

Sexual Dimorphism and Pair Spawning into a Sponge by the Filefish, *Brachaluteres ulvarum*, with a Description of the Eggs and Larvae

Izumi Akagawa, Youichi Tsukamoto¹ and Muneo Okiyama

Ocean Research Institute, University of Tokyo, 1–15–1 Minamidai, Nakano-ku, Tokyo 164, Japan

¹ Present address: National Research Institute of Fisheries Science,
2–12–4 Fukuura, Kanazawa-ku, Yokohama, Kanagawa 236, Japan

(Received September 9, 1994; in revised form November 11, 1994; accepted December 7, 1994)

Abstract Sexual dimorphism, reproductive behaviour and early development of a small filefish, *Brachaluteres ulvarum*, were studied in the field and an aquarium. Males were larger than females (twice body weight) and showed a remarkable colour change during male-male competition during the reproductive season. A single male often followed a gravid female, although a pair-bond was not fixed. Only the larger male with more intense nuptial colouration continued to court until spawning. When the gravid female assumed a spawning position on the osculum of the calcareous sponge, *Grantessa mitsukurii*, the male also pushed his abdomen onto the osculum. Spawning by the female took 20–30 sec, whereas the male quickly departed. Parental care was not observed after mating. The eggs were demersal and adhesive, being the largest recorded (0.82 mm in diameter) among monacanthids. Hatching occurred 6–8 days after spawning (19–22°C), newly-hatched larvae measuring 1.93–2.35 mm in total length. Sexual dimorphism and pair spawning into the sponge are discussed in comparison with other monacanthids.

Various sexual dimorphisms have been studied in relation to the two types of sexual selection, female (male) choice and male-male (female-female) competition. For example, male nuptial colouration and female choice have been analyzed in guppies (Houde, 1987) and sticklebacks (Milinski and Bakker, 1990), male size and frequency of copulation in lizards (Trivers, 1976) and large-male advantage for access to females in a salamander (Mathis, 1991). Nuptial colouration is also used as a signal to drive off competing males in male-male competition in sticklebacks (Rowland, 1982) as well as to court females.

The purpose of the present study of reproductive behaviour and sexual dimorphism in size and colouration of a small filefish, *Brachaluteres ulvarum* (family Monacanthidae), was to examine the relationship between sexual dimorphism and male-male competition in the species. This fish is found mainly in seaweed beds, being distributed along the Pacific coast of southern Japan (Matsuura, 1984). The fishes in this genus are known to be poor swimmers with cryptic habits in seaweeds (Hutchins and Swainston, 1985). Little is known about their reproductive behaviour and early ontogeny, including that of *B. ulvarum*, probably because of their small popula-

tion sizes and restricted distribution. *Brachaluteres ulvarum* occurs in southern Japan, *B. jacksonianus* in southern Australia, *B. taylori* in Micronesia and *B. fahaqa* in the Red Sea (Hutchins and Swainston, 1985).

In other monacanthids, various reproductive guilds (Balon, 1975, 1984) and characteristics of eggs and larvae have been reported; in *Stephanolepis cirrhifer* (Fujita, 1955; Tsukashima and Kitajima, 1981), *Thamnaconus modestus* (Kitajima et al., 1964), *Aluterus monoceros* (Kitada et al., 1985; Imura et al., 1986), *Oxymonacanthus longirostris* (Barlow, 1987), *Paramonacanthus japonicus* (Nakazono and Kawase, 1993; Kawase and Nakazono, 1994a), *Rudarius ercodes* (Nakamura, 1942; Kawase and Nakazono, 1994a; Akagawa and Okiyama, in press), and *Cantherhines pardalis* (Kawase and Nakazono, 1994b). All these monacanthids spawn small, demersal eggs (Fujita, 1988), but vary in their mating systems and parental care; viz. monogamous, polygynous or promiscuous and biparental, maternal or no care, respectively.

The spawning of *B. ulvarum* into a sponge (*Grantessa mitsukurii*), as reported here, is the first example known among monacanthids. The relevancy of this specific feature, spawning behaviour and sexual di-

morphism is discussed, and the morphology of embryos and hatched larvae of *B. ulvarum* described.

Materials and Methods

Collection of fish and sponge

The sampling sites were along the breakwater on the south part of Koajiro Bay (35°09'35''N, 139°37'20''E) and among seaweed beds at the mouth of Aburatsubo Bay (35°09'15''N, 139°36'50''E), the bays being located side by side on the west coast of Miura Peninsula, Kanagawa Prefecture, Japan. Thirty-five specimens of *Brachaluteres ulvarum* (13 females and 22 males) were collected by hand net from a boat in Koajiro Bay in June and July 1991, and 2 (a female and male) and 10 (6 females and 4 males) by SCUBA diving in Aburatsubo Bay in June 1991 and 1993, respectively. All collections were made during the reproductive season, owing to the fish being rarely found at other times.

Two sponges, *Halichondria japonica* 12 specimens and *Grantessa mitsukurii* 8 specimens, were collected in Aburatsubo Bay on 24 June 1993, and examined for eggs of *B. ulvarum*. Parts of them were used as spawning substrates during aquarium observations.

Gonad examination

After aquarium observations all specimens were preserved in 10% seawater-buffered formalin. The standard length (SL) and body weight (BW) of 26 males and 19 females were measured. Gonad weights of 23 males and 17 females were measured, the remaining fish being used for artificial fertilization. The gonads of 5 males and 6 females were sliced in 7 µm paraffin sections, stained with haematoxylin and eosin, and examined histologically under dissecting binocular and light microscopes.

Reproductive behaviour

Aquarium observations were conducted with or without sponges as a spawning substrate. A pair of *B. ulvarum* captured in Aburatsubo Bay on 25 June 1991, when the male was following the smaller gravid female, was kept in an aquarium (60×30×30 cm) lacking a spawning substrate and observed from 25 June to 4 July. Several males and gravid females, captured in Koajiro Bay on 28 June 1991, were held

in aquaria (90×40×40 cm) in various combinations (1 female and 2–3 males, 2–3 females and 1 male, and 2–3 females and 2–3 males). Each aquarium included rocks and several kinds of seaweeds (*Ecklonia cava*, *Padina arborescens*, *Sargassum* spp. and red algae), the sea grass, *Zostera marina*, and the sea squirt, *Pyura michaelsoni*, which were all common in Aburatsubo Bay, as a spawning substrate, but lacked sponges. The water temperature was held at 22–24°C, and the aquaria kept in the dark until the beginning of observations. Fifteen hrs of observations were made from 28 June to 4 July.

Three males and three gravid females captured in Aburatsubo Bay between 16 and 24 June 1993, were housed in an aquarium (60×30×30 cm) containing two specimens of the sponge, *Halichondria japonica* on 24 June, and two of *Grantessa mitsukurii* on 25 and 26 June. The water temperature was held at 19–22°C, and the aquarium kept in the dark until the beginning of observations. Reproductive behaviour was observed and recorded by video camera for 6 hrs.

Field observations were conducted by SCUBA diving, totalling 40 hrs each for the periods from 24 June to 4 July 1991 and 15 to 30 June 1993. The study area covered 200 m² of seaweed beds (1–5 m deep) in Aburatsubo Bay. Reproductive behaviour of *B. ulvarum* was recorded by underwater video camera for 4 hrs. The water temperature was 22–24°C in 1991, and 19–22°C in 1993.

Ten-minute observations of a female and following male were conducted, when such a pair was found in the observation area. Eleven pairs were observed on separate occasions, but without individual recognition.

Eggs and larval development

The eggs spawned into the sponge in the aquarium on 24 June 1993, were taken out and incubated in flowing seawater at 19–22°C. In addition, artificial fertilization involving the most gravid female (41.2 mm SL) and the dominant male (60.9 mm SL) was carried out on 26 June and the resulting eggs incubated as above. On the third day following fertilization, the eggs were incubated in still water, which was changed twice a day, and larvae transferred to a rearing tank (30 cm in diameter, 15 cm in height) after hatching. One third of the water in the latter was changed daily. The larvae survived for 6 days without feeding, representative speci-

mens being removed daily and preserved in 2% paraformaldehyde-2% glutaraldehyde mixture in 0.1 M cacodylate buffer (pH 7.4) for subsequent morphological observations. The methods of measurements and terminology follow Leis and Rennis (1983). After observation, the specimens were post-fixed in 2% OsO₄ for 2 hrs, dehydrated through a graded ethanol series, dried in a critical-point dryer and mounted on a brass disc. They were subsequently sputter-coated with gold (150 Å) and observed by scanning electron microscopy (SEM).

Results

Sexual dimorphism and gonad condition

Body proportions of *Brachaluteres ulvarum* were similar between the sexes, although the species showed remarkable sexual size dimorphism. Of fish collected in Koajiro Bay in 1991, males (mean \pm SD = 55.9 ± 5.4 mm SL, $n = 22$) were significantly longer than females (42.2 ± 2.9 mm SL, $n = 13$) (Mann-Whitney test, $U = 11$, $z = -4.4$, $p < 0.0005$), their BW's being 10.19 ± 2.23 g and 5.65 ± 1.12 g, respectively. Of fish collected in Aburatsubo Bay in 1993, males (58.9 ± 3.6 mm SL, $n = 4$) were also significantly longer than females (39.0 ± 1.8 mm SL, $n = 6$) ($U = 0$, $p < 0.01$), their BW's being 11.30 ± 2.43 g and 4.28 ± 0.63 g, respectively. All the specimens longer than 50 mm SL (8 g BW) were males, only 2 (out of 26 males) being smaller than 50 mm SL (38.9 and 43.4 mm SL). The size ratio (male size/female size; Parker, 1992) was around 2.

Body colouration of males and females was basically similar, but the former showed a marked change during male-male competition for mates (see next section). Preserved male specimens sometimes retained a black stain on the abdomen, being the only trace of the nuptial colouration.

The gonosomatic indices (GSI) of males ranged between 0.16–0.62 (mean = 0.36, $n = 23$), the lower values being consistent with testes filled with spermatozoa (Fig. 1A). Female GSI ranged between 4.40–12.45 (mean = 7.18, $n = 17$). Most ovaries were occupied by oocytes in various stages of development (Fig. 1B).

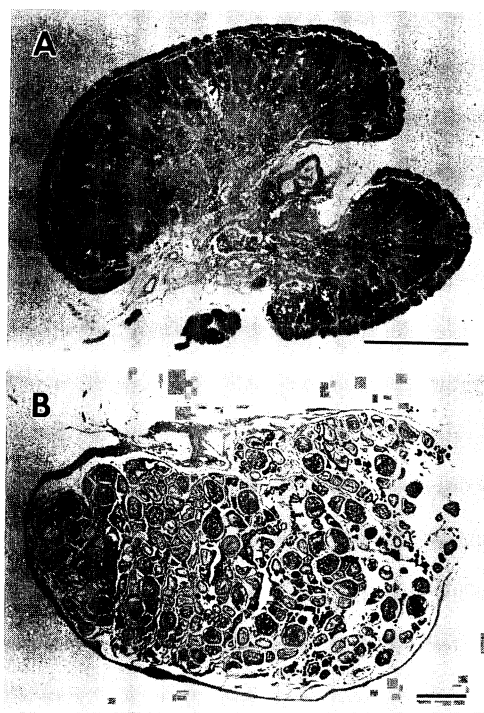


Fig. 1. Gonad structure of *Brachaluteres ulvarum* collected in Koajiro Bay on 28 June 1991. A) Testis showing active spermatogenesis from a specimen, 53.8 mm SL, GSI = 0.34; B) ovary with various stages of oocytes from a specimen, 42.5 mm SL, GSI = 6.5. Scale bars indicate 1 mm.

Male body colouration during male-male competition and courtship

During the field investigations, 2–5 individuals (not individually recognised) were observed in the study area in Aburatsubo Bay every day. Fish were often found in pairs, but sometimes singly. When in pairs, the larger fish was always following the smaller. Collection and subsequent gonad examination showed the smaller fish to be a female and the larger a male.

When a male met another male while following a gravid female, both males performed lateral display with their body colour changed gradually (Fig. 2). This involved three phases: phase 1, showing conspicuous, broken horizontal lines on the lateral sur-

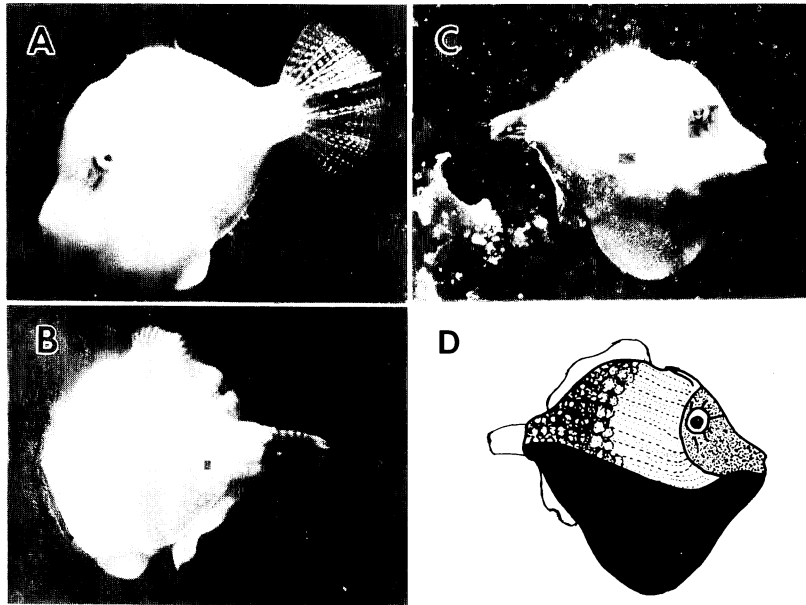


Fig. 2. Changes in male body colouration during lateral display in an aquarium. A) Before display: lateral lines indistinct; B) phase 1, lateral lines and knitting-like patterns clearly apparent; C) phase 2, flap spread downward and colour changed to gray; D) phase 3, lower part of body completely black and face yellowish-orange.

face of the body and knitting-like patterns rearwards while folding the tail (Fig. 2B); phase 2, extending the ventral flap downward, the flap itself becoming gray (Fig. 2C); phase 3, changing the lower part of the body to completely black with some sparkling blue lines, and the face to bright yellowish-orange (Fig. 2D). The broken lines and knitting-like patterns are clearly shown on the upper body in Figure 2D. Such lateral display with conspicuous colour changes continued for 3–5 minutes or more, finishing when the smaller male with the less intense colour fled. When two males were equally-matched during the display contest, they vigorously lunged at and chased each other.

When in pairs, the male sometimes courted the female by lateral display, quickly raising and lowering the dorsal spine and spreading and quivering the caudal fin. Subsequently, broken horizontal lines appeared clearly on the body of the male and the abdomen became black, but the colouration change was less obvious in courtship than in male-male competition.

Pair-bonding

During 5 of the pair observations using SCUBA, another male appeared, both males then competing by displaying laterally at each other, while the female moved around feeding. In at least one of these competitions, the original male was defeated and the new male followed the female. On 3 other occasions, the original male followed the same female continuously without competition, but on the remaining 3, the males stopped following and became separated from the females, with one of the former beginning to follow another gravid female. Thus, male-male competition was severe and a pair-bond was not fixed.

Spawning into a sponge

In June 1993, lateral display, following and courtship were observed daily in Aburatsubo Bay. At about 6:00 h on 24 June 1993, 6–7 individuals of *B. ulvarum* were observed gathered around a concrete

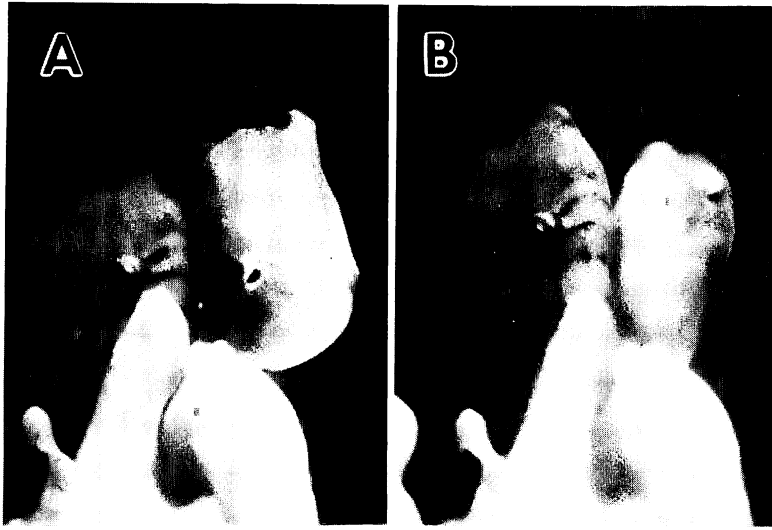


Fig. 3. Courtship and spawning in an aquarium. A) Female (right) examination of sponge osculum, with cheek-to-cheek approach by male; B) female (right) assumption of oblique upward posture for spawning. Male about to assume similar posture, prior to fertilization.

column in the water. Several calcareous sponges, *Grantessa mitsukurii*, were attached to the column. Three gravid females sometimes looked into the oscula of the sponges in turn. Aggressive behaviour was observed, both between males and between females; males often showed lateral display, the largest one with the most intense nuptial colouration lunging at the others, while females also lunged at and chased each other, but without any accompanying display. The largest and most aggressive male drove other males away and approached face to face to a female, which kept looking into the sponge, repeatedly opening and closing his mouth quickly, but without noticeable colour change (Fig. 3A). Other males did not approach the pair.

After investigation of several sponges, the female bit pieces off a selected sponge to widen the osculum. At 6:37 h, the female suddenly assumed an upward-oblique posture and pushed her abdomen onto the osculum (Fig. 3B). A few seconds later, the male which had courted at her side took a similar posture, pushing his abdomen onto the osculum. The female retained the position for 20–30 sec, whereas the male departed after 1–2 sec.

Sneaking behaviour of neighboring males was not observed. Afterward, no fish approached the sponge. Although eggs and sperm were not seen at spawning, fertilized eggs were later found in the sponge. Judging from their embryonic development, they had

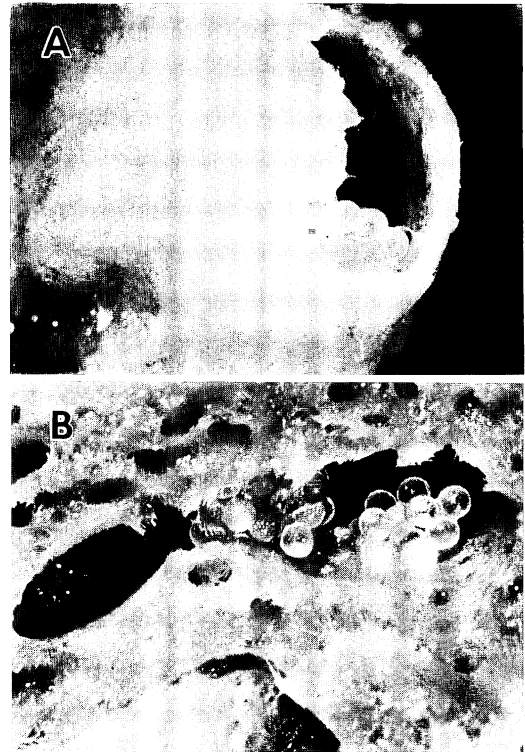


Fig. 4. Eggs deposited in the sponge, *Grantessa mitsukurii*. A) Eggs visible in the osculum which had been enlarged by biting before spawning; B) eggs adhering to the canal.

resulted from the pair observed above.

Of 8 specimens of calcareous sponges (*G. mitsukurii*) collected, three had had the osculum enlarged by biting and two contained eggs in the osculum (Fig. 4A). Each sponge specimen was 5–10 cm in diameter and 5 cm in height. One of the sponges had a total of 661 eggs adhered to the exhalant canal, reaching deeply into the canal, but without obstructing it (Fig. 4B). The developmental stages of these eggs (see later) showed that 160 were spawned on the day of collection, with the remainder having been spawned the day before. *Grantessa mitsukurii* was not common in Aburatsubo Bay, fewer than 20 specimens being located in the observation area. No eggs of *B. ulvarum* were found associated with other substrates, including seaweeds, sea grasses, sea squirts, rocks and sandy bottoms.

Preference for spawning substrate

In the aquaria with seaweeds, sea grasses, sea squirts and rocks, but without sponges, spawning did not occur, although subsequent gonad examination revealed that the gravid females had mature eggs and all the males had testes filled with sperm. When 2–3 males were housed in an aquarium, they often showed lateral display and lunged at each other. Only the predominant male followed and courted a gravid female continuously and frequently lunged at the other males. When 2–3 gravid females were housed in an aquarium, the predominant male followed the females one after another.

In the aquarium containing the soft, flat sponge, *Halichondria japonica*, the gravid females looked into the osculum repeatedly. One of the females spawned on the osculum 4 hrs after the onset of observations,

but the eggs were spread over the sponge surface around the osculum. The predominant male did not assume the ejaculating posture but instead ate the eggs.

In the aquarium with the calcareous sponge, *G. mitsukurii*, both males and females began looking into the osculum soon after the onset of observations. Spawning occurred between the predominant male and a gravid female following the same pattern as that seen in the field, after about 20 min of observations.

Eggs and larvae

The spherical eggs (0.82 ± 0.03 mm [mean \pm SD, $n=10$] in diameter) were demersal and adhesive, with a colourless transparent chorion and a slightly yellowish yolk containing more than 20 oil globules of various size (0.03–0.13 mm in diameter). The main features of embryonic development are summarized in Table 1 and Figure 5A–C. Hatching occurred between 6–8 days after spawning.

General morphology.—The newly-hatched larvae, measuring 1.85–2.20 mm notochord length (NL), and with 20 myomeres, had a round head, short trunk and long tail (Fig. 5D). The body became deeper with growth (Fig. 5E), but the proportion of preanal length to NL did not change (Table 2).

In the newly-hatched larvae, the yolk sac was ovoid in shape, measuring 0.60 ± 0.05 mm long ($n=5$), and had an oil globule half as long as the yolk sac, located in the anterior part of the latter. Absorption of the yolk and the oil globule was completed within 4–5 days after hatching.

In the newly-hatched larvae, the mouth and anus were not open (Fig. 5D). The formation of these

Table 1. Embryonic development of *Bracharuteres ulvarum*

Time after spawning	Developmental stage or episode
15 min	Elevation of blastodisc
2 hrs 30 min	2-cell stage (Fig. 5A)
21 hrs	Blastula stage
36 hrs	Closure of blastopore
39 hrs	Formation of optic vesicle, 4 myomeres
41 hrs	Formation of Kupffer's vesicle, 8 myomeres (Fig. 5B)
52 hrs 30 min	Formation of lens, beginning of tail formation
55 hrs	Formation of otic capsule
57 hrs	Disappearance of Kupffer's vesicle
70 hrs	Appearance of melanophores on the yolk and head (Fig. 5C)
74 hrs	Beginning of heart pulse
6–8 days	Hatching (Fig. 5D)

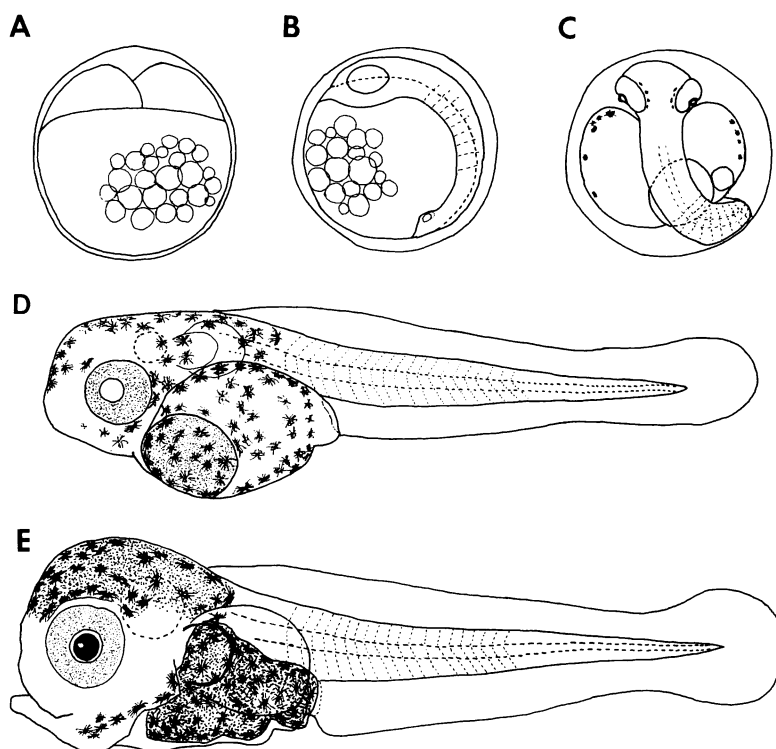


Fig. 5. Embryonic development and external morphology of *Brachaluteres ulvarum* larvae. A) 2 hrs 30 min after spawning; B) 41 hrs after spawning; C) 70 hrs after spawning; D) newly-hatched larva, 2.47 mm TL; E) preflexion larva, 5 days after hatching, 2.82 mm TL.

parts and the convolution of the alimentary canal were completed three days after hatching. The anus was situated anterior to the middle of the body (Fig. 5E).

Minute "cell-like" granules spread over the entire surface of the newly-hatched larvae, followed a narrow, polygonally-patterned zone except along the contour of the finfold. Observations by SEM showed them to be mesh-like, epidermal structures with raised ridges around the margin (Fig. 6).

Pigmentation.—Melanophores on the head and abdomen first appeared in the embryo around 70 hrs after spawning (Fig. 5C). In the newly-hatched larvae, numerous branched melanophores were distributed from the snout to the nape and on the abdomen (Fig. 5D). These increased in number with growth. One day after hatching, melanophores appeared in the eyes. In four-day old larvae, the head and entire abdomen were completely black (Fig. 5E).

Table 2. Body sizes and proportions of *Brachaluteres ulvarum* larvae*

Days after hatching	Total length (mm)	Notocord length (mm)	Measurements in % of notochord length		
			Head length	Preanal length	Body depth
0	2.28–2.58 (2.47)	1.85–2.20 (2.04)	16.0–18.0	38.2–40.5	17.7–20.5
2	2.31–2.81 (2.56)	1.93–2.35 (2.20)	18.2–22.0	35.9–42.3	22.0–24.4
4	2.65–2.97 (2.80)	2.18–2.45 (2.31)	21.4–23.9	39.0–42.3	26.3–30.7
6	2.77–2.93 (2.85)	2.42–2.57 (2.51)	21.4–24.8	38.5–43.9	24.0–28.7

* Ranges of 5 larvae are shown with means in parentheses.

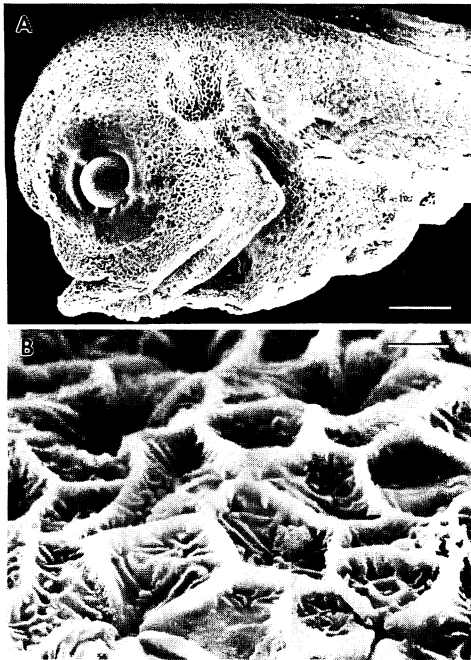


Fig. 6. SEM photomicrographs of *Brachaluteres ulvarum* larva. A) Head of 5-day old larva. Scale bar indicates 80 μm ; B) magnification of epidermal structure. Scale bar 4 μm .

Discussion

Spawning into the sponge

The present study established for the first time that the filefish, *Brachaluteres ulvarum*, spawns into the exhalant canal of the calcareous sponge, *Grantessa mitsukurii*, and conducts no parental care. This type of reproductive guild has been called “a hider in live invertebrates” by Balon (1975, 1984). Among monacanthids, there is no other record of this guild.

Some other fish species are also known to exploit sponges as spawning substrates, but the ways of exploitation and the species of sponges differ (Breder, 1939, 1941; Warfel and Merriman, 1944; Moreno, 1980; Munehara, 1991). The only other fish that hides eggs inside sponges, without parental care, is the little dragon sculpin, *Blepsias cirrhosus* (Munehara, 1991).

The benefits and costs to the eggs for *Brachaluteres ulvarum* seem to be similar to those for *Blepsias cirrhosus*. The benefits are the avoidance of predation and the assurance of oxygen resulting from

sponge respiration. The cost is the possible restriction of reproduction by limited availability of suitable sponges, as shown by the aquarium experiments in this study.

The choice of the calcareous sponge, *Grantessa mitsukurii*, as a spawning substrate may be due to *Brachaluteres ulvarum* lacking an ovipositor. Accordingly, the fish has to widen the osculum before spawning by biting pieces off and adhere the numerous small eggs to the bent wall of the canal, via the osculum, so as not to block the former. Under these circumstances, the choice of the tall (5 cm), hard sponge by *Brachaluteres ulvarum*, instead of a very soft, thickened (2–3 cm) sponge, such as that chosen by *Blepsias cirrhosus*, appears to be somewhat logical.

Eggs and larvae

Small, demersal eggs, coupled with poorly-developed larvae at hatching, are common characteristics of monacanthids (Table 3). *Brachaluteres ulvarum* has the largest known eggs in the family, its long incubation time and high cumulative temperature also being noteworthy (Table 3). However, the newly-hatched larvae of *B. ulvarum* are not well developed. At that time, their mouths are unopened, as in other monacanthids (Table 3), and the yolk persists some two days after opening of the former. Such time delay from mouth opening to yolk absorption, unlike the situation in *Aluterus monoceros* or *Rudarius ercodes*, in which species yolk absorption is complete when the mouth opens, is a significant advantage for *B. ulvarum* when food is scarce.

Among the three types of monacanthid larval morphs (Aboussouan and Leis, 1983; Leis and Rennis, 1983), the larvae of *B. ulvarum* fall into type C. Five-day old larvae (Fig. 5E) were similar in both proportion and pigmentation to a 2.5 mm *Brachaluteres* larvae figured by Leis and Rennis (1983: fig. 72A).

The pre-larvae of *B. ulvarum* could be distinguished from those of the other four Japanese monacanthids by pigmentation. The former had well-developed melanophores on the dorsal part of the head, but none on the ventral part of the tail. No melanophores occur dorsally on the head in *R. ercodes* (Nakamura, 1942; Kawase and Nakazono, 1994a), *Stephanolepis cirrhifer* (Fujita, 1955), *Thamnaconus modestus* (Kitajima et al., 1964) and *Paramonacanthus japonicus* (Kawase and Nakazono, 1994a) all have melanophores on the ventral part of the tail.

The raised epidermal ridges observed during SEM examinations of larval *B. ulvarum* (Fig. 6) may have a protective function. *R. ercodes* lacks such raised ridges on the epiderm (Akagawa, unpubl. data) and there are no reports of such structures in other monacanthids. The larvae of *Gasterosteus aculeatus*, which hatch in a nest under the sand, have a remarkable epidermal structure, that may protect the larvae from abrasion (Tsukamoto and Okiyama, unpubl. data). Similarly, the larvae of *B. ulvarum* are subject to abrasion against the hard, rough wall of the calcareous sponge and would benefit from protective ridges.

Spawning behaviour and sexual dimorphism

In monacanthids, various mating systems are known: *Rudarius ercodes* shows promiscuous mating (Akagawa and Okiyama, in press), *Oxymonacanthus longirostris* is monogamous (Barlow, 1987), *Paramonacanthus japonicus* is monogamous or occasionally polygamous (Nakazono and Kawase, 1993) and *Stephanolepis cirrhifer* is polygynous (H. Kawase, pers. comm.). Although mating systems vary among the species, all except *R. ercodes*, conduct pair spawning with monogamous or polygynous behaviour. Other than that in *B. ulvarum*, there are no reports of conspicuous sexual size dimorphism in monacanthids, although various other examples of sexual dimorphism have been reported; e.g., the body proportions of *P. japonicus* (Matsuura, 1984), the elongated second soft-ray in the dorsal fin of male *S. cirrhifer* (Fujita, 1955) and the gaudy orange pelvic flap in

male *O. longirostris* (Barlow, 1987). There are no known examples of hermaphroditism in monacanthids or balistids.

Pair spawning in *B. ulvarum* occurred both in the field and in the aquarium, but the pair-bond was not fixed. Only the largest male with the most intense body colouration monopolized the gravid female(s). Because the male and female spawned side by side with their abdomens pushing onto the sponge osculum, single female-multiple male spawning would be unlikely to occur. Sneaking by other males, by ejaculating into the osculum before or after pair spawning as in some bitterlings (Wickler, 1973; Shinabe et al., 1993), was at no time observed. Larger size in males appeared to be appropriate in this situation, even if the GSI index was low. Thus, selection may have favoured males becoming larger than females (Harvey and Bradbury, 1991).

Sexual dichromatism in *B. ulvarum* may have a function not only in courtship but also in severe male-male combat. As in sticklebacks (Rowland, 1982), the conspicuous body colouration change in *B. ulvarum* seemed to be a signal used to drive off competing males. Such short-term colour intensification occurred especially during male-male competition, with the more intensely-coloured males tending to be more aggressive.

Acknowledgments

We thank T. Kuwamura for his helpful suggestions and critical reading of the manuscript. We are

Table 3. Comparison of embryonic and larval sizes and incubation times of monacanthids

	Eggs size (mm)	Onset of hatching (hrs after fertiliza- tion)	Cumulative temperature before onset of hatching (°C·hrs)*	Newly- hatched larvae (mm TL)	MO, YA (days after hatching)	Reference
<i>Paramonacanthus japonicus</i>	0.53	29	841–850	1.94	2, —	Kawase and Nakazono (1994a)
<i>Stephanolepis cirrhifer</i>	0.61–0.66	57	1026–1226	1.80–2.07	3, 4	Fujita (1955)
	—	50	1225–1260	2.1	2, —	Tsukashima and Kitajima (1981)
<i>Thamnaconus modestus</i>	0.6–0.64	40	960–1000	1.8	—, 3	Kitajima et al. (1964)
<i>Rudarius ercodes</i>	0.52	36	965–1030	1.8	—, 1.5	Nakamura (1942)
	0.53	62.5	1283–1331	1.86	2, 2	Kawase and Nakazono (1994a)
<i>Aluterus monoceros</i>	0.68	55	1342–1611	2.47	2, 2	Imura et al. (1986)
<i>Oxymonacanthus longirostris</i>	0.7	53.5	1445–1530	2.5	2, 5	Barlow (1987)
<i>Brachaluteres ulvarum</i>	0.82	150	3225–3600	2.47	3, 5	Present study

* Cumulative temperature was calculated by multiplication of temperature range by onset of hatching (hrs after fertilization). MO, mouth opening; YA, yolk absorption; —, no data in the reference.

very grateful to the late S. Tanita for identification of the sponge. M. Morisawa and T. Sato provided the facilities for our study in Misaki Marine Biological Station. We thank H. Suzuki, M. Sekimoto and M. Sekifuji for their useful advice and help in collecting fishes, M. Hara for assistance with SEM techniques, and Y. Kurita, R. Masuda, Y. Sakakura, M. Kanda, J. Aoyama and Y. Iwatsuki for stimulating discussion. Y. Tohyama and K. Tanaka gave support in making the underwater videos.

Literature Cited

- Aboussouan, A. and J. M. Leis. 1983. Balistoidei: development. Pages 450–459 in H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr. and S. L. Richardson, eds. Ontogeny and systematics of fishes. Am. Soc. Ichthyol. Herpetol., Spec. Publ. No. 1.
- Akagawa, I. and M. Okiyama. In press. Reproductive behaviour of the filefish, *Rudarius ercodes*: male spawning parades and female choice. Env. Biol. Fish.
- Balon, E. K. 1975. Reproductive guilds of fishes: a proposal and definition. J. Fish. Res. Bd. Can., 32: 821–864.
- Balon, E. K. 1984. Patterns in the evolution of reproductive style in fishes. Pages 35–53 in G. W. Potts and R. J. Wootton, eds. Fish reproduction: strategies and tactics. Academic Press, London.
- Barlow, G. W. 1987. Spawning, eggs and larvae of the longnose filefish *Oxymonacanthus longirostris*, a monogamous coralivore. Env. Biol. Fish., 20: 183–194.
- Breder, C. M., Jr. 1939. On the life history and development of the sponge blenny, *Paraclinus marmoratus* (Steindachner). Zoologica, 24: 487–496.
- Breder, C. M., Jr. 1941. On the reproductive behavior of the sponge blenny, *Paraclinus marmoratus* (Steindachner). Zoologica, 26: 233–236.
- Fujita, S. 1955. On the development and prelarval stages of the file-fish, *Monacanthus cirrhifer* Temminck et Schlegel. Sci. Bull. Fac. Agr., Kyushu Univ., 15: 229–234. (In Japanese with English summary.)
- Fujita, S. 1988. Monacanthidae. Pages 967–975 in M. Okiyama, ed. An atlas of the early stage fishes in Japan. Tokai University Press, Tokyo. (In Japanese.)
- Harvey, P. H. and J. W. Bradbury. 1991. Sexual selection. Pages 203–233 in J. R. Krebs and N. B. Davies, eds. Behavioural ecology. Third edition. Blackwell Scientific Publications, Oxford.
- Houde, A. E. 1987. Mate choice based upon naturally occurring color-pattern variation in a guppy population. Evolution, 41: 1–10.
- Hutchins, J. B. and R. Swainston. 1985. Revision of the monacanthid fish genus *Brachaluteres*. Rec. West. Aust. Mus., 12: 57–78.
- Imura, N., N. Yoshida and T. Arakawa. 1986. Embryonic [sic], larval and juvenile developments of laboratory-reared unicorn filefish, *Aluterus monoceros* (Linnaeus). Bull. Nagasaki Pref. Inst. Fish., 12: 37–42. (In Japanese.)
- Ishinabe, T., K. Mochizuki and K. Yamashita. 1993. Reproductive behavior in aquarium of *Tanakia lanceolata* (subfamily Acheilognathinae, family Cyprinidae) from Chiba, Japan. J. Nat. Hist. Mus. Inst., Chiba, 2: 133–143. (In Japanese with English summary.)
- Kawase, H. and A. Nakazono. 1994a. Embryonic and pre-larval development and otolith increments in two filefishes, *Rudarius ercodes* and *Paramonacanthus japonicus* (Monacanthidae). Japan. J. Ichthyol., 41: 57–63.
- Kawase, H. and A. Nakazono. 1994b. Reproductive behavior of the honeycomb leatherjacket, *Cantherhines pardalis* (Monacanthidae), at Kashiwajima, Japan. Japan. J. Ichthyol., 41: 80–83.
- Kitada, T., N. Yoshida, N. Imura and M. Yoshida. 1985. Spawning behavior of unicorn filefish, *Aluterus monoceros* (Linnaeus) in rearing tank. Bull. Nagasaki Pref. Inst. Fish., 11: 25–27.
- Kitajima, C., M. Kawanishi and T. Takeuchi. 1964. Egg development and post-larval stages of a file-fish, *Navodon modestus* (Günther). Suisanzoushoku, 12: 49–54.
- Leis, J. M. and D. S. Rennis. 1983. The larvae of Indo-Pacific coral reef fishes. New South Wales University Press, Sydney. 240 pp.
- Mathis, A. 1991. Large male advantage for access to females: evidence of male-male competition and female discrimination in a territorial salamander. Behav. Ecol. Sociobiol., 29: 133–138.
- Matsuura, K. 1984. Family Monacanthidae. Pages 359–361 in H. Masuda, K. Amaoka, C. Araga, T. Uyeno and T. Yoshino, eds. The fishes of the Japanese Archipelago. English text. Tokai University Press, Tokyo.
- Milinski, M. and T. C. M. Bakker. 1990. Female sticklebacks use male coloration in mate choice and hence avoid parasitized males. Nature, 344: 330–333.
- Moreno, C. A. 1980. Observation on food and reproduction in *Trematomus bernacchii* (Pisces: Nototheniidae) from the Palmer Archipelago, Antarctica. Copeia, 1980: 171–173.
- Munehara, H. 1991. Utilization and ecological benefits of a sponge as a spawning bed by the little dragon sculpin *Blepsias cirrhosus*. Japan. J. Ichthyol., 38: 179–184.
- Nakamura, M. 1942. Notes on three species of Japanese bitterlings spawn in autumn. Bull. Biogeogr. Soc. Japan, 11: 97–100.
- Nakazono, A. and H. Kawase. 1993. Spawning and biparental egg-care in a temperate filefish, *Paramonacanthus japonicus* (Monacanthidae). Env. Biol. Fish., 37: 245–256.
- Parker, G. A. 1992. The evolution of sexual size dimorphism in fish. J. Fish Biol., 41 (Supplement): 1–20.

- Rowland, W. J. 1982. The effects of male nuptial coloration on stickleback aggression: a reexamination. *Behaviour*, 80: 118-126.
- Trivers, R. L. 1976. Sexual selection and resource accruing abilities in *Anolis garmani*. *Evolution*, 30: 253-269.
- Tsukashima, K. and C. Kitajima. 1981. Rearing and development of larval and juvenile filefish, *Stephanolepis cirrhifer* (Temminck et Schlegel). *Bull. Nagasaki Pref. Inst. Fish.*, 7: 39-46. (In Japanese with English summary.)
- Warfel, H. E. and D. Merriman. 1944. The spawning habits, eggs, and larvae of the sea raven, *Hemitripterus americanus* in southern New England. *Copeia*, 1944: 197-205.
- Wickler, W. 1973. Breeding behavior of aquarium fishes: an introduction to the biology of their reproduction. T. F. H. Publications, Neptune City. 192 pp.

アオサハギの性的二型とカイメンへの産卵及び初期発生

赤川 泉・塚本洋一・沖山宗雄

カワハギ科の小型魚アオサハギの性的二型・繁殖行動・初期発生を親魚の採集・潜水観察・飼育観察によって明らかにした。神奈川県三浦半島で1991年と1993年に採集したアオサハギの雄は、雌より有意に大きく（体重で約2倍）、繁殖期の雄間競争では顕著な体色変化が見られた。雄が腹部の膨満した雌を藻場で追尾しているのがしばしば観察されたが、ペアは固定しておらず、より著しい婚姻色を示す、より大型の雄のみが産卵まで雌の追尾を続けた。雌がセツカイカイメンの大孔に腹部を押しつけ産卵の姿勢をとると、雄も並んで同じく腹部を押しつけた。雌は20-30秒かけて産卵したが、雄は2-3秒で離れた。卵は直径0.82mmの沈性付着卵で、カワハギ科では最大であった。親による卵保護は行われなかった。卵は6-8日で孵化し（19-22°C）、孵化仔魚の全長は1.93-2.35mmであった。本種の雄の示す婚姻色は、求愛のみならず、雄間競争において、signalとしての機能を持つことが示唆された。雄が雌より大きいという性的二型は、乱婚でありながら、カイメンへのペア産卵をおこなうために、雄間競争が激しいことと関連していると考察された。

（〒113 東京都中野区南台 1-15-1 東京大学海洋研究所 資源生物部門；塚本 現住所：〒236 横浜市金沢区福浦 2-12-4 中央水産研究所）