these body colors and sizes with gonadal sexes indicated that fish of types B and E were only secondary males which showed the terminal color phase, whereas types A, C, and D certainly showed the initial color phase, but their gonads were a complex of various stages of sex succession from female to secondary male. Ovaries, secondary testes and transitional gonads were found abundantly among these three types.

2) Elongation of the second ventral ray: Although the presence of a long second ventral ray had been considered one of the specific characteristics in *C. temmincki*, the present authors surmised that remarkable elongation of the ray was seen only in the larger fish and it gradually extended with growth in body length or progress of sex succession. We investigated the possibility of correlation between length of the ray and gonadal sex using the following index:

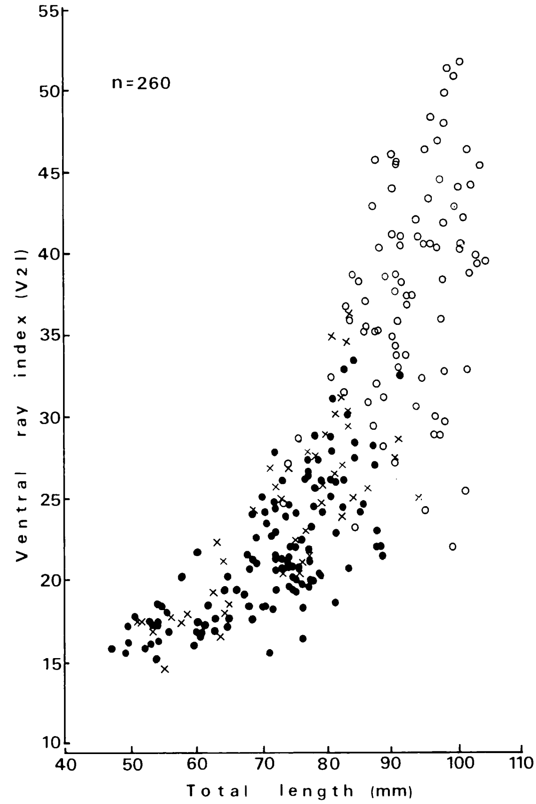

Fig. 7. Relationship between the index of the second ventral ray ($V_2I=(V_2L/TL)\times 10^2$; V_2L, length of the second ventral ray; TL, total length of fish) and total length in *Cirrhilabrus temmincki*. Closed circles, female; open circles, male; cross marks, transitional fish.

$$V_2I=(V_2L/TL)\times 10^2$$

where V_2L is the length of the second ventral ray, and TL is the total length of the fish.

Two of the 262 fish collected monthly were excluded as their ventral rays were partially missing. Of the remaining 260 fish (45.7–104.5 mm TL), 128 females (45.7–104.5 mm TL) showed an index of 15.2–33.3, 45 transitional fish (51.0–94.0 mm TL) gave 14.6–36.3, and 87 males (73.5–104.5 mm TL) gave 22.0–51.7. Thus, a positive correlation was obtained between the length of the second ventral ray and gonadal sex and/or body growth (Fig. 7).

Discussion

The process of gonadogenesis and gonadal sex differentiation in *C. temmincki* from Suruga Bay was established by histological observations. Gonads of the present species began to differentiate at a young stage of approximately 20 mm TL in a typical gonadogenetic process known as the parovarian type (Shimizu and Takahashi, 1980). This is the first report on the gonadogenetic process among the fishes belonging to the family Labridae. The early ovarian structure began to be formed in juvenile fish of less than approximately 30 mm TL. No histological evidence was found for the occurrence of primary males in *C. temmincki*. Almost all fish of the present species showed steady development of the gonad exclusively as an ovary for the first maturation as a female. These females, in general, eventually changed their gonadal sex to become secondary males after the reproductive season in a typical protogynous process. However, in some specimens, an early intersexual phase was seen not only among mature ovaries after function but also among immature ovaries or among mature ones before first reproduction as females. In *C. temmincki*, the sex succession from female to male showed substantial evidence of belonging to a category defined as protogynous hermaphroditism. According to Atz (1964), this term is defined as "hermaphroditism in which the individual functions first as a female, and later in life as a male". According to the present study, in *C. temmincki*, a major part of the hermaphroditic phenomenon clearly fitted the definition of Atz but a minor proportion did not appear to coincide his definition because the fish were thought to function only as females or only as males during their life cycle. Atz (1964) also pointed out the phenomenon of "non-functional but normal hermaphroditism, that is, normal hermaphroditism exhibited by an individual that functions only as a male or only as a female"; this was defined as "rudimentary hermaphroditism". Atz (1964) referred to Liu (1944) and Liem (1963) who used the term of hermaphroditism for "protogynous hermaphrodites like the *Monopterus* in which the entire gonad appears to change from an ovary into a testis", but Atz disagreed with that difinition because it did not clearly explain this sexual phenomenon. Our findings in *C. temmincki*, however, seemed to differ from the definition of rudimentary hermaphroditism given by Atz (1964), while bearing a close resemblance to the case of *Monopterus*. Several authors have hitherto reported the existence of prematurational sex succession among protogynous species, occurring in the stage previous to female sexual function, in other teleosts such as the fishes belonging to the families Parapercidae, Sparidae, and Scaridae (Lissia Frau and Casu, 1968; Huang et al., 1974; Warner and Robertson, 1978; Nakazono et al., 1985; Alekseev, 1982). In *C. temmincki*, prematurational sex change from female to male was thought to occur rather commonly, but it did not seem to conform to normal hermaphroditism. According to histological observations, transitional gonads appeared in fish up to about 38 mm TL and the secondary males up to about 58 mm TL among these specimens. These individuals were markedly smaller than the minimal size of sexual maturation and the monthly sizing composition of the fish specimens. No male specimens of such a small size were obtained during the reproductive season. These fish also produced several intersexual gonads in which both numerous seminal lobules and developing oocytes, from the yolk vesicle stage to the ripe stage, coexisted in the ovigerous lamellae of one gonad. However, it was doubtful whether these should be defined as 'protogynous' or 'prematurational protogynous' phenomena (Robertson and Warner, 1978; Warner and Robertson, 1978), because in young fish there was no evidence that these findings related to their reproductive tendency. In the diandric Caribbean wrasses, Warner and Robertson (1978) pointed out that a sex change occurred as "a large proportion of those (initial phase) males had transitional gonads. We feel that this indicates rapid transition of the secondary males into the terminal phase," and they referred to the study of Reinboth (1973) who proposed that "no transitionally colored secondary male had transitional gonads." Warner and Robertson (1978) further reported a correlation between the change of body color and gonadal sex in the monandric Caribbean wrasses, concluding that "sex change occurs over a small size range," or "sex change probably precedes color change, which is common in the monandric parrotfishes," and "in none of the monandric species is there any tendency to early sex change (i.e., prematurational or early post-maturational), which is common in the monandric parrotfishes." The present *C. temmincki* is an effectively monandric species as Bell (1983) reported, but its initial color phase extends to transitional fish and some males as well as females. Their body lengths therefore overlap broadly, ranging from 30.0–94.0 mm TL within a total range of 11.4–104.5 mm TL, and sex change occurs in the prematurational stage as well as in young fish distant from maturation or sexual function.

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駿河湾におけるイトヒキベラの生殖腺形成と雌雄同体現象

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駿河湾産のイトヒキベラ *Cirrhilabrus temmincki* について生殖腺の組織学的研究と外部形態の観察によって，幼期における生殖腺形成ならびに生殖機能と雌雄同体現象の関連を検討した．全長 11.4–19.5 mm の個体の生殖腺は性的に未分化の状態にあるが，全長 21.1–29.6 mm の個体では，減数分裂前期の生殖細胞が増加して肥大卵母細胞も出現し，parovarian type の卵巣形成を開始して，全長 31.0–40.4 mm で生殖腺の卵巣分化が明らかとなり，未分化生殖腺から精巣に分化する例は見出されなかった．卵巣は両性生殖腺を経由して二次精巣に変わる．駿河湾における本種の繁殖期は 6–9 月で，卵巣機能を果たす最小の個体の大きさは全長 50.4 mm，精巣機能を果たす最小の個体の大きさは全長 88.2 mm であった．雌雄両相が共存する生殖腺は，繁殖期をはさむ 4–7 月と 9–10 月にそれぞれ見出された．ただし，4–6 月の両性生殖腺には雌相から雄相への移行の進展傾向は認められず，これらは当年の繁殖期には卵巣機能を果たすものと判断された．一方，7–10 月の間性像は明らかに雌性先熟雌雄同体現象の過程に含まれるものであった．また，4 月に小型個体だけで成る群から採集された標本中には，全長約 38 mm の個体の生殖腺に雄性化が発現し，二次精巣が全長約 58 mm の個体に出現している．本種は一次雄が存在しない monandric type である．体色が明瞭な終相を呈する個体は二次雄で，始相を呈する個体には雌，性移行中の個体，二次雄の 3 者が存在する．本種の特徴とされる糸状の腹鰭第 2 軟条は，体の成長に伴って伸長し，結果的に雄では著しい伸長が見られることが明らかにされた．

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