Japan. J. Ichthyol.
41(3): 261-274, 1994

魚類学雑誌
41(3): 261-274, 1994

Reproductive Behavior, Eggs and Larvae of a Caesionine Fish, *Pterocaesio digramma*, Observed in an Aquarium

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(*Received May 19, 1994; in revised form September 1, 1994; accepted September 13, 1994*)

Abstract Reproductive behavior and early life history of *Pterocaesio digramma* were described from aquarium observations. Spawning occurred between a pair plus sneakers (usually about 5 individuals) during the period before sunset from the beginning of May to the beginning of July, 1993. Six easily distinguishable behavior patterns were involved in the spawning sequence: 1) Up and down swimming; 2) Courtship; 3) Rushing; 4) Pair spawning; 5) Sperm release by sneakers; and 6) Post spawning. The species was considered to be a group spawner. Fertilized eggs were spherical, transparent, buoyant and unpigmented. They averaged 0.84 mm in diameter, and contained a single oil globule averaging 0.16 mm in diameter. Hatching began 23 hours after fertilization, 70% of the eggs having hatched within the following 2 hours, at 24.0±0.5°C. Immediately after hatching, larvae were 2.06-2.34 mm in total length and had a large ellipsoidal yolk. An oil globule with a few melanophores was situated at the anterior margin of the yolk. Larval development of *P. digramma* was described during the first 15 days after hatching, 15 day-old larvae being characterized by a large head, a relatively elongated and laterally compressed body, conspicuous preopercular spines and serrate spines in the dorsal and pelvic fins (characteristically long second dorsal and pelvic spines). They also possessed several large and clearly defined dendritic melanophores on the membrane between the second and third dorsal spines.

Early life histories of a number of species within the family Lutjanidae (*sensu* Johnson, 1993) have been studied in recent decades. Leis (1987) provided an extensive review of the family, with additional reports by Kojima (1988), Mori (1988), Potthoff et al. (1988), Iwatsuki et al. (1989), Soletchnik et al. (1989), Iwatsuki et al. (1990) and Hamamoto et al. (1992). The last-mentioned described embryonic development and larvae of *Lutjanus stellatus* and discussed important characteristics of eight lutjanid species.

In the subfamily Caesioninae, egg and larval development are very poorly known, except in preflexion to flexion larvae of *Caesio cuning* (Leis and Rennis, 1983). Accordingly, larvae of the subfamilies Lutjaninae and Caesioninae remain difficult to separate, because of the lack of information on larval characters.

Thresher (1984) and Grimes (1987) reviewed the limited field and in-captivity information on spawning in the family. Reproductive behavior in the Lutjaninae has been reported five times, twice in the field (Wiklund, 1969; Starck, 1971) and the rest in-captivity (Arnold et al., 1978; Suzuki and Hioki, 1979; Hamamoto et al., 1992), but only once in the Caesioninae, Bell and Colin (1986) describing the reproductive behavior of *Caesio teres* in the field.

This paper describes reproductive behavior of *Pterocaesio digramma* reared in an aquarium, being the second report for caesionine fishes, in addition to embryonic development from newly hatched to 15-day old larvae, as the first report for caesionine fishes, and provides comparisons of reproductive behavior, embryonic development and larvae between *P. digramma* and other lutjanid species.

Materials and Methods

Observation of reproductive behavior

The adult brood stock of 2,133 *Pterocaesio di-*

gramma were captured mainly by a drive-in net (oikomi-ami) in the sea off Motobu, Okinawa Prefecture. Initial collections were made on Nov. 13, 1992 (309 specimens) and Dec. 22, 1992 (1,750 specimens). The fish were reared in a rectangular concrete tank at the Okinawa Expo Aquarium, Okinawa Prefecture, about 1,600 individuals being alive by the end of April, 1993. They were further supplemented by 74 specimens captured between May 11–22, 1993. The sizes of parental *P. digramma* were estimated from two specimens, preserved after being used for artificial insemination. The parental male measured 190 mm in standard length (SL) and was 139 g in body weight (BW), and the female 213 mm SL and 190 g BW. Other parental fishes were almost the same size, their estimated ages being from 2–3 years, based on their duration in captivity and size when first collected.

The concrete tank (27.0 m × 12.0 m × 3.5 m deep; water capacity 1,100 t) had two adjacent acrylate panels (27.0 m × 3.5 m high and 12.0 m × 3.5 m high) and three acrylate windows (2.0 m × 0.4 m high) of concrete wall except in the two acrylate panels for viewing by aquarium visitors. The surface of the tank allowed indirect natural light to enter from the northeast side, after being reflected from the glass ceiling (10 m × 8 m) of an adjacent tank. Water circulated at 440 t/hr, with natural sea water being supplied at 200 t/hr. Observations of reproductive behavior were primarily made through the two panels and from the surface of the tank. The fishes were fed around about 15:30 every day, except Sunday. Water temperature was measured every day at 9:00 throughout 1993.

In addition to *P. digramma* and 6 further lutjanid species, the tank contained 41 other species of marine fishes, totaling approximately 1,600 individuals, *viz.* Carangidae (15 species), Carcharhinidae (4 species), Scombridae (4 species), Dasyatididae (3 species), Rhinobatidae (2 species), Acanthuridae, Coryphaenidae, Echeneididae, Girellidae, Kyphosidae, Lethrinidae, Mobulidae, Myliobatididae, Orectolobidae, Rachycentridae, Rhincodontidae, Rhinopteridae and Serranidae (1 species each), following Masuda et al. (1984). The additional lutjanid fishes included *Aprion virescens* (2 individuals), *Lutjanus bohar* (1 individual) and *L. malabaricus* (1 individual) (all Lutjaninae *sensu* Allen and Talbot, 1985), and *Caesio caerulaurea* (23 individuals), *P. trilineata* (3 individuals) and *P. tile* (6 individuals) (all Caesioninae *sensu* Carpenter, 1987). The Japanese name considered applicable to *P. digramma* is "Takasago." Although both "Takasago" and "Nise-takasago" have been used and confused for both *P. digramma* and *P. marri* in Japan (Masuda et al., 1975; Akazaki, 1984, 1988; Shimada, 1993), we follow Shinohara (1966) who is considered to have initially differentiated between the two species on the basis of specimens in Japan.

Reproductive behavior of *P. digramma* was observed from the beginning of May to the beginning of July, 1993. Rapid photographic (3.5 times per sec.) and 8 mm movie camera records were used for the analyses of behavior. The number of spawnings in a 5 minute interval during each period (20 min) from the first spawning time to the end was also counted from June 26–30, 1993.

The parental specimens used for artificial insemination and serial samples eggs and larval specimens observed during the study were deposited in the Department of Animal Science, Fisheries Science Course, Miyazaki University (MUFS): adult male, MUFS 9090; adult female, MUFS 9091; eggs, MUFS 9980–10000 and larvae, MUFS 10001–10029.

Rearing of eggs and larvae

Eggs naturally spawned on June 13, 1993, were mainly used for observations of embryonic and prelarval development. Furthermore, eggs fertilized by the dry method on June 18, 1993, were used to confirm the identity of the former on the basis of development and melanophore patterns. Both sets of eggs were maintained in a 1 *l* glass beaker, the temperature during the rearing trial being kept at 24.0 ± 0.5°C (mean ± standard deviation [SD]).

Additional, buoyant, fertilized eggs, which were spawned on June 13, 1993, were used for larval rearing and observations. Just after spawning, the eggs were collected by net, about 160,000 eggs being transferred into a 500 *l* polycarbonate tank containing weakly aerated sea water. After hatching, half or one-third of the water was changed every day. The temperature during the rearing trial varied from 26.3 to 29.4°C. Larvae were initially fed with unfiltered S-type rotifers, *Brachionus* spp., the food subsequently being altered to both S-type rotifers, *Brachionus* spp. and *Artemia* nauplii. Cultured marine chlorella, *Nannochloropsis oculata*, for the rotifers, were added daily in the polycarbonate tank. Throughout the rearing period, the larvae gradually decreased in number. The last individuals died 17 days after

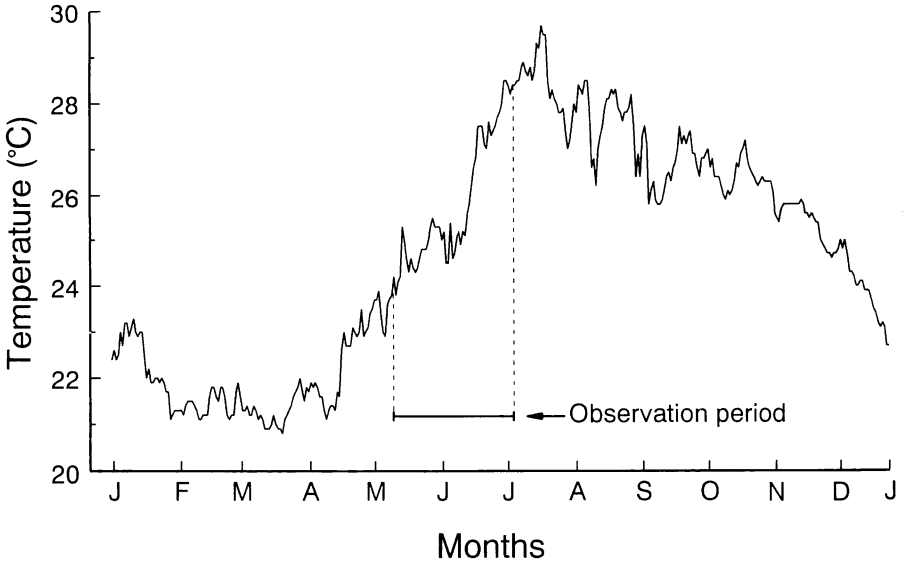

Fig. 1. Observation period (concurrent with spawning period) of reproductive behavior of *Pterocaesio digramma*, and daily changes of tank water temperature in 1993. Horizontal solid line represents observation period: March 10–June 4, 1993.

hatching.

Illustrations of live specimens were made with the aid of a drawing attachment on a microscope, and many live color photographs were also taken. All size data were from live specimens. Proportional measurements of the larvae followed Leis and Rennis (1983), in which body length (BL) corresponded to notochord length in preflexion and flexion larvae. Additional measurements included upper jaw length (UJL), diameter from anterior tip to posterior tip of yolk and diameter of oil globule. Count method of myotomes followed Leis and Rennis (1983), in which postanal myotomes included terminal myomere from which urostyle will form.

Results

Reproductive behavior

Reproductive behavior of *Pterocaesio digramma* was observed every day from May 10 to July 4, 1993, in water temperatures ranging from 23.8 to 28.5°C (Fig. 1). Spawning was observed between about 16:00 and 19:00, corresponding to 3.5–0.5 hours before sunset (Fig. 2). Reproductive behavior was not affected by the switching off (around 18:30) of the aquarium lights during the observations. On the other hand, reproductive behavior was frequently disturbed by large sharks and rays in the same tank because of their frequent penetration of the *P. digramma* school. Six easily distinguishable behavior patterns were recognized in the spawning sequence (Figs. 3A, B and 4A–D).

Up and down swimming.—For most of the day the fish were usually quiet, forming several schools at the bottom near the three acrylate windows. However, the spawners started to aggregate at the surface in the corner on the north-northeast side of the aquarium at around 16:00, being situated in a flow of natural sea water from a large inflow pipe. They periodically rose to the surface, ascending almost vertically as a column (Fig. 3A) and descending at once in a similar manner (Fig. 3B). The school was estimated to comprise about 1,500 individuals, including most of the *P. digramma* in the tank. At the same time, a rapid sequence of low sounds (gulu, gulu, gulu,...) was emitted by the spawner, but the mechanism of sound production could not be determined.

Courtship.—There was no obvious sexual dimorphism in *P. digramma*, but just before spawning female fish had a considerably swollen abdomen. Some individuals (10–20) remained near the surface longer as their spawning approached after ascents to the surface. Subsequently, courtship behavior of a

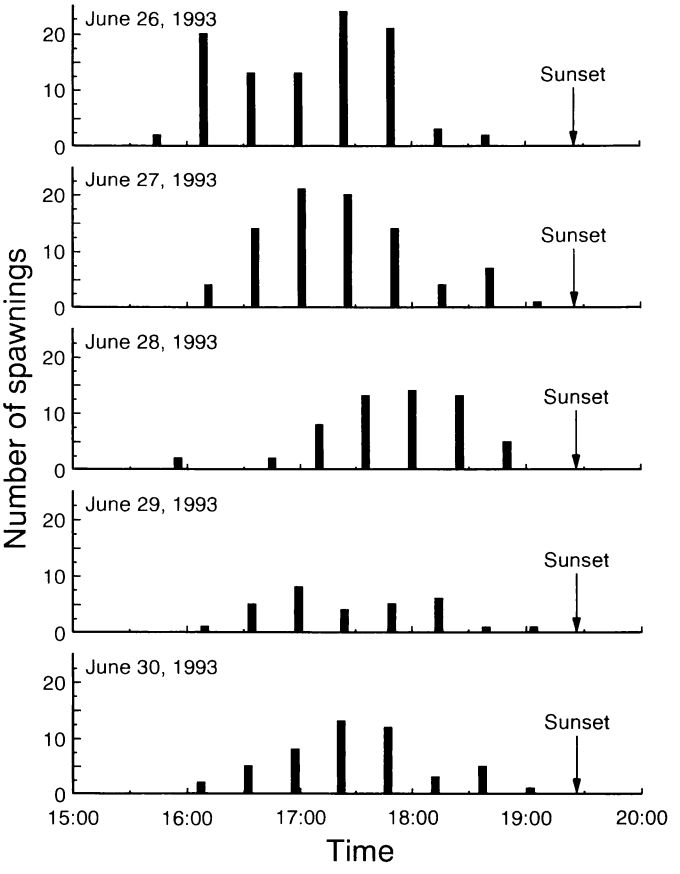

Fig. 2. Total number of spawnings in a 5 minute interval during each period (20 min) from the first spawning time to the end of *Pterocaesio digramma*, showing the relationship between spawning activity and time. Arrows indicate sunset: 17:25 (June 26–27, 1993) and 17:26 (June 28–30, 1993).

male toward a selected female was initiated by the preceding pecking and pushing the female's swollen abdomen with his snout, as the aggregation rose to the surface (Fig. 4A).

Rushing.—The male pushed the female forward, and the couple began to swim in a semicircle in a short burst. In addition, about 10–15 sneakers within the mass pursued the couple (Fig. 4B).

Pair spawning.—The initial couple released eggs and sperm at the surface, their abdomens being orientated towards each other (Fig. 4C).

Sperm release by sneakers.—Just after the initial spawning, about 5 of the leading sneakers released sperm together at the pair spawning spot (Fig. 4D).

Post spawning.—After the release of gametes, the initial couple and sneakers, plus the remaining sneakers (which did not release sperm), scattered, returning to the school and participating in up and down swimming. However, just after the release of sperm by the sneakers, a large number of other spawners within the mass quickly darted over to the gamete cloud and engulfed the eggs. Spawnings were observed in many places, with about 10 spawnings being recorded in a one minute period during peak activity.

Eggs and embryos

Embryonic development is shown in Table 1 and Figure 5. The fertilized eggs were spherical, transparent, buoyant and unpigmented. Eggs ranged from 0.82 to 0.88 mm in diameter (mean = 0.84 ± 0.02 mm, $n = 60$) (mean ± standard deviation [SD]) and had a single oil globule (slightly yellowish) measuring 0.14–0.17 mm in diameter (mean = 0.159 ± 0.007 mm, $n = 60$), a clear and unsculptured cho-

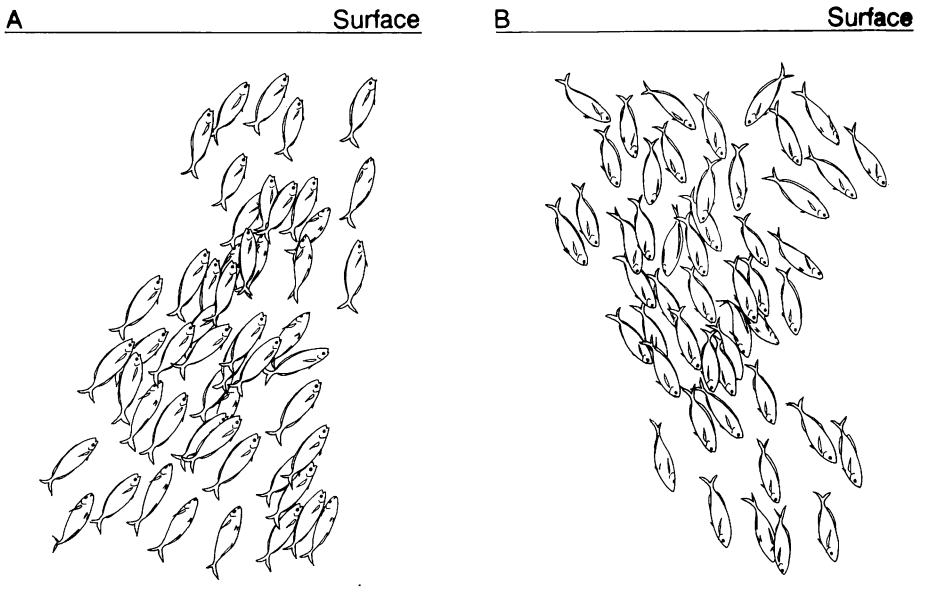

Fig. 3. Diagrammatic representation of up and down swimming movements of *Pterocaesio digramma* in an aquarium. A) Up swimming movement; B) down swimming movement.

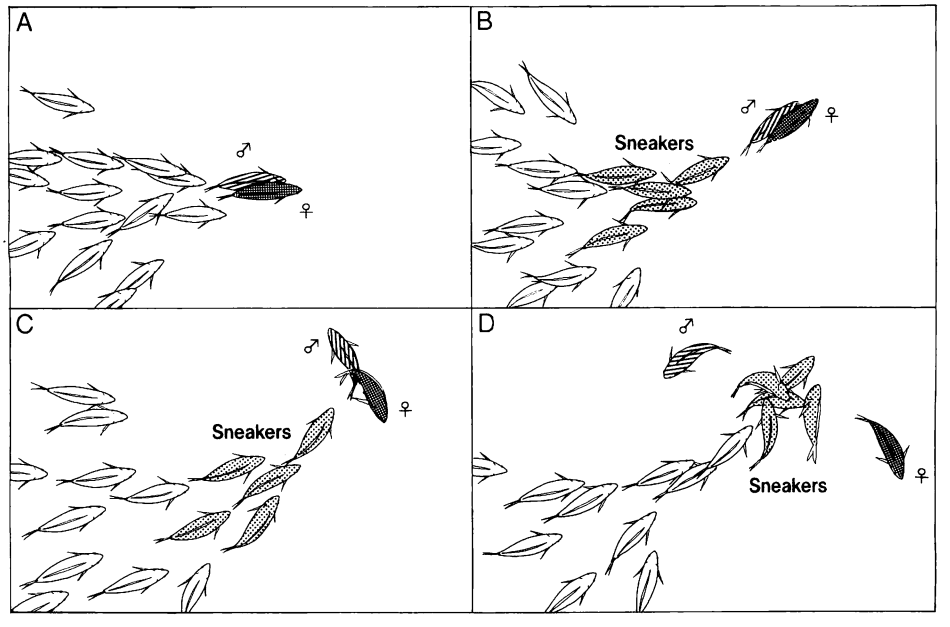

Fig. 4. Four stages of the spawning sequence of *Pterocaesio digramma* in an aquarium as observed from the water surface. See text for explanation.

rion and homogeneous, unsegmented yolk.

Forty-three minutes after fertilization, the eggs reached the four-cell stage (Fig. 5A), at 2 hr 50 min, the morula stage (Fig. 5B) and at 6 hr 55 min, the gastrula stage (Fig. 5C). At 9 hr 1 min, the blastoderm covered two-thirds of the yolk and the embryonic body was visible (Fig. 5D); at 10 hr 33 min, 4 myotomes appeared (Fig. 5E); at 11 hr 16 min, 5

myotomes and optic and Kupffer's vesicles were visible (Fig. 5F); at 12 hr 1 min, 10 myotomes were seen, in addition to three punctate melanophores appearing dorsally on the embryo (Fig. 5G); at 12 hr 31 min, 14 myotomes and melanophores on the oil globule in all eggs, and the yolk in 1 out of 10 individuals examined, were visible; at 13 hr 10 min, 15 myotomes and auditory vesicles were seen; at 14 hr 27 min, 18 myotomes and the optic lenses were visible (Fig. 5H), and at 17 hr 3 min, 25 myotomes and the pectoral fin rudiments were observed. Immediately before hatching, 28 myotomes were apparent, the posterior half of the body being separated from the yolk. In addition, 1–2 punctate or dendritic melanophores were observed on the dorsal surface of each myotome (Fig 5I). Hatching began 23 hours after fertilization, 70% of the eggs having hatched within the following 2 hours, at 24.0±0.5°C.

Morphology of Larvae

Just-hatched larvae (Fig. 6A) were transparent, ranging from 2.06 to 2.34 mm (mean=2.19±0.11 mm, $n=5$) in total length (TL, including the anterior portion of the yolk protruding beyond the larval snout) and from 1.72 to 2.10 mm (mean=1.91±0.13 mm, $n=5$) in BL. The larvae had a large yolk, no mouth and limited swimming abilities. The anus was not contiguous with the posterior end of the yolk. Small granules on the surface of the finfold and yolk, and a tortoiseshell-like pattern of short lines on the surface of the finfold were observed, but are not illustrated. The granules became thickened in 6-hour old larvae (2.44–2.64 mm TL, $n=5$; Fig. 6B), but along with the pattern of short lines had mostly disappeared in a 10-day old larva (4.48 mm TL, $n=1$). The total number of myomeres ranged from 28 in just-hatched larvae (2.06–2.34 mm TL, $n=5$; Fig. 6A) to 25–27 in 15-day old larvae (4.64–5.46 mm TL, $n=5$; Fig. 7D). Preanal myomeres numbered 10 to 9; postanal, 18 to 16.

The body was particularly elongated in just-hatched to 18-hour old larvae (mean 2.19–mean 3.10 mm TL, $n=20$; Fig. 6A–C), with the body depth changing gradually owing to the development of a steeper profile to the forehead (first seen in a 6-day old larva [3.36 mm TL, $n=1$]). The body was deeper at the pelvic base than at the anus on a 7-day old larva (3.54 mm TL, $n=1$). In a 15-day old larva (5.46 mm TL, $n=1$; Fig. 7D), the body was relatively elongated and laterally compressed.

Just-hatched larvae (2.06–2.34 mm TL, $n=5$; Fig.

Table 1. Embryonic development of *Pterocaesio digramma* at water temperatures of 24±0.5°C

Time after spawning	Developmental stages observed
29 min	2-cell stage
43 min	4-cell stage (Fig. 5A)
58 min	8-cell stage
1 hr 6 min	16-cell stage
1 hr 25 min	32-cell stage
1 hr 36 min	64-cell stage
2 hr 50 min	Morula stage (Fig. 5B)
3 hr 23 min	Blastula stage
6 hr 55 min	Gastrula stage (Fig. 5C)
9 hr 1 min	Beginning of embryo formation (Fig. 5D)
10 hr 33 min	Appearance of 4 myotomes (Fig. 5E)
11 hr 16 min	5-myotome stage: formation of optic and Kupffer's vesicles (Fig. 5F)
12 hr 1 min	10-myotome stage: appearance of melanophores on embryo (Fig. 5G)
12 hr 31 min	14-myotome stage: appearance of melanophores on oil globule in all eggs and yolk in 1 individual (out of 10 examined)
13 hr 10 min	15-myotome stage: formation of auditory vesicles
14 hr 27 min	18-myotome stage: formation of optic lenses (Fig. 5H)
15 hr	19-myotome stage: disappearance of Kupffer's vesicle
15 hr 48 min	20-myotome stage: appearance of heart
16 hr 34 min	21-myotome stage: beginning of heart pulse
17 hr 3 min	25-myotome stage: appearance of pectoral fin rudiments
18 hr 10 min	26-myotome stage: beginning of embryonic movement
23 hr 5 min	28-myotome stage: immediately before hatching (Fig. 5I)

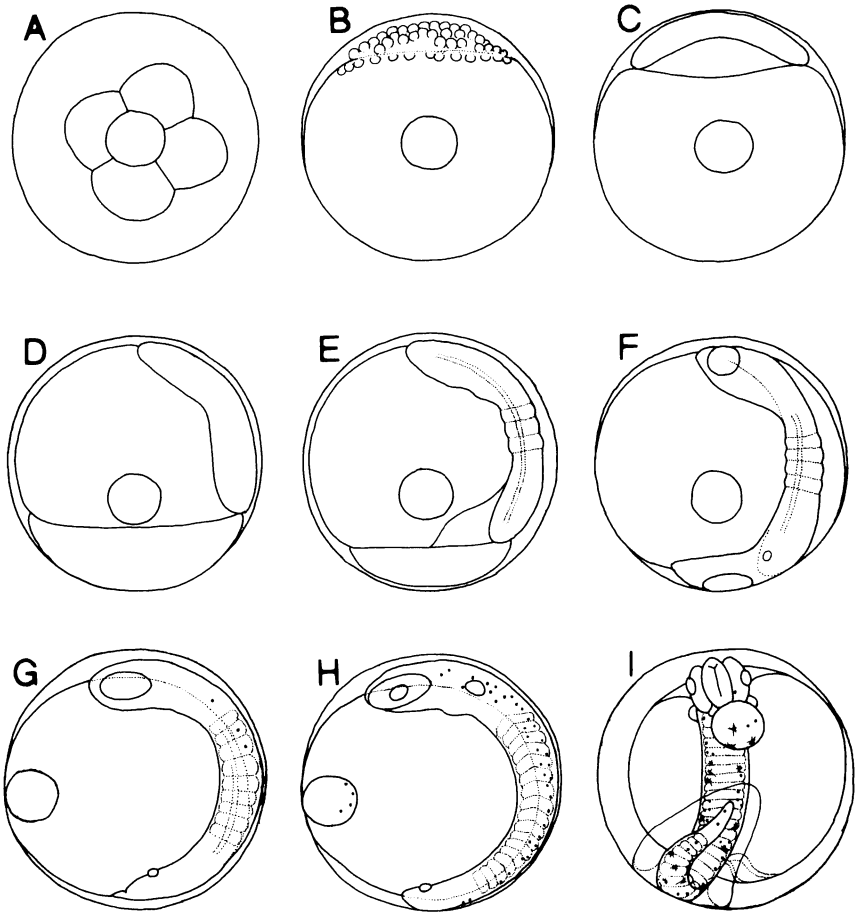

Fig. 5. Embryonic development of eggs of *Pterocaesio digramma*. A) 4-cell stage, 43 min after fertilization, MUFS 9981; B) morula stage, 2 hr 50 min, MUFS 9986; C) gastrula stage, 6 hr 55 min, MUFS 9988; D) beginning of embryo formation, 9 hr 1 min, MUFS 9991; E) appearance of 4 myotomes, 10 hr 33 min, MUFS 9992; F) 5-myotome stage, 11 hr 16 min, MUFS 9993; G) 10-myotome stage, 12 hr 1 min, MUFS 9994; H) 18-myotome stage, 14 hr 27 min, MUFS 9996; I) 28-myotome stage, 23 hr 5 min, MUFS 10000.

6A) had a large ellipsoidal yolk sac that extended anteriorly beyond the snout, and an oil globule situated close to but protruding slightly beyond the anterior margin of the yolk. Absorption of the yolk and oil globule was rapid, both being completely absorbed in 3-day old larvae (3.16–3.30 mm TL, $n=5$; Fig. 7A). The mouth opened in 36-hour old larvae (3.08–3.28 mm TL, $n=5$; Fig. 6D), with food being first observed in the gut of 3-day old larvae (3.16–3.30 mm TL, $n=5$; Fig. 7A). The gut began to coil in 18-hour old larvae (3.02–3.20 mm TL, $n=5$; Fig. 6C), and was tightly coiled in a 7-day old larva (3.54 mm TL, $n=1$).

The first inflation of the gas bladder was observed in 3-day old larvae (3.16–3.30 mm TL, $n=5$; Fig. 7A), but in a 10-day old larva (4.48 mm TL, $n=1$), the gas bladder was inconspicuous because of extensive shielding by pigment.

In a 15-day old larva (5.46 mm TL, $n=1$; Fig. 7D), the head was moderately large and compressed, and the mouth was large and somewhat oblique, the corner being behind the level of the anterior margin of the eye. The snout began to be pointed in 3-old day larvae (3.16–3.30 mm TL, $n=5$; Fig. 7A). Subsequently the head profile became more rounded (first seen in a 6-day old larva [3.36 mm TL, $n=1$]), with the snout becoming less pointed (Fig. 7C, D). Two pairs of conical teeth were formed anteriorly on

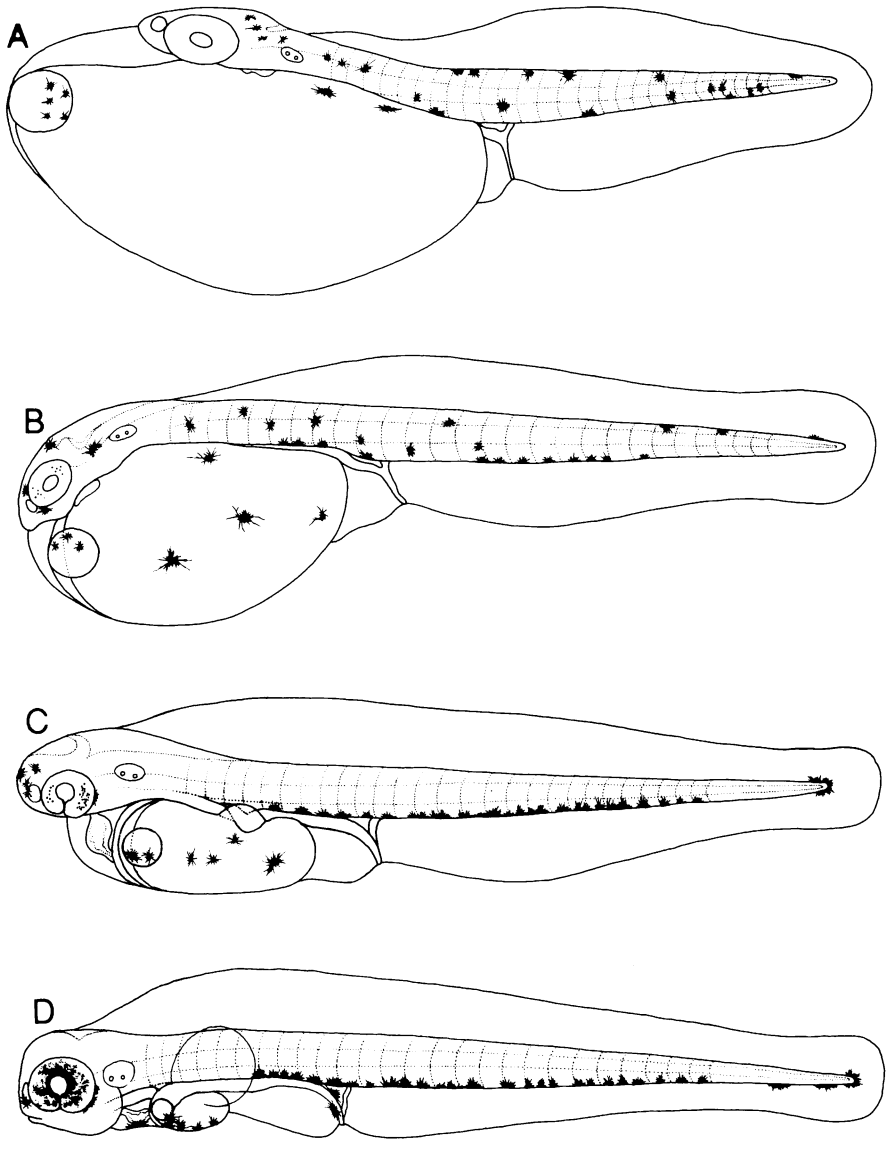

Fig. 6. Yolk-sac larval stage of *Pterocaesio digramma*. A) Just-hatched larva, 2.34 mm TL, MUFS 10001–10003; B) 6 hr after hatching, 2.64 mm TL, MUFS 10004–10005; C) 18 hr after hatching, 3.20 mm TL, MUFS 10009–10010; D) 36 hr after hatching, 3.28 mm TL, MUFS 10015–10016.

the premaxilla in a 10-day old larva (4.48 mm TL, $n=1$). These had increased to three pairs and a pair of similar dentary teeth were formed, in a 12-day old larva (4.62 mm TL, $n=1$). The former had increased further to seven pairs in a 15-day old larva (5.46 mm TL, $n=1$; Fig. 7D).

Head spines were smooth, with the ridges lacking serrations. Spines were found on the preopercle, interopercle, posttemporal and supracleithrum in a 15-day old larva (5.46 mm TL, $n=1$; Fig. 7D). The preopercular spines developed on two borders, a 5-day old larva (3.42 mm TL, $n=1$; Fig. 7B) having two spines on the inner border and one on the outer. Subsequently, the spines gradually increased in number, the inner spines numbering four in an 8-day old larva (3.90 mm TL, $n=1$; Fig. 7C) and the outer spines five in a 10-day old larva (4.48 mm TL, $n=1$). In a 15-day old larva (5.46 mm TL, $n=1$; Fig. 7D),

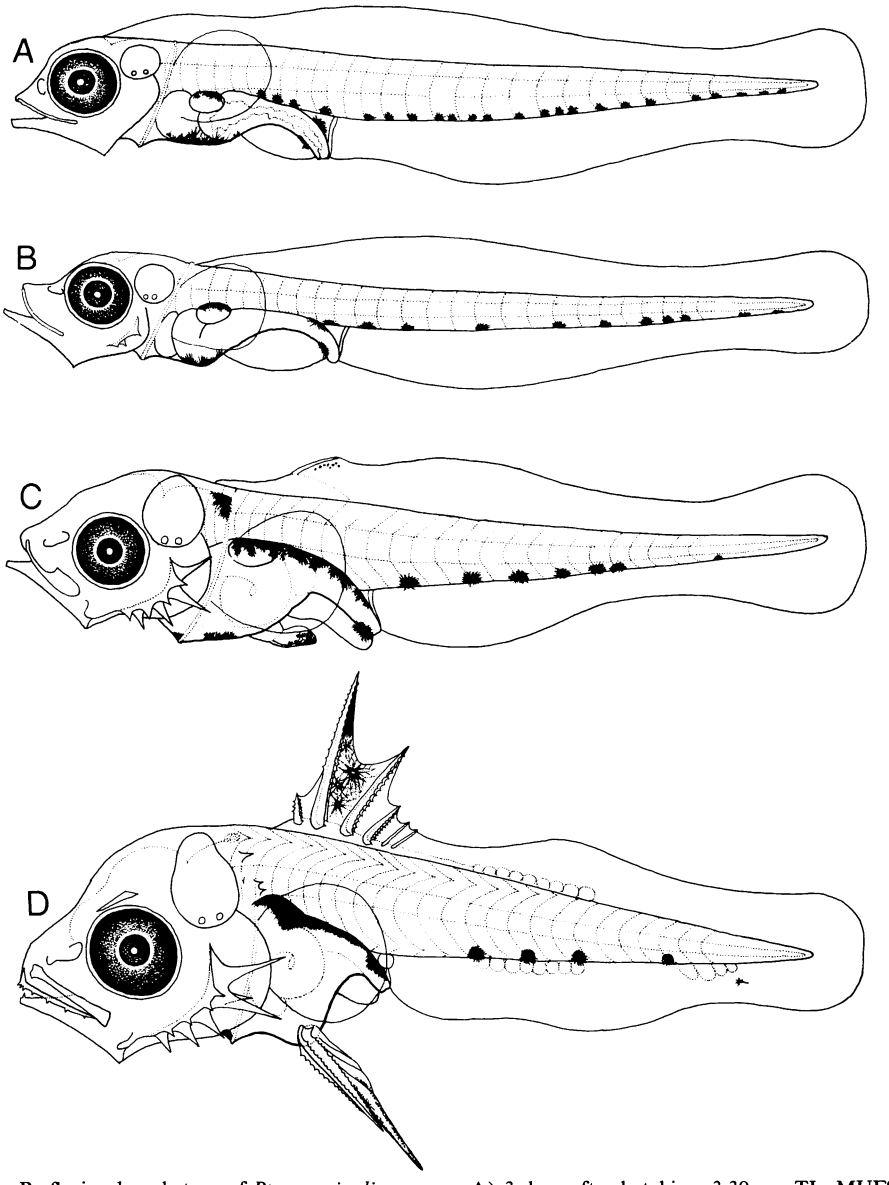

Fig. 7. Preflexion larval stage of *Pterocaesio digramma*. A) 3 days after hatching, 3.30 mm TL, MUFS 10019; B) 5 days after hatching, 3.42 mm TL, MUFS 10021; C) 8 days after hatching, 3.90 mm TL, MUFS 10025–10026; D) 15 days after hatching, 5.46 mm TL, MUFS 10029.

a small spine on the interopercle and a smooth supraocular ridge were apparent. Single spines on the posttemporal and supracleithrum were first observed in a 10-day old larva (4.48 mm TL, $n=1$), with second spines being apparent on these elements in a 15-day old larva (5.46 mm TL, $n=1$; Fig. 7D).

Dorsal and pelvic fin rudiments were apparent in a 7-day old larva (3.54 mm TL, $n=1$), the second dorsal and pelvic spines having appeared on the rudiments in an 8-day old larva (3.90 mm TL, $n=1$; Fig. 7C). The dorsal spines had increased to six in a 15 day-old larva (5.46 mm TL, $n=1$; Fig. 7D). The edges of both the dorsal and pelvic spines had serrations, which first appeared on the second dorsal and pelvic spines concurrent with the dorsal spines increasing to four (apparent in a 10-day old larva [4.48

mm TL, $n=1$]). The second dorsal spine was V-shaped in cross-section, the V opening posteriorly; the anterior edge was smooth and the posterior edges coarsely serrated. The pelvic spine was trapezoidal near the base and rounded near the tip in cross section; all four edges were coarsely serrated. In a 15-day old larva (5.46 mm TL, $n=1$; Fig. 7D), the anterior edge of the first and second dorsal spines and both the posterior edges of the first to fourth dorsal spines were coarsely serrated. Furthermore, at that stage rudiments of the anal fin and caudal fin rays had appeared.

Morphometrics of larvae

Proportional changes of various parts of the body against BL are shown in Table 2. Body proportions (PAL, BD, HL and ED) relative to BL decreased, and the proportion of SnL to BL slightly increased until the larvae attained 3.00–3.16 mm BL ($n=5$), when completely absorption of the yolk took place (3-day old). During the preflexion stage after absorption of the yolk, the development of the head and gut by feeding resulted in the body proportions (PAL, BD, HL, ED and especially SnL) increasing relative to BL. The proportion of PDL to BL slightly increased to 0.30–0.31 in larva 7–15 days after hatching (mean 3.24–mean 4.73 mm BL, $n=25$). The proportion of DSL[a] and P_2SL to BL increased to 0.05–0.15 and 0.02–0.12, respectively, in larva 8–15 days after hatching (mean 3.65–mean 4.73 mm BL, $n=20$). The proportion of UJL to BL increased to 0.06–0.10 in larva 2–15 days after hatching (mean 3.07–mean 4.73 mm BL, $n=50$).

Pigmentation of larvae

Just-hatched larvae (2.06–2.34 mm TL, $n=5$; Fig. 6A) had many dendritic melanophores along the body axis from the head to the caudal section. In 18-hour old larvae (3.02–3.20 mm TL, $n=5$; Fig. 6C), the melanophores on the body were confined to the ventral midline of the trunk and the tail posterior to the fifth myotome, with one or two dendritic melanophores also appearing on the posterior tip of the notochord. However, the latter had disappeared in 3-day old larvae (3.16–3.30 mm TL, $n=5$; Fig. 7A). The number of melanophores on the ventral part of the body began to decrease from 15–23 on 3-day old larvae (3.16–3.30 mm TL, $n=5$; Fig. 7A), numbering 3–10 on 15-day old larvae (4.64–5.46 mm TL, $n=5$; Fig. 7D).

Just-hatched larvae (2.06–2.34 mm TL, $n=5$; Fig. 6A) had 3–9 melanophores on the surface of the oil globule, and 1–4 melanophores on the surface of the yolk (in 6 out of 10 individuals examined). At mean 2.50 mm TL (6-hour old, $n=5$; Fig. 6B), all individuals examined had melanophores on the yolk. In 36-hour old larvae (3.08–3.28 mm TL, $n=5$; Fig. 6D), most of the melanophores on the yolk were situated on the ventral midline. The melanophores on the yolk subsequently covered the anteroventral part of the gut after absorption of the yolk in 3-day old larvae (3.16–3.30 mm TL, $n=5$; Fig. 7A), but in a 15-day old larva (5.46 mm TL, $n=1$; Fig. 7D), these had disappeared.

In 36-hour old larvae (3.08–3.28 mm TL, $n=5$; Fig. 6D), single dendritic melanophores appeared on the dorsal and ventral surfaces of the posterior part

Table 2. Changes in body proportions (relative to body length) during the first 15 days of development of *Pterocaesio digramma*

Body parts	Yolk-sac larvae	Preflexion larvae after absorption of yolk
Pre-anal length (PAL)	0.54–0.40	0.40–0.45
Body depth (BD)	0.34–0.13	0.11–0.24
Head length (HL)	0.22–0.16	0.19–0.27
Eye diameter (ED)	0.10–0.07	0.07–0.09
Snout length (SnL)	0.03–0.04	0.07–0.11
Diameter of yolk	0.58–0.08	—
Diameter of oil globule	0.08–0.02	—
Pre-dorsal fin length (PDL)	—	0.30–0.31
2nd dorsal fin spine length (DSL[a])	—	0.05–0.15
Pelvic fin spine length (P_2SL)	—	0.02–0.12
Upper jaw length (UJL)	0.06	0.07–0.10

of the gut. In 3-day old larvae (3.16–3.30 mm TL, $n=5$; Fig. 7A), a few dendritic melanophores appeared on the dorsal part of the gas bladder, and together with those on the gut had become strongly dendritic on an 8-day old larva (3.90 mm TL, $n=1$; Fig. 7C). However, the melanophore of the posteroventral part of the gut had disappeared in a 15-day old larva (5.46 mm TL, $n=1$; Fig. 7D).

A small, punctate melanophore, first observed on the cleithral symphysis in a 7-day old larva (3.54 mm TL, $n=1$), had become strongly dendritic in a 10-day old larva (4.48 mm TL, $n=1$), but was reduced in size in older larvae (Fig. 7D).

Just-hatched larvae (2.06–2.34 mm TL, $n=5$; Fig. 6A) had several dendritic melanophores on the head, but the eye was unpigmented. Eye pigmentation started in 6-hour old larvae (2.44–2.64 mm TL, $n=5$; Fig. 6B), with the melanophores on the head disappearing in 3-day old larvae (3.16–3.30 mm TL, $n=5$; Fig. 7A). One punctate melanophore was present on the dorsal side of the hindbrain in a 6-day old larva (3.36 mm TL, $n=1$), becoming strongly dendritic in a 10-day old larva (4.48 mm TL, $n=1$). Subsequently, the melanophore became smaller, and in a 15-day old larva (5.46 mm TL, $n=1$; Fig. 7D), was barely visible.

At the time of formation of the dorsal and pelvic fin spines in an 8-day old larva (3.90 mm TL, $n=1$; Fig. 7C), several punctate or dendritic melanophores had appeared on the dorsal finfold and pelvic fin rudiments. However, at no time during the observations were the dorsal and pelvic spines pigmented (Fig. 7C, D). In a 10-day old larva (4.48 mm TL, $n=1$), the melanophores on the dorsal fin were located only on the membrane between the second and third dorsal spines. In a 12-day old larva (4.62 mm TL, $n=1$), a single large dendritic melanophore was clearly visible on the membrane between the second and third dorsal spines. In a 15-day old larva (5.46 mm TL, $n=1$; Fig. 7D), the melanophores on the membrane had increased to four, with a single stellate melanophore having appeared on the rear portion of the ventral finfold.

Discussion

Reproductive behavior

Being a group spawner, *Pterocaesio digramma* was similar to other lutjanid fishes, *viz. Lutjanus synagris* (Wiklund, 1969), *L. kasmira* (Suzuki and Hioki, 1979), *L. stellatus* (Hamamoto et al., 1992) and *Caesio teres* (Bell and Colin, 1986).

Two points of difference between the subfamilies Caesioninae and Lutjaninae were noted. In its natural habitat, the reproductive behavior of *C. teres* essentially takes place before sunset, the onset of spawning occurring between 67 minutes before sunset to 7 minutes after sunset, being associated with tidal changes (Bell and Colin, 1986). Spawning of *P. digramma* in this study began from about 3.5 hours before sunset, spawning taking place every day, with no evidence of lunar cycling. However, this species may exhibit lunar periodicity in spawning in its natural habitat. Thresher (1984, pers. comm. of Doherty) reported spawning of *P. digramma*, at One Three Island, Great Barrier Reef, shortly before the full moon at dusk in early summer, a large school spawning a few feet off the bottom on the windward side of the reef, in approximately 18 m of water. On the other hand, spawning in the Lutjaninae had been observed during the crepuscular period, to about 2 hours after sunset (Wiklund, 1969; Suzuki and Hioki, 1979; Hamamoto et al., 1992). Such spawning differences may be explained by differences in life-style, namely, the Caesioninae are diurnal fishes, whereas the Lutjaninae are nocturnal in many cases (our observation and Randall et al., 1990). Furthermore, in the Caesioninae, large schools (*C. teres*, ca. 1,000 individuals; *P. digramma*, ca. 1,500 individuals) of spawners performed up and down swimming movements during spawning, whereas in the Lutjaninae, such movements by a large school have not been observed (Wiklund, 1969; Suzuki and Hioki, 1979; Bell and Colin, 1986; Hamamoto et al., 1992). Thus, up and down swimming as a part of the spawning sequence may be unique to the Caesioninae, within the Lutjanidae.

Eggs

The embryonic development of *Pterocaesio digramma* did not differ significantly from other lutjanid fishes for which information is available, *viz. Lutjanus kasmira* (Suzuki and Hioki, 1979), *L. campechanus* (Rabalais et al., 1980; Minton et al., 1983), *L. russelli* (Liu and Hu, 1980), *L. vitta*? from Iwatsuki et al. (1993) (Lu, 1981), *L. erythropterus* (Zhang et al., 1985), *L. lutjanus* (Zhang et al., 1985) and *L. stellatus* (Hamamoto et al., 1992). All had embryonic development typical of the Percoidei. However,

melanophores were observed on the oil globule during embryonic development in *P. digramma* (Fig. 5H, I), but not so in the Lutjaninae (Suzuki and Hioki, 1979; Rabalais et al., 1980; Lu, 1981; Zhang et al., 1985; Hamamoto et. al., 1992). In *P. digramma*, both egg diameter (0.82–0.88 mm) and oil globule diameter (0.14–0.17 mm) were almost the same as those of other lutjanid fishes (0.65–1.02 and 0.05–0.20 mm, respectively) (Leis, 1987).

Larvae

Larval development in *Pterocaesio digramma* was similar that in other lutjanid fishes for which information is available, *viz. Rhomboplites aurorubens* (Laroche, 1977), *Lutjanus kasmira* (Suzuki and Hioki, 1979), *L. campechanus* (Collins et al., 1980; Rabalais et al., 1980; Minton et al., 1983), *L. griseus* (Richards and Saksena, 1980), *L. russelli* (Liu and Hu, 1980), *L. vitta*? from Iwatsuki et al. (1993) (Lu, 1981), *L. ophuysenii* (Mori, 1984), *L. erythropterus* (Zhang et al., 1985), *L. lutjanus* (Zhang et al., 1985) and *L. stellatus* (Hamamoto et. al., 1992), all possessing a tightly coiled gut, small gas bladder, similar body pigment pattern, and early formation of head spination and pelvic and dorsal fin spines (Leis and Rennis, 1983).

However, in just-hatched larvae, melanophores on the oil globule, present in *P. digramma* (Fig. 6A), are absent in the Lutjaninae (see above) (Suzuki and Hioki, 1979; Rabalais et al., 1980; Lu, 1981; Zhang et al., 1985; Hamamoto et al., 1992). Furthermore, differences in the degree of development of melanophores on the dorsal fin membrane of larvae were apparent between *P. digramma* and lutjanine species (Laroche, 1977; Collins et al., 1980; Richards and Saksena, 1980; Mori, 1984). In the former, several large, well-defined dendritic melanophores were present on the membrane between the second and third dorsal spines in the late-preflexion stage (Fig. 7D). Similar dendritic melanophores are shown on the illustration of a natural juvenile of *Caesio* sp., given by Kojima (1988: 516). However, in the Lutjaninae, such well developed melanophores have not been observed on the dorsal fin membrane at any time during the larval stage (Collins et al., 1980; Richards and Saksena, 1980; Mori, 1984). Therefore, melanophores on the oil globule in just-hatched larvae and well developed melanophores on the dorsal fin membrane in late-preflexion larvae might be characteristic of *P. digramma* or, possibly, of a higher (subfamilial) level.

Acknowledgments

We are most grateful to Mr. Senzou Uchida and Mr. Tasuku Nagasaki, Okinawa Expo Aquarium, Japan, for permission for our study and provision of many facilities. We are greatly appreciative of Dr. Jeffrey M. Leis and Ms. Sally E. Reader, Australian Museum, Sydney, Australia, not only for critical comments on the manuscript, but also for great help with English. Furthermore, we thank Dr. Seishi Kimura, Mie University, Japan, for comments on the figures. Lastly, we thank Dr. Graham S. Hardy, Thames, New Zealand, for further assistance with English and critical comments.

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タカサゴ亜科魚類タカサゴ *Pterocaesio digramma* の飼育下における産卵行動とその卵内発生及び仔魚

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タカサゴ亜科魚類タカサゴ *Pterocaesio digramma* の飼育下における産卵行動とその卵内発生及び孵化後 15 日目までの仔魚を記載した．本種の産卵は，1993 年 5 月 10 日から同年 7 月 4 日まで毎日観察された．産卵行動はおよそ 16 時から 19 時の約 3 時間の間，ほぼ連続的に観察された．産卵行動は 6 つの段階に分けられた．1) 親魚は，まず天然海水の注水口がある水槽内北北東側の隅で約 1,500 尾の群れを作り，その群れ全体が水面に対して

ほぼ垂直な上下運動を繰り返した．2) 親魚が水表面まぎわに達した時，群れの中のある1尾の雄が1尾の雌に対し求愛を行い，3) その後，その雄雌は水面近くを水平方向に向かって突進し，さらに約10–15尾のスニーカーがそれを追尾した．4) ペアによる産卵が行われた後，5) 約5尾のスニーカーによる放精が行われた．6) 放卵，放精を終えた親魚は分散し，再び群れに戻った．

本種の受精卵は，油球1個を有する卵径0.82–0.88 mmの球形分離浮遊卵で，水温24±0.5°Cで受精後23時間で孵化を開始し，その2時間後に全体の約70%の卵が孵化した．孵化直後の仔魚は平均全長2.19 mm，卵黄は長円形で大きく，その先端は吻端より前方に突出し，油球は卵黄の先端に位置していた．孵化後3日目の仔魚の全長は3.16–3.30 mmで，卵黄及び油球は完全に吸収された．孵化後5日目（全長3.42 mm）より頭部の棘の形成が始まった．孵化後7日目（全長3.54 mm）で，背鰭と腹鰭の原基が出現し，孵化後8日目（全長3.90 mm）で，それぞれの原基に1本の棘が現れた．孵化後10日目（全長4.48 mm）より，背鰭棘と腹鰭棘に鋸歯状のものが形成され始めた．孵化後15日目（全長5.46 mm）で，背鰭棘は6本になり，その内の第1棘から第4棘までが鋸歯状になった．仔魚は孵化後17日目まで飼育ができたが，仔魚の形態は孵化後15日目のものと相違は認められなかった．

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