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Mating Behavior and Larval Development of *Pseudobagrus ichikawai* (Siluriformes: Bagridae)

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Abstract Mating behavior and larval development of *Pseudobagrus ichikawai* (Siluriformes: Bagridae) were observed in captivity. The mature male showed aggressive behavior, apparently forming a territory around its shelter. Mating behavior by 8 pairs was observed two hundred and sixteen times in and around the male's shelter, 20–45 hr after HCG injection of females. Mating behavior comprised either the male leading the female to or the female visiting the shelter, embrace, spawning, and the female stirring the eggs and leaving the shelter. Mating behavior sequences were repeated with intervals of several minutes, the number of eggs spawned at each time decreasing from over 100 to 0. The species appeared to have a sequential polygynous mating system with male parental care. Females had about 400–1800 developed ovarian eggs. The eggs, measuring 1.6–2.1 mm in diameter, hatched out some 60–80 hr after fertilization in 21–24°C W.T. Newly-hatched larvae measured 4.1–5.1 mm TL, with yolk absorption nearly completed and feeding initiated 4 days after hatching, at 8.4–9.3 mm TL. Full fin ray complements developed as follows: caudal and pectoral (10.6–11.3 mm TL), dorsal and anal (12.0 mm TL), and pelvic (13.7–14.2 mm TL). The adipose fin separated from the caudal fin at about 16.0 mm TL. Male filial cannibalism was observed in all pairs, and sibling cannibalism in which the larvae fed on the eggs was also implied.

Siluriforms are extremely divergent in reproductive styles, including, for example, parental care and no-care types, mouth-brooders, and at least one brood parasite (Breder and Rosen, 1966; Blumer, 1982; Sato, 1986). However, the reproductive ecology of Bagridae, one of the largest siluriform families, has been poorly studied (Breder and Rosen, 1966; Burgess, 1989; Ferraris, 1991). Although some breeding habits of this family have been reported, e.g., breeding sites and male parental care of *Pseudobagrus fulvidraco* (Nikol'skii, 1954) and larval feeding on secretions from the parent's belly skin in some South Asian species (Ferraris, 1991), mating behavior has never been reported in East Asian species.

Pseudobagrus ichikawai (=*Coreobagrus ichikawai*), an endemic species in Japan, is found in restricted regions in the middle of Honshu (Nakamura, 1963; Miyadi et al., 1976). The species is sexually size dimorphic, having larger males, and has an adult sex ratio biased toward females. It has been suggested as having a polygynous mating system (Watanabe, 1994). However, mating behavior of this fish has not been previously recorded, owing to the difficulty in the observations. The species is nocturnal and probably spawns in a cave or crevice along a river bank or under a boulder.

This paper describes the mating behavior in captivity and discusses some other aspects of reproduction of *P. ichikawai*. Early development of embryos and larvae is also described, and larval ecology discussed.

Materials and Methods

Mature examples of *Pseudobagrus ichikawai* were captured in the Kawaura River (Nagara River system), Minokamo City, Gifu Prefecture, Japan (35°30′N, 137°01′E). The experiments were carried out in an educational laboratory, Miwa Elementary School, Minokamo City, in 1991 (1 male, 103.0 mm SL; 7 females, 76.5–91.0 mm SL), and at the Laboratory of Ichthyology, Tokyo University of Fisheries, in 1993 (2 males, 104.0 and 108.5 mm SL; 8 females, 62.5–94.0 mm SL). Sex determination of the adult fish was based on the swollen abdomen of ripe females, and the dark body color and extended genital papilla anterior to the anal fin origin of mature males (Watanabe, 1994).

Because intensive aggression was observed when two or more males were kept in an aquarium, each male was reared in a separate aquarium (60–120 *l*) in which a domed shelter had been placed on the gravel substrate before mating. For observations of male aggressiveness, other individuals were sometimes put temporarily into an aquarium in which a male was being reared. One or more females were reared in a single aquarium (20–60 *l*). Water temperature during the experiments ranged from 21 to 24°C in 1991 and from 20 to 26°C in 1993.

Human chorionic gonadotropin (HCG) was injected into the dorsal muscle of both female and male fish (ca. 100 units/1 g). For each mating experiment, an ovulated female was transferred into the male's aquarium, observations on mating behavior being recorded under light conditions by an 8 mm video camera. After the number of eggs released per spawning attempt had decreases considerably, the female was removed.

After spawning, some of the eggs were transferred into another aquarium, at the same water temperature, for observations of embryonic and larval development. *Artemia* nauplii and minced, frozen chironomid larvae were supplied as food. Total lengths (TL) of the larvae were measured when fresh, with morphological observations being made on specimens fixed with 5% buffered formalin and preserved in 70% ethyl alcohol. Specimens were subsequently deposited in the National Science Museum, Tokyo (NSMT-P 36057).

The total weight of the ovaries and number of ovarian eggs belonging to the largest-size mode were measured for 14 mature females (52.8–83.7 mm SL) collected from the Kawaura River in June 1990 and 1993, and preserved in 10% formalin (NSMT-P 36042–36046, 36049–36052, June 20, 1990; NSMT-P 36047–36048, June 5, 1990; NSMT-P 36053, June 27, 1993; NSMT-P 36054–36055, June 10, 1993). The total number of ovarian eggs was calculated from the total weight of the ovaries and number of eggs on one side.

Since *P. ichikawai* is an endangered species, which has been designated as a "natural monument" for preservation purposes, all experiments were carried out with the permission of the Japanese National Agency for Cultural Affairs.

Results

Reproductive behavior

Pre-mating behavior.—Before spawning, mature male *Pseudobagrus ichikawai* swam around the shelter, sometimes digging the substrate under the shelter by beating their tail. They attacked other individuals introduced to the aquarium.

Mating behavior.—Mating behavior was observed between 8 pairs, made up from 8 females and 3 males (Table 1). The time lag between the last HCG injection of the females and first spawning ranged from 20 to 45 hr ($n=8$, mean$\pm$SD$=29.0\pm8.0$ hr).

Mating behavior was observed two hundred and sixteen times ($n=8$, mean$\pm$SD$=27.0\pm17.0$/pair, range: 7–56) (Table 2), having the following pattern.

Table 1. Parental fish used for observations on the mating behavior of *Pseudobagrus ichikawai*, and selected experimental data

Name	Sex	SL (mm)	BW (g)	Date of mating	HCG-spawning time (hr)[a]	Partner	Pair No.
M1	♂	103.0	10.6	Jul. 3–7, 1991	—	F1, F2, F3	1, 2, 3
M2	♂	108.5	23.2	Jul. 10–20, 1993	—	F4, F5, F6, F7	4, 5, 6, 7
M3	♂	104.0	19.6	Jul. 15, 1993	—	F8	8
F1	♀	83.5	13.0	Jul. 3, 1991	33	M1	1
F2	♀	84.0	12.2	Jul. 7, 1991	24[b]	M1	2
F3	♀	84.5	12.6	Jul. 7, 1991	<25[b]	M1	3
F4	♀	94.0	18.6	Jul. 10, 1993	20[b]	M2	4
F5	♀	72.5	9.8	Jul. 13, 1993	26	M2	5
F6	♀	84.5	10.0	Jul. 19, 1993	25	M2	6
F7	♀	62.5	4.6	Jul. 20, 1993	45	M2	7
F8	♀	82.5	11.0	Jul. 15, 1993	34[b]	M3	8

[a] Time lag between last HCG injection and first spawning; [b] more than one injection.

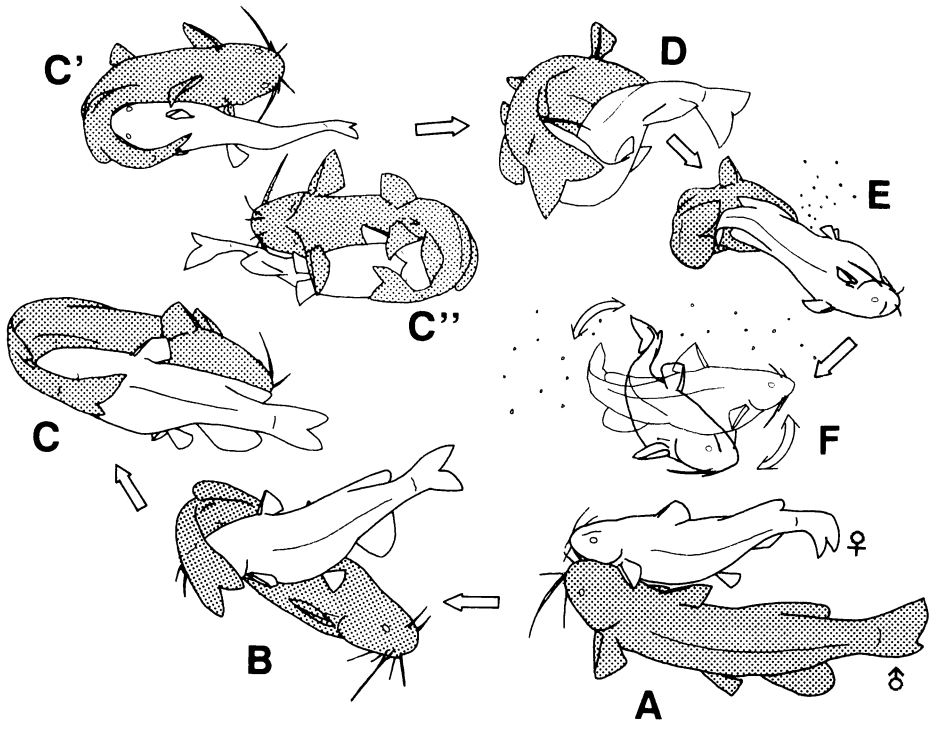

Fig. 1. Mating behavior of *Pseudobagrus ichikawai*. A) Courting; B) start of embrace; C) embrace (C′—dorsal view, C″—ventral view); D) termination of embrace; E) spawning; F) egg stirring. See text for detailed explanations.

On the introduction of a ripe female to a male aquarium, the male started to pursue the former, nudging its belly (Courting; Fig. 1A). The female was then led to or visited voluntarily the male shelter in most cases (94.0%, $n=213$). Subsequently, either in the shelter (usually) or outside, the male wrapped its body around the head and abdomen of the female, with the female's head against the male's caudal peduncle (Embrace; Fig. 1B, C, C′, C″ and Fig. 2), remaining in the position for 5.2–9.2 sec (6.1–7.8 sec on average for each pair) (Table 2). The female, firmly held by the male's pectoral, pelvic, anal and caudal fins, slowly beat its caudal fin during the embrace. The direction of the embrace (side of the

Table 2. Some aspects of mating behavior of *Pseudobagrus ichikawai*, observed in the aquarium

Pair No.[a]	Number of matings	Duration of embrace (sec)[b]	Position of male's head on female			Interval between successive matings (min)[d]
			Left	Right	Bias[c]	
1	20	7.8±0.5 (17)	8	9	NS	5.7±5.2 (17)
2	10	7.3±0.4 (10)	3	7	NS	4.9±3.2 (9)
3	7	7.5±0.6 (7)	4	3	NS	1.7±0.5 (6)
4	56	7.4±0.5 (55)	29	27	NS	3.8±0.9 (54)
5	20	6.5±0.5 (19)	17	3	**	7.0±2.0 (18)
6	28	6.5±0.4 (27)	19	9	*	6.5±2.3 (27)
7	28	7.0±0.4 (28)	13	15	NS	6.9±1.8 (27)
8	47	6.1±0.6 (46)	16	31	*	5.0±1.6 (45)

[a] See Table 1; [b] mean±SD (n); [c] binomial test: NS: $p\geq0.05$, *: $p<0.05$, **: $p<0.01$; [d] mean±SD (n), excluded data longer than 15 min.

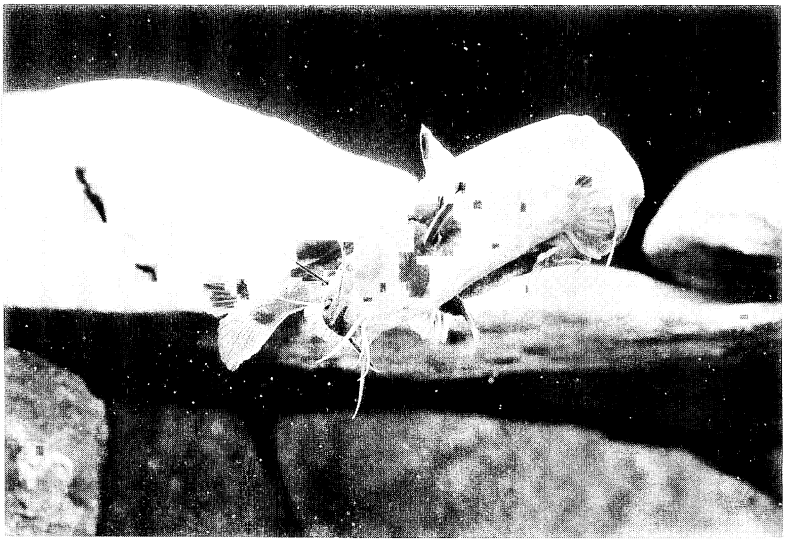

Fig. 2. Embrace during mating sequence in *Pseudobagrus ichikawai* (photo by R. Uchiyama). *Front*—male (M2, 108.5 mm SL); *behind*—female (F6, 84.5 mm SL).

male's head for the female) was significantly biased in 3 of the 8 pairs (binomial test; $p<0.05$) (Table 2), but the sequence of the direction was not significant in each pair (runs test; $p>0.1$).

The embrace was terminated by spawning, with the female often turning its abdomen upwards when releasing eggs (Fig. 1D and 1E). Neither conspicuous ejaculatory behavior by the male nor turbidity caused by semen was observed. Immediately after spawning, the female stirred the eggs by quickly swinging its body (Fig. 1F). The eggs were adhesive, sticking to the substrate or sides of the shelter. Subsequently, the female left the spawning site or was chased away by the male.

After several minutes, the female either returned voluntarily or was led back by the male to the shelter, and the above behavior pattern repeated. The mean interval between successive spawnings ranged from 1.7 to 7.0 min (Table 2), the variation of the intervals among the 8 pairs being significant (one-way ANOVA; $p<0.001$).

The number of eggs per spawning attempt ranged from more than 100 to 0, decreasing on each occasion. The total number of eggs released by each female over successive spawnings was not counted exactly, but roughly estimated at between 100–500.

Immediately following spawning, all males were seen to forage for eggs. Following the experiment, about 70 eggs were found in the stomach contents flushed from male "M3" (Pair No. 8).

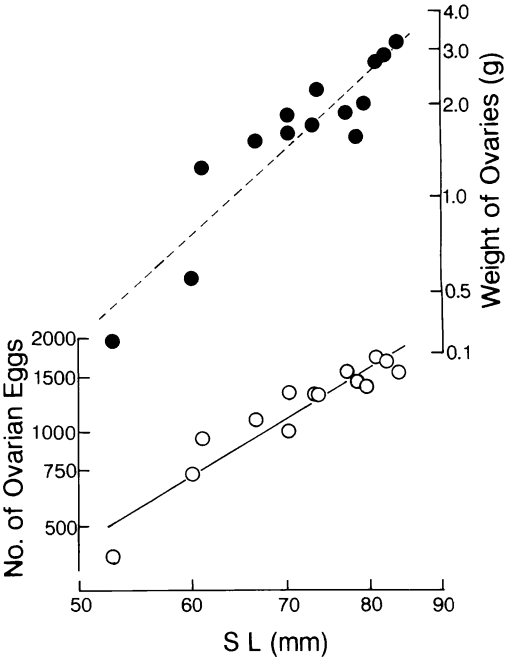

Fig. 3. Relationships between standard length and number of ovarian eggs (○), weight of ovaries (●) in *Pseudobagrus ichikawai*.

Parental care.—Although the males did not exhibit features of parental care, such as fanning or egg-cleaning, they continued to tend the shelter and attack other fish introduced to the aquarium after

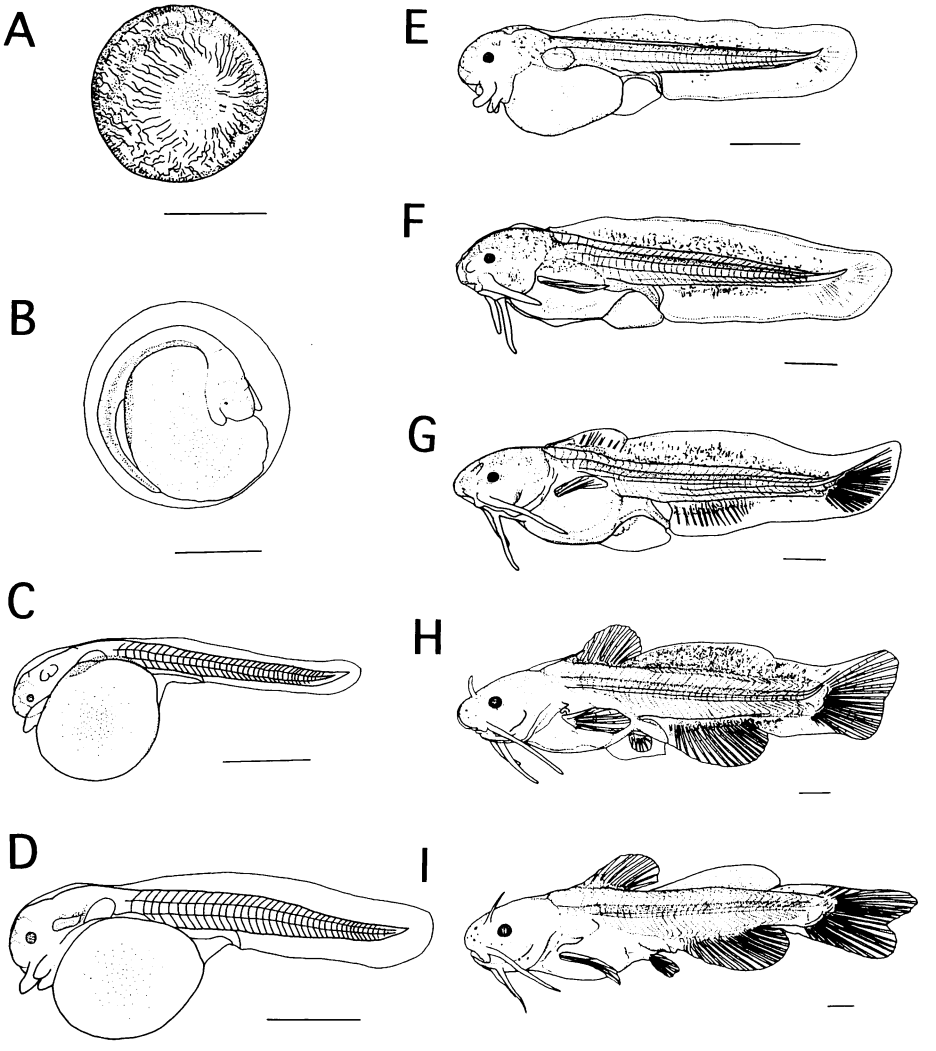

Fig. 4. Eggs, larvae and juveniles of *Pseudobagrus ichikawai*. A) Eggs; B) 40 hr after fertilization; C) newly-hatched larva, 4.3 mm TL; D) day 0, 4.8 mm TL; E) day 1, 5.6 mm TL; F) day 4, 8.4 mm TL; G) day 7 10.6 mm TL; H) day 14, 14.2 mm TL; I) day 23, 17.0 mm TL. Scale bar indicates 1 mm.

spawning or hatching.

Fecundity and weight of ovaries

In 52.8–83.7 mm SL (3.8–13.5 g in weight) females, the number of developed ovarian eggs and weight of ovaries ranged from 407 to 1751, and from 0.35 to 3.12 g, respectively. The relationships between female size (SL: mm) and number of ovarian eggs (NO), and female size and total weight of ovaries (WO: g), respectively, are given by the following equations: $NO = 9.55 \times 10^{-3} \times SL^{2.75}$ ($r^2 = 0.89$, $n = 14$), and $WO = 3.56 \times 10^{-8} \times SL^{4.12}$ ($r^2 = 0.85$, $n = 14$) (Fig. 3). The total weight of the ovaries ranged from 9.6 to 24.1% (mean $\pm$ SD = 18.7 $\pm$ 4.8%) of body weight.

Early development

The eggs spawned from Pair Nos. 1, 4, 6, 7 and 8 were maintained until the juvenile stage. The following description of the early development of *P. ichikawai* was based mainly on the progeny of Pair No. 1, which were maintained separately from the paren-

tal fish.

Eggs.—The eggs were covered with a sticky, jelly-like coat, with many, irregular radiating ridges on the surface (Fig. 4A). The yellowish eggs were spherical and rather depressed in shape, measuring 1.7–2.0 mm (1.6–2.1 mm in all females) in diameter. After fertilization, the blastula stage was reached after 8 hr, the gastrula stage after 15 hr, and the neurula stage after 20 hr. Optic cups were observed after 24 hr. After 30 hr, auditory vesicles occurred and undulating movement began. After 40 hr, a pair of maxillary barbel rudiments were observed (Fig. 4B), and after 60 hr, eyes were pigmented.

Larvae and juveniles.—Hatching occurred between 60 and 80 hr after fertilization. The newly-hatched larvae were 4.1–5.1 mm TL, and had 12–13 +24–26=36–39 myomeres (Fig. 4C). Pectoral fin buds were already present. Two pairs of mandibular barbels were formed about this time, and the auditory region became pigmented (Fig. 4D). The larvae attached themselves to the substrate or wall of the aquarium using the adhesive surface of the head and barbels, some 2–3 days after hatching.

One day after hatching, at 5.5–6.3 mm TL, the mouth opened, and the mandibular became movable (Fig. 4E). The larvae avoided light, gathering in shaded areas. The caudal and pectoral fin rays started to differentiate at 7.8–8.1 mm TL, 3 days after hatching.

The yolk was nearly absorbed at 8.4–9.3 mm TL, 4 days after hatching (Fig. 4F), at which time feeding started. A pair of nasal barbels had developed, and pigmentation on the head, body and fin-fold increased. In addition, the dorsal fin had started to separate from the fin-fold, and the pectoral spine had appeared. Differentiation of the anal fin rays was observed at 9.5–10.0 mm TL, 5 days after hatching, and that of the dorsal fin rays at 10.6–11.3 mm TL, 7 days after hatching (Fig. 4G). The caudal and pectoral fin ray complements were completed 7 days after hatching; C: 7–8+8–9, P_1: i+7. The pelvic fin buds were formed at 11.9–12.6 mm TL, 8 days after hatching. The dorsal and anal fin ray complements (D: ii+7, A: 16–18), and dorsal fin–fin-fold separation were completed, and caudal fin bifurcation initiated at ca. 12.0 mm TL, 10 days after hatching. The anal and caudal fins separated at 12.9–15.4 mm TL, 13 days after hatching. The pelvic fin rays started to differentiate 13 days after hatching, being completed (P_2: 6) at 13.7–14.2 mm TL, one day later, i.e., all fin ray complements were completed by this stage (Fig. 4H). Serrations on the posterior edge of the pectoral spine appeared 14 days after hatching, with the anterior edge of the spine remaining smooth throughout the larval period. The adipose and caudal fins separated at ca. 16.0 mm TL, 23 days after hatching (Fig. 4I). The juveniles reached 15.0–20.0 mm SL (mean, 17.5 mm) 60 days after hatching, and 19.0–26.0 mm SL (mean, 23.2 mm) after 90 days.

Of the larvae born to Pair No. 4, those reared in the male's aquarium showed higher growth rates than those reared in a separate aquarium, although the latter were well-fed. After 12 days, the former measured 14.2–17.6 mm TL, having all fin ray complements completed, whereas the latter measured 12.3–13.9 mm TL, with incomplete pelvic fin rays. Although four mating experiments (Pair Nos. 4–7) were performed successively over 10 days involving the "M2" male in the same aquarium (Table 1), only larvae from the first mating (No. 4) were collected from the aquarium at the conclusion of the experiments. During the third and fourth mating experiments (Nos. 6 and 7), larvae from the first, which had already started to feed, appeared from retreats just after spawning, actively swimming and foraging around the shelter. Only undifferentiated matter was found in the stomachs of those larvae.

Discussion

Mating behavior and reproductive style

The occurrence of intensive aggressive behavior and active swimming (patrolling?) around the shelter by male *Pseudobagrus ichikawai* is suggestive of the territorial behavior. In addition, males might dig a depression in the substrate under the shelter during the pre-mating period, in order to prepare a spawning site. Mating behavior was performed mainly in the male's shelter. In its natural habitat, *P. ichikawai* would spawn in a cave or crevice along the river bank, which is used as a shelter by the male. Although some spawnings were observed outside the shelter in the aquarium, they could not be considered unusual, because the artificial shelter may have been much narrower than a natural shelter.

Conspicuous components of the mating behavior of *P. ichikawai* were "embrace" and "egg stirring." A spawning embrace has been widely observed in other catfish species, such as scatter-spawners,

Silurus asotus and *S. biwaensis* (Siluridae) (Katano et al., 1988; Maehata et al., 1990), a nest-builder, *Clarias batrachus* (Clariidae) (cf., Burgess, 1989), and a copulative woodcat, *Parauchenipterus insignis* (Auchenipteridae) (cf., Burgess, 1989). Although some characteristics, such as form and time of the embrace, differ among these species, the basic behavioral feature seems to be rather common in siluriforms. Similarly, egg stirring behavior just after spawning has also been reported in other catfishes, such as *Silurus biwaensis* (Maehata et al., 1990) and *Heteropneustes fossilis* (Siluridae) (Roy and Pal, 1986), in which both sexes exhibit this behavior. Egg stirring behavior has a function of scattering eggs around the nest, probably helping to protect them from predation by both the male parent and other fishes in *Pseudobagrus ichikawai.*

A single female spawned eggs repeatedly at intervals of several minutes. A female (52.8–83.7 mm SL) usually contains from 400 to 1800 developed ovarian eggs, most of which are released during the breeding season, being a period of less than one month (Watanabe, 1994; Watanabe, unpubl. data).

It has been shown in field surveys that male *P. ichikawai* grow larger than females, but decrease in number faster than the latter in both the Tagiri (tributary of the Inabe River) (Watanabe, 1994) and Kawaura Rivers (Watanabe, unpubl. data). Territorial behavior of adult males has also been observed in the Kawaura River (Watanabe, unpubl. data). Because spawning takes place in the male's shelter, the maintenance and defense of the shelter must be one of the most important factors for male reproductive success. This suggests that the sex ratio bias in adults observed in natural populations has resulted from male–male competition for spawning sites. Sexual size dimorphism is associated with a polygynous mating system in many species, attributed to the operation of sexual selection (Selander, 1965; Bartholomew, 1970; Clutton-Brock and Harvey, 1984). Because of the reiterative spawning by the female, the possibility exists that *P. ichikawai* mates promiscuously. However, the occurrence of spawning in the (fewer overall) male shelter and sexual size dimorphism imply significant mate-choice by females, suggesting a tendency for sequential polygynous mating in this species.

In the related species, *P. fulvidraco*, males have been reported to guard both the eggs and larvae in the nest hole, previously dug by the male in the clay bottom (Nikol'skii, 1954). In *P. ichikawai*, although no evidence of male parental care except patrolling was observed, the aggressive behavior exhibited by males against fish approaching the shelter may have a function of guarding the eggs and larvae.

Early development and ecology

Significant differences in early development occur between *Pseudobagrus ichikawai* and related species, such as *P. tokiensis* (referred to as *P. aurantiacus*) (Okada and Seiishi, 1937, 1938), *P. aurantiacus* (Takeshita and Kimura, 1994), and *P. longirostris* (referred to as *Leiocassis longirostris*) (Zhang and He, 1991). The eggs of *P. ichikawai* (1.6–2.1 mm in diameter) are smaller than those of *P. tokiensis* (ca. 2.3 mm) and *P. aurantiacus* (2.4–2.7 mm). Similarly, the size of newly-hatched larvae of *P. ichikawai* (4.1–5.1 mm TL) is smaller than that in *P. tokiensis* (6.2 mm) and *P. aurantiacus* (5.3–5.5 mm). Yolk absorption and initial feeding in *P. ichikawai* (4 days after hatching, 21–24°C) occur earlier than in *P. tokiensis* (6–7 days, 27°C), *P. aurantiacus* (7 days, 18–23°C), and *P. longirostris* (5–6 days, 21–27°C). The completion of fin development by separation of the adipose and caudal fins is attained at a smaller size in *P. ichikawai* (ca. 16 mm TL) than in *P. tokiensis* (ca. 20 mm) and *P. aurantiacus* (21–23 mm). As in the adults (Nakamura, 1963), the lower number of anal fin rays (16–18) in *P. ichikawai* larvae is a diagnostic feature within the Japanese bagrids (>18 in the other three species), although, since the species are distributed allopatrically (Nakamura, 1963), there should be no problems in field identification.

One day after hatching, the larvae of *P. ichikawai* were observed to avoid light. Since the larvae attached themselves to the substrate using a cephalic and barbel adhesive mechanism during the first 2–3 days, it is considered that they stay in the male's shelter at least during that period, soon after starting to feed. Sequential matings in the shelter therefore make sibling cannibalism a distinct possibility. The undifferentiated stomach contents of the larvae collected from the "M2" male's aquarium (progeny of Pair No. 4) seemed to comprise eggs from later spawnings (Pair Nos. 6 and 7). However, since neither eggs nor early larvae have been collected in

the field, the elucidation of the reproductive and larval ecology in the natural habitat remains a subject for the future.

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ネコギギ（ナマズ目ギギ科）の配偶行動と初期発育

渡辺勝敏

ネコギギ *Pseudobagrus ichikawai* の配偶行動と初期発育を室内飼育によって観察した．成熟雄は非常に攻撃的であり，シェルターの周りにテリトリーを形成しているようであった．産卵はHCGを注射後20–45 hrに開始された．8ペアによる計216回の配偶行動についてビデオで解析したところ，配偶行動は，雄のシェルターへの雄による雌の誘導あるいは雌自身による訪問に始まり，雄による雌の頭腹部への抱擁，産卵，雌による卵の撹拌，そして雌の産卵場所からの退去，という連鎖からなっていた．産卵は数分おきに多数回繰り返され，最初，1回に100粒以

上が放卵されたが，後半にはほとんど0粒となった．雄のシェルター内での産卵とこれまでの野外調査の知見から，本種は雄による子の保護を伴う連続的一夫多妻的繁殖様式を持つと考えられた．孕卵数は約400–1800粒であった．直径1.6–2.1 mmの受精卵は，水温21–24°Cで受精後60–80時間後に孵化した．孵化仔魚は全長4.1–5.1 mmで，4日後，全長8.4–9.3 mmで卵黄が吸収され，摂餌が開始された．鰭条の定数化は尾鰭および胸鰭(10.6–11.3 mm)，背鰭および臀鰭(12.0 mm)，腹鰭(13.7–14.2 mm)の順に起こり，脂鰭と尾鰭は全長約16.0 mmで分離した．全てのペアで雄親による食卵が観察され，また仔稚魚による卵の捕食も示唆された．

(〒108 東京都港区港南4–5–7　東京水産大学魚類学研究室)