

# Occurrence patterns and ontogenetic development based on the swimming- and feeding-related characters in larval and juvenile Japanese whiting (*Sillago japonica*) in the innermost Tokyo Bay, central Japan

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**Abstract:** Occurrence patterns of the larval and juvenile Japanese whiting, *Sillago japonica*, were investigated in Tokyo Bay by monthly samplings using the following two types of gear: a small seine net towed at three tidal-flat stations around the river mouth of Tama-gawa River from May 2006 to September 2009; and a ring net towed at a station in the offshore water of the Tama-gawa River mouth from January 2006 to May 2008. Their functional development was also observed mainly by osteological characters on the basis of 111 cleared and stained specimens of 2.0–21.1 mm in body length (BL). Specimens collected from the offshore water were 30 in number with  $4.6 \pm 1.6$  (mean  $\pm$  SD) mm BL, ranging from 2.0 to 8.5 mm BL, and those from the tidal flats were 232 with  $15.7 \pm 5.6$  mm BL from 6.1 to 49.3 mm BL. Based on the functional development of swimming- and feeding-related characters, the larvae and juveniles were divided into five and four developmental phases, respectively. Improvements of swimming and feeding functions observed at about 3 mm BL were considered to assist the early larvae in migrating shoreward, and the specimens of 6.0–8.9 mm size classes occurred in both the offshore and tidal flat stations. Thereafter on tidal flats, the number of individuals increased and reached a peak at about 15 mm BL, when the juveniles acquired functional swimming and feeding abilities. The juveniles  $> 15$  mm BL decreased in number, and then those ca. 30 mm BL had scarcely appeared on the tidal flats. The Japanese whiting juveniles  $> ca. 30$  mm BL in the innermost Tokyo Bay are most likely to move into deeper waters.

**Keywords :** *Japanese whiting, early life history, habitat shift, functional development*

## 1. Introduction

The Japanese whiting, *Sillago japonica*, distrib-

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uted in the coasts of Japan from the southern part of Hokkaido to Kyushu, Korea, China and Taiwan (HAYASHI and HAGIWARA, 2013), is known as an important commercial fish (SANO and MOCHIZUKI, 1984). In Tokyo Bay, which is located in the southeast coast of central Japan and the inner bay of which is surrounded by the Tokyo metropolitan area, the Japanese whiting is also a target fish for fisheries and angling. Therefore,

many studies have been conducted for knowing the biological aspects of the species as follows: the spawning patterns (SULISTIONO *et al.*, 1999a), age and growth (SULISTIONO *et al.*, 1999c), feeding habits (SULISTIONO *et al.*, 1999b; ARAYAMA and KOHNO, 2004), and concentrations of radioactive cesium (YANAGITA *et al.*, 2016; TEISHIMA *et al.*, 2017). Furthermore, their occurrence patterns have been studied in offshore-surface waters by ring nets (e.g. KANOU *et al.*, 2002a; NAGAIWA *et al.*, 2005), tidal flats/surf zones by seine nets (e.g. NASU *et al.*, 1996; KANOU *et al.*, 2000; ARAYAMA *et al.*, 2002; AOKI *et al.*, 2016; UMEDA and KOHNO, 2017), and offshore-bottom waters by beam trawl nets (YONEYAMA *et al.*, 2009; BUREAU OF ENVIRONMENT, TOKYO METROPOLITAN GOVERNMENT, 2018).

McKAY (1992) compiled the information about habitat, biology and fisheries of the species. However, no studies are available on the development of swimming- and feeding-related characters, the functional development, nor the ontogenetic intervals; although OOZEKI *et al.* (1992) divided laboratory-reared larvae and early juveniles into 10 stages and 3 phases on the basis of morphological and histological characters, no detailed descriptions were given and their phases corresponded to yolk-sac, from pre- to post-flexion and transformation larvae of KENDALL *et al.* (1984).

This study aims to establish the ontogenetic intervals during the early life history of the Japanese whiting based on the development of swimming- and feeding-related characters. The occurrence patterns of larvae/juveniles are also investigated in offshore waters and on tidal flats in the inner Tokyo Bay, and the relationships between the ontogenetic intervals and occurrence patterns are clarified to elucidate how each area of the inner Tokyo Bay provide habitats for the species.

## 2. Material and methods

Specimens used in this study were sampled from four sampling sites in the inner Tokyo Bay (Fig. 1). Two types of sampling gear were used as follows: a 0.8 mm mesh size small seine net (cf., KANOU *et al.*, 2002b) was monthly or bimonthly towed for about 100 m<sup>2</sup> at about 1m depth tidal flat during day time from May 2006 to September 2009 in three stations around the river mouth of Tama-gawa River, the northwestern innermost Tokyo Bay; and a 1.3 m diameter ring net with 0.5 mm mesh size was towed for 15 minutes by one to two knots through surface waters during day time from January 2006 to May 2008 (not sampled in March and July 2006, and January, March, July and September 2007) in one station off the mouth of Tama-gawa River by a 19 ton T/S *Hiyodori* of Tokyo University of Marine Science and Technology. Water temperature and salinities were measured after the samplings from January (offshore) or May (tidal flats) 2006 to May 2008, and the sediment was collected from the bottom of tidal flats for the measurements of particle-size distribution and mud-content percentage (cf., KOHNO *et al.*, 2014) from March 2008 to September 2009.

Collected specimens were fixed in 5% seawater formalin and later preserved in 70% ethanol. Species identification follows OKIYAMA (2014). The body length (BL: *sense* LEIS and TRNSKI, 1989) of each specimen was measured to the nearest 0.1 mm using a micrometer attached to a binocular dissecting microscope or a digital caliper.

Out of the specimens collected, 111 individuals (2.0–21.1 mm BL) were randomly selected for the morphological study to establish the ontogenetic intervals. These specimens were cleared and stained by the method of POTTHOFF (1984), and the following characters were observed: as the swimming-related characters, fin supports

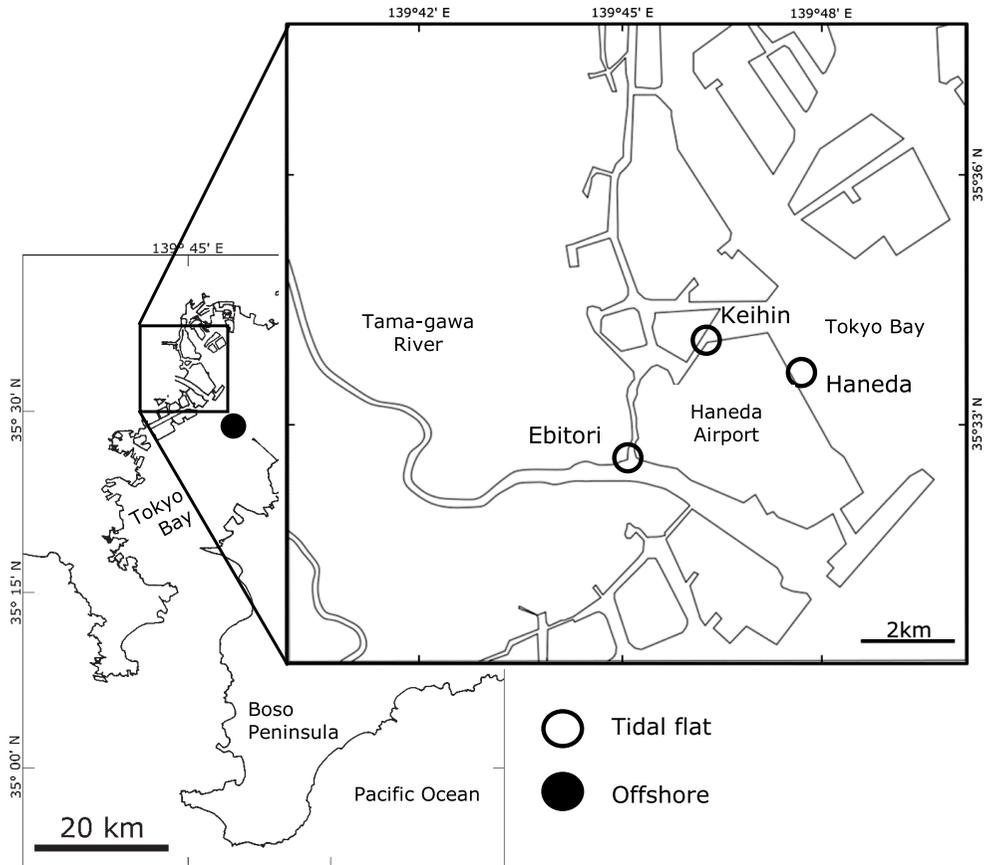


Fig. 1 Map showing the locations of one offshore and three tidal-flat sampling stations in the inner Tokyo Bay, central Japan.

and rays, the angle of notochord flexion (measured until the urostyle appeared and the notochord tip disappeared), vertebral centra, hemal and neural arches and spines, and the greatest body depth and its position measured from the snout tip to the vertical line at the greatest body depth; and as feeding-related characters, the structure of upper jaw (maxilla and premaxilla), the structure of lower jaw (Meckel's cartilage, dentary, angular and retroarticular), mouth width, ratio of premaxilla to gape, numbers of jaw teeth, pharyngeal teeth, and prevomer teeth, suspensorium, opercular bones, hyoid arch, and number of branchiostegal rays. The histogram

method of developmental events by 1 mm BL fish size intervals employed by SAKAI (1990) and the key character method of KOHNO and SOTA (1998) and KOHNO *et al.* (2000) were both applied to determine the ontogenetic intervals (cf., SHINAGAWA *et al.*, 2002). In this study, the description was based on the body length in the state of ethanol preservation and on the smallest specimen when the developmental phenomena and events were first observed.

### 3. Results

#### 3.1 Physical conditions of water and sediment

The water temperature in the offshore and

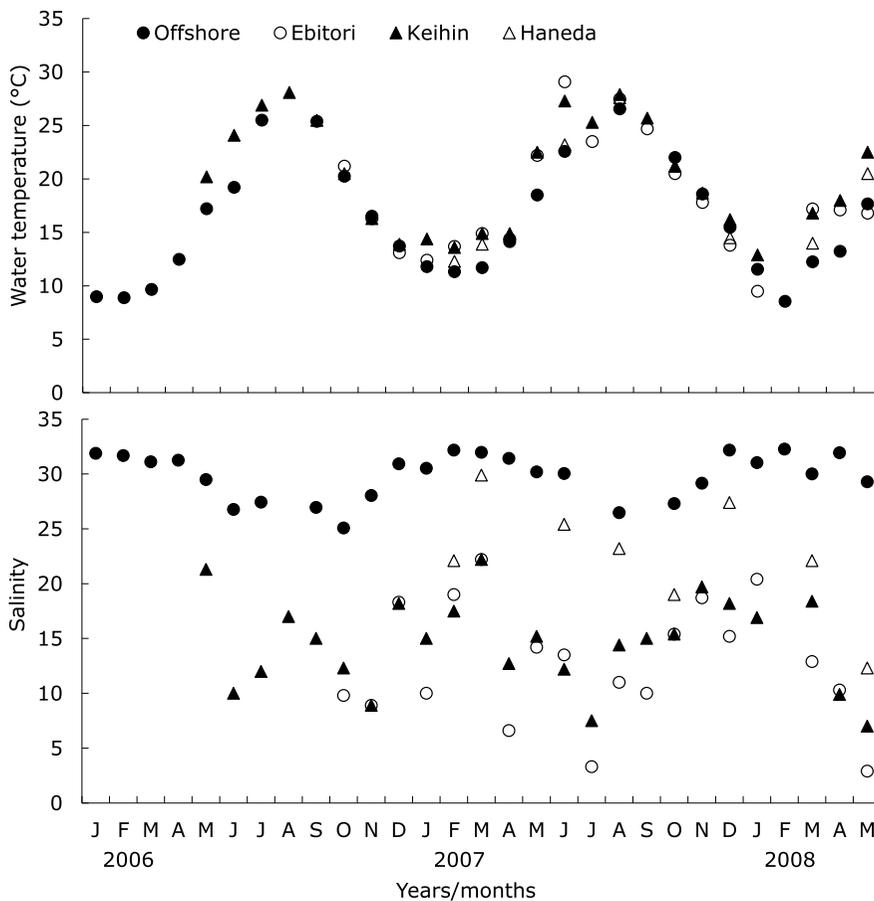


Fig. 2 Water temperature and salinities of the offshore and three tidal-flat sampling stations in the inner Tokyo Bay.

tidal-flat stations showed such the same tendency as increasing during the summer season and decreasing during the winter season, and no remarkable differences were detected between the stations (Fig. 2). The highest temperature, 29.1 °C, was recorded at the river tidal flat station, Ebitori, in June 2007 and the lowest, 8.5 °C, at the offshore station in February 2008.

The salinity was the highest in the offshore station, ranging from 25.1 to 32.3 with the mean  $\pm$  SD = 29.9  $\pm$  2.1, followed by the forehead tidal-flat station, Haneda, ranging from 12.3 to 29.9 with 22.8  $\pm$  4.1 (Fig. 2). In the river-mouth

and river tidal-flat stations, Keihin and Ebitori, the salinities were relatively low and varied from 3.0 to 22.2 with 14.4  $\pm$  3.9 and from 0.1 to 22.2 with 11.4  $\pm$  5.2, respectively.

Regarding the bottom sediment, the median particle size was the largest and the mud-content percentage was the lowest in Haneda, varying from 326.8 to 1,358.3  $\mu\text{m}$  (mean  $\pm$  SD = 621.4  $\pm$  307.2  $\mu\text{m}$ ) and from 0.6 to 8.0 % (1.2  $\pm$  0.4 %), respectively (Fig. 3). No remarkable differences were observed in the bottom sediment between Keihin and Ebitori; the median particle size and mud-content percentages fluctuated

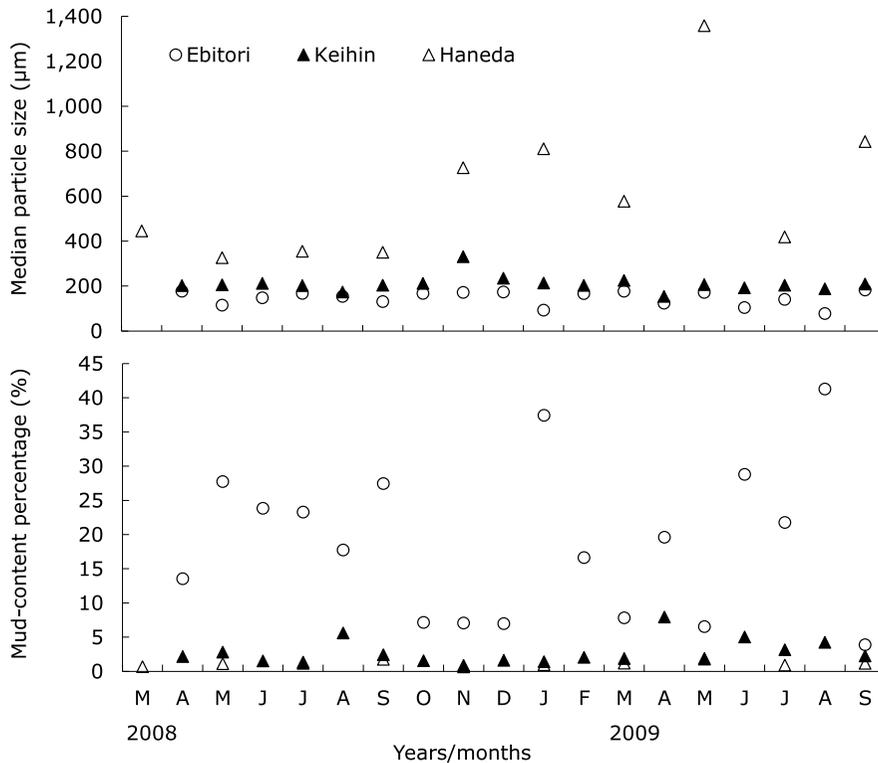


Fig. 3 Median particle size and mud-content percentage of the bottom sediment at three tidal-flat sampling stations around the Tama-gawa River mouth in the inner Tokyo Bay.

from 154.3 to 331.1  $\mu\text{m}$  ( $209.7 \pm 34.2 \mu\text{m}$ ) and from 0.7 to 8.0 % ( $2.8 \pm 1.8 \%$ ) in the former and from 78.1 to 182.7  $\mu\text{m}$  ( $146.9 \pm 31.2 \mu\text{m}$ ) and from 3.9 to 41.3 % ( $18.8 \pm 10.8 \%$ ) in the latter.

### 3.2 Occurrence patterns

The total number of Japanese whiting collected from the offshore station was 30 with the size of  $4.6 \pm 1.6 \text{ mm BL}$  (mean  $\pm$  SD), ranging from 2.0 to 8.5 mm BL, with a mode of 3.0–3.9 mm BL (Fig. 4). The months of occurrence were limited to August ( $3.4 \pm 1.0 \text{ mm BL}$ ,  $n = 8$ ), September ( $5.9 \pm 2.0 \text{ mm BL}$ , 7) and October ( $4.7 \pm 1.3 \text{ mm BL}$ , 15) (Fig. 5). In the three tidal-flat stations, no specimens were collected from the river tidal flat station, Ebitori. The total number of

specimens collected from the other two tidal-flat stations, Keihin and Haneda, was 232 with the size of  $15.7 \pm 5.6 \text{ mm BL}$ , ranging from 6.1 to 49.3 mm BL and a mode of 14.0–14.9 mm BL (Fig. 4). The BL of specimens collected from the offshore and tidal-flat stations were overlapped in 6.0–8.9 mm size classes (Fig. 4).

The specimens collected from the river mouth tidal flat station, Keihin, numbered 95, ranging from 6.1 to 49.3 mm BL ( $17.2 \pm 6.3 \text{ mm BL}$ ) with a mode of 14.0–14.9 mm BL (Fig. 6). The months of occurrence were limited to the period from July to September, and the number and size of specimens by the months were  $n = 4$  and  $14.8 \pm 3.9 \text{ mm BL}$  ranging from 10.0 to 18.5 mm BL in July, 57 and  $19.3 \pm 7.2 \text{ mm BL}$  from 6.1 to 49.3

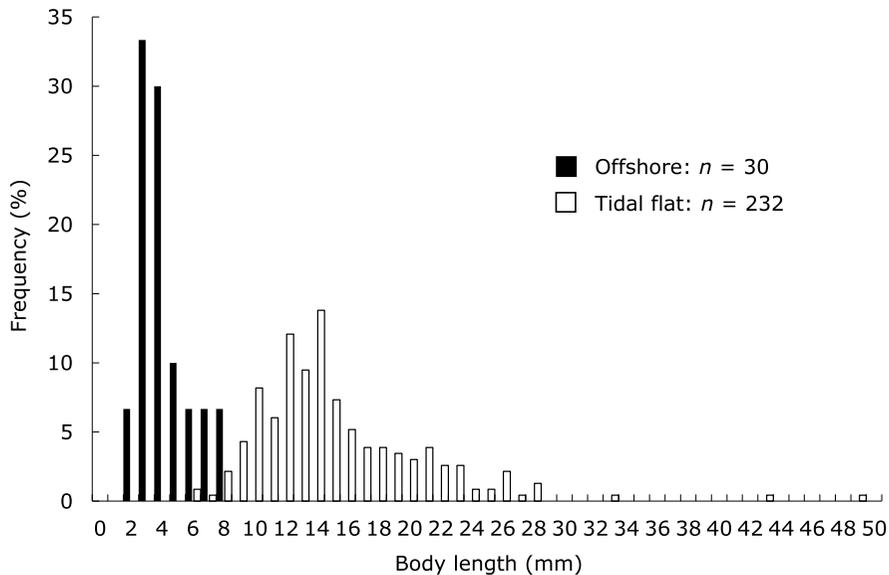


Fig. 4 Size composition of the Japanese whiting, *Sillago japonica*, collected from the offshore and three tidal-flat sampling stations in the inner Tokyo Bay.

mm BL in August, and 34 and  $14.0 \pm 1.8$  mm BL from 10.3 to 17.5 mm BL in September (Fig. 7).

In the forehead tidal flat station, Haneda, the number of specimens collected was 137 ranging from 6.4 to 43.2 mm BL ( $14.7 \pm 4.7$  mm BL) with a mode of 14.0–14.9 mm BL (Fig. 6). These specimens were collected from July to October, and the monthly changes of their individual number and size were as follows (Fig. 7):  $n = 7$  and  $12.9 \pm 4.8$  mm BL (mean  $\pm$  SD) with a range from 8.9 to 21.3 mm BL in July; 46 and  $16.1 \pm 4.8$  mm BL from 8.8 to 28.0 mm BL in August; 9 and  $12.6 \pm 4.1$  mm BL from 8.7 to 22.2 mm BL in September; and 75 and  $14.2 \pm 4.7$  mm BL from 6.4 to 43.2 mm BL in October.

### 3.3 Functional development

#### 3.3.1 Swimming-related characters

*Flexion of the notochord end:* Flexion of the notochord end was first evident at 3.4 mm BL with the angle of  $6^\circ$ , although the largest specimen with a straight notochord end was 4.2 mm BL

(Fig. 8A). Notochord flexion was complete at about 5 mm BL with the angle of about  $40$  to  $50^\circ$ .

*Caudal fin supports and fin rays:* No elements of the caudal skeleton were detected until 2.8 mm BL, when three cartilaginous buds of parhypural and hypurals 1 + 2 and 3 + 4 were observed. The cartilaginous buds of neural and hemal arches and spines of the future preural centrum 4 appeared at 5.3 mm BL and those of the preural centra 2 and 3 and three epurals at 6.2 mm BL. The cartilaginous bud of hypural 5 appeared at 6.5 mm BL, when all the cartilaginous elements were observed; in addition, the hypurals 1 + 2 and 3 + 4 started ossifying. The parhypural, hemal and neural arches and spines of the preural centrum 4, those of the preural centra 2 and 3, and hypural 5 started ossifying at 6.8 mm BL, 7.3 mm BL, 7.6 mm BL, and 7.8 mm BL, respectively. Ossification was perceived in the epurals 1–3 at 11.1 mm BL, and thus all cartilaginous elements started ossifying. The bony urostyle and uroneurals 1 and 2 were first ob-

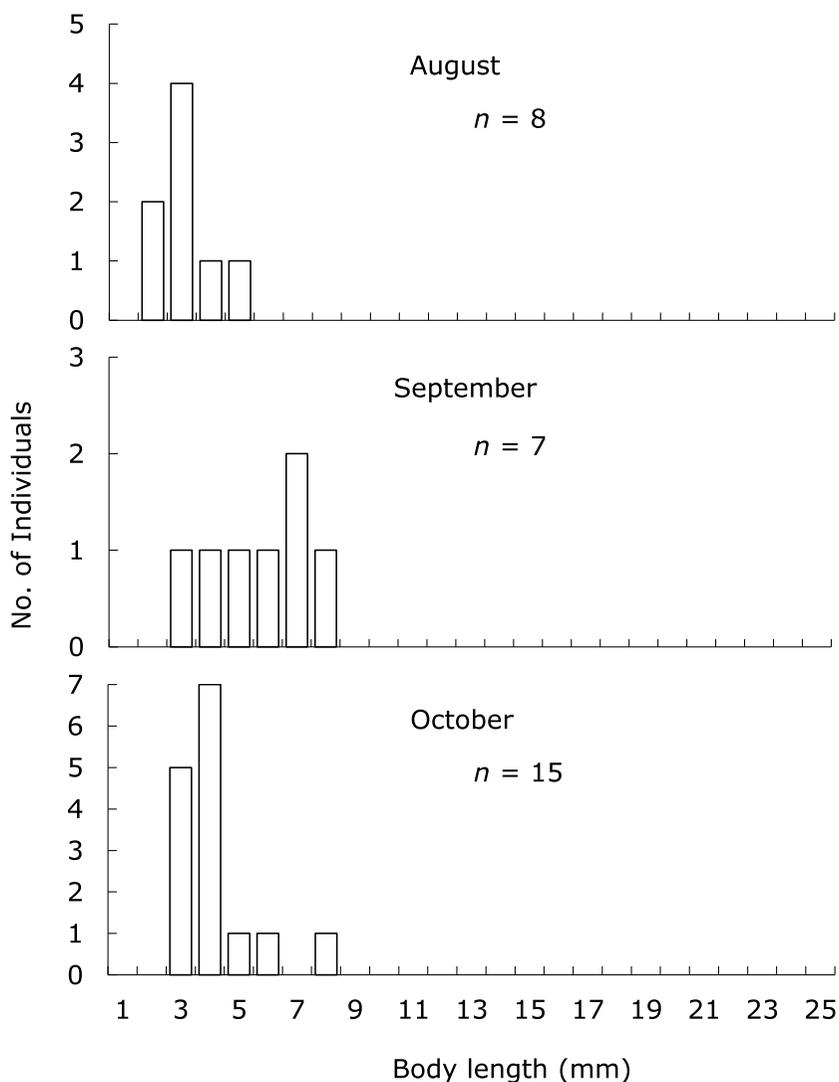


Fig. 5 Monthly changes of the size composition of Japanese whiting, *Sillago japonica*, collected from the offshore sampling station in the inner Tokyo Bay.

served at 5.9 mm BL, 8.3 mm BL and 10.6 mm BL, respectively.

Principal caudal fin rays were first discerned at 2.8 mm BL, when four rays were counted (Fig. 8B). The adult complement of 9 + 8 principal caudal fin rays was attained at 4.9 mm BL.

*Dorsal fin supports and fin rays:* The smallest specimen with dorsal fin supports was 4.8 mm

BL, in which 23 cartilaginous pterygiophores were observed. All the pterygiophores appeared by 5.9 mm BL. Ossification of five pterygiophores was first observed at 7.9 mm BL, and all elements started ossifying at 13.2 mm BL.

Dorsal fin rays were first discerned at 4.6 mm BL, when 14 soft fin rays were observed (Fig. 8C). The adult complement of 32–35 rays

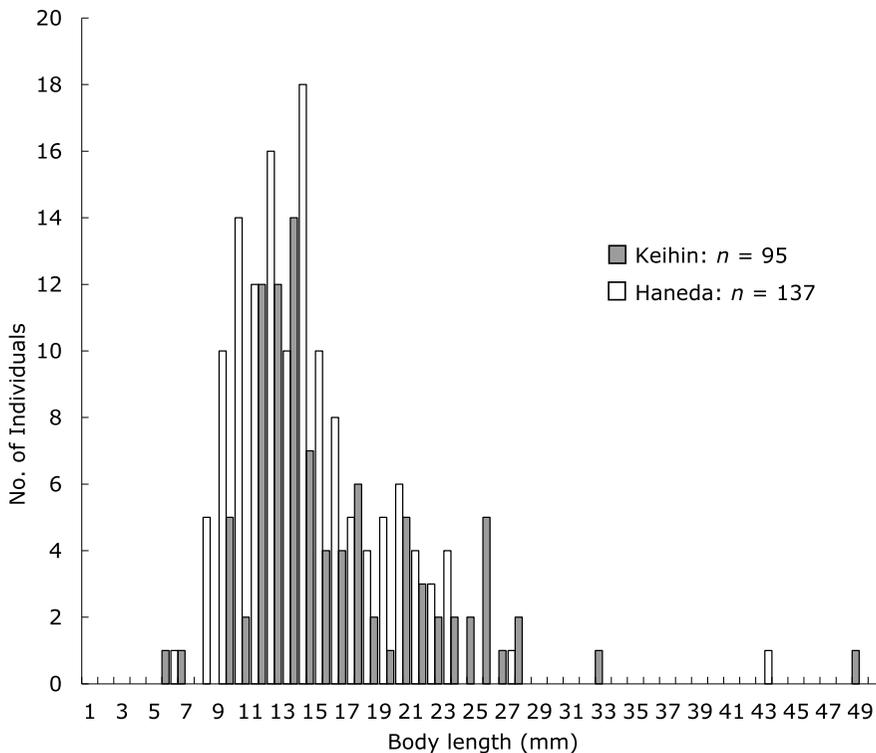


Fig. 6 Size composition of the Japanese whiting, *Sillago japonica*, collected from two tidal-flat sampling stations, the river-mouth tidal flat, Keihin, and the forehead tidal flat, Haneda, in the inner Tokyo Bay.

was attained at 5.9 mm BL.

*Anal fin supports and fin rays:* Nineteen cartilaginous pterygiophores were first observed at 4.8 mm BL, and all the pterygiophores appeared by 5.9 mm BL. Ossification was first discerned at 7.9 mm BL, and all elements started ossifying at 14.0 mm BL.

Anal fin rays were first discerned at 4.6 mm BL, when 15 soft fin rays were observed (Fig. 8D). The adult complement of 23–26 rays was attained at 5.9 mm BL.

*Pectoral fin supports and fin rays:* A rod-shaped bony cleithrum, a coraco-scapular cartilage and a cartilaginous plate, which later grew into actinosts, were observed in the smallest specimen examined of 2.0 mm BL. The bladelike

cartilage was divided into four actinosts at 5.9 mm BL. Ossification of the coraco-scapular cartilage and actinosts was first perceived at 7.9 mm BL and 8.5 mm BL, respectively. The bony supracleithrum and posttemporal were observed at 3.6 mm BL and the postcleithrum at 9.4 mm BL.

The pectoral fin rays were first discerned at 5.3 mm BL, when six were noted (Fig. 8E). The adult complement of 15–17 rays was attained at 6.1 mm BL.

*Pelvic fin supports and fin rays:* The pelvic fin support, the basipterygium, was first observed at 5.9 mm BL, and the ossification started at 9.3 mm BL.

The pelvic fin rays were first discerned at 7.2

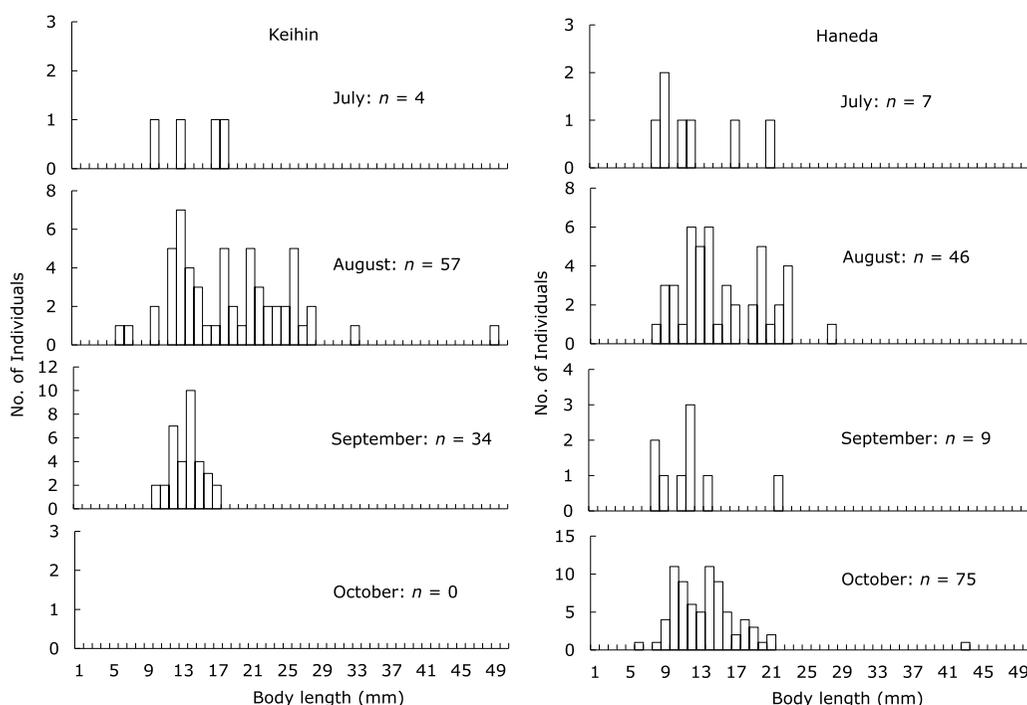


Fig. 7 Monthly changes of the size composition of Japanese whiting, *Sillago japonica*, collected from two tidal-flat sampling stations, Keihin and Haneda, in the inner Tokyo Bay.

mm BL, when four rays were observed (Fig. 8F). The adult complement of six rays was attained at 9.4 mm BL.

**Vertebra:** The smallest specimen possessing vertebral elements was 2.8 mm BL, in which 21 centra, 16 cartilaginous neural arches and spines, and seven cartilaginous hemal arches and spines were observed. The adult complement of 35 centra was attained at 5.9 mm BL. Both the hemal and neural arches and spines started ossifying at 6.2 mm BL and became complete in number at 7.7 mm BL. All arches and spines started ossifying at 7.9 mm BL.

**Maximum body depth and its position:** The ratio of the maximum body depth to BL was 23.5 % in the smallest specimen examined of 2.0 mm BL, although the ratio varied from 11.5–28% until about 8 mm BL (Fig. 8G). The ratios converged

and decreased gradually to 15–20% at about 10 mm BL and became stable thereafter.

The position of maximum body depth varied from 10% at 2.0 mm BL to 35% at 4.0 mm BL (Fig. 8H). The ratios became stable at about 10–25% in specimens of about 9–14 mm BL, but increased to 30–35% thereafter.

### 3.3.2 Feeding-related characters

**Mouth width:** The mouth opened in all specimens examined. The mouth width was 0.13 mm in the smallest specimen of 2.0 mm BL and increased rapidly to about 5 mm BL (Fig. 9A). The growth rate became then more or less slow until about 13 mm BL and rapid again, with the largest specimen examined of 21.1 mm BL possessing a 1.88-mm-wide mouth.

**Jaw structure:** The smallest specimen of 2.0

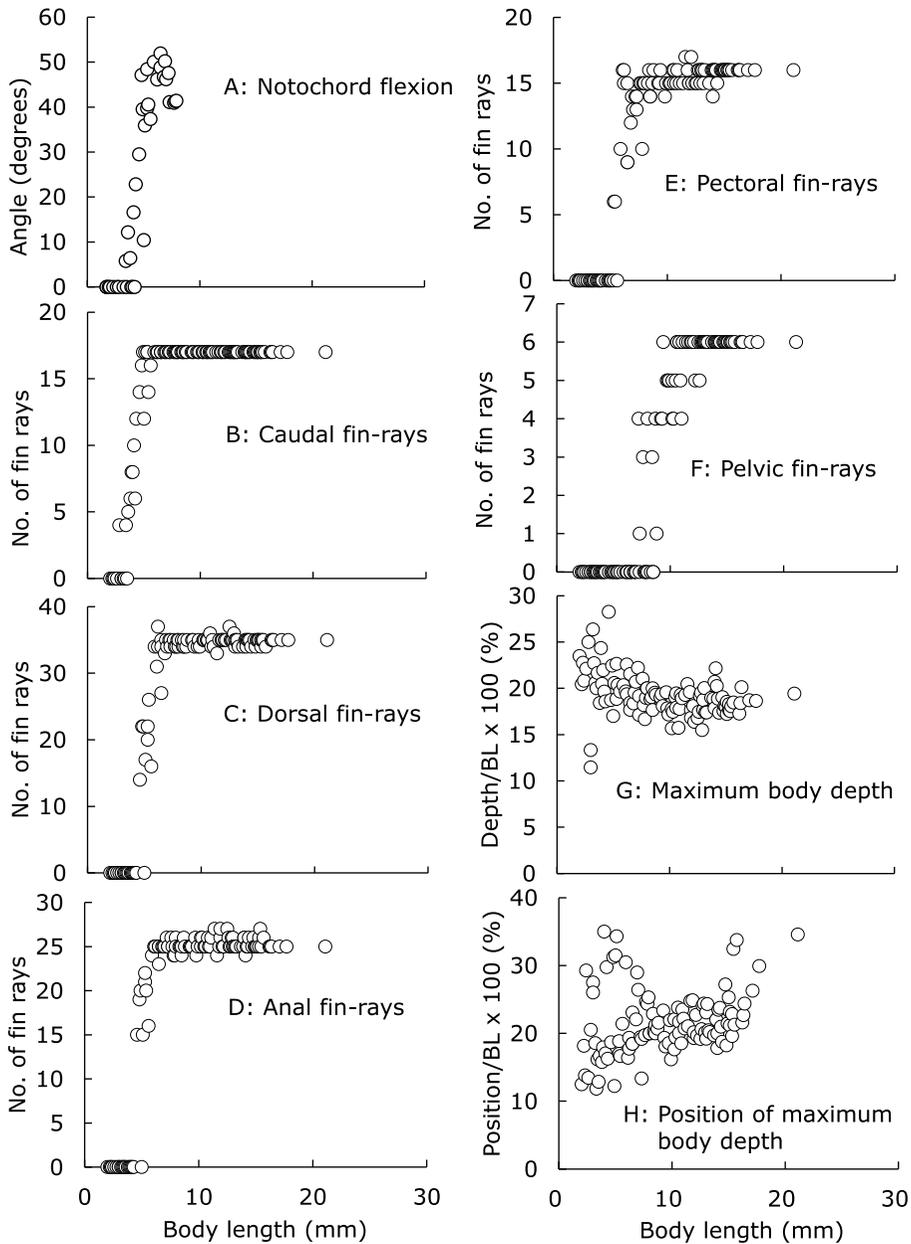


Fig. 8 Changes in swimming-related characters with growth in the Japanese whiting, *Sillago japonica*.

mm BL possessed the maxilla and Meckel's cartilage. Premaxilla and dentary appeared at 2.8 mm BL, the angular at 3.6 mm BL and retroarticular at 4.1 mm BL.

*Premaxilla length/gape*: The ratio of premaxilla to gape was 52% at 2.8 mm BL, when the premaxilla appeared first (Fig. 9B). The ratio increased rapidly to about 85% at about 4 mm BL

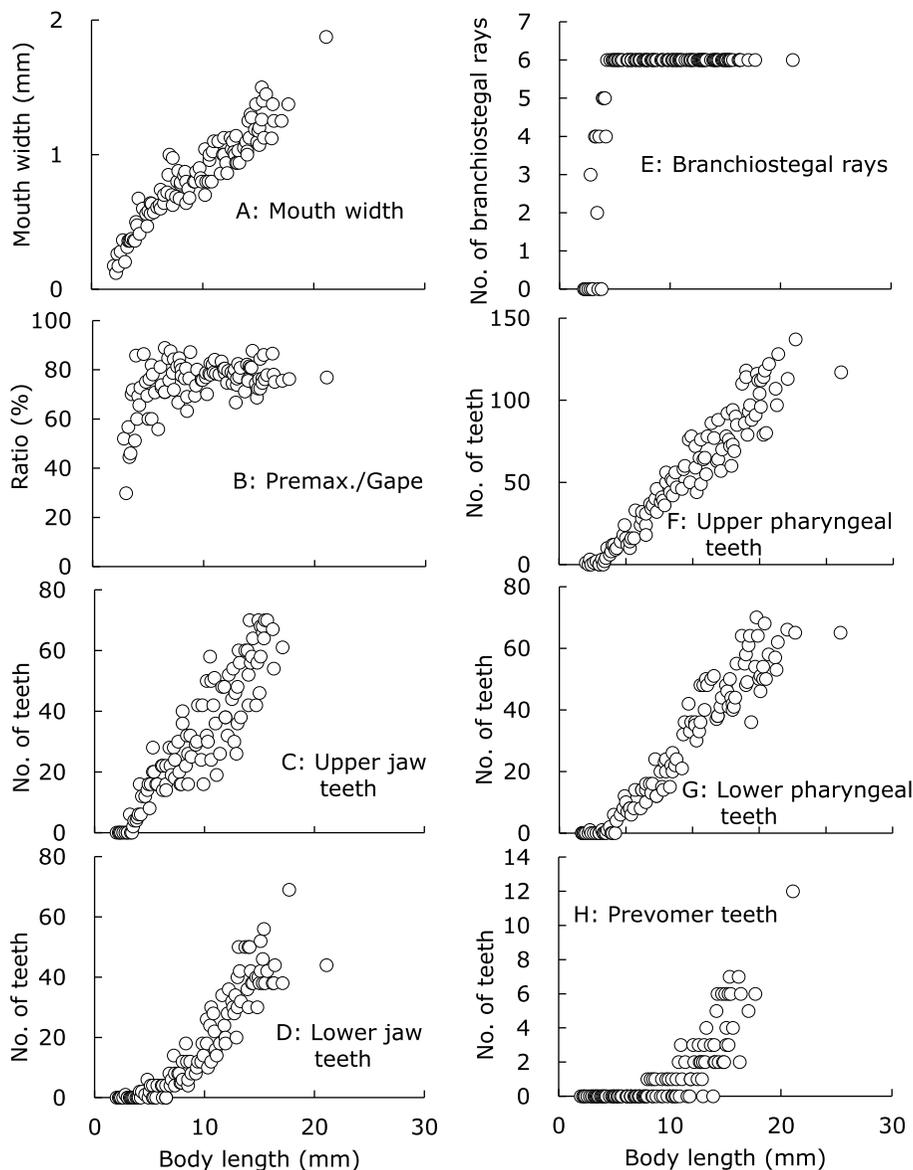


Fig. 9 Changes in feeding-related characters with growth in the Japanese whiting, *Sillago japonica*.

and became stable at 70–85% thereafter.

**Jaw teeth:** The first upper jaw teeth observed were six in number at 3.2 mm BL (Fig. 9C). The number of upper jaw teeth increased rapidly to about 6 mm BL and exponentially thereafter with a maximum number of 84 at 17.7 mm BL.

Although the first lower jaw tooth was observed at 2.8 mm BL, the increase of number was slow up to 7 mm BL with a maximum number of six (Fig. 9D). The number of lower jaw teeth increased exponentially up to about 13 mm BL with a maximum number of 50, and the in-

crease ratio became slow thereafter and varied from 40 to 70 in number.

*Suspensorium*: The smallest specimen of 2.0 mm BL possessed the palato-quadrates and hyomandibular-symplectic cartilages. The cartilaginous palatine was first observed at 2.6 mm BL. The quadrates, metapterygoid, symplectic and hyomandibular started ossifying at 5.9 mm BL, and the palatine at 6.5 mm BL. The bony ectopterygoid and endopterygoid were first observed at 4.1 mm BL and 8.0 mm BL, respectively.

*Hyoid arch and branchiostegal rays*: The hypohyal, cerato-epihyal, and interhyal cartilages were first observed at the smallest specimen of 2.0 mm BL. The interhyal, ceratohyal and epihyal started ossifying at 6.5 mm BL, and the hypohyal at 6.8 mm BL.

Three branchiostegal rays were first observed at 2.8 mm BL, and the adult complement of six rays was attained at 4.3 mm BL (Fig. 9E).

*Opercular bones*: A bony opercle appeared first at 2.0 mm BL, followed by the preopercle at 3.4 mm BL, subopercle at 3.8 mm BL and interopercle at 4.1 mm BL.

*Pharyngeal teeth*: One upper pharyngeal tooth was first discerned at 2.0 mm BL (Fig. 9F). The number of upper pharyngeal teeth increased and reached a maximum number of 137 at 17.7 mm BL. On the other hand, one lower pharyngeal tooth was first observed at 2.3 mm BL (Fig. 9G). The number increased and reached a maximum number of 70 at 14.8 mm BL.

*Prevomer teeth*: One prevomer tooth was observed in specimens from 8.0 to 12.9 mm BL (Fig. 9H). The second prevomer tooth appeared at 10.8 mm BL, and the number increased slowly with a maximum number of 12 at 21.1 mm BL.

## 4. Discussion

### 4.1 Developmental phases

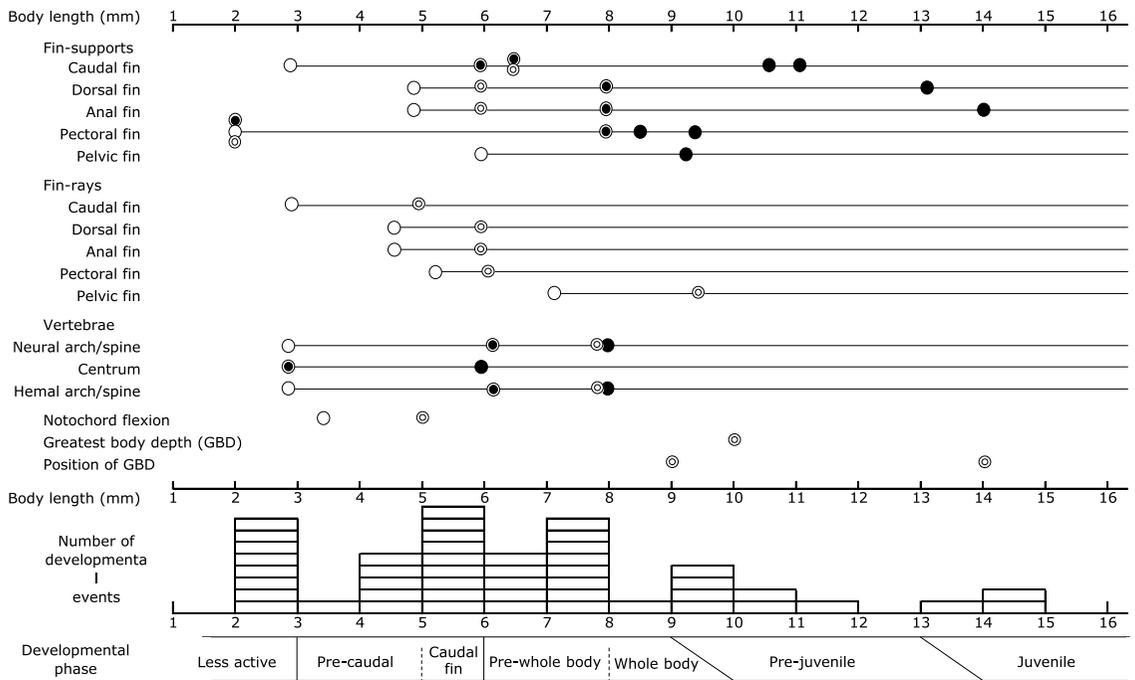
#### 4.1.1 Developmental phases of swimming function

Based on the development of swimming-related characters shown in Figure 10, the Japanese whiting larvae and juveniles were divided into the following five developmental phases.

*The phase of less active swimming (from 2 mm BL to 3 mm BL)*: No swimming-related characters appeared, other than the pectoral fin elements such as the cleithrum, coraco-scapular cartilage and cartilaginous plate, which developed later into actinosts. No fin rays appeared, and all the fins were composed of fin-fold. Therefore, the larvae in this phase are considered to drift passively rather than to swim actively.

*The phase of caudal fin propulsion (from 3 mm BL to 6 mm BL)*: This phase is divided into two sub-phases, pre-caudal and caudal fin propulsion sub-phases, at about 5 mm BL. In the former sub-phase, notochord end flexion started and was completed. Caudal fin supports started appearing, and the caudal fin rays started appearing and were completed in number. The hemal and neural arches and spines and the vertebral centra started appearing. The flexion of notochord end as well as the completion of caudal fin rays in number indicate that the beating of caudal fin produces weak propulsion (KOHNO *et al.*, 1983). In the latter sub-phase, on the other hand, the dorsal, anal and pectoral fin supports and rays started appearing and reached the adult complement, indicating that the body balance became stable (GOSLINE, 1971) and thus the beating ability of caudal fin would increase (KOHNO and SOTA, 1998).

*The phase of whole body propulsion (from 6 mm BL to 9–10 mm BL)*: This phase is also divided into two sub-phases, pre-whole and whole body propulsion sub-phases, at about 8 mm BL.



**Fig. 10** Schematic representation of the development of swimming-related characters with growth, showing the developmental phases in the Japanese whiting, *Sillago japonica*, collected from the inner Tokyo Bay. ○: cartilaginous elements and fin rays start appearing or notochord flexion begins; ◎: all cartilaginous elements appear, numbers of fin rays and vertebral elements and notochord flexion become complete, or flexion points of morphometric characters appear; ●: bony elements start appearing, or cartilaginous elements start ossifying; ●: all cartilaginous elements start ossifying, or all bony elements start appearing. Developmental events are shown by boxes, and developmental phases are also shown in the bottom.

The vertebral centra were completed in number; therefore, the strong body axis and completed dorsal and anal fins allow larvae to swim powerfully by propagating the beat of the whole of the body posterior to generate propulsion (OMORI *et al.*, 1996). In addition, at about 8 mm BL, the neural and hemal arches and spines were completed in number and started ossifying, and all the dorsal and anal fin supports started ossifying. The completed dorsal and anal fin supports and rays prevent the larvae from rolling caused by whole-body beating (GOSLINE, 1971). The pectoral fin supports were also completed, and the pelvic fin support and rays appeared and were completed,

indicating that the specimens became a juvenile stage with possessing the completed, adult number of fin rays at 9.4 mm BL. The development of paired fins indicates the improvement of maneuverability (LAGLER *et al.*, 1977; MATSUOKA, 1987; NARISAWA *et al.*, 1997).

*The phase of pre-juvenile swimming (from 9–10 mm BL to 13–14 mm BL):* All bony elements appeared and all cartilaginous elements started ossifying in the caudal fin support. Flexion points occurred in the greatest body depth and its position; changes of the body depth and position are considered to be the improvement of swimming in fish (ALEEV, 1963).

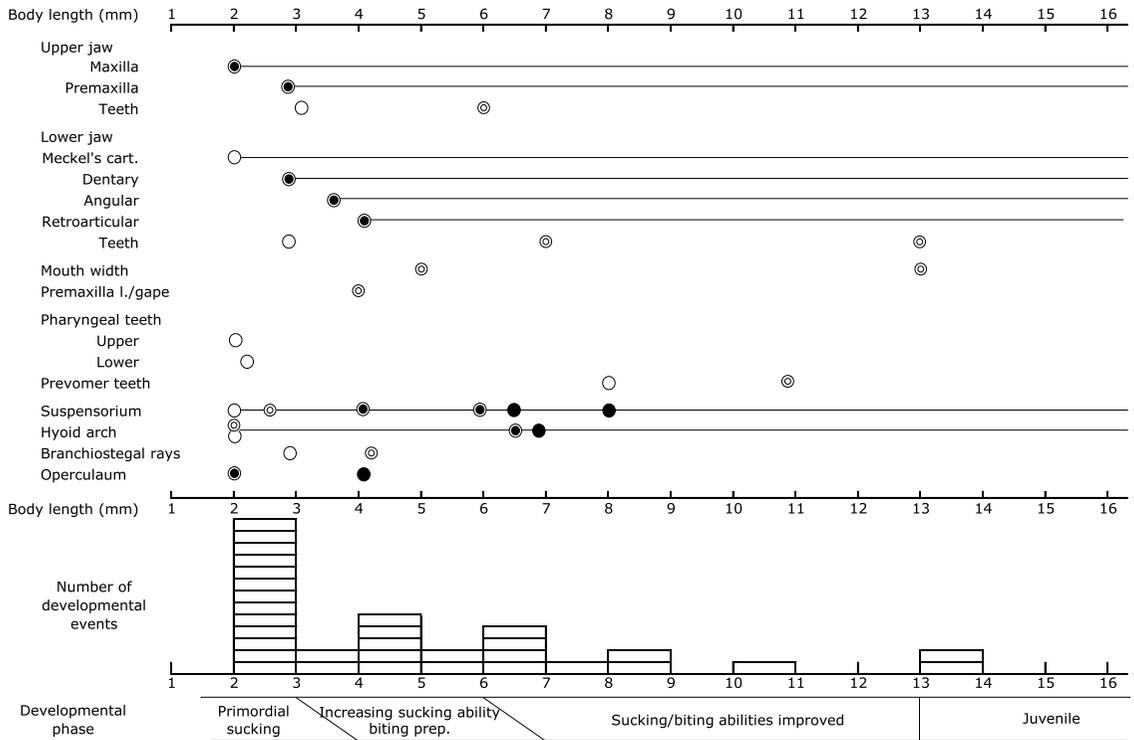


Fig. 11 Schematic representation of the development of feeding-related characters with growth, showing the developmental phases in the Japanese whiting, *Sillago japonica*, collected from the inner Tokyo Bay. ○: cartilaginous elements and fin rays start appearing or notochord flexion begins; ⊙: all cartilaginous elements appear, numbers of fin rays and vertebral elements and notochord flexion become complete, or flexion points of morphometric characters appear; ●: bony elements start appearing, or cartilaginous elements start ossifying; ●: all cartilaginous elements start ossifying, or all bony elements start appearing. Developmental events are shown by boxes, and developmental phases are also shown in the bottom.

*The phase of functional, juvenile swimming (over 13–14 mm BL):* All characters concerning swimming function became complete in number and started ossifying, and the position of greatest body depth became stable. Therefore, juveniles larger than 13–14 mm BL were considered to have acquired the functional, juvenile swimming mode.

#### 4.1.2 Developmental phases of feeding function

Based on the development of feeding-related characters shown in Figure 11, the Japanese

whiting larvae and juveniles were divided into the following four developmental phases.

*The phase of primordial sucking (from 2 mm BL to 3–4 mm BL):* The oral cavity was enclosed by the maxilla, Meckel's cartilage, a part of suspensorium and hyoid arch, indicating that the feeding mode is sucking. However, these elements, other than the small bony maxilla, are cartilaginous, and thus negative pressure for sucking is considered to be low (e.g. KOHNO *et al.*, 1997).

*The phase of increasing sucking ability and biting preparation (from 3–4 mm BL to 6–7 mm*

BL): The gape elements of the premaxilla, dentary and angular started appearing, indicating that gape opening and closing ability increase (SHINAGAWA *et al.*, 2002). In addition, the ossification of suspensorium and appearance of branchiostegal rays, opercular bones and retroarticular would increase the sucking ability (TAMURA *et al.*, 2013). Although the number is low, the upper and lower jaw and pharyngeal teeth started appearing in this phase. The functions of the jaw and pharyngeal teeth are to bite/capture and to propel acquired food organisms to the digestive tract, respectively (GOSLINE, 1971). Therefore, this phase is also recognized as a phase of biting preparation.

*The phase of sucking/biting abilities improved (from 6–7 mm BL to 13 mm BL)*: All characters concerning feeding function, except for the number of jaw, pharyngeal and vomer teeth, became complete not only in number but ossification. The larvae/juveniles of this stage are considered to improve their feeding abilities.

*The phase of functional, juvenile feeding (over 13 mm BL)*: The number of lower jaw teeth became stable, and the flexion point of mouth width, which determines the size of food organisms (HUNTER, 1981), was noticed. Therefore, the functional, juvenile feeding mode was considered to be acquired in juveniles over 13 mm BL.

#### 4.2. Habitat shifts corroborated by functional development

The smallest Japanese whiting larva collected in this study was 2.0 mm BL, in which the yolk was completely absorbed. OOZEKI *et al.* (1992) reported that a newly hatched larva was 1.2 mm BL and the yolk was completely absorbed at 2.5 mm BL of five days after hatching. Considering the lack of yolk and the shrinkage of body size as pointed out by OOZEKI *et al.* (1992), the smallest larva of 2.0 mm BL collected in this study would

be older than five days after hatching. Although the size of larvae collected from the offshore water in this study ranged from 2.0 to 8.5 mm BL, the dominant size class was 3.0–3.9 and 4.0–4.9 mm BL (Fig. 4), which occupied 33.3 and 30.0 % of the total number of offshore specimens. Swimming and feeding modes of the dominant larvae were the pre-caudal propulsion and sucking ability increasing/biting preparation, and thus the larvae occurred in the offshore water in this study do not swim actively but drift passively or swim weakly nor feed actively. The dominant size of the offshore specimens would be attained by one to two weeks after hatching, according to the results of OOZEKI *et al.* (1992).

The larvae > 6 mm BL started appearing on tidal flats, and the number increased after 8 mm BL and reached to a peak of occurrence at the 14.0–14.9 mm BL size class (Fig. 4). During the size from 6 to 14 mm BL, the swimming mode progressed from pre-whole body propulsion to pre-juvenile phases, which were divided at about 10 mm BL (Fig 10). In the former phase, which would correspond to two to three weeks after hatching (OOZEKI *et al.*, 1992), the larvae are considered to migrate shoreward by not strong but spontaneous swimming as well as by utilizing water currents, and they became juveniles morphologically at 9.4 mm BL by the completion in number of all fin rays. In the latter, pre-juvenile phase, the increase of individual number on tidal flats was accounted by the active shoreward migration supported by the improvement of swimming ability. On the other hand, the feeding abilities of both the sucking and biting were improved during the size from 6 to 14 mm BL (Fig. 11). ARAYAMA *et al.* (2003) reported that the main food of the species between 7.0 and 13.9 mm BL was calanoid copepods, and after 14 mm BL polychaet larvae were added; this change of feeding pattern is in accord with the change of

swimming and feeding modes revealed in this study.

The number of juveniles > 15 mm BL decreased gradually on tidal flats, and those > ca. 30 mm BL were absent besides exceptionally large individuals of 33, 43 and 49 mm BL (Fig. 4). KRÜCK *et al.* (2009) suggested a possibility that a niche shift would occur in sillaginid fishes > 20 mm BL in Moreton Bay, Australia, which more or less agrees with our results of the disappearance pattern from tidal flats. Although a habitat shift occurred from intertidal pools to adjacent subtidal waters in Moreton Bay (KRÜCK *et al.*, 2009), no habitats after the tidal flats which corresponding to the subtidal waters in Moreton Bay could be detected for the Japanese whiting in the innermost Tokyo Bay. ARAYAMA *et al.* (2003) indicated that, in Tateyama Bay of the outer Tokyo Bay, an offshore area within 100 m from the shoreline at the depth < 1 m is an important nursery area for the Japanese whiting and that the occurrence of larvae/juveniles in the shoreline area corresponding to the tidal flats in this study would be accidental. However in the innermost Tokyo Bay, we could not find nursery areas corresponding to the offshore area of ARAYAMA *et al.* (2003); those > ca. 30 mm BL in the innermost Tokyo Bay are most likely to move into deeper waters.

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