Abstract: The ontogeny of *Ilisha elongata* was reviewed, and their early distribution was examined because information on the early life history of this species is limited. Revision in ontogeny revealed several unique characteristics to this species, such as two chorions in the egg and a more anterior pelvic bud (fin) position. These characteristics contrast strikingly with the clupeid fishes, suggesting that this species belongs to the Pristigasteridae and not to the Clupeidae. Data from ichthyoplankton collected in March, May, July and November suggest that *I. elongata* spawned just off river mouths in summer and attained peak spawning in June. The larvae with elliptical eyes migrated inside the rivers, where the waters were more turbid. Thus, the spawning and nursery grounds of *I. elongata* almost entirely overlapped with those of the clupeid *Sardinella zunasi* both temporally and spatially, which may result in larval competition between the two species.

Keywords: Ariake Sound, early life history, egg, *Ilisha elongata*, larva

Introduction

Recently, *Ilisha elongata* (Bennett, 1830) was reassigned to the family Pristigasteridae (subfamily Pelloninae) (Nelson et al. 2016). Although once considered a subfamily of the family Clupeidae (Nelson 1967), Nelson (1970) and Grande (1985) elevated it to the rank of superfamily owing to the unique characteristics of these fish. Di Dario (2002) determined this superfamily to be a basal group of Clupeoidei. There is no doubt that this group is at least independent from Clupeidae, being farthest from Pristigasteridae, as reported by Whitehead (1985).

In the western Pacific, *I. elongata* is widespread in the Java Sea, along the northern coast of Australia to Queensland, and from the South and East China Seas to Peter the Great Bay, i.e., from tropical to cooler humid waters (Whitehead 1985, Mohsin & Ambak 1996, Isa et al. 1998, Carpenter & Niem 1999). In Japan, *I. elongata* is present from Okinawa to western Niigata facing the Japan Sea, and to eastern Hokkaido facing the Pacific, principally in Shimabara Bay, Kyushu, and the Seto Inland Sea (Uchida 1958, Whitehead 1985, Yamada et al. 2007, Aonuma & Yagishita 2013).

Shimabara Bay is the largest tidal flat region with the highest tidal range in Japan, of which the Ariake Sound is the innermost part, and contains brackish, highly turbid water with strong tidal currents (Inoue 1980, Yagi et al. 2011). The importance of this upper estuary as a nursery ground has been demonstrated for diverse fish, including clupeid fish, i.e., *I. elongata*, *Coilia nasus* Temminck & Schlegel, 1846, *Sardinella zunasi* (Bleeker, 1854) and Ko-
nosirus punctatus\textsuperscript{(*)} (Temminck \& Schlegel, 1846), which lead their early life history stages there, from spring to summer, with the periods overlapping between the species (Yagi 2010, Yagi et al. 2011). It is speculated that some niche isolation should occur to avoid competition within the estuaries. The early life histories of the engraulid $C. nasus$ and the clupeid $S. zunasi$, both of which are abundant in summer, have been studied in Ariake Sound (Takita 1966, 1967, Ishida \& Tsukahara 1972, Yagi 2010, Simanjuntak et al. 2015, Simanjuntak 2016, Ito et al. 2018). The eggs and larvae of the clupeid $K. punctatus$ are present from late winter to early summer in various waters in Japan and the Korean Peninsula, but they have not been reported in Ariake Sound (Yoshida 1937, Matsushita \& Nose 1974, Kawasaki et al. 2006). Although the reproductive ecology of $I. elongata$ has been examined in Ariake Sound and the Seto Inland Sea (Zhang \& Takita 2007, Zhang et al. 2009, Masui et al. 2016), its early life history has only been investigated sporadically in the Geum estuary in western Korea, around the Hangzhou estuary in central China, and in Ariake Sound. Accordingly, little is known about the distribution of the egg and larval stages of this species in any region (Yabe 1938, Sha \& Ruan 1981, Yagi et al. 2011).

In this paper, we reviewed the ontogeny of $I. elongata$, and examined their egg and larval distributions in Ariake Sound to better understand its early life history. Furthermore, we assessed its early stages to understand the distribution dynamics.

**Materials and Methods**

Early-stage fish specimens were collected in the Ariake Sound in Shimabara Bay during each spring tide in March, May, July and November 2019 (Table 1). Pelagic eggs and larvae were collected by oblique tows using a larva net with a 1.3-m mouth diameter. The mesh aperture of the larva nets were 0.5 mm at the sea stations (outside river: Stns. 1–8, 16, 17, 33–38, 47–54, 61, 62 and 70 in Fig. 1), and 1.0 mm at river stations (inside river: Stns. 0–5, 6–13, 30, 37, 38, 48, 49, 50–52 and 73) to avoid clogging of the net. The eggs and larvae of the clupeid $K. punctatus$ are present from late winter to early summer in various waters in Japan and the Korean Peninsula, but they have not been reported in Ariake Sound (Yoshida 1937, Matsushita \& Nose 1974, Kawasaki et al. 2006). Although the reproductive ecology of $I. elongata$ has been examined in Ariake Sound and the Seto Inland Sea (Zhang \& Takita 2007, Zhang et al. 2009, Masui et al. 2016), its early life history has only been investigated sporadically in the Geum estuary in western Korea, around the Hangzhou estuary in central China, and in Ariake Sound. Accordingly, little is known about the distribution of the egg and larval stages of this species in any region (Yabe 1938, Sha \& Ruan 1981, Yagi et al. 2011).

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Beam trawl (width, 1.5 m; height, 0.25 m; 2-mm mesh aperture), modified according to the description of Kuipers (1975), conducted at Stns. 0–8, 16, 17, 33–38, 47–54, 61, 62 and 73 for collecting demersal juveniles. The towing distance of the beam trawl was monitored by GPS (GPSMAP 64s, Garmin).

The number of individuals ($n$) was converted to density ($N$: inds. 100 m$^{-2}$) using the following equations;

\[ N_{LN} = \frac{n \times d \times 100}{A \times D} \]

where $A$ is the area (m$^2$) of the larva net, $D$ is the towing distance (m), and $d$ is the towing depth (m) for the larva net;

\[ N_{BT} = \frac{n \times 100}{w \times D} \]

where $w$ is the width (m) of beam trawl, and $D$ is the towing distance (m) for the beam trawl.

A small seine net (1×4 m, 1-mm mesh aperture) (Kinoshita et al. 1988) was also used to collect larvae and juveniles that migrated to the littoral zone at Miike beach during all months except November.

All samples were initially fixed with ca. 10% seawater formalin. Eggs and larvae were immediately sorted and preserved in 10% formalin and 99% ethanol, respectively. Eggs and larvae of $Ilisha elongata$ was distinguished from other eggs and larvae in the Ariake Sound by the following characteristics: double chorions; oil globule to egg diameter proportions; the moderate perivitelline space for eggs; the extremely posterior oil globule in the yolk for yolk-sac larvae; the myomere counts of 54–58 for larvae; the anal ray counts of 43–49 for larvae and juveniles (Yabe 1938, Uchida 1958, Mito 1966, Sha \& Ruan 1981). The developmental stages of eggs, larvae and juveniles were counted based on the ontogeny of the embryo (A–C, Nakai 1962), notochord tip and completion of fin rays (Kendall et al. 1984), respectively. Unlabeled lengths indicate body length (BL) (notochord length for prefexion and flexion larvae, and standard length for postflexion larvae and juveniles). Other measurements such as eye diameter, body depth, pre-pelvic, preanal, head and snout lengths were performed according to the work of Okiyama (2014). The sample collected in July 2016 was used to describe early postflexion larvae because there was a lack of appropriate specimens in 2019. A representative series of specimens used in this study have been deposited in the Usa Institute of Marine Biology, Kochi University (UKU94000–94008).

At each sampling station, water temperature (°C), salinity and turbidity were observed at 0.5-m intervals from the surface to the bottom using a Compact-CTD (ASTD102, JFE Advantech). The current velocity was measured using an ACP (WHSZ1200-I-UG12, RD Instruments) at 0.5-m depth intervals from a depth of 1 m to the bottom.

**Results**

**Physical environment**

Of four parameters (Fig. 2), only temperatures exhibited seasonal variations, and showed small differences between rivers, estuaries and the open bay. Drastic haloclines

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(*) Temminck & Schlegel, 1846
Table 1. Survey schedule in Ariake Sound in 2019.

| Station | Latitude (N) | Longitude (E) | Date |
|---------|--------------|---------------|------|
|         |              |               | 20–24 March | 16–20 May | 2–3, 14–17 July | 11–15 November |
| 0       | 33°12.418'   | 130°8.235'    | +     | +         |                | +               |
| 1       | 33°11.734'   | 130°8.354'    | +     | +         | +               | +               |
| 2       | 33°11.730'   | 130°10.071'   | +     | +         | +               | +               |
| 3       | 33°12.005'   | 130°7.89'     | +     | +         | +               | +               |
| 4       | 33°12.159'   | 130°8.585'    | +     | +         | +               | +               |
| 5       | 33°11.817'   | 130°12.8'     | +     | +         | +               | +               |
| 6       | 33°11.383'   | 130°13.917'   | +     | +         | +               | +               |
| 7       | 33°9.833'    | 130°13.667'   | +     | +         | +               | +               |
| 8       | 33°7.733'    | 130°14.583'   | +     | +         | +               | +               |
| 9       | 33°4.233'    | 130°13.75'    | +     | +         | +               | +               |
| 10      | 33°0'        | 130°13.5'     | +     | +         | +               | +               |
| 11      | 33°56.117'   | 130°16.367'   | +     | +         | +               | +               |
| 12      | 33°54.633'   | 130°13.95'    | +     | +         | +               | +               |
| 13      | 33°53.583'   | 130°11.85'    | +     | +         | +               | +               |
| 14      | 33°51.635'   | 130°12.459'   | +     | +         | +               | +               |
| 15      | 33°54.517'   | 130°11.033'   | +     | +         | +               | +               |
| 16      | 33°9'        | 130°16'       | +     |           |     | +               |
| 17      | 33°13.239'   | 130°21.799'   | +     | +         | +               | +               |
| 18      | 33°12.442'   | 130°20.470'   | +     | +         | +               | +               |
| 19      | 33°11.179'   | 130°20.397'   | +     | +         | +               | +               |
| 20      | 33°9.538'    | 130°19.828'   | +     | +         | +               | +               |
| 21      | 33°8.484'    | 130°20.316'   | +     | +         | +               | +               |
| 22      | 33°7.583'    | 130°17.433'   | +     | +         | +               | +               |
| 23      | 33°9.140'    | 130°27.683'   | +     |           |     | +               |
| 24      | 33°8.777'    | 130°27.140'   | +     | +         | +               | +               |
| 25      | 33°8.295'    | 130°27.215'   | +     | +         | +               | +               |
| 26      | 33°7.803'    | 130°26.780'   | +     | +         | +               | +               |
| 27      | 33°7.301'    | 130°26.450'   | +     | +         | +               | +               |
| 28      | 33°6.813'    | 130°26.069'   | +     | +         | +               | +               |
| 29      | 33°5.243'    | 130°24.790'   | +     | +         | +               | +               |
| 30      | 33°3.858'    | 130°24.507'   | +     | +         | +               | +               |
| 31      | 33°7.878'    | 130°5.771'    | +     | +         | +               | +               |
| 32      | 33°7.856'    | 130°6.431'    | +     | +         | +               | +               |
| 33      | 33°7.532'    | 130°7.273'    | +     | +         | +               | +               |
| 34      | 33°7.281'    | 130°7.763'    | +     | +         | +               | +               |
| 35      | 33°6.1'      | 130°9.867'    | +     | +         | +               | +               |
| 36      | 32°51.501'   | 130°5.229'    | +     |           |     | +               |
| 37      | 32°52.282'   | 130°6.137'    | +     |           |     | +               |
| 38      | 32°53.069'   | 130°7.814'    | +     |           |     | +               |
| 39      | 32°53.663'   | 130°8.98'     | +     |           |     | +               |
| 40      | 32°52.512'   | 130°10.063'   | +     |           |     | +               |
| 41      | 32°51.17'    | 130°11.241'   | +     |           |     | +               |
| 42      | 32°51.284'   | 130°11.587'   | +     | +         | +               | +               |
| 43      | 32°53.67'    | 130°9.521'    | +     | +         | +               | +               |
| 44      | 33°4.256'    | 130°22.573'   | +     |           |     | +               |
| 45      | 33°15.001'   | 130°24.606'   | +     | +         | +               | +               |
| 46      | 33°0.712'    | 130°24.508'   | +     | +         | +               | +               |

+: surveyed stations.
were observed between the estuary and the upper reach of the rivers in all seasons, caused by the tidal exchange of water. Salinity in July was relatively lower than that in other months, because the survey was conducted at the conclusion of the rainy season. While it was notably less turbid in the open bay and Isahaya inlet in all seasons, waters around estuaries were more turbid in the Rokkaku and Hayatsue Rivers than in the Shiota and Yabe Rivers; turbidities were highest in the Rokkaku and lowest in the Yabe Rivers. Currents more than 1.5 kt were frequently measured inside and outside the estuaries during flood or ebb tides, but the velocities were constant inside Isahaya inlet. Miike beach was similar to the open bay with regards to temperature, salinity and turbidity, but velocity was weaker.

Fig. 1. Map showing stations where fish were collected in Ariake Sound, Japan. Open circles (Stns. 0–13, 30, 33–38, 42–62, 70, 73), solid circles (Stns. 0–8, 16, 17, 33–38, 47–54, 61, 62, 73) and the solid triangle (Miike beach) indicate the stations where collections were made by a larva net for pelagic eggs and larvae, beam trawl for demersal juveniles and seine net for larvae and juveniles entering the littoral zone, respectively, in March, May, July and November 2019.

Description of the eggs and larvae

Because the ontogeny of this species from the egg to juvenile stages has already been reported by Uchida (1958) and Sha & Ruan (1981), the following description will be limited to results that describe unique principal characteristic morphometries.

The pelagic eggs are spherical, 1.70–2.20 mm (principally 1.8–2.1 mm) in diameter, with a single, yellowish, relatively large oil globule 0.30–0.44 mm in diameter. The egg has moderate perivitelline space, a largely segmented yolk, and clear, smooth chorions, which are uniquely double. Pigments are utterly absent during the early stages (Fig. 3a, b), after an embryo tail is freed from the yolk, distinctive scattered melanophores begin to form dorsally on the occipital, shoulder, and oil globule, and ventrally on the separating point of the tail from the yolk (Fig. 3c).

In the larvae (ca. 5 mm) which are still consuming the
Fig. 2. Horizontal distribution of water temperature, salinity, turbidity (at 0.5 m depth) and current magnitude (at 1 m depth) when fish were collected at each station in March, May, July and November 2019. Solid and shaded arrows indicate flood and ebb tides, respectively.
yolk, the mouth, oil globule, anus and pectoral fin does not open yet, is present at the end of the yolk, opens at ca. 79% BL, and buds, respectively. Patches of small, scattered melanophores are distributed on the frontal head, dorsal shoulder, ventral abdomen, back oil globule, and ventrally just before the anus. The eye remains unpigmented (Fig. 3d).

The long, straight gut reaches 77–80% BL during the prefexion and flexion stages, and subsequently, the anus migrates gradually forward until it reaches ca. 68% BL in ca. 22 mm juveniles (Figs. 3, 4a). Initially, the head length, snout length and body depth are ca. 15, 3 and 8% BL, respectively, and gradually increase to ca. 24, 6 and 15% BL, respectively, by ca. 22 mm juvenile (Figs. 3, 4b–d). The eye is elliptical (long/short axes of 1.3–1.7) and subsequently becomes more round (long/short axes of ca.
1.1) with growth until entering the juvenile period (Figs. 3, 4f).

The ca. 8 mm larva bears no hypurals, which begin to differentiate at ca. 9 mm. Some hypurals start to push up the notochord tip at ca. 12 mm (Fig. 3e, f). Notochord flexion is almost complete at ca. 14 mm (Fig. 3g). Dorsal and anal anlagen are present at ca. 8 mm, and the number of myomeres between the dorsal termination and anal origin is 10 (Fig. 3e). Dorsal and anal rays with both rays being completely developed by ca. 18 mm larva (Fig. 3e–h). The pelvic bud is present at ca. 39% BL in ca. 17 mm postflexion larva, hardly migrating by ca. 22 mm juvenile with a completed pelvic fin (Figs. 3g, i, 4e).

Externally the visible gas bladder is differentiated with small pigments in ca. 18 mm postflexion larvae, thereafter being considerably expanded in ca. 22 mm juveniles (Fig. 3h, i).

Melanophores are distributed posteriorly to the cleithral symphysis, laterally on the foregut, irregularly along the ventral margin of the hindgut, above the rectum, on the posterior anal anlagen, the ventral margin of the caudal peduncle, the dorsal margin, and the bottom of the undifferentiated hypurals with the notochord tip between, the latter being positioned more along the caudal rays with more developed upper and lower lobes (Fig. 3e). When starting notochord flexion, the melanophores are also distributed anterior to the cleithral symphysis (Fig. 3f). Just prior to flexion completion, melanophores are absent along the hindgut and on the dorsal notochord tip (Fig. 3g). After postflexion, small melanophores appear along the cleithrum, and increase in number during the juvenile period (Fig. 3h, i). Melanophores occur on the frontal and ventral mouth tip, the dentary in two rows, dorsal margin of the caudal peduncle, and internally on the otic and hypural region in juveniles (Fig. 3i).

**Distribution of the eggs and larvae**

A total of 493 eggs, 416 larvae (4.4–21.8 mm, with a modal size at 14–15 mm), and two juveniles (22.2–22.7 mm) of *Ilisha elongata* were collected by the larva net, and a total of 13 larvae (11.5–19.3 mm, with a modal size at 13–14 mm) and four juveniles (22.5–82.7 mm) were collected by the beam trawl (Fig. 5). No eggs, larvae or juveniles were present at Miike beach in March, May, July. Most eggs were collected in May, being utterly absent in March and November (Fig. 6). November collections only

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**Fig. 4.** Ontogenetical morphometries in various parts of *Ilisha elongata* collected in the present study.

**Fig. 5.** Comparison of size and developmental stage frequencies of *Ilisha elongata* between larva net (upper) and beam trawl (lower) collection in Ariake Sound. Juveniles larger than 40 mm BL were captured in November.
Early life history of *Ilisha elongata* yielded three juveniles (40.9–82.7 mm), one from each of Stns. 5, 7 and 38, by the beam trawl (Fig. 5). Eggs were typically distributed around estuaries, of which the Shiota River produced the most abundant yield. Some yolk-sac larvae were found around the Shiota and Rokkaku estuaries in May. Thereafter, more developed larvae were more widely and abundantly distributed around all the estuaries, with the Hayatsue River having the highest density of larvae. Compared with eggs, larvae migrated further into the upper reaches of most of the rivers. Although the beam trawl was only able to collect a few larvae and juveniles, which tended to be larger than those collected by the larva net, their spatial distribution was nearly the same as the larvae caught by the larva net.

**Discussion**

Delsman (1930) collected certain eggs from the coasts of the western Java Sea and hatched them, and he provisionally identified these eggs and hatched larvae as *Ilisha elongata* by their characteristics, because it was the commoner *Ilisha* species along the north coast of the western Java Sea. However, this identification is likely suspect, because more than five species of *Ilisha* are distributed around that...
detailed the ontogeny of eggs to juveniles, where the eggs were likely caught in the field, but information regarding whether the subsequent larvae and juveniles were collected from field or reared is missing. Furthermore, regarding the relative positions of the dorsal and anal fins, these two fins in the 14.91 mm postflexion larvae in Plate 2 in Sha & Ruan (1981) are evidently closer together than those in the report by Uchida (1958) and our specimens (Fig. 3). Accordingly, that specimen is not I. elongata but is probably the engraulid Setipinna tenuifilis (Valenciennes, 1848), as reported by Young et al. (1995).

Compared with the pelagic, oil-globuliferous eggs and larvae of various clupeid fishes (Uchida 1958, Takita 1966, Noichi 2014), I. elongata bears two chorions, a much larger oil globule, narrower perivitelline space in their eggs, and a much more anteriorly positioned pelvic bud (fin) and gas bladder (Figs. 3, 4). These characteristics may indicate that I. elongata belongs to the Pristigasteridae and not to Clupeidae.

The larvae bore elliptical (narrow) eyes, which are also found in the larvae of the oxudercids [Odontamblyopus lacepedii (Temminck & Schlegel, 1845) and Tridentiger barbatus (Günther, 1861)], which are endemic to Ariake Sound (Tojima 2020), and found especially in mesopelagic myctophid fish (Moser et al. 1984), and clupeids from Lake Tanganyika (Tshibangu & Kinoshita 1995), likely suggesting adaptation to low-light environments, such as turbid waters, the deep sea and deep lakes. Uchida (1958) made no references to the above significant morphological characteristics.

Ilisha elongata eggs and larvae were more abundant in May and July, respectively. Temperatures at which eggs and larvae were collected ranged from 20.8 to 25.5°C (generally ca. 22°C) and from 21.6 to 27.3°C (generally 24–27°C), respectively. The salinities ranged from 13.6 to 31.2 (mainly 29–31) and from 1.2 to 30.9 (mainly 3–16), respectively (Figs. 2, 6). Considering these physical phenomena, it is likely that this fish temporally spawns with the most actively in June, and spatially just off the river mouth. This spawning period is almost in accordance with the results estimated by GSI and histological examinations in Ariake Sound (Zhang et al. 2009). In the Seto Inland Sea, which is another water body with high productivity, I. elongata was estimated to spawn from June to August, according to GSI observations (Masui et al. 2016), likely one month later than in Ariake Sound, and this might be attributable to differences in seasonal temperatures between the two locations.

In a western Korean estuary facing the Yellow Sea, I. elongata spawned in the upper reaches (salinity: 22–23), ca. 10 km from the river mouth (Yabe 1938). In Ariake Sound, salinities are less than 22 over the 2–8 km upper reaches from all river mouths (Fig. 2). These differences in salinity may be attributable to differences in maximum tidal distances, which is ca. 10 m in western Korea vs. ca. 6 m in Ariake Sound (Inoue 1980, Okada 1987). Thus, it is likely that the Korean spawners migrate to within the river with the greater flood tide.

In Ariake Sound, more larvae (chiefly flexion stage) than eggs were distributed inside most of the rivers (Fig. 6). This suggests that I. elongata larvae migrate upstream during development. In comparison with the larva net, the beam trawl barely collected any larvae, but it was able to collect a few large juveniles (Figs. 5, 6). The extremely low numbers of juveniles caught suggests that I. elongata do not remain in this habitat after reaching juvenile stage. No larvae or juveniles were found in the littoral zone of a tidal flat (Miike beach) (Fig. 6) and they were absent throughout the year (Hibino et al. 2002). Takita et al. (2003) reported that juveniles and adults were collected more offshore. These facts suggest that I. elongata juveniles and adult are distributed in offshore waters, rarely migrating inshore.

The larvae of Konosirus punctatus were widespread throughout Ariake Sound, including in the open bay area, estuaries and littoral zone of Miike beach, where large numbers of larvae have been found in May and June (Hibino et al. 2002, Yagi et al. 2011), so that Miike beach is likely used as their main nursery ground. In other waters such as Tosa Bay, Shikoku, K. punctatus is the most abundant species in Ariake Sound. S. zunasi can encounter I. elongata and C. nasus during the larval period. Thus, it is likely that niche competition between these two species occurs in the lower reaches of the rivers. Takita (1966) and Yagi (2010) reported that Sardinella zunasi uses the estuary off river mouths, so that the spawning and nursery grounds of S. zunasi and I. elongata almost entirely overlap both temporally and spatially. Differences in larval diet may be necessary to avoid competition between the two species. Further studies on the larval feeding ecology and the vertical distribution of these clupeoid fish are needed to sufficiently understand niche partitioning among these species in Ariake Sound.

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