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Early Morphogenesis of flyingfish, *Cypselurus heterurus doederleini* (Teleostei: Exocoetidae)

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Abstract: Embryonic and larval developments of a flyingfish, *Cypselurus heterurus doederleini* were studied. Egg was large and lacking in oil globule, but with long, thin and sticky thread-like filaments around the chorion. In the early embryonic stage, the pigments and the pectoral fin were formed and the vitelline circulated, preceding the formation of the heart. In the later stage, the mouth started being opened and the pectoral, ventral and caudal fins became elongated and moved. The eye was darkened. After eight days of incubation, first two larvae hatched-out which started from sunset to sunrise and continued for two days at the temperature ranges from 22.5°C to 23.5°C. No hatching at night. The average total length of the newly-hatched larvae was 6.07 mm.

Newly-hatched larva was heavily pigmented and exhibited yellowish-pinkish color patterns. Organs were fully formed and they actively swam. They fed actively after the absorption of an eggyolk at one-day. Larvae grew faster and almost doubled its total length within 11 days, but exhibited negative allometry, making the body form more elongate and slender.

Key words: *Cypselurus heterurus doederleini, egg, larva, development.*

INTRODUCTION

A flyingfish, *Cypselurus heterurus doederleini* (Steindachner) is common and one of the most important commercial fishes in Japan. It belongs to the largest flyingfishes thriving in the water of Japan. Its developmental informations can be found in many literatures (Nayudu, 1923; Bruun, 1935; Breder, 1938; Hubbs and Kampa, 1946; Imai, 1959). These studies depend largely on the description of acquired wild eggs and larvae and no study has been conducted for artificially inseminated materials. Data for the development such as behaviour, color pattern and variation, feeding habit, temperature and physical response to light are inadequate. The advance in the seed production technology for the past decades has led to the production of several marine fishes using artificial insemination technique (Arias, 1976; Akazaki and Hashimoto, 1978). Recently, various scientific informations on the early life history and development were generated (Matsuoka, 1987; Fukuhara, 1991; Kestemont and Stalmans, 1992). The purpose of this study is to investigate the developmental process of artificially inseminated eggs and larvae of the highly oceanic *Cypselurus heterurus doederleini* as a possible potential information for seed production in aquaculture and marine ranching industries.

MATERIALS AND METHODS

Eggs of *Cypselurus heterurus doederleini* were collected off Iburi, Tosashimizu, Kochi Prefecture on May 11, 1997. During the hauling of set-net (Oshiki ami), two males and three females

with fully mature gonad were selected. The eggs (ova) were taken out from the genital pore by pressing over the abdomen. The same method was done in taking out the semen. At about 7:30 AM, the ova and the semen were immediately mixed in 1,000 ml beaker for fertilization called artificial insemination.

Fertilized eggs were washed before they were put inside the plastic bag containing about 20 liters sea water with the temperature of 19°C. The plastic bag was filled with oxygen gas and was put inside the cooler. A small amount of ice were put inside the cooler to maintain the temperature during 3-4 hours travel for transportation. The eggs were transported to the seed production center of Usa Marine Biological Institute with temperature ranged from 16°C to 17°C. They were acclimatized to 21°C for an hour before they were put inside the hatching tank. Hatching temperature was gradually adjusted and maintained at 23°C in a 500 liters cylendrical hatching tank. Since the eggs of a flyingfish, *Cypselurus heterurus doederleini* lack in oil globule to float them, a net was fixed as an attaching substratum inside the hatching tank with a running water. Developmental stages of the eggs were observed and sketched.

After hatching, the larvae were transfered to 1,000 liters cylendrical rearing tank. To maintain the water quality uniform, about one-half of the used water in the tank was changed every morning after wild copepods and brine shrimps were fed to them. Chorella was added in the water to maintain oxygen supply. The feed was given twice a day. Samples of the larvae were fixed in 10% formalin solution and observed under the microscope with a camera lucida. Body measurements were conducted from sketches based on the scale. Regression of all statistically significant measurements was presented with the body length as a predictor (x trait), because most of the multiple components of the body size are highly covariant (McKinney and McNamara, 1991). Ratio of length of homologous distances in two forms was considered as dilatation and coded with 1.00 as relative isometry, >1.00 as positive allometry, and <1.00 as negative allometry (Bookstein *et al.*, 1985).

RESULTS

Egg development

The egg was spherical and transparent, 1.7-1.8 mm in diameter. It sank and was protected by a tough chorion adorned with 55-56 filaments with 13-15 mm long (Fig. 1A-B). Fertilization occurred immediately after the ova and the semen were mixed in 1,000 ml beaker. Meroblastic fertilized eggs were hatched through several stages, the cleavage, morula, blastula and gastrula at the water temperature of 22.5°C-23.5°C. The egg, embryonic and the larval chronological developments were summarized in Table 1 and illustrated in Figs. 1 and 2.

The egg became 8-cell stage at 5 hours after fertilization (Table 1 and Fig. 1B). It became 16-cell stage at 6 hours (Fig. 1C), 32-cell stage at 7 hours (Fig. 1D) and morula stage at 8 hours (Fig. 1E).

At 9 hours (Table 1 and Fig. 1F), the egg became blastula stage. The cells became micromeres or blastomeres over the perivitelline space.

At 10 hours (Table 1 and Fig. 1G), the cells became blastoderm, giving rise to the embryo.

At 1 day and 7 hours (Fig. 1H), the egg became gastrula stage, the early stage of embryonic development. At this stage, the embryonic shield started being formed and the blastoderm covered almost 3/4 of the yolk surface.

At 2 days and 1 hour (Table 1 and Fig. 1I-J), the gastrulation continued with the formation of Kupffer's vesicle, optic vesicle, notochord and myomeres.

At 2 days and 6 hours (Table 1 and Fig. 1K-L), the gastrulation stage continued. The head, brain vesicle, auditory vesicle, optic cup and the heart started being formed. Heart started beating.

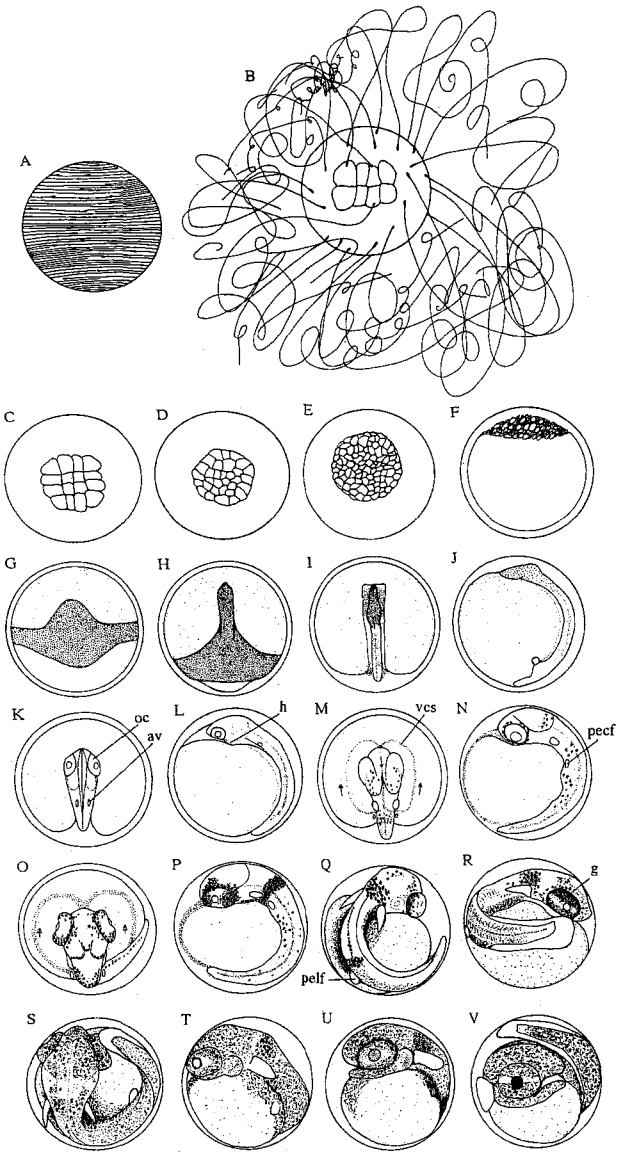

Fig. 1. Embryonic development in *Cypselurus heterurus doederleini*. A) unfertilized ovarian egg with coiling filaments; B) 8 cell stage with tendrils; C) 16 cell stage (tendrils removed); D) 32 cell stage; E) morula stage; F) blastula stage; G) blastoderm started to cover yolk; H) gastrula stage, embryonic shield formed, blastoderm covered almost 3/4 of yolk surface; I-J) Kupffer's vesicle formed, optic vesicle, notochord and myomeres appeared; K-L) head, auditory vesicle (*av*), optic cup (*oc*) and heart (*h*) formed; M-N) melanophores appeared, pectoral fin rudiments (*pecf*) and vitelline circulatory system (*vcs*) formed, vitelline circulated (↑, indicates direction); O-P) increased pigments, tail moved and cross bond formed; Q) increased pigments, pectoral fins moved and pelvic fin rudiments (*pelf*) formed; R) increased pigments, dorsal and anal fins formed, guanophores (*g*) horizontal to eye formed; S-T) increased pigments on head and body, lower jaw, operculum and gills formed; formation of lower jaw, operculum and gills; U) lower jaw moved and mouth opened, eyeball became dull brown; V) eyeball blackened and yolk became small. (See Table 1).

Table 1. Embryonic development in *Cypselurus heterurus doederleini* fertilized at 7 : 30 of May 11, 1997 at the water temperature ranging from 22.5°C to 23.5°C.

Time	*Period After Fertilization (Day : Hr :Min)*	*Water Tempt. (°C)*	*Developmental Stage*
07 : 30	00 : 00 : 00	20.0	Fertilization
12 : 30	00 : 05 : 00	23.0	8 cell stage (Fig. 1B)
13 : 30	00 : 06 : 00	23.0	16 cell stage (Fig. 1C)
14 : 33	00 : 07 : 03	23.0	32-cell stage (Fig. 1D)
15 : 33	00 : 08 : 00	23.0	Morula stage (Fig. 1E)
16 : 30	00 : 09 : 00	23.0	Blastula stage (Fig. 1F)
17 : 30	00 : 10 : 00	23.0	Blastoderm started to cover yolk (Fig. 1G).
14 : 25	01 : 06 : 55	23.0	Gastrula stage began; embryonic shield formed; blastoderm covered almost 3/4 of yolk surface (Fig. 1H).
08 : 45	02 : 01 : 15	22.5	Kupffer's vesicle formed; optic vesicle appeared; notochord and myomeres appeared (Fig. 1I-J).
13 : 32	02 : 06 : 02	23.0	Head formed (brain vesicle, optic cup developed); auditory vesicle appeared; heart developed (heartbeat started) (Fig. 1K-L).
08 : 35	03 : 01 : 05	23.0	Melanophores appeared, pectoral fins and vitelline circulatory system formed, vitelline circulated (Fig. 1M-N).
08 : 35	04 : 01 : 05	22.5	Increased pigmentations; cross bond pigments formed; tail moved (sway) (Fig. 1O-P).
15 : 35	05 : 08 : 05	23.0	Increased pigmentations; pectoral fins elongated and moved; ventral fin formed (Fig. 1Q).
17 : 50	05 : 10 : 20	23.5	Increased pigmentations; dorsal and anal fin membrane formed; guanophores horizontal to the eye formed (Fig. 1R).
08 : 25	06 : 00 : 45	22.5	Increased pigmentations on the head and body; lower jaw, operculum and gills formed (Fig. 1S-T).
17 : 45	06 : 10 : 15	23.0	Lower jaw moved and mouth opened; eyeball became dull brown, yolk-sac became small (Fig. 1U).
08 : 30	08 : 01 : 00	23.0	Eyeball became dark, yolk-sac became small (Fig. 1V).
18 : 30	08 : 11 : 00	23.0	First two eggs hatched, average total length 6.07 mm. Hatching continuous until dawn.
18 : 30	09 : 11 : 00	23.0	Hatching of second batch and continuously until dawn.
08 : 30	10 : 01 : 00	23.0	All eggs hatched.

At 3 days and 1 hour (Table 1 and Fig. 1M-N), the pectoral fin rudiments started forming. The melanophores started appearing on the head dorsally, around the optic cup and the front and rear of the pectoral fin rudiment hypaxially. The vitelline circulatory system became apparent with the vitelline circulating from the anterior of the snout to between the auditory vesicles and pectoral fin rudiments. It circulated around both the left and right peripheries of the head (Fig. 1M and O).

At 4 days and 1 hour (Fig. 1O-P), the melanophores on the body increased. The pigments started appearing on the optic cups, more on the head, and the body cross bond started being formed anterior to the pectoral fin rudiments. The sparse pigments were scattered on the body. The tail started moving bilaterally.

At 5 days and 8 hours (Table 1 and Fig. 1Q), the melanophores on the body increased and the pectoral fin rudiments became large and started moving. The pelvic (ventral) fin rudiments started being formed.

At 5 days and 10 hours (Table 1 and Fig. 1R), the dorsal and the anal finfolds started being formed. The guanophores appeared on the horizontal of the eyes.

At 6 days and 1 hour (Table 1 and Fig. 1S-T), the pigment cells were intensified on the head and over the body. The lower jaw, gill arches and opercular rudiments were visible.

At 6 days and 10 hours (Table 1 and Fig. 1U), the mouth became functional. The eyeball became dull brown in color.

At 8 days and 1 hour (Table 1 and Fig. 1V), the eyeball became black and yolk-sac became small.

At 8 days and 11 hours (Table 1), the first two larvae were hatched out, which started after sunset and continued hatching thereafter until dawn. Hatching stopped in daylight.

At 9 days and 11 hours (Table 1), the second batch of eggs were hatched which started after sunset and continued until dawn.

At 10 days and 1 hour (Table 1), all of the eggs were hatched just before sunrise with a total of 13,000 individuals.

Larval external development and growth

Larval development were observed at the water temperature of 21°C-23°C. The newly-hatched larvae have an average total length of 6.07 mm ($n = 5$) with a small peripheral egg yolk (Table 2 and Fig. 2A). They exhibited color variation from pale-brown to dark-brown with the heavy pigmentations around the body and the head. At night, the larvae had exhibited yellowish-pinkish color with positive phototaxic behaviour. The large fan-blade-like shape pectoral fins were transparent except the base where the pigmentation started (Figs. 2A and 3A1). The pelvic fins were elongated with sparse pigments (Figs. 2A and 3A2). Both pectoral and pelvic fins were widely spread during at rest, particularly at night. The caudal fin was marginally rounded with small and sparce pigments (Figs. 2A and 3A3). The dorsal and anal fins were transparent. They swam actively at any direction on the water surface.

Table 2. Larval growth in *Cypselurus heterurus doederleini*. Measurement in mm of total length, mean, range, standard deviation (SD) and percentage (%) of growth in 11 days rearing period.

Day-old	TOTAL LENGTH		% of growth
	Range (mm)	Mean ± SD	
Newly-hatched	5.950 - 6.190	6.070 ± 0.170	----
One-day-old	6.150 - 6.580	6.370 ± 0.157	5%
Two-day-old	6.850 - 7.510	6.830 ± 0.230	17%
Three-day-old	6.940 - 7.870	7.300 ± 0.298	20%
Four-day-old	7.050 - 8.030	7.620 ± 0.361	26%
Five-day-old	7.050 - 8.530	7.960 ± 0.395	31%
Six-day-old	7.940 - 9.160	8.710 ± 0.453	44%
Seven-day-old	8.840 - 9.960	9.000 ± 0.533	48%
10-day-old	10.910 - 12.130	11.380 ± 0.434	87%
11-day-old	10.520 - 14.370	12.040 ± 1.459	99%

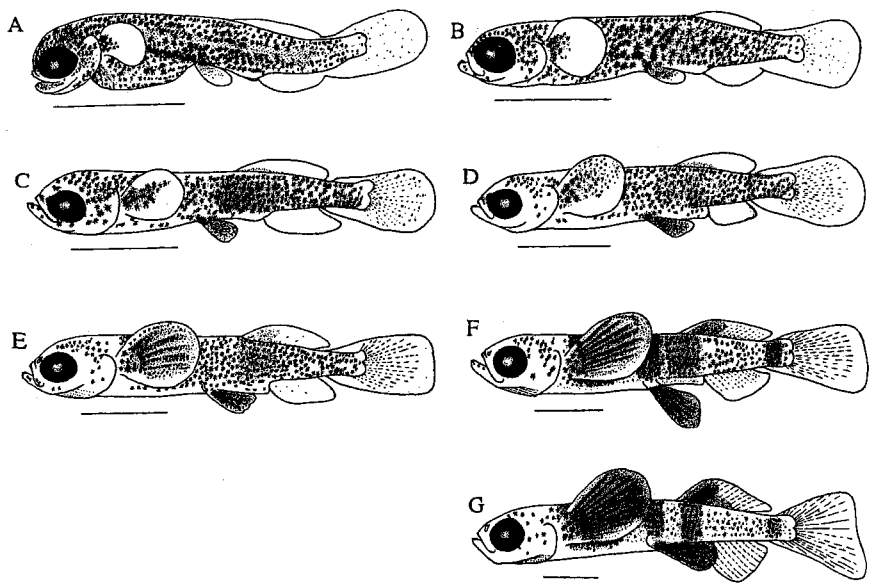

Fig. 2. Larval development in *Cypselurus heterurus doederleini.* A) newly-hatched larvae; B) one-day-old larvae; C) three-day-old larvae; D) five-day-old larvae; E) seven-day-old larvae; F) 10-day-old larvae; G) 11-day-old larvae. (See Table 1). Bars = 1 mm.

At one-day-old (Table 2 and Fig. 2B), they attained an average total length of 6.37 mm (n = 10). The yolk was fully absorbed. The teeth became apparent and started feeding actively on wild copepods. They swam sluggishly and descended slantlingly with a few centimeters to catch food.

At three-day-old (Table 2 and Fig. 2C), they attained an average total length of 7.30 mm (n = 10). The finfolds disappeared gardually. The pigmentations spread heavily over the central part of the pectoral fin (Fig. 3B1), over the pelvic fin (Fig. 3B2), at the base of the dorsal fin (Fig. 2C) and moderately scattered on the caudal fin (Fig. 3B3). Pigments on the caudal fin looked like broken lines (Fig. 3B3, C3, D3, E3 and F3).

At five-day-old (Table 2 and Fig. 2D), they attained an average total length of 7.96 mm (n = 10). The pigments on the pectoral fins spread heavily over its dorsal half. The pectoral (Fig. 3C1) and the pelvic fins became wider (Fig. 3C2).

At seven-day-old (Table 2 and Fig. 2E), they attained an average total length of 9.00 mm (n = 7). The pigments on the pectoral and pelvic fins changed gradually into a dusky color and extended over the few anterior fin rays (Fig. 3D1, D2).

At 10-day-old (Table 2 and Fig. 2F), they attained an average total length of 11.38 mm (n = 5). Four vertical dusky bonds started appearing on the rear of the pectoral fin base, at the pelvic fin base, just behind the pelvic fin base and on the caudal peduncle. The caudal fin became truncate (Figs. 2E, 3E3). The lower half of the caudal fin became slightly larger than the upper one. They started schooling and swimming against the current (current from aeration) for the search of foods. Stressed individuals swam downward to the bottom.

At 11-day-old (Table 2 and Fig. 2G), they attained an average total length of 12.04 mm (n = 6). The organs such as pectoral, pelvic, anal, dorsal and caudal fins, eyes, mouth, opercles and the body form were almost completely developed. The pigment cells (melanophores) on the

head and between the cross bonds became thinner. Silver color (guanophores) on the ventral part of the body and the opercle became conspicuous. The caudal fin became asymmetrical with elongate lower lobe. The body became elongated. Juvenile started gliding at the maximum distance of about 12 cm.

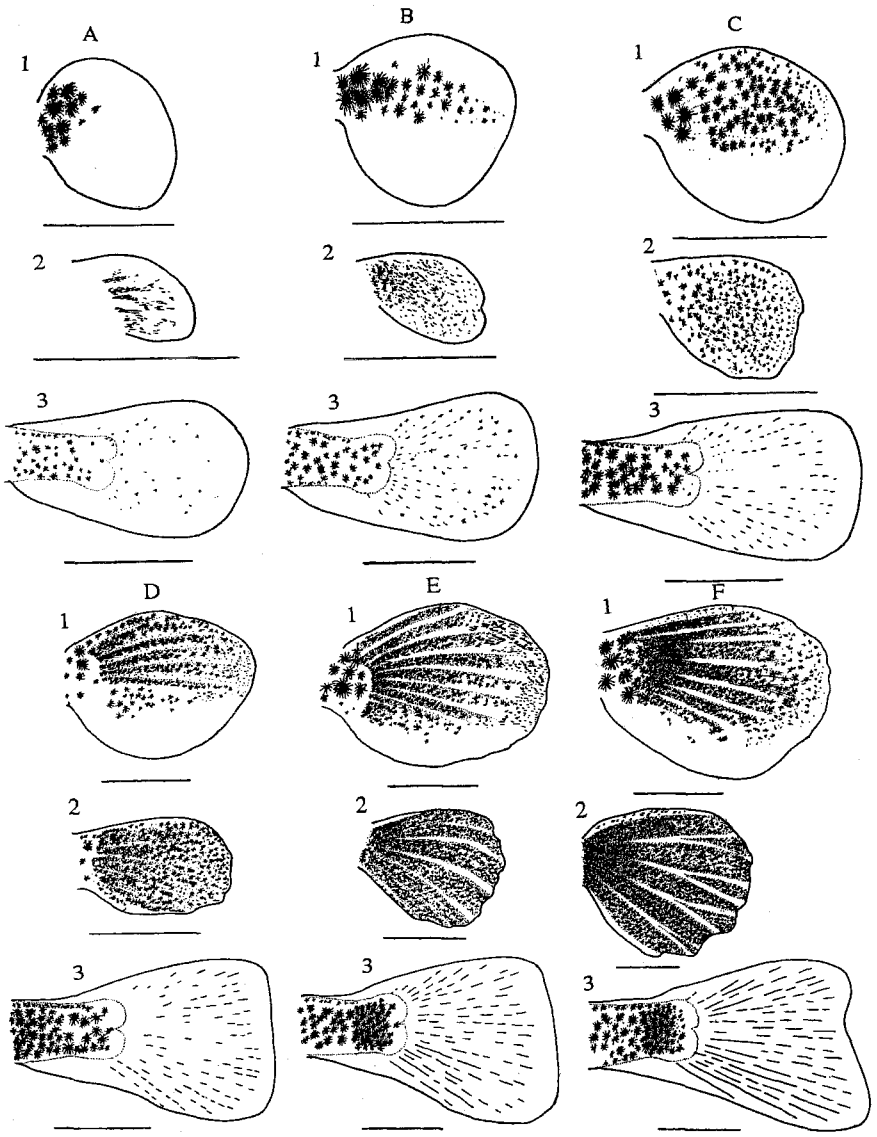

Fig. 3. Development and color pattern of pectoral (1), ventral (2) and caudal (3) fins of *Cypselurus heterurus doederleini*. A) newly-hatched larvae; B) three-day-old larvae; C) five-day-old larvae; D) seven-day-old larvae; E) 10-day-old larvae; F) 11-day-old larvae. (See Table 1). Bars = 1 mm.

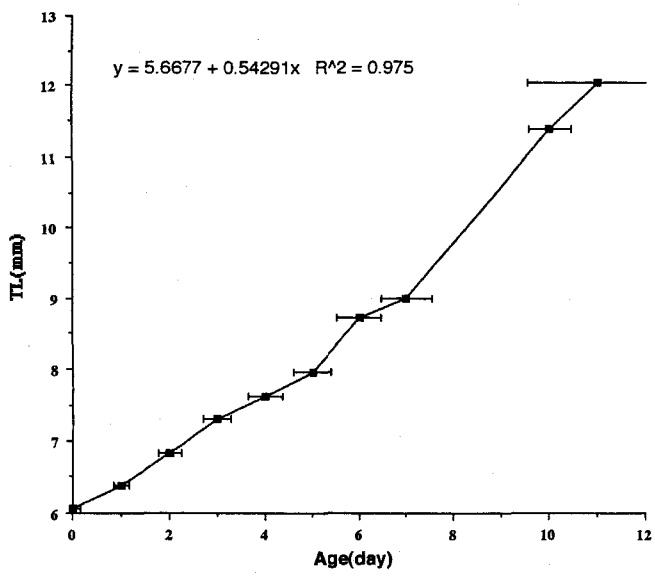

Fig. 4. Graph of growth in 11 day-old *Cypselurus heterurus doederleini* with regression and correlation value. Line, trendline; ⊢■⊣, standard deviation (SD).

The general body form developed allometrically (Table 3 and Fig. 5). All the body metrics exhibited shortening ranging from $b = 0.078$ to $b = 0.571$ during development.

Table 3. Description of body morphometric characters and corresponding regression and correlation values of 11 day-old larvae in *Cypselurus heterurus doederleini*.

Body Metrics	Regression and Correlation Values
PD - predorsal length	$y = 0.331 + 0.497x \quad r^2 = 0.995$
PA - preanal length	$y = 0.135 + 0.571x \quad r^2 = 0.996$
PV - preventral length	$y = 0.231 + 0.389x \quad r^2 = 0.991$
HL - head length	$y = -2.348e + 0.217x \quad r^2 = 0.974$
POL - preorbital length	$y = -0.164 + 0.115x \quad r^2 = 0.938$
ED - eye diameter	$y = 0.200 + 6.852e - 2x \quad r^2 = 0.894$
SNL - snout length	$y = -4.850e - 2 + 3.227e - 2x \quad r^2 = 0.950$
HW - width of head	$y = 0.340 + 0.121x \quad r^2 = 0.982$
BW - body width	$y = 0.599 + 4.800e - 2x \quad r^2 = 0.322$
HD - depth of head	$y = 0.224 + 0.139x \quad r^2 = 0.968$
BD - body depth	$y = 0.793 + 7.841e - 2x \quad r^2 = 0.373$
PFL - pectoral fin length	$y = -1.269 + 0.335x \quad r^2 = 0.972$
VFL - ventral fin length	$y = -1.038 + 0.279x \quad r^2 = 0.967$
ULF - upper lobe of caudal fin	$y = -0.286 + 0.197x \quad r^2 = 0.977$
LLF - lower lobe of caudal fin	$y = -0.497 + 0.231x \quad r^2 = 0.989$

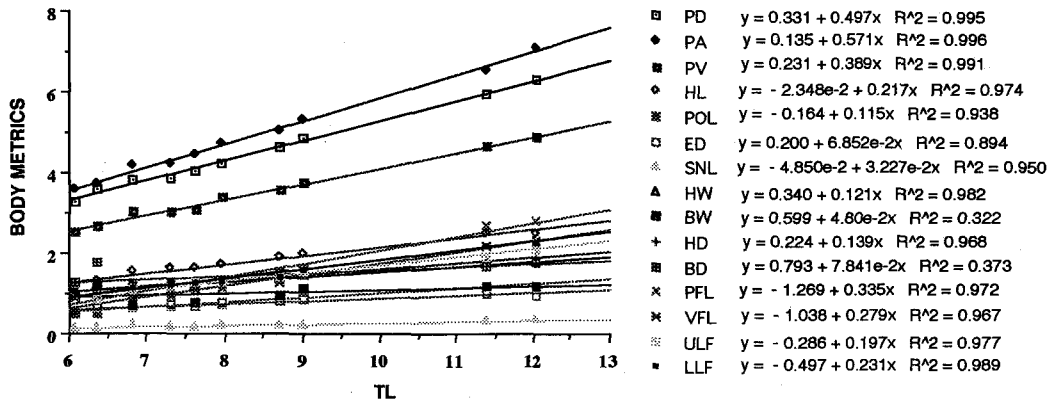

Fig. 5. Graph of relationships between the total body length (TL) and the body metrics with fitted curve lines in 11 day-old *Cypselurus heterurus doederleini*. Description of legends in Table 3.

DISCUSSION

Eggs

Morphology and general development— Our study on the morphogenesis of flyingfish, *Cypselurus heterurus doederleini* revealed various unique characteristics. The egg was demersal in nature, heavier than water and no oil globule to float it. It follows the general mitotic developmental process. Although eggs were fertilized at the same time, they took two hatching batches. For the first batch, it took eight days and 11 hours incubation to hatch the first few eggs starting from sunset and continued until sunrise. Hatching stopped in daylight. The second batch started hatching at the next sunset at nine days and 11 hours incubation period. All eggs hatched before sunrise at 10 days and one hour (Table 1). It took a total of 38 hours (one day and 14 hours) to hatch all eggs from the initial hatching.

At two days of incubation, the organs were formed followed by the beating of the heart. Melanophores started being formed on the head, optic cup and on the base of pectoral fin rudiments with the formation of vitelline circulatory system at three days period. At 6 days, the mouth started opening, preceding its formation with simultaneous dull-brown coloration of the eyeball and the darkening of the eye at 8-day-old.

Comparative and developmental analysis— The egg of flyingfishes is provided with the long numerous filaments and uniformly spaced around the chorion, except *Exocoetus* which is devoid of filaments (Imai, 1959; Parin, 1960; Collette *et al.*, 1984). Egg with 1.7-1.8 mm in diameter in this study is smaller than the egg from the wild taken from Fukuoka described by Imai (1959) with 1.8-2.2 mm, but relatively similar to D'Ancona (1931) which is 1.5-1.9 mm and Breder (1938) which is 1.6-1.8 mm. The length, the number and the arrangement of filaments differs from species to species (Collette *et al.*, 1984). In *Cypselurus heterurus doederleini*, there are 55-56 filaments around the chorion with the length ranging from 13-15 mm. These filaments serve as the attaching gadget to the floating objects such as seaweeds, woods, twigs or entangling to each other in the natural condition (Parin, 1960).

A relatively long incubation period is a typical character of the flyingfishes, but the period differs from species to species (Kovalevskaya, 1982). The incubation period of *C. heterurus doederleini* differs from its congener *Cypselurus pinnatibarbatus japonicus* having an incubation period of 14 days, but almost similar to *Cypselurus opisthopus hiraii* of 9 days (Imai, 1957). In

C. heterurus doederleini, the two hatching batches with a total of 38 hours is a rare condition.

At the early embryonic development, melanophores started being formed on the head, on the optic cup and on the base of pectoral fin rudiments (Fig. 1). The melanophore formation of *C. heterurus doederleini* at 3 days incubation period is earlier than *C. pinnatibarbatus japonicus* and *C. opisthopus hiraii* showing 6 days and 9 days, respectively, but all are heavily pigmented upon hatching. The pigmentation which started from the early embryonic stage in flyingfish, *C. heterurus doederleini* and other flyingfishes might be functional to protect the body from sunlight and other ultra rays at the water surface.

The formation of vitelline circulatory system is one of the common character of demersal eggs (Kendal *et al.*, 1984). In *C. heterurus doederleini*, the vitelline circulatory system was formed following the formation of the heart, allowing the blood to circulate (Fig. 1M and O). At 6 days incubation period, the mouth became functional, followed by the darkening of the eyes and the complete formation of the body organs in the later stage. These conditions show the readiness of the larvae to search preys and eat foods upon hatching.

Larvae

Morphology and general development — Upon hatching, the larvae were well formed with considerably large fins, and capable of swimming and capturing foods. They were protected by heavy and uniform epidermal pigmentation over the entire body with individual variations (Figs. 2 and 3). Larvae were phototaxic, actively swimming at the surface and around the light. At night, they were motionless with their pelvic and their pectoral fins widely opened.

The growth rate of the larvae were low in a week-old stage but accelerated in postlarval stage (Fig. 4). Larvae attained the length almost twice after 11 days (Table 2) with negative allometric growth ranging from $b = 0.078$ to $b = 0.571$ (Table 3).

Comparative and developmental analysis — The size at hatching in this study has an average total length (TL) of 6.07 mm with a peripheral egg yolk larger than that described by Imai (1959). This comparison bears a question, because the newly hatched larvae (6.07 mm TL) from the artificially inseminated eggs with 1.7-1.8 mm in diameter in this study were larger than the newly hatched larvae (4.7 mm TL) from the wild eggs with 1.8-2.2 mm in diameter described by Imai (although the number of specimens observed was not mentioned).

The color variation between day and night in each larva has an adaptive process. The melanophores that were exhibited by day protect the body and its appendages from sunlight and other external influences. Likewise, xanthophores at night might do the same. However, the absorption of some light rays changes the colors and reflect yellowish-pinkish color at the outer layer of the skin. The heavy pigmentations through-out the developments suggest a high resistance from the external damaging factors. At night, larvae were motionless with their pelvic and their pectoral fins widely open. This behaviour maintains the body against pitching and rolling while at rest.

The growth of larvae was considerably higher in the postlarval stage. This curve may be related with the ability to search foods and to feed actively. The negative allometry was related with the elongation of body structure. This evolutionary body transformation resulting in the elongate and slender body (Fig. 5) is homologous to the elongation of the pectoral fins, pelvic fins, lower lobe fin and the initial gliding at the postlarval stage or at the early juvenile stage.

Prospective — The importance of flyingfish, *Cypselurus heterurus doederleini* (tsukushi tobiuo) as a potential economic species has received little attention in any wide-range for the biologists and aquaculturists. As described above, an artificial seed production of the flyingfish is one of the possible alternatives for marine aquaculture, though seed production problems such as the occurrence of diseases, high mortality rate and other cultural problems may possibly occur.

More biological and cultural studies are therefore needed to provide vital informations for whatever may have in near future.

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