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FULL PAPER

Occurrence of Ayu (*Plecoglossus altivelis*) larvae in northern Vietnam

Hau Duc Tran · Izumi Kinoshita · Thuy Thi Ta · Kensaku Azuma

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Abstract The early life history of Ayu (*Plecoglossus altivelis*) was investigated in the Kalong and Tien Yen River systems, northern Vietnam, which is probably the most southern distribution locality for this species, during the period of November 2010 to February 2011. A total of 248 larvae were captured in the Kalong, and none were collected in the Tien Yen. There was little difference in development between the Kalong larvae and those of *P. a. altivelis* and *P. a. ryukyuensis*. Temperatures and salinities when the larvae were collected ranged from ca. 12 to 21°C and from ca. 3.5 to 30 psu. The preflexion to flexion larvae (primarily preflexion with yolk, 5.2–12.9 mm BL) occurred in the central current from December to February, with a peak abundance in early January. The flexion to postflexion (primarily postflexion, 14.1–23.8 mm BL) larvae occurred in the bank waters from early January to late February. The larval occurrence in the Kalong was 1–2 months later than for *P. a. altivelis* in Japan and *P. a. ryukyuensis* in the Ryukyu Islands, probably because of the delay until a reasonable photoperiod for the start of spawning in the lower latitudinal region. The larvae were never collected from the sea, where the temperatures were lower than in the river and estuary in January and February, unlike in Japan.

Keywords Ayu larvae · Ontogeny · Distribution · Kalong River · Vietnam

H. D. Tran (✉) · I. Kinoshita
Usa Institute of Marine Biology, Kochi University,
Tosa, Kochi 781-1164, Japan
e-mail: tdhauzoo@yahoo.com

I. Kinoshita
e-mail: muhomatu@kochi-u.ac.jp

T. T. Ta
Hanoi National University of Education,
136 Xuan Thuy, Cau Giay, Hanoi, Vietnam

K. Azuma
Nishinihon Institute of Technology, Shimanto Research Center,
2-1-13 Watarigawa, Shimanto, Kochi 787-0050, Japan

Introduction

The Ayu, *Plecoglossus altivelis* (Osmeridae) (sensu Nelson 2006), is an amphidromous fish with an annual life cycle, spawning in the lower reaches of rivers in autumn. Newly hatched larvae are immediately swept downstream to the sea, where they spend the winter months until ascending rivers as juveniles in spring. This species is distributed from the Panke Pond, Hokkaido (ca. 45°N), to the Ryukyu Islands (ca. 26°N) in the Japanese Archipelago, and from Chongjin, northern Korea (ca. 42°N), around the Korean Peninsula, along Chinese coasts (Liaoning, Hebei, Shandong, Zhejiang, Fujian, Guangxi, and Taiwan), to the Kalong River (the Bac-Lon River in Chinese), northern Vietnam (ca. 21°30′N) on the continent (Guangxi Huangzu Zizhiqu Institute of Fisheries and Institute of Zoology Academia Sinica 1981; Kawanabe and Sakurai 1982; Hosoya 2002; Shan et al. 2005). It should be determined whether the distributional regions of this species are the most latitudinally expanded of all amphidromous fishes.

The *P. altivelis* distributed in the Japanese Archipelago had been divided into two subspecies, i.e., the Ayu *Plecoglossus altivelis altivelis* from Hokkaido to the Yakushima Island and the Ryukyu-ayu *Plecoglossus altivelis ryukyuensis* in the Ryukyu Islands (Nishida 1988; Yonezawa et al. 2010). On the other hand, although the Chinese Ayu was recently nominated as a subspecies (*Plecoglossus altivelis chinensis*), differing from either

P. a. altivelis or *P. a. ryukyuensis* (see Shan et al. 2005), on the basis of morphology, this differentiation is problematic because of having too poor characters to compare among the Ayu populations. Thus, the status of continental populations is uncertain.

In Japan, it was found that Ayu larvae appeared abundantly in the surf zone of sandy beaches (Senta and Kinoshita 1985), and subsequently it was shown that a proportion of Ayu larvae and juveniles remains and grows within the estuary (Tsukamoto et al. 1989; Takahashi et al. 1990; Aljamali et al. 2006). However, little is known about the early life history of the continental Ayu.

Recently, the Ayu population has decreased greatly in Japan, and it was hypothesized that this phenomenon can be attributed to an increase in sea water temperatures and more frequent larval mortality due to higher temperatures because of global warming (Takahashi et al. 1999, 2003). Is this true? We fortunately were able to collect Ayu larvae in the Kalong River, which is probably their southernmost distributional area. Therefore, we could ask how Ayu lead their early life history in tropical waters. Our goal was to answer this question and to compare the early life history of the Kalong Ayu with that of *P. a. altivelis*. In this study, we provide a detailed description of the larval Vietnamese Ayu, and information on the seasonal and spatial distribution of the larvae.

Materials and methods

We investigated two rivers, the Kalong and Tien Yen River systems, northern Vietnam, from November 2010 to February 2011 (Fig. 1). Of these, the former yielded Ayu larvae. Accordingly, we should document using materials from the Kalong River. The Kalong River flows into the northernmost Vietnamese coast on the Gulf of Tonkin, the headwaters are located in China, and the lower part of the river runs along the border with China. The Kalong estuary has a large area of tidal flats with an average tidal range of 3–4 m (Vietnam Administration of Seas and Islands, Marine Hydrological Center 2010).

Surveys for dynamic sampling of the Ayu larvae, which were categorized into early and late larval periods, were made monthly from November to December 2010 and bimonthly from January to February 2011. Because of aggregation at the surface in the early larval period (Tago 2002a; Aljamali et al. 2006; Yagi et al. 2006; Zhong 2006), we made horizontal tows only at the surface, in the center of the current, with a larva net (1-m mouth diameter, 0.5 mm mesh-aperture) at stations L0–L12. For the immigrated larvae, a small seine net (1 × 4 m, 1-mm mesh aperture) (Kinoshita et al. 1988) was used at stations S1–S13 in the bank waters around the Kalong River system. A day's collection usually consisted of one to four hauls at each bank water station. Most of stations were surveyed regularly, but stations L0, L1, L1′, L10, and L12 for the larva net and stations S2, S3, S6–S8, and S12′ for the seine net had to be temporarily surveyed in each monthly collection according to the tidal schedules (Fig. 1).

Samples were fixed in 10% formalin in November and December, and directly in ca. 80% ethanol in January and February for a future molecular study. Immediately sorted Ayu specimens were transferred to 80% ethanol, with their sizes subsequently being measured by developmental stages (Kendall et al. 1984). In this study, unlabeled lengths indicate body length (BL) (notochord length for preflexion and flexion larvae and standard length for postflexion larvae). The size ranges of the larvae on which the descriptions were based were: preflexion with yolk, 5.2–7.8 mm ($n = 11$); preflexion without yolk, 5.8–10.9 mm ($n = 21$); flexion, 11.5–14.1 mm ($n = 5$), and postflexion, 16.1–23.8 mm ($n = 13$). Observations and drawings of Ayu larvae were made with a binocular microscope and camera lucida. A representative series of samples used in this study were deposited at the Usa Institute of Marine Biology (UKU-194001001–194001009), Kochi University. In the present study, *Plecoglossus altivelis* is used as the scientific name, because we do not know whether the Vietnamese Ayu is identified as the *P. a. altivelis* or other subspecies.

Water temperatures (°C) and salinities (psu) were measured at the surface and bottom of each bank water station (stations S1–S13) and at 1-m-depth intervals from the surface to the bottom of each station along the center of current (stations L0–L13) using a Water Quality Checker (WQC-22A, TOA DDK). At station L13, water parameters were only measured in December and early January.

Results

Description of larvae (Figs. 2, 3)**.** Flexion larvae (Fig. 2e) were identified to the species based on the myomere counts (62–65), distinctive pigmentation on the dorsal margin of the caudal peduncle, and formation of dorsal and anal fins (Uchida 1958). Identification of larvae at a stage earlier than flexion was verified by melanophore patterns traced back from the flexion-stage larvae. Additionally, our larvae could be distinguished from salangid fishes, whose larvae morphologically and meristically resemble Ayu larvae, but with closely located dorsal and anal fins.

The larvae are very elongate and have 60–65 myomeres (40–45 + 19–21). The straight, long gut reaches to 76–78% BL, and the anus hardly migrates throughout the larval period (Figs. 2, 3a). Initially, the body depth, head

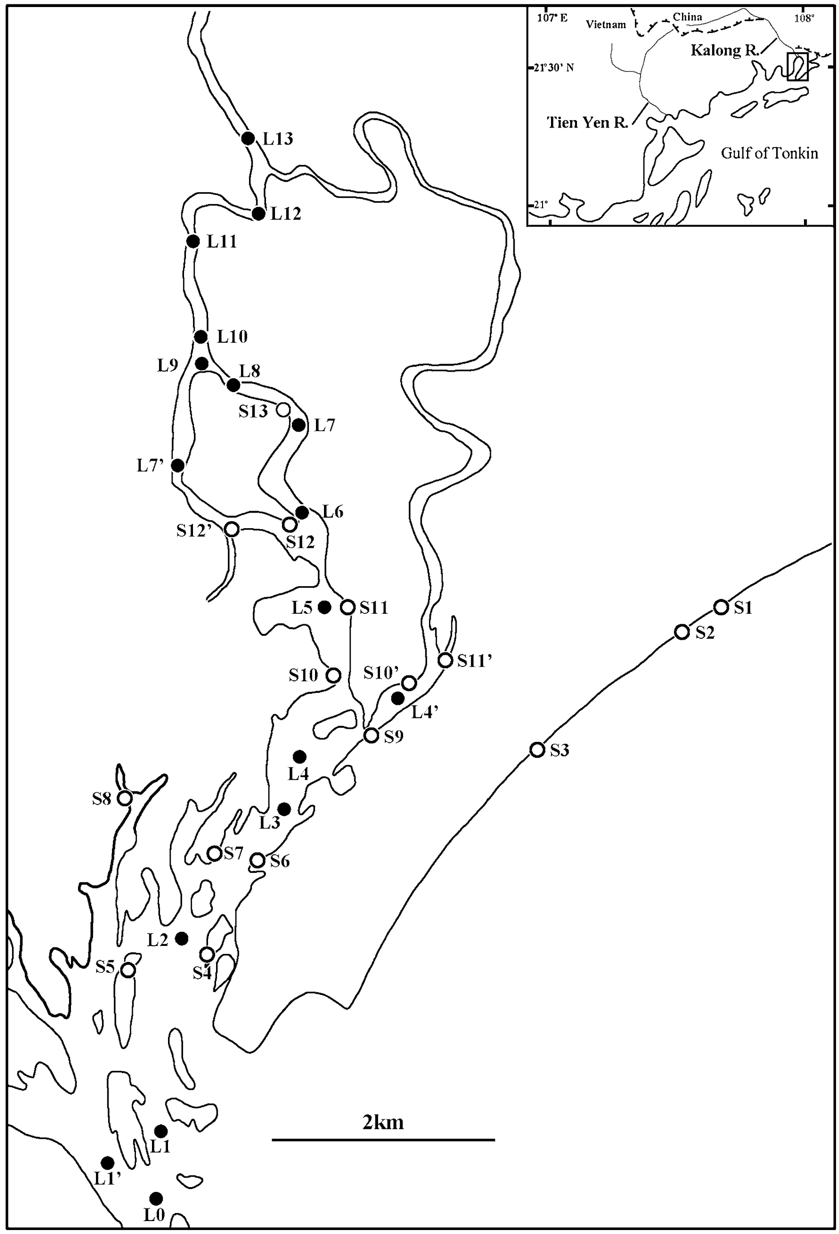

Fig. 1 Chart showing stations where surveys were carried out in the Kalong River system, northern Vietnam, from November 2010 to February 2011. Stations where Ayu larvae were sampled are indicated by *solid circles* (stations L0–L12, larva net) and *open circles* (stations S1–S13, seine net)

length, and eye diameter are ca. 8, 15, and 6% BL, and gradually decrease to ca. 5, 11, and 3% BL, respectively, until ca. 12 mm, after which they all begin to increase, and attain ca. 9, 16, and 5% BL, respectively, at ca. 20 mm (Figs. 2, 3b–d). This turning point occurs during the flexion larval period. The snout length increases from ca. 1 to 4% BL with growth (Figs. 2, 3e). Most of larvae smaller than 8 mm retain some the yolk, which is completely consumed by about 9 mm (Fig. 2a, b). Larvae less than 9 mm have only the pectoral fin placed low on the body (Fig. 2a, b). Incipient pectoral rays are present at ca. 24 mm (Fig. 2i). The caudal anlage begins to develop at ca. 9 mm, pushing up the notochord tip during 14–15 mm, with notochord flexion and the rays being completed at ca. 16 mm (Fig. 2c–f). The anal and dorsal anlagen are present at ca. 12 and 14 mm, respectively (Fig. 2d, e), with myomeres between two anlagen numbering ca. 15 (Fig. 2e); their incipient rays start to differentiate in larvae smaller than 16 mm (Fig. 2f), and the full complements of these fin rays are present at ca. 20 mm (Fig. 2g). The pelvic bud appears slightly anterior to the dorsal-fin origin (myomere 20–21) at ca. 21 mm (Fig. 2h). The adipose fin, located directly over the anal fin, begins to form at ca. 14 mm as a gradual thickening of the finfold.

The operculum does not cover the posterior-most gill filaments at least until ca. 24 mm (Fig. 2e–i). The nasal pit is differentiated by ca. 14 mm and starts to divide at 20 mm (Fig. 2e, g).

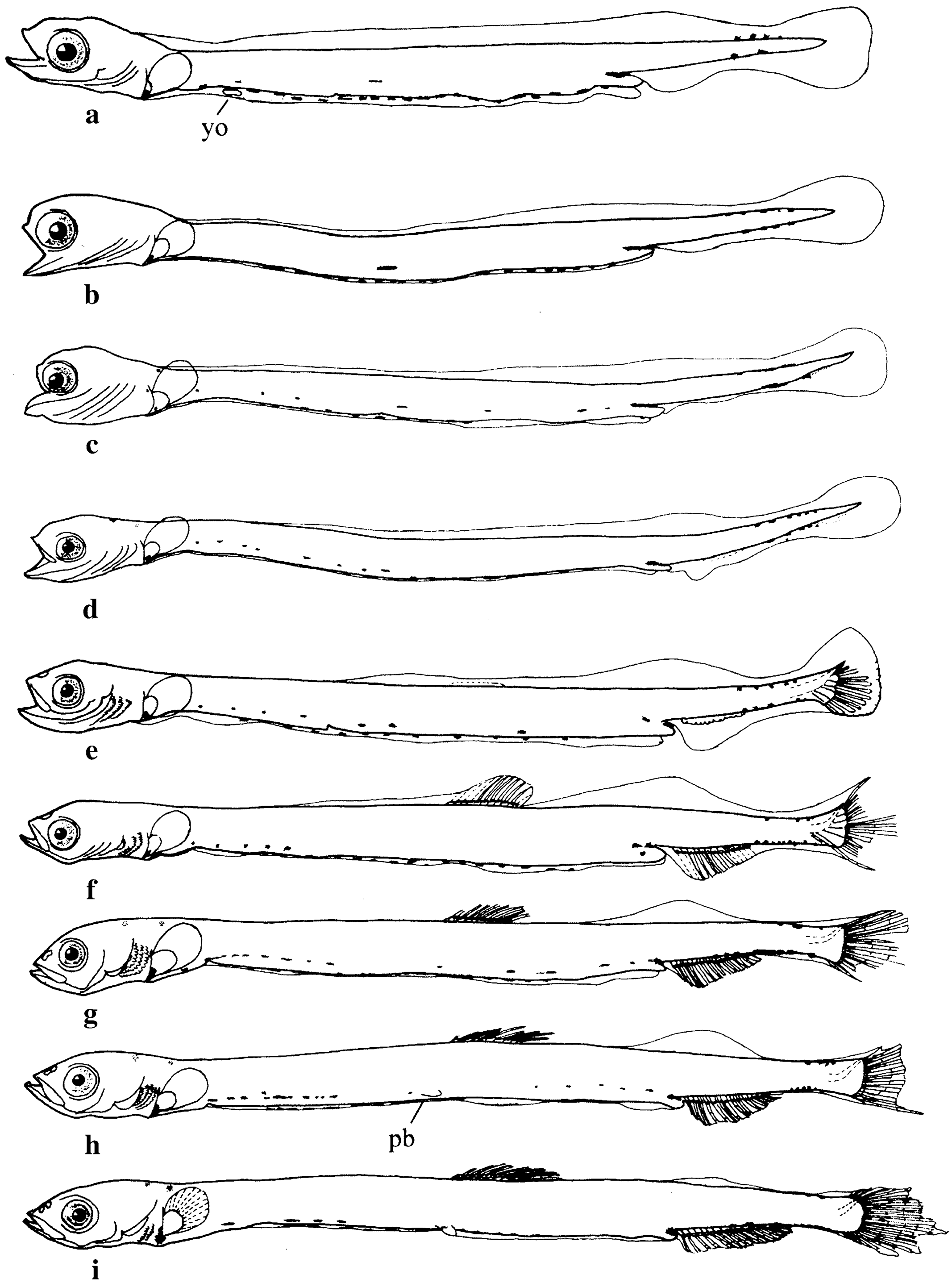

Fig. 2 Developmental stages of Ayu *Plecoglossus altivelis* from the Kalong River system. **a** The 5.2-mm preflexion larva with yolk (UKU-194001001); **b** 5.8-mm preflexion larva without yolk (UKU-194001002); **c** 9.3-mm preflexion larva without yolk (UKU-194001003); **d** 11.5-mm flexion larva (UKU-194001004); **e** 14.1-mm flexion larva (UKU-194001005); **f** 16.1-mm postflexion larva (UKU-194001006); **g** 20.0-mm postflexion larva (UKU-194001007); **h** 21.3-mm postflexion larva (UKU-194001008); **i** 23.8-mm postflexion larva (UKU-194001009). **a–d** and **e–i** Specimens taken from river channel and bank water, respectively. *pb* Pelvic bud, *yo* yolk

Initially melanophores are distributed behind the cleithral symphysis, dorsal to the anus, along the dorsal and ventral margins of tail posterior to the anus; a single row of melanophores is found along the ventral midline of the gut; and two rows of melanophores at long intervals dorsolaterally on the fore- and midgut (Fig. 2). The latter rows are

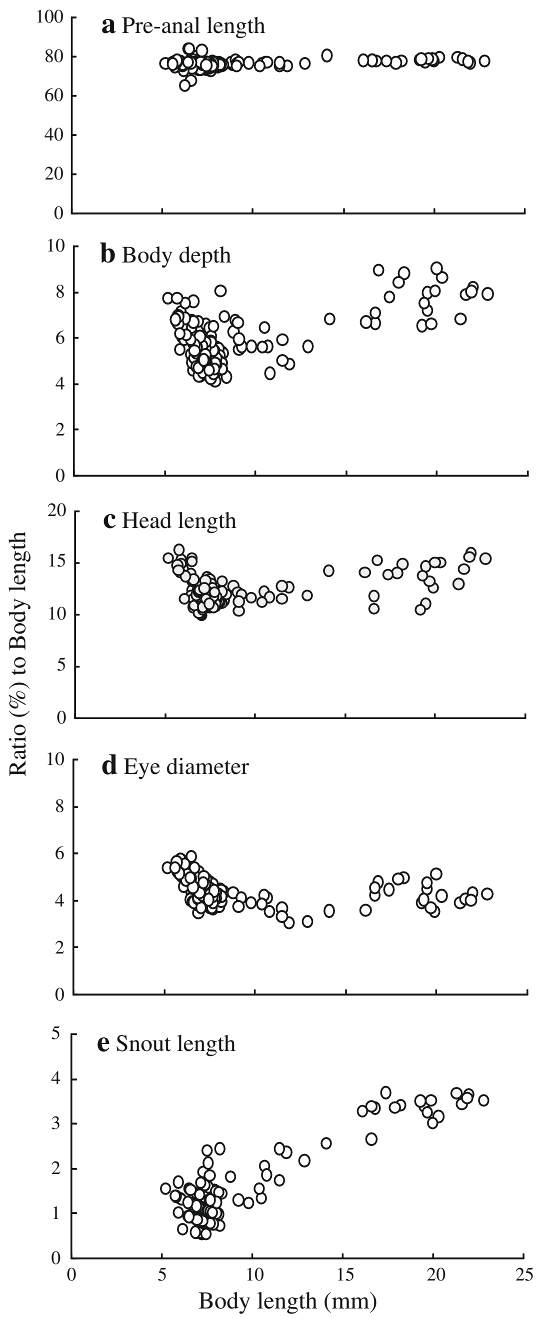

Fig. 3 Sequence of changes in the ratio of each measured part to the body length of the Vietnamese Ayu larvae

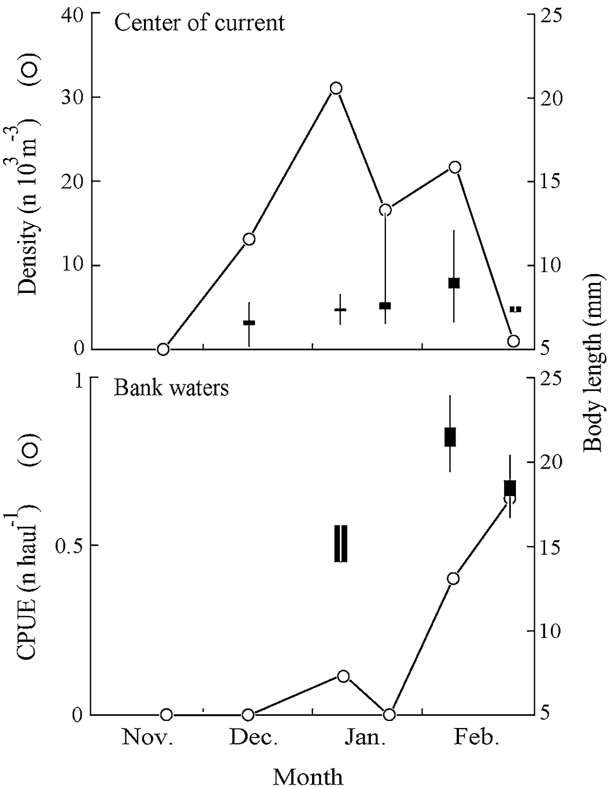

Fig. 4 Seasonal occurrence of the Ayu larvae in two habitats in the Kalong River system from November 2010 to February 2011. *Vertical lines* and *thick bars* denote ranges and mean values (±SE) of body length, respectively

gradually denser with growth. In postflexion larvae, the caudal fin membrane and anal fin base begin to bear melanophores (Fig. 2f). From the flexion larval stage, internal melanophores appear irregularly in the occiput to shoulder (Fig. 2d–i).

Distribution of larvae in the center of the current. A total of 227 Ayu larvae were collected from December to February, with a peak abundance in early January (Figs. 4, 6). They were preflexion to flexion larvae (chiefly preflexion with yolk), ranging from 5.2 to 12.9 mm in size. Larvae less than 8 mm were predominant, and only 30 larvae were larger than 8 mm (Fig. 5). The mean size did not change seasonally except that larger larvae occurred from middle January to middle February (Fig. 4). The larvae were collected only at the river stations (stations L6–L12) from December to early January, and gradually expanded to be distributed toward the estuary until middle February; subsequently few appeared in late February (Fig. 6).

The Kalong River system was vertically well mixed and received tidal exchange of water, except for a stratification in temperature in late February (Fig. 7). The river temperatures were over 20°C until December and decreased suddenly to around 15°C in early January. The temperatures and salinities when the larvae were collected ranged from 12.1 (middle January) to 21.3°C (December), and from 3.5 (December) to 29.8 psu (middle January), respectively.

Distribution of larvae in the bank waters. A total of 21 larvae were collected in the bank waters in January and February (Figs. 4, 6). They were composed of flexion and postflexion larvae (mostly postflexion), ranging from 14.1

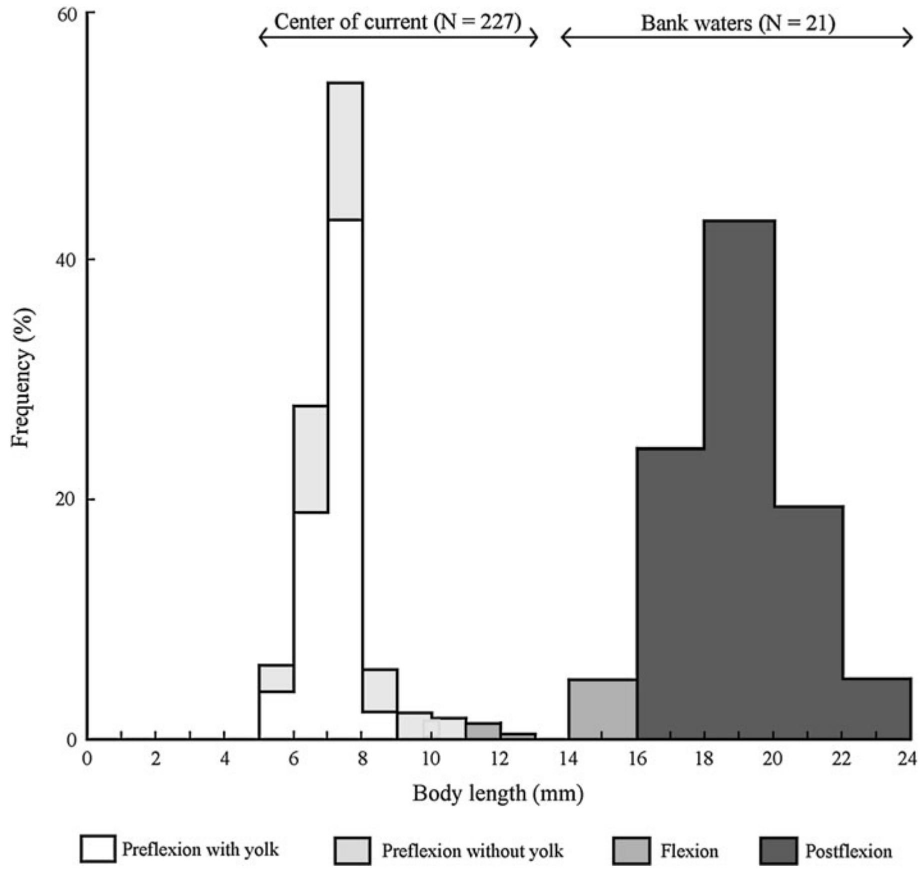

Fig. 5 Comparisons of sizes and developmental stages of the Ayu larvae collected between two habitats in the Kalong River system from November 2010 to February 2011

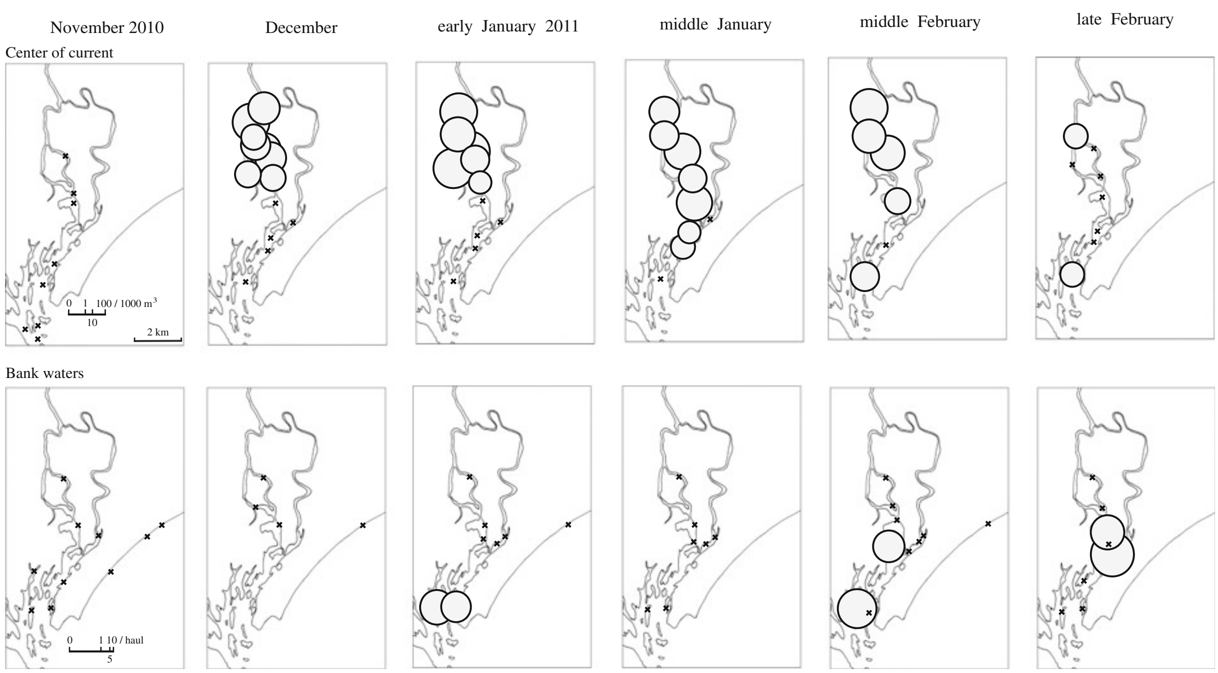

Fig. 6 Seasonal changes of horizontal distributions of the Ayu larvae collected in the center of current by a larva net and the bank waters by a seine net around the Kalong River system from November 2010 to February 2011. The diameter of each *circle* is drawn in proportion to the cube root of density (n/1,000 m^3) in the *upper* and CPUE [n/haul (ca. 50 m)] in the *lower* panels. *Crosses* represent no Ayu larvae

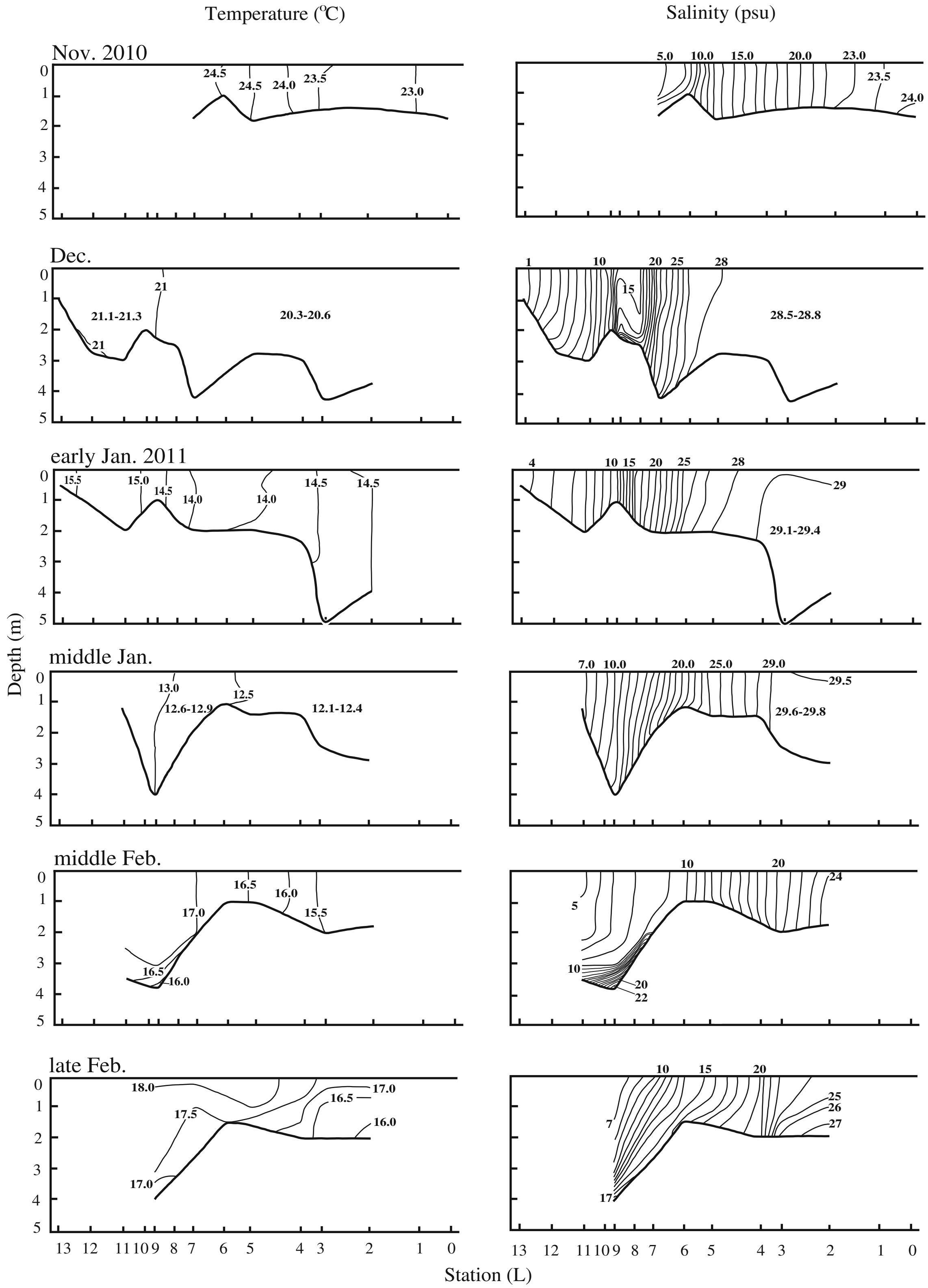

Fig. 7 Seasonal change in the vertical profiles of physical parameters along an axis from station L13 to L0 in the Kalong River system from November 2010 to February 2011 (see Fig. 1)

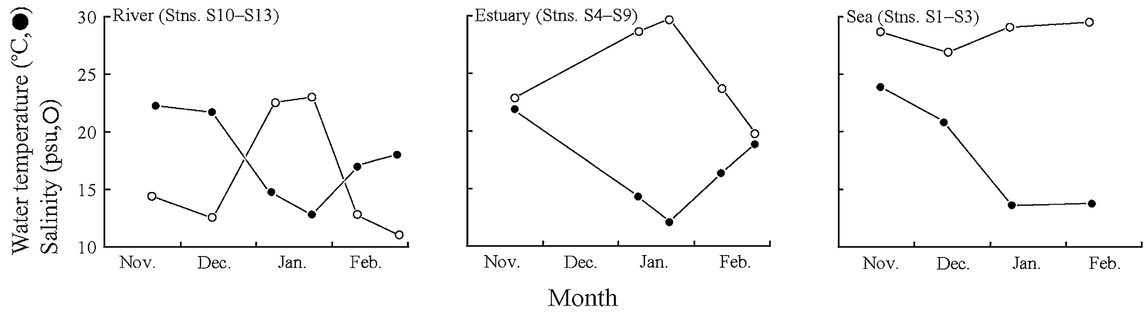

Fig. 8 Seasonal changes of mean temperatures and salinities in bank waters around the Kalong River system from November 2010 to February 2011. Surveyed stations were topographically categorized into a river (stations S10–S13), estuary (stations S4–S9), and sea (stations S1–S3) areas (see Fig. 1)

to 23.8 mm, with a mode at 18–20 mm (Fig. 5). The larval sizes changed irregularly, with the largest mean value in middle February (Fig. 4). The CPUE increased seasonally until late February, except for no larvae in middle January, then subsequently tended to continue to rise after February. The larvae occurred only at the estuarine stations in January and started to be found at the river stations in February. No larvae were found at the sea stations (Fig. 6).

Seasonal changes in average water temperatures and salinities divided by three topographical areas are shown in Fig. 8. The average temperature was lowest in middle January in the river and estuary, and in January in the sea. Salinity was higher in the sea area. Seasonal relationship between the temperature and salinity revealed a reciprocal pattern. However, lower temperature of the river and estuary in January seemed to be not seasonally but tidally influenced by colder water from the sea.

Discussion

When *Plecoglossus altivelis* larvae from Vietnam were compared with *P. a. altivelis* (see Uchida 1958; Tachihara and Kimura 1991; Saruwatari 1995; Takahashi et al. 2000; Azuma 2005) and *P. a. ryukyuensis* (see Tachihara and Kawaguchi 2003), there were few differences in morphology or pigmentation. Among three types, the developmental sequence of fins hardly showed differentiation, and the developmental progress to size could not be found, probably because of a disturbance by different temperatures in which each type of larva was distributed. Although Tachihara and Kawaguchi's *P. a. ryukyuensis* larvae were reared, comparing morphometrically among the three types, a proportional turning point occurred at ca. 12, 14–18, and 15 mm in the Vietnamese Ayu, *P. a. altivelis* and *P. a. ryukyuensis*, respectively. Furthermore, the proportional body depth of the three types was similar until each turning point; thereafter, the three types had different body depths, with *P. a. altivelis* the most slender and *P. a. ryukyuensis* the deepest. A planned genetic study will be necessary to determine whether the Vietnamese Ayu are *P. a. altivelis*, *P. a. ryukyuensis*, or another subspecies.

The preflexion larvae with yolk were found from 12 December to 24 February, but were not common. If the embryonic period was the same as that of *P. a. altivelis* and *P. a. ryukyuensis*, the Vietnamese Ayu would have spawned from late November to middle February. This is 1 and 2 months later than *P. a. altivelis* in southern and northern Japan, respectively, and less than 1 month later than *P. a. ryukyuensis* (see Kishino and Shinomiya 2004; Kishino 2009). In late November when the Vietnamese Ayu are presumed to have started to spawn, the daylight length and temperature were estimated at ca. 11 h and 22°C (http://www.timeanddate.com; Figs. 7, 8). On the other hand, daylight length was ca. 12 h at the spawning time of *P. a. altivelis* and <11 h in *P. a. ryukyuensis*, and the temperature was <20°C in the both the Japanese subspecies (Kishino and Shinomiya 2004). Therefore, the temperature was much higher when the Vietnamese Ayu were presumed to spawn, but there was little difference in daylight length among the three types. Accordingly, if shortening a photoperiod can stimulate gonadal development (Shiraishi and Takeda 1961; Shiraishi 1965), the Vietnamese Ayu surely should begin to spawn latest because of delay until a reasonable photoperiod for start of spawning in the lower latitudinal region.

The *P. a. altivelis* larvae immigrate to the bank waters in estuaries or the sea from October to May with the greatest abundance in November or December (Senta and Kinoshita 1985; Azuma et al. 1989; Takahashi et al. 1990; Tago 2002b; Aljamali et al. 2006), but little is known about distributional duration for *P. a. ryukyuensis* (see Oka et al. 1996). Compared with *P. a. altivelis*, the Vietnamese larvae occurred ca. 2 months later in estuarine bank waters, and their CPUE was much lower during the study period. Considering the delay occurrence, it is conceivable that the Vietnamese larvae aggregate in March and April like the *P. a. altivelis*.

A number of the larval remainders of *P. a. altivelis* were found in some estuaries of Japan (Tsukamoto et al. 1989; Takahashi et al. 1990; Aljamali et al. 2006). In the present study, no larvae in any of the sea stations seemed to demonstrate the same phenomenon as *P. a. altivelis*. Our sampling in the sea was limited, so it is possible that the Vietnamese Ayu is found in the sea, albeit infrequently. The Vietnamese remainders were likely attributable to the following two factors: (1) our preflexion larvae with yolk were not just hatched, but had consumed much of their yolk. This fact might suggest a long lapse following hatching, which could allow the larvae to be swept from their spawning grounds to the estuary. (2) In spite of a tropical area, the temperatures of the sea were lower than those of the river and estuary in January and February (Figs. 7, 8), when the larvae were predominant. In the same months in Japan, however, temperatures are much higher in the sea than in rivers and estuaries (Takahashi et al. 1990; Aljamali et al. 2006). In northern Vietnam, this thermal situation possibly makes the larvae less likely to be swept into the sea.

Why were the sea temperatures of the coast facing the northern Gulf of Tonkin so cold? A southwest cold current passes the Taiwan Strait probably from the Yellow Sea as a reaction against the Kuroshio Current flowing northeastward along the eastern edge of Taiwan (Sverdrup et al. 1961; Wyrtki 1961; Endo 1987). This cold current flows counter-clockwise along the northern Vietnamese coasts.

Few flexion larvae of around 12 mm were collected both in the center of the current and bank waters (Fig. 5). In *P. a. altivelis* larvae of Japan, flexion larvae are aggregated at the surface or dispersed vertically when the water column is stratified or mixed, respectively (Tago 2002a; Aljamali et al. 2006; Yagi et al. 2006). In the Kalong River system, the water column was mixed during the present study (Fig. 7). Accordingly, the flexion larvae seemed to be dispersed vertically, and there was little occasion for them to be sampled because of their extremely lower density. In any case, it is clear that the larvae immigrate to bank waters when they attain the postflexion stage beyond 16 mm.

The Ayu larvae were absent in the Tien Yen River during the sampling period. There seem to be two possibilities to explain this: (1) that this river is beyond the southernmost border of the distribution, and (2) some features of the Tien Yen make it unsuitable for Ayu spawning grounds.

It is significant that temperatures of the river and estuary were much higher in the Kalong River than in any of the Japanese rivers during the early life period of the Ayu, and the present study could reveal that they are still breeding in the tropical region.

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