

Occurrence patterns and ontogenetic intervals based on the development of swimming- and feeding-related characters in larval and juvenile Japanese sea bass (*Lateolabrax japonicus*) in Tokyo Bay

Yasushi TAMURA, Masato MOTEKI, Toshihiro YOKOO and Hiroshi KOHNO*

Abstract: Occurrence patterns of the sea bass (*Lateolabrax japonicus*) larvae and juveniles were examined in Tokyo Bay by monthly samplings using the following two types of gear; a small seine net on tidal flats around the mouth of the Tama River from January 2007 to December 2008, and a ring net in offshore waters from December 2005 to March 2008. Their functional development was also observed by the osteological method on the basis of 47 cleared-and-stained specimens of 3.0–30.1 mm BL. The specimens collected from offshore waters were 391 in number, 3.67 ± 1.37 (mean \pm SD) mm body length (BL) in ranging from 1.8 to 8.1 mm BL and yolk-sac and preflexion larvae in developmental stages, while those from tidal flats were 580 with 21.9 ± 11.0 mm BL from 11.4 to 123.5 mm BL and varied from flexion larvae to juveniles. No specimens from 8 to 11 mm BL were collected in this study. The sea bass larvae spawned and hatched offshore waters near the mouth of Tokyo Bay are likely to migrate passively to inshore waters and then swim weakly with poorly developed swimming characters to inshore waters. In this study, few sea bass specimens smaller than 13.5 mm BL and larger than about 30 mm BL were collected in tidal flats, and thus the tidal flats of inner Tokyo Bay provide a nursery ground mainly for 13.5–30.0 mm BL juveniles. The 13.5–20.0 mm BL juveniles start acquiring functional, juvenile swimming and feeding abilities.

Keywords: Japanese sea bass, early life history, shoreward migration, functional development, Tokyo Bay

1. Introduction

The Japanese sea bass (*Lateolabrax japonicus*), distributed on the coast of Japan from Hokkaido south to Kyushu and the southern coast of the Korean Peninsula (HATOOKA, 2002), is known as a typical euryhaline fish, migrating from the sea to brackish/fresh waters, and as an important commercial fish, not only for fisheries but for angling in Japan (SHOJI *et al.*, 2002). Therefore, in Ariake Bay,

the gross biology of sea bass has been well studied, especially their early life histories; eggs are spawned and larvae hatch in offshore/open waters, remaining there up to about 8 mm in body length (BL), before moving to coastal surf zones, where the larvae are divided into two migratory groups, one remaining in the surf zone and the other swimming up rivers (MATSUMIYA *et al.*, 1985; HIBINO *et al.*, 2002, 2006). In Tokyo Bay, central Japan, many studies of the sea bass have been conducted to date, and their spawning ground has been identified as the mouth of Tokyo Bay (WATANABE, 1965; SUZUKI, 1982), with larvae collected by ring nets in offshore waters (KANOU *et al.*, 2002a; NAGAIWA *et al.*, 2005) and juveniles using seine nets in coastal tidal

Laboratory of Ichthyology, Tokyo University of Marine Science and Technology (4-5-7 Konan, Minato, Tokyo 108-8477, Japan)

* Corresponding author: Hiroshi KOHNO
Tel; +81-3-5463-0529
Fax; +81-3-5463-0523
E-mail; hirokun@kaiyodai.ac.jp

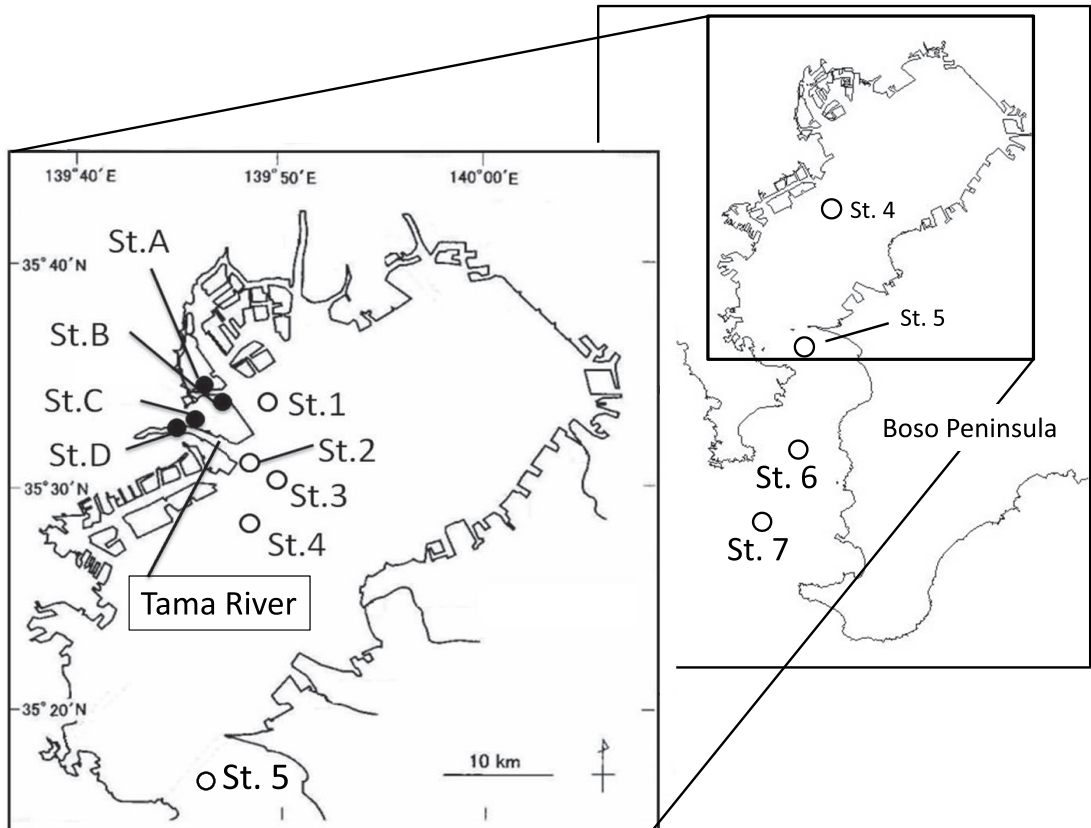


Fig. 1. Map of Tokyo Bay, central Japan, indicating the locations of sampling stations. A–D, stations for seine-net samplings; 1–7, those for ring-net samplings.

flats/surf zones (KANOU *et al.*, 2000; ARAYAMA *et al.*, 2002; KOHNO *et al.*, 2008; MOTEGI *et al.*, 2009).

As survival during the larval stage affects recruitment and population fluctuations in the sea bass, the early life history and ecology of the species were reviewed by ISLAM *et al.* (2011). However, no studies are available on the relationships between occurrence patterns and the functional development of larvae and juveniles of the sea bass. This study aimed to clarify the relationships between ontogenetic habitat shifts and the functional development of swimming and feeding abilities of the sea bass in Tokyo Bay. These relationships will indicate whether the larvae/juveniles move actively or passively, and represent important, basic information for elucidating the ways in which each area of Tokyo Bay provides habitats for the sea bass and for managing sea bass

resources in Tokyo Bay.

2. Materials and methods

The specimens used in this study originated from three sources and were collected using two types of sampling gear. A small seine net with 1-mm mesh size, as described by KANOU *et al.* (2002b), was deployed monthly at four sampling sites [stations (Stns.) A–D; Fig. 1] on tidal flats around the mouth of the Tama River located on the innermost, western coast of Tokyo Bay from January 2007 to December 2008 (except February 2008). A 1.3 m diameter ring net with 0.5-mm mesh size was towed for 15 minutes by 2 knots through surface waters during day time; two vessels, a 19-ton training ship (T/S) *Hiyodori* and a 277-ton T/S *Seiyomaru*, of the Tokyo University of Marine Science and Technology were operated. The *Hiyodori* samples were collected monthly from

four stations (Stns. 1–4; Fig. 1) located in the innermost offshore waters of Tokyo Bay from January 2006 to March 2008, while those of *Seiyo-maru* were collected from the inner Stn. 4 and three stations (Stns. 5–7) in outer Tokyo Bay in December 2005. The aim of the *Seiyo-maru* samples was to compare sizes and developmental stages between inner and outer Tokyo Bay. The collected specimens were fixed in 5% buffered seawater formalin and later preserved in 70% ethanol. The identification followed the method of KINOSHITA and FUJITA (1988) for the larvae larger than about 9 mm BL, and the series method of LEIS and TRNSKI (1989) was applied for those smaller than about 9 mm BL. The sizes of specimens collected were measured to the nearest 0.1 mm using a micrometer attached to a binocular dissecting microscope for specimens smaller than 10 mm BL and callipers for specimens 10 mm BL and larger; developmental stages were determined by the methods of KENDALL *et al.* (1984). Specimens collected by ring-nets were all measured, while those by seine nets were measured at most 30 individuals by each station/month.

Of the specimens sampled, 47 (19 of 3.0–8.1 mm BL collected by *Hiyodori* from the innermost waters and 28 of 11.4–30.1 mm BL collected by seine net from tidal flats) were selected for the morphological study to determine functional development. These specimens were cleared and stained by the method of POTTHOFF (1984), and the following characters were observed: fin supports and fin rays, the angle of notochord flexion, the vertebral centra, hemal and neural arches and spines and the greatest body depth and its position as swimming-related characters and the structure of the upper jaw (maxilla, premaxilla and supramaxilla), the structure of the lower jaw (Meckel's cartilage, dentary, angular and retroarticular), jaw teeth, mouth width, premaxilla/gape, pharyngeal teeth, suspensorium, hyoid arch, branchiostegal rays and opercular bones as feeding-related characters. Developmental phases were determined by the method of KOHNO and SOTA (1998), in which both the histogram method of developmental events by 0.5-mm BL fish size intervals employed by

SAKAI (1990) and the key character method were applied. 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 observed.

3. Results

3.1. Occurrence patterns

The total number of sea bass larvae collected offshore by ring nets towed by both *Hiyodori* and *Seiyo-maru* was 391 with size of 3.67 ± 1.37 mm BL (mean \pm SD), ranging from 1.8 to 8.1 mm BL, with a mode of 3.00–3.49 mm BL (Fig. 2). In the innermost offshore waters of Stns. 1–4, without regard to sampling vessel, the number of specimens collected was 191 of 4.44 ± 1.39 mm BL, ranging from 1.8 to 8.1 mm BL, and with a mode of 3.50–3.99 mm BL; water temperature and salinities varied from 7.8 to 15.1°C and from 26.0 to 32.3, respectively. The specimens collected from the outer Tokyo Bay of Stns. 5–7 numbered 200, with 2.93 ± 0.84 mm BL ranging from 1.8 to 6.3 mm BL and with a mode of 3.00–3.49 mm BL; water temperature and salinities varied from 15.4 to 16.1°C and from 33.3 to 34.3, respectively. The months of occurrence were limited to the period from December to March.

The sizes of the 230 *Seiyo-maru* samples collected in December 2005 were as follows by sampling station (Fig. 3): Stn. 4, $n=30$, mean \pm SD = 3.15 ± 0.93 mm BL, ranging from 1.8 to 6.1 mm BL; Stn. 5, 99, 3.43 ± 0.49 mm BL, 1.8–5.6 mm BL; Stn. 6, 11, 3.62 ± 1.45 mm BL, 1.8–6.3 mm BL; and Stn. 7, 90, 2.29 ± 0.57 mm BL, 1.8–4.8 mm BL. The sizes of these specimens were significantly different among stations and between Stn. 7 and others (Tukey's test, $P < 0.01$).

Of the 391 larvae collected offshore, 88 (22.2%) were yolk-sac larvae and the remainder of 303 were preflexion larvae. Of 200 larvae collected in outer Tokyo Bay, 83 (41.5%) were yolk-sac larvae and the remainder of 117 were preflexion larvae. Of 191 larvae collected in inner Tokyo Bay, 5 (2.6%) were yolk-sac larvae and the remainder of 186 were preflexion larvae.

All the specimens collected offshore in inner

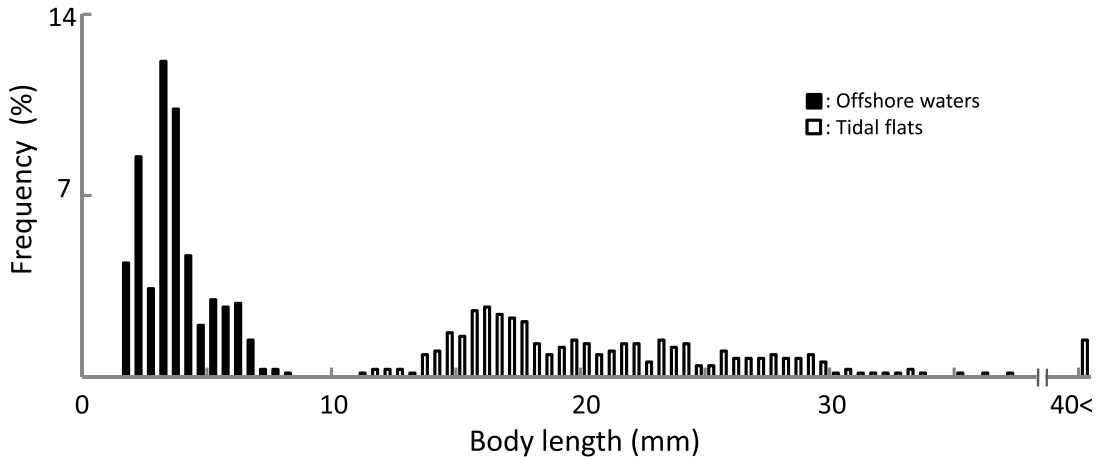


Fig. 2. Body length (BL) frequencies of larval and juvenile *Lateolabrax japonicus* collected from offshore waters ($n=391$) and tidal flats ($n=311$) in Tokyo Bay.

Tokyo Bay by *Hiyodori* were preflexion larvae.

The total number of sea bass collected from tidal flats was 580, varying from 11.4 to 123.5 mm BL with 21.9 ± 11.0 mm BL and a mode of 16.0–16.5 mm BL (Fig. 2); water temperature and salinities fluctuated from 12.3 to 30.5°C and from 0.1 to 29.9, respectively. These specimens were collected from January to August, and their developmental stages varied from flexion larvae to juveniles. Monthly changes in their body sizes are shown in Fig. 4. The sea bass grew in the tidal flats from January (12.3 ± 0.9 mm BL: $n=2$) to April 2007 (19.2 ± 3.6 mm BL: $n=54$) and from March (16.2 ± 1.1 mm BL: $n=59$) to May 2008 (40.9 ± 12.5 mm BL: $n=12$).

Specimens of 8.2–11.3 mm BL were not collected either from offshore waters or from tidal flats, and in the latter, few specimens were larger than about 30 mm BL (Fig. 2).

3.2. Functional development

3.2.1. Swimming-related characters

Flexion of the notochord end: Flexion of the notochord end was not detected in the specimens collected from offshore waters, the largest of which was 8.1 mm BL (Fig. 5A). Notochord flexion was complete in the smallest specimen collected from the tidal flat, 11.4 mm BL, and the angle was stable at about 40°–47°.

Caudal fin supports and fin rays: No

elements of the caudal skeleton were detected until 5.5 mm BL, when two cartilaginous buds of hypurals 1–2 were observed. The cartilaginous buds of the parhypural and hypural 3 appeared at 6.9 mm BL and hypural 4 at 8.1 mm BL. In addition, the smallest specimen from the tidal flats (11.4 mm BL) possessed the cartilaginous bud of hypural 5 as well as those of the hemal and neural spines of the future pleural centra 2 and 3 and epurals 1–3. The bony urostyle and pleural centra 2 and 3 were observed in the 11.4-mm BL specimen. In a 13.8-mm BL specimen, ossification was perceived in the parhypural, hypurals 1–5 and the hemal and neural spines of future pleural centra 2 and 3. All cartilaginous elements, including epurals 1–3, started ossifying at 15.4 mm BL.

Principal caudal fin rays were first discerned at 5.5 mm BL, when four rays were counted (Fig. 5B). The adult complement of 8 + 7 principal caudal fin rays was attained at 11.4 mm BL.

Dorsal fin supports and fin rays: The smallest specimen with dorsal fin supports was 11.4 mm BL, in which an adult complement of 25 cartilaginous pterygiophores was observed. The ossification of three of these was first perceived at 14.2 mm BL. All pterygiophores started ossifying at 17.5 mm BL.

Dorsal fin rays were first discerned at 11.4 mm BL, when 12 soft fin rays were observed (Fig. 5C). Two spines were first perceived at

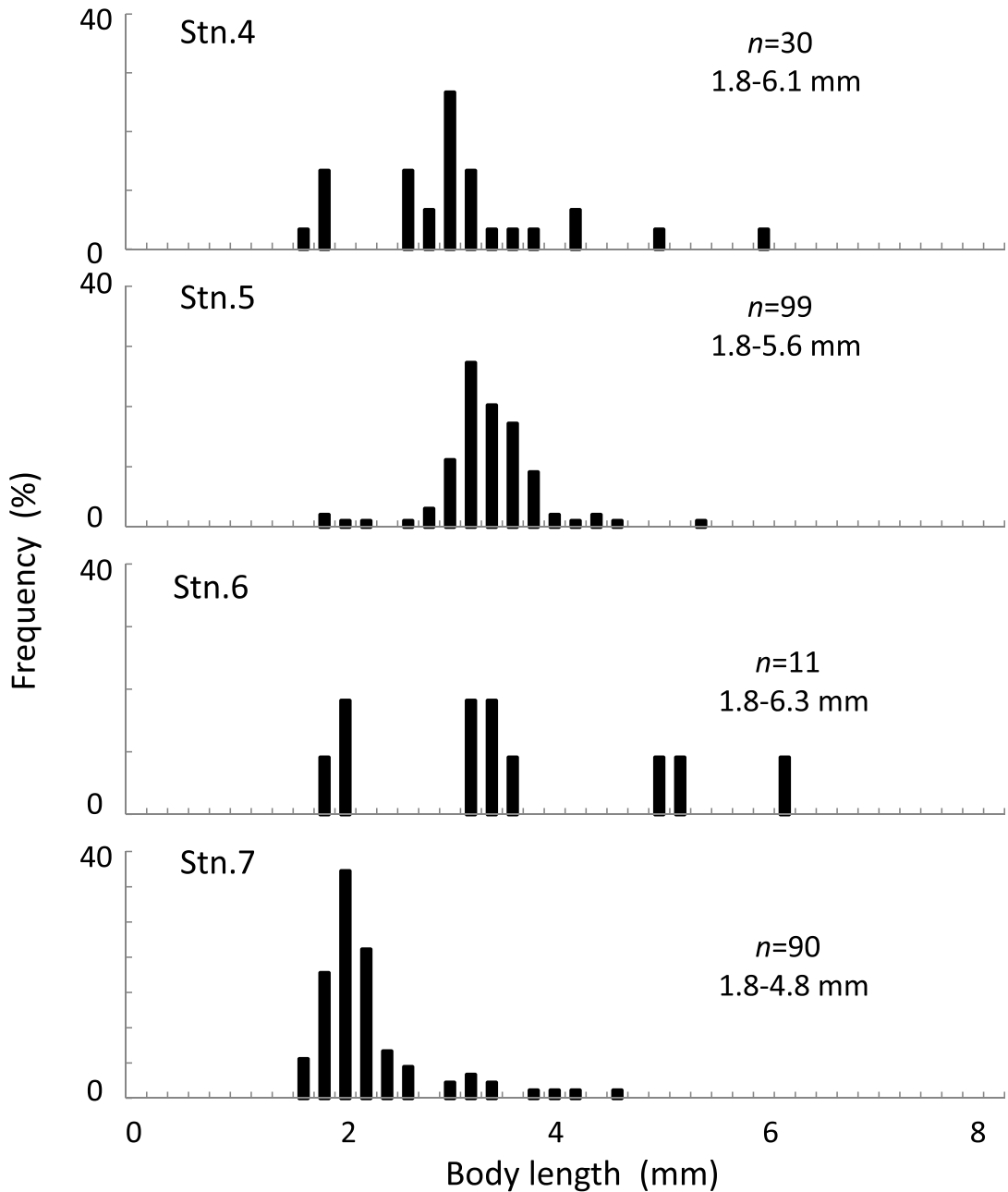


Fig. 3. Body length (BL) frequencies of larval *Lateolabrax japonicus* collected from Tokyo Bay offshore waters in December 2005 by the training ship *Seiyo-maru*, shown by ring-net sampling sites (Stns. 4–7). For sampling stations, see Figure 1.

11.7 mm BL, and the adult complement of 26–28 rays was attained at 13.0 mm BL.

Anal fin supports and fin rays : The adult complement in number of eight cartilaginous

pterygiophores was first discerned at 11.4 mm BL. Ossification of two pterygiophores was first observed at 14.2 mm BL, and all elements started ossifying at 17.5 mm BL.

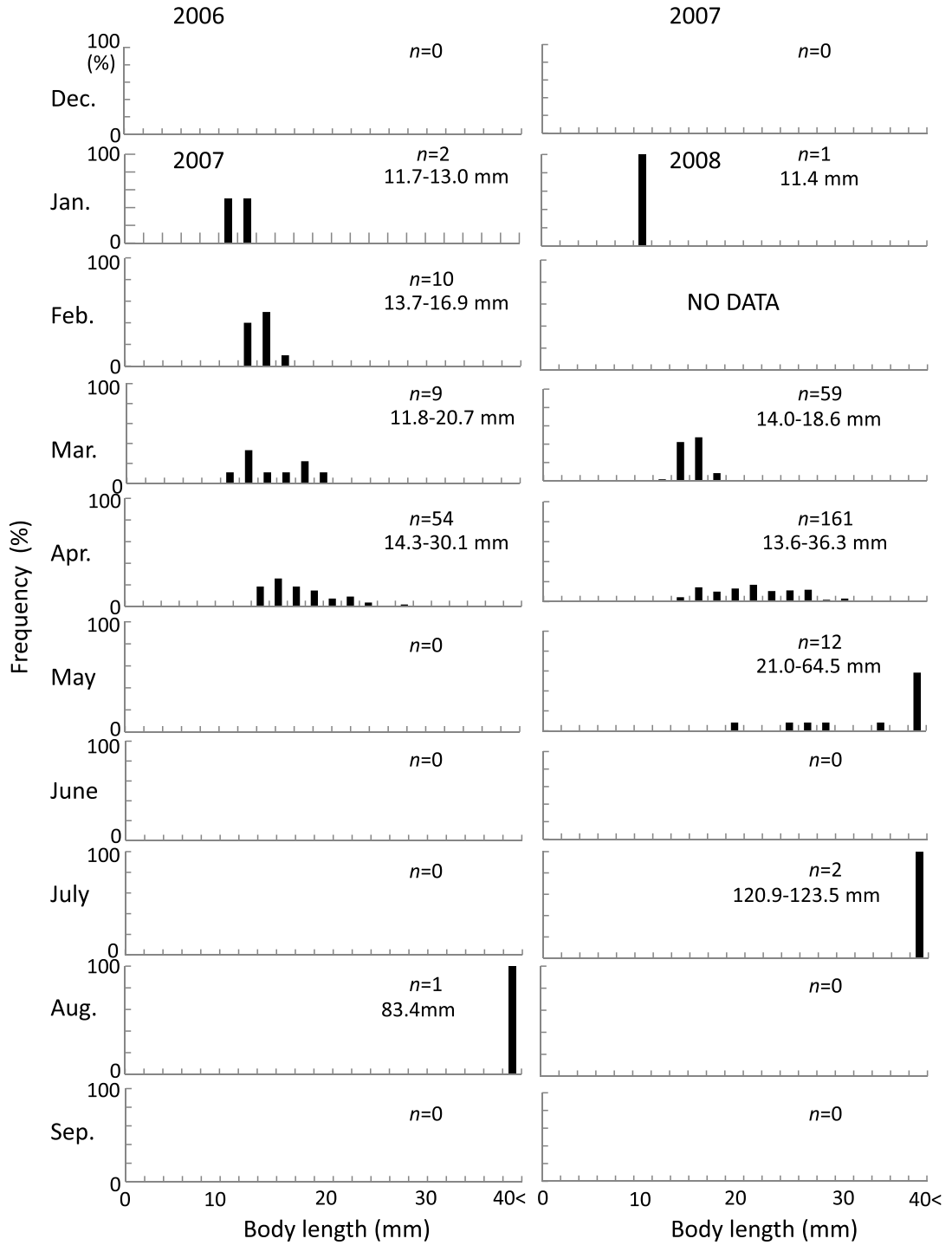


Fig. 4. Monthly changes in body length (BL) frequencies of larval and juvenile *Lateolabrax japonicus* collected from Tokyo Bay tidal flats.

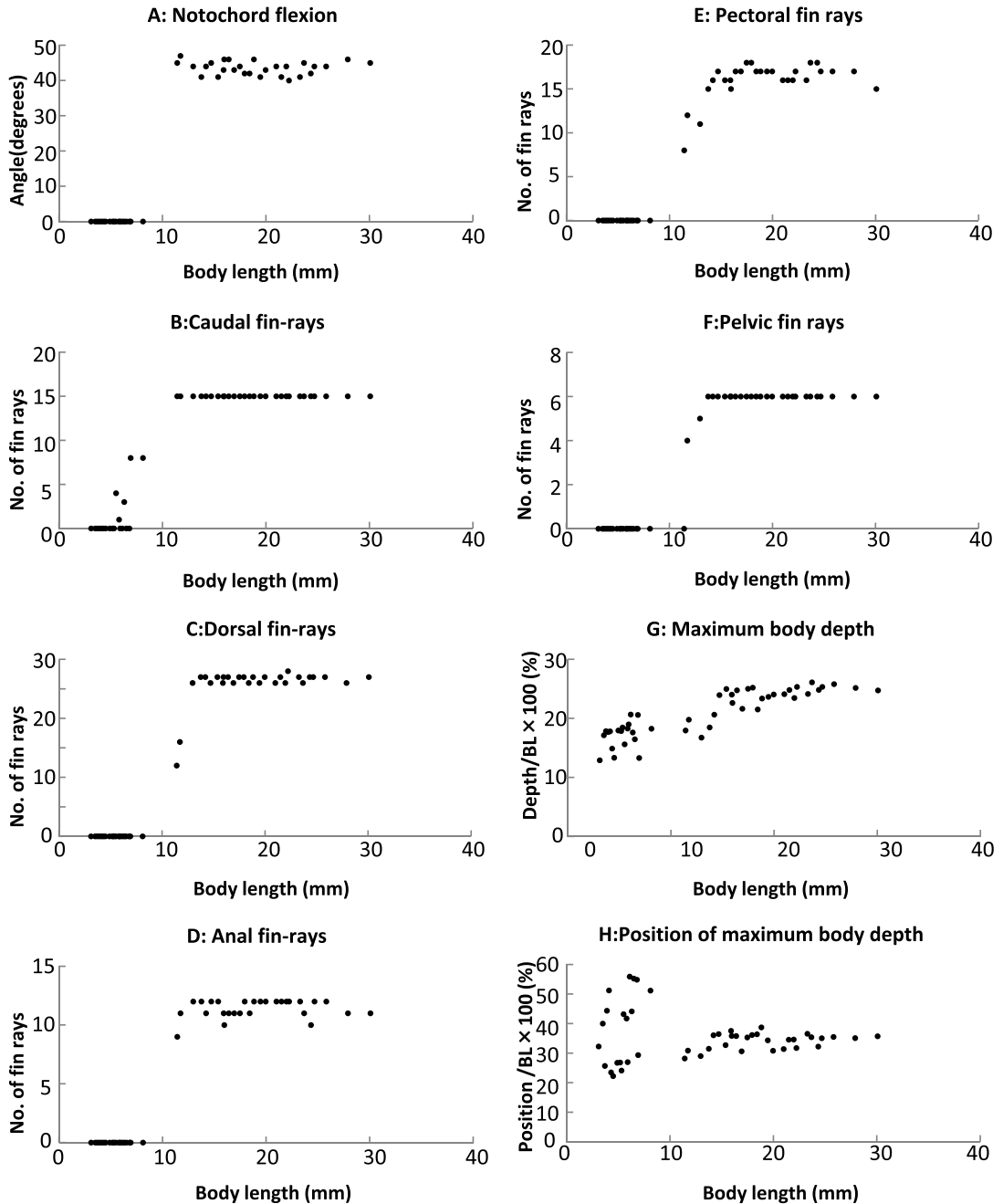


Fig. 5. Changes in swimming-related characters with growth in *Lateolabrax japonicus* collected from Tokyo Bay.

The anal fin rays were first discerned at 11.4 mm BL with one spine and eight soft rays (Fig. 5D). The adult complement of 10–12 rays was attained at 11.7 mm BL.

Pectoral fin supports and fin rays: The pectoral fin supports of a rod-shaped bony cleithrum, a coraco-scapular cartilage and a bladeli-like cartilage, which later grew into

actinosts, were observed in specimens of 3.1–8.1 mm BL collected from offshore waters. A supracleithrum and posttemporal were observed at 11.4 mm BL. Ossification of the coraco-scapular cartilage and actinosts was first perceived at 15.4 mm BL.

The pectoral fin rays were first discerned at 11.4 mm BL, when eight were noted (Fig. 5E). The adult complement of 15–18 rays was attained at 13.8 mm BL.

Pelvic fin supports and fin rays : The pelvic fin support, the basipterygium, was first discerned at 11.4 mm BL, and ossification started at 15.4 mm BL.

The pelvic fin rays were first discerned at 11.7 mm BL, with one spine and three soft rays (Fig. 5F). An adult complement of six rays was attained at 13.8 mm BL.

Vertebra: No vertebral elements were recognised in the specimens collected from offshore waters, up to 8.1 mm BL. In the smallest specimen collected from the tidal flat (11.4 mm BL) all hemal and neural arches and spines and centra were observed, with the ossification of the first three neural arches and spines. All arches and spines started ossifying at 14.2 mm BL.

Maximum body depth and its position : The ratio of the maximum body depth to BL was 13% in the smallest specimen examined of 3.1 mm BL, and varied from 13% to 20% in specimens up to 14.2 mm BL (Fig. 5G). Thereafter, the ratios were stable at about 22–26%.

The position of maximum body depth varied from 23% at 4.3 mm BL to 56% at 6.1 mm BL (Fig. 5H) and became stable from 28% to 39% thereafter.

3.2.2. Feeding-related characters

Mouth width : The mouth opened in all specimens examined. The mouth width was 0.3 mm in the smallest specimen of 3.1 mm BL and increased gradually in specimens from offshore waters (Fig. 6A). The growth rate became more or less rapid in specimens from 11.4 to about 20 mm BL and slowed thereafter, with the largest specimen examined (30.1 mm BL) possessing a 4.2-mm-wide mouth.

Jaw structure : The smallest specimen of 3.1 mm BL possessed the maxilla and Meckel's

cartilage. Premaxilla, dentary and angular were discerned at 5.5 mm BL, the retroarticular at 13.0 mm BL and supramaxilla at 14.7 mm BL.

Premaxilla length/Gape : The ratio of premaxilla to gape was 66% at 5.5 mm BL (Fig. 6B). Although the ratio tended to increase in specimens collected from offshore waters, the ratio varied from 70% to 90% in the specimens from tidal flats.

Jaw teeth : The first upper jaw teeth observed were six in number at 5.5 mm BL (Fig. 6C). The number of upper jaw teeth increased exponentially up to about 20 mm BL, with a maximum of 198 at 19.5 mm BL and varying from 100 to 150 thereafter. The lower jaw teeth were first observed at 11.4 mm BL with four noted (Fig. 6D). The lower jaw teeth increased up to about 20 mm BL with a maximum number of 112 at 19.5 mm BL, and the number became stable thereafter.

Suspensorium : The palatoquadrate and hyomandibular-symplectic cartilages were first observed at 3.1 mm BL and the bony ectopterygoid and endopterygoid at 11.4 mm BL. The quadrate, hyomandibular and symplectic started ossifying at 13.0 mm BL and the palatine and metapterygoid began at 13.8 mm BL.

Hyoid and branchiostegal rays : The ceratohyal-epihyal and interhyal cartilages were first observed at 3.1 mm BL and the hypohyal cartilage was noted at 11.4 mm BL. The ceratohyal and epihyal started ossifying at 13.0 mm BL, the interhyal began at 13.8 mm BL and the hypohyal started at 15.4 mm BL.

A branchiostegal ray was first observed at 5.5 mm BL, and the adult complement of seven rays was attained at 11.4 mm BL (Fig. 6E).

Pharyngeal teeth : The first upper pharyngeal teeth, 10 in number, were observed at 5.5 mm BL (Fig. 6F). The number of teeth increased exponentially with the maximum number of 134 at 22.0 mm BL.

The first lower pharyngeal tooth, 1 in number, was observed at 8.1 mm BL (Fig. 6G). The number of teeth increased exponentially with the maximum number of 132 at 22.0 mm BL.

Opercular bones : The first opercular bones to appear were the preopercle and opercle at 5.5

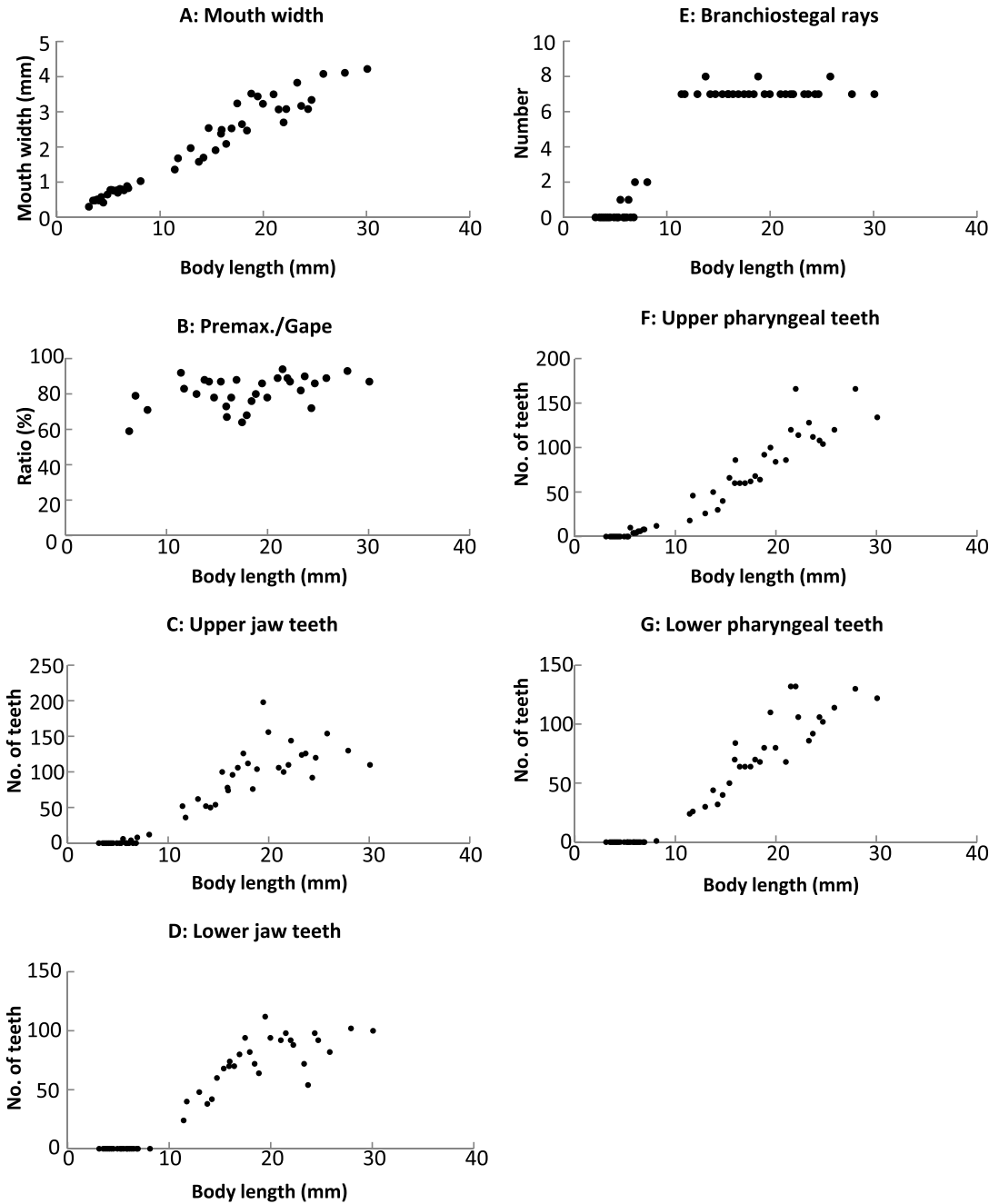


Fig. 6. Changes in feeding-related characters with growth in *Lateolabrax japonicus* collected from Tokyo Bay.

mm BL. The interopercle and subopercle were first observed at 11.4 mm BL.

4. Discussion

4.1. Developmental phases of Japanese sea bass larvae and juveniles

The development of characters concerning the swimming and feeding functions of the

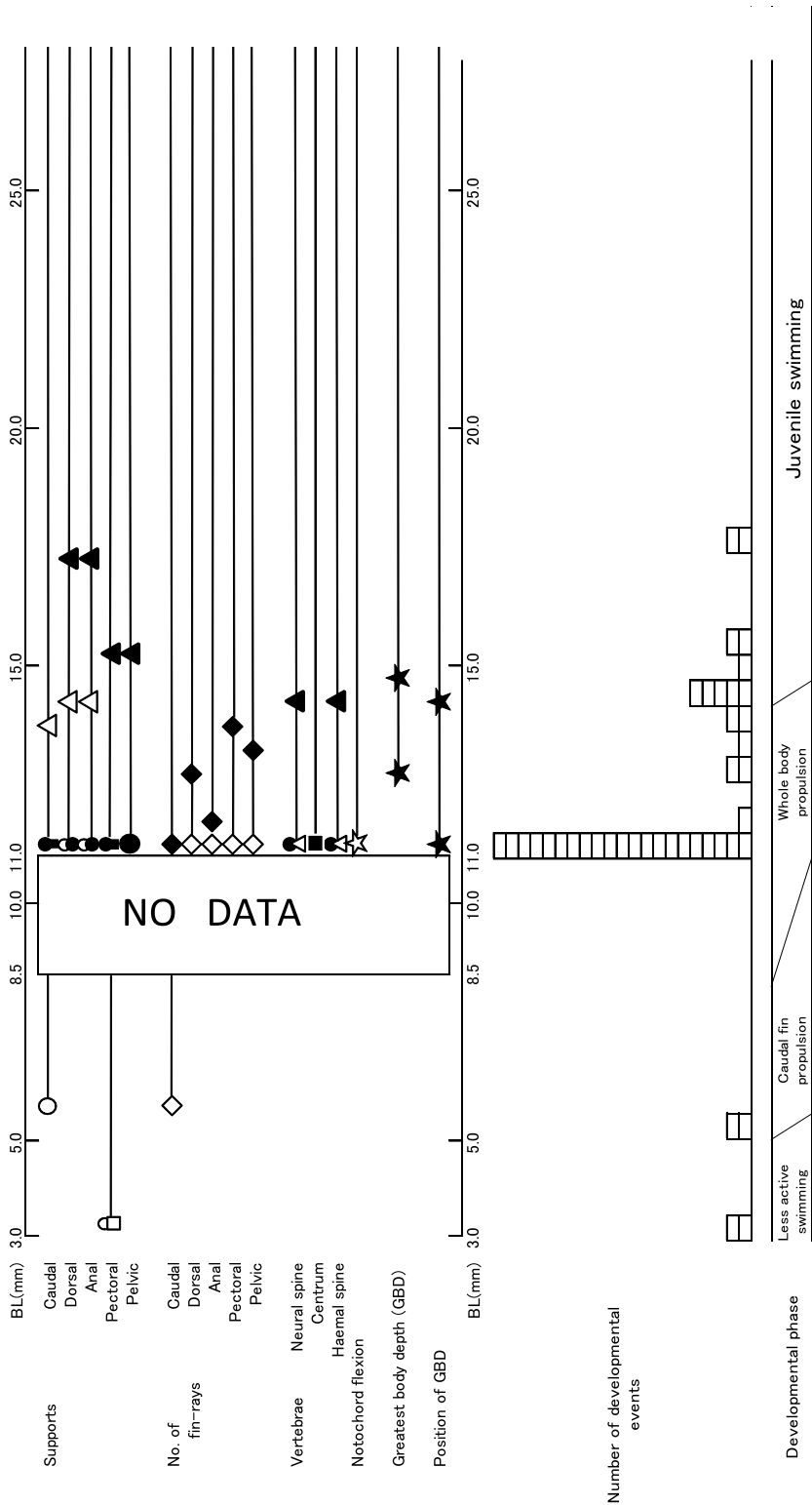


Fig. 7. Schematic representation of the development of swimming-related characters with growth (body length, BL) in *Lateolabrax japonicus* collected from Tokyo Bay. Open circles, cartilaginous elements start appearing; closed circles, all cartilaginous elements start appearing; open squares, bony elements start appearing; closed squares, all bony elements start appearing; open triangles, cartilaginous elements start ossifying; closed triangles, all cartilaginous elements start ossifying; open diamonds, fin rays start appearing; open diamonds, fin rays become complete in number; an open star, notochord flexion becomes complete; closed stars, flexion points of morphometric characters are observed.

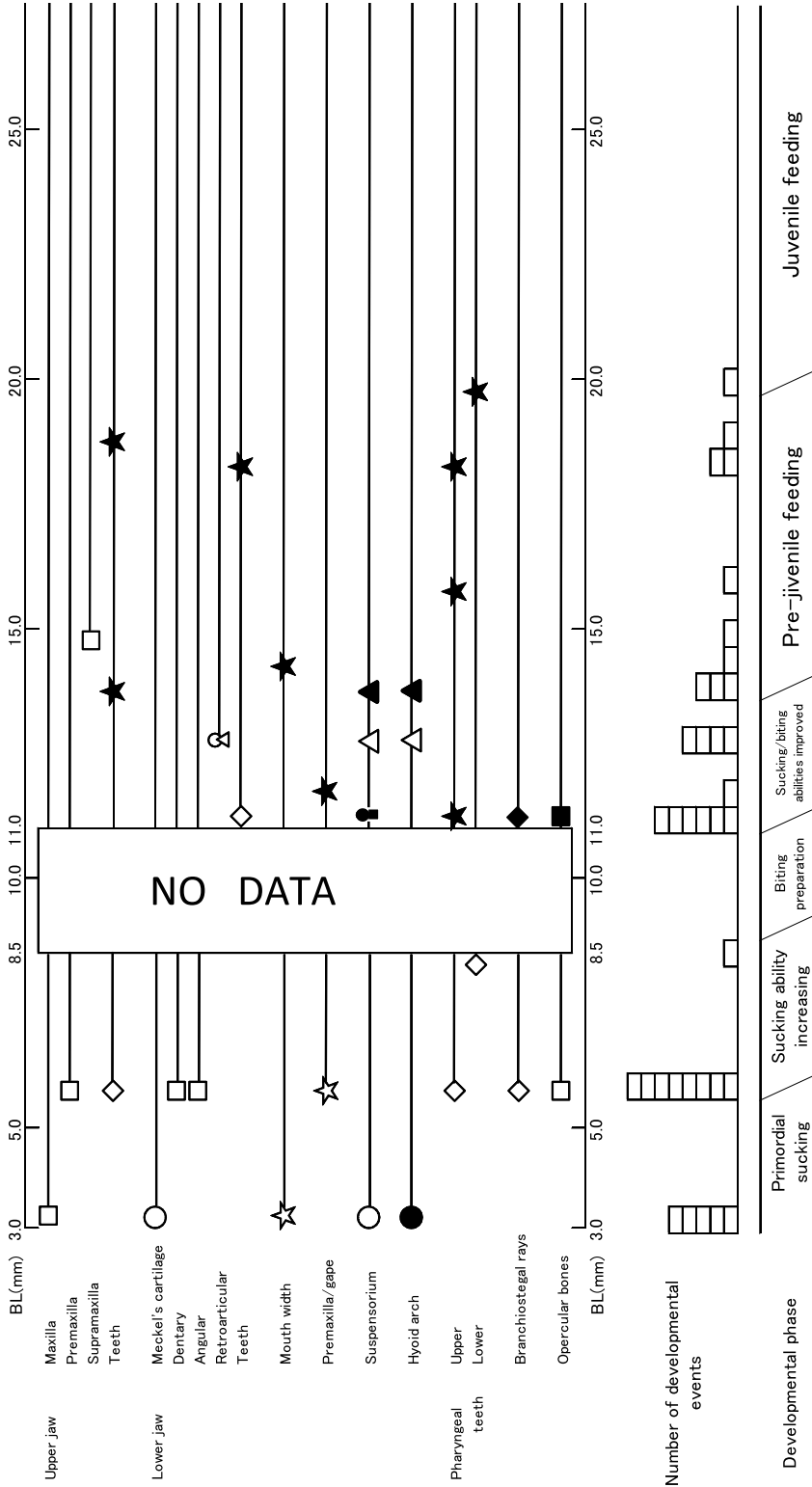


Fig. 8. Schematic representation of the development of feeding-related characters with growth (body length, BL) in *Lateolabrax japonicus* collected from Tokyo Bay. Open circles, cartilaginous elements start appearing; closed circles, all cartilaginous elements start appearing; open squares, bony elements start appearing; closed squares, all bony elements start appearing; open triangles, cartilaginous elements start ossifying; open stars, all cartilaginous elements start ossifying; open diamonds, teeth and branchial rays start appearing; a closed diamond, branchial rays become complete in number; open stars, mouth opens and premaxilla start appearing; closed stars, flexion points of teeth number and morphometric characters are observed.

Japanese sea bass larvae and juveniles obtained in this study are shown in Fig. 7 and 8.

4.1.1. Developmental phases of swimming function

Based on the development of characters related to swimming function, sea bass larvae and juveniles were divided into the following four phases.

1) The phase of less active swimming (3.0–5.5 mm BL)

No swimming-related characters appeared, other than the pectoral fin elements such as the cleithrum, coraco-scapular cartilage and fan-like cartilaginous plate, which developed later into actinosts. The larvae in this phase are therefore considered to drift passively rather than to swim actively.

2) The phase of caudal fin propulsion (5.5–8.5/11.0 mm BL)

In this phase, the caudal fin supports and fin rays started appearing. However, no other characters related to swimming were detected; therefore, this phase was judged as the caudal fin propulsion phase, during which the beating of the caudal fin produces propulsion. Larvae of 8.5–11.0 mm BL were not examined in this study, and thus the end of this phase and the beginning of the next phase were not precisely determined.

3) The phase of whole body propulsion (8.5/11.0–14.0 mm BL)

The neural and hemal arches and spines and the vertebral centra started appearing and were completed in number during this phase. These characters are considered to reinforce the body axis (KOHNO *et al.*, 2000). Notochord flexion was also completed, all the elements of caudal fin supports appeared and the number of caudal fin rays reached the adult complement during this phase, indicating that the beating ability of the caudal fin would increase (KOHNO and SOTA, 1998). The strong body axis and completed caudal fin allow larvae to swim powerfully by propagating the beat of the whole of the body posterior to generate propulsion (OMORI *et al.*, 1991). The dorsal and anal fin supports and fin rays were also completed during this phase; these characters prevent the larvae from rolling caused by whole-body

beating (GOSLINE, 1979). In addition, the pectoral and pelvic fin rays started appearing during this phase. The development of paired fin rays indicates the improvement of manoeuvrability (NARISAWA *et al.*, 1997).

4) The phase of functional, juvenile swimming (over about 14.0 mm BL)

All characters concerning swimming function became complete in number, and ossification started in all related elements. Therefore, larvae/juveniles larger than about 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 characters related to feeding function, sea bass larvae and juveniles were divided into the following five phases.

1) The phase of primordial sucking (3.0–5.5 mm BL)

The oral cavity was enclosed by the maxilla, Meckel's cartilage, a part of the suspensorium and hyoid arch, indicating that the feeding mode in this phase is sucking. However, these elements, other than the small bony maxilla, are cartilaginous, and thus negative pressure for sucking is considered to be low (see KOHNO *et al.*, 1997).

2) The phase of increasing sucking ability and biting preparation (5.5–8.5/11.0 mm BL)

The gape elements of the premaxilla, dentary and angular started appearing in this phase, indicating that gape opening and closing abilities increase (SHINAGAWA *et al.*, 2002). The appearance of branchiostegal rays and opercular bones would increase the sucking ability during this phase.

Although the upper jaw and pharyngeal teeth started appearing during this phase, no lower jaw teeth were recognised until 11.4 mm BL. 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). No specimens were examined between 8.5 and 11.0 mm BL in this study, and thus the larval size when the feeding mode of biting started could not be determined;

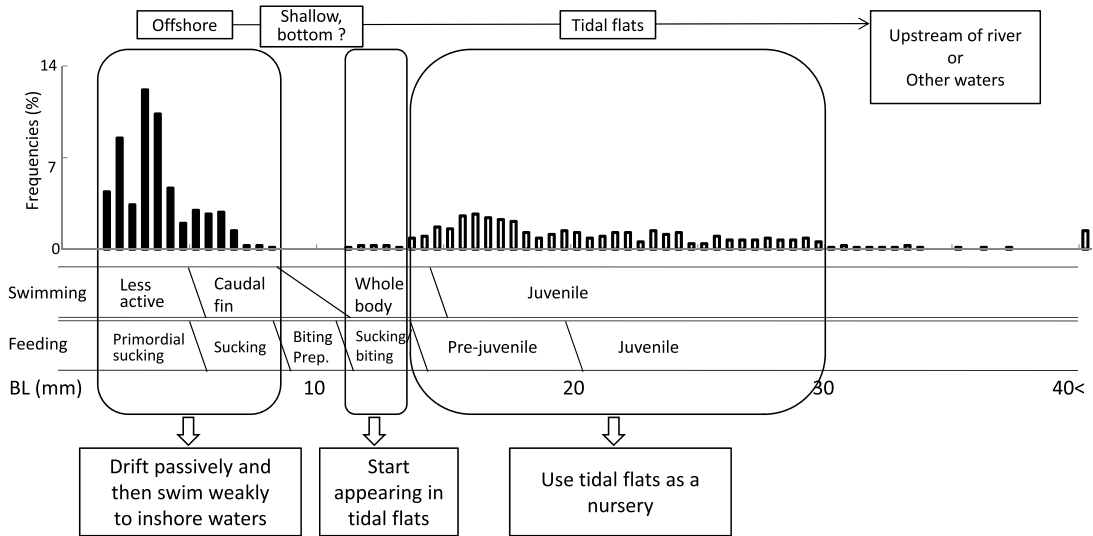


Fig. 9. Schematic representation summarizing the appearance patterns, habitat shifts, and functional development of swimming and feeding abilities, shown with growth (body length, BL), of the larval and juvenile *Lateolabrax japonicus* in Tokyo Bay.

therefore, this phase was tentatively recognised as biting preparation.

3) The phase in which sucking and biting abilities improved (8.5/11.0–13.5 mm BL)

In this phase, sucking ability was improved by the appearance of all the suspensorium and opercular bone elements. The numerical completion of the branchiostegal rays also helps to generate more or less strong negative pressure for sucking. In addition to sucking, the feeding mode of biting is gained by the appearance of lower jaw teeth. The stable ratio of premaxilla length to gape of 70–90% is considered to allow gape opening and closing to function well and thus to improve biting ability.

4) The phase of pre-functional, juvenile feeding (13.5–20.0 mm BL)

All the characters concerning feeding function except for the number of jaw and pharyngeal teeth became complete in number, and ossification began in all related elements. Therefore, larvae/juveniles of 13.5–20.0 mm BL are considered to have acquired a pre-functional, juvenile feeding mode.

5) The phase of functional, juvenile feeding (over about 20 mm BL)

The number of jaw and pharyngeal teeth became stable, and the functional, juvenile

feeding mode was considered to be acquired in juveniles of over 20 mm BL.

4.2. Relationships between developmental stages and distribution patterns

The relationships between the developmental phases obtained in this study and the appearances of Japanese sea bass larvae and juveniles in Tokyo Bay are schematically shown in Fig. 9.

4.2.1. Spawning and ontogenetic shoreward migration

In this study, yolk-sac larvae were mainly collected from outer Tokyo Bay, and the sizes of offshore specimens were significantly different among stations and between Stn. 7 and others. These results support the results of WATANABE (1965) and SUZUKI and ITOH (1984), according to whom the spawning ground of sea bass in Tokyo Bay was considered to be located in waters of the bay mouth, with hatching larvae moving to the inner waters of Tokyo Bay with growth. Also, in Ariake Bay, the spawning ground is located in the central region of the bay, and the eggs and larvae disperse toward the inner region (HIBINO, 2002; HIBINO *et al.*, 2002). These spawning grounds are located

in thermohaline frontal regions formed between the outer and inner bay waters, and eggs are densely distributed in these regions (WATANABE, 1965; NAKATA and IWATSUKI, 1991; HIBINO *et al.*, 2007).

This study revealed that nearly all the larvae collected offshore that were smaller than 5.5 mm BL would drift passively with primordial characters related to their swimming function, and even larger larvae up to about 8 mm BL would swim only weakly using caudal fin propulsion (Fig. 9). These results support the suggestion that the inshore ontogenetic migration of sea bass early larvae depends on shoreward currents. OHMI (2002) speculated that the gravitational circulation in Wakasa Bay in the Sea of Japan plays an important role in larval drift to the inshore region through the middle to bottom layer, and HIBINO *et al.* (2007) showed that in Ariake Bay, larvae temporally expand their distribution into the inner, shallow water regions via the middle layer. In this period of shoreward migration, the first feeding larvae prey on smaller zooplankton, based on the estimated mouth size (ISLAM and TANAKA, 2005). Sea bass larvae smaller than about 8 mm BL likely generate low negative pressure to suck food organisms with a poorly developed oral cavity.

4.2.2. Habitat shifts with development

The largest larva collected from offshore waters in Tokyo Bay was 8.1 mm BL, and the smallest larva from the innermost tidal flats was 11.4 mm BL in this study. Dodging behaviour by sea bass larvae larger than 8 mm BL is very unlikely because KANOU *et al.* (2002a) collected larger, more active fish larvae such as a 39.4 mm BL juvenile of atherinid *Hypoatherina valenciennesis*, a 28.4 mm BL juvenile of carangid *Seriola quinqueradiata* and a 24.6 mm BL mugilid *Mugil cephalus cephalus* using the same gear and methods as those used in this study. OHMI (2002) reported that sea bass of 8–14 mm BL appeared in sandy bottom waters of 5–10 m depth off the Yura River mouth of Wakasa Bay. Therefore, sea bass larvae of 8–11 mm BL would be distributed in shallow, bottom waters of Tokyo Bay (Fig. 9).

The larvae and juveniles collected from the

tidal flats ranged from 11.4 to 123.5 mm BL in this study. However, few fish measuring 13.5 mm BL and smaller were collected, and numbers decreased suddenly at about 30 mm BL and larger, with a mean of 21.9 mm BL and mode of 16.0–16.5 mm BL. The juvenile stage was attained at 13.8 mm BL when the fin rays reached their adult complements in number. Therefore, the tidal flats of inner Tokyo Bay provide a nursery ground mainly for 13.5–30-mm BL juvenile sea bass (Fig. 9). This study showed also that sea bass early juveniles starting at 13.5 mm BL acquire functional, juvenile swimming and feeding abilities.

The early juveniles appearing in the tidal flats swim actively and select this area as a habitat. The complete juvenile feeding mode was acquired at 20 mm BL, with the stability of tooth numbers. NIP *et al.* (2003) reported that sea bass of 11–20 mm BL fed on copepods and cladocerans, shifting to decapods and amphipods at 20 mm BL in Tolo Harbour, Hong Kong. FUJITA *et al.* (2007) also indicated that sea bass larger than 20 mm BL fed exclusively on mysids in Ariake Bay. HIBINO *et al.* (2006) showed that in the sand flats of the eastern part of Ariake Bay, sea bass juveniles of 16.7 and 22.9 mm BL on an average at the spring and neap tides, respectively, migrate to shallow water after sunrise to feed on copepods before emigrating from there after sunset.

4.2.3. Importance of larval and juvenile habitats for the Tokyo Bay sea bass

Tokyo Bay has been a leading location for the catch of sea bass, with the production from the bay accounting for about 30% of the total catch in the 2009 fiscal year (Fisheries AGENCY, 2011). As pointed out by SHOJI *et al.* (2002), the Tokyo Bay sea bass catch has been favourably retained since the 1990s, indicating that the recruitment of sea bass has been stable. A major factor affecting recruitment variability is the survival rate during the early life history (HOUDE, 1987). The Tokyo Bay sea bass, as a migratory fish, is considered to face two major challenges during the egg, larval and juvenile stages, one being the long-distance migration from the spawning to nursery grounds, and the being other the selection of a

nursery ground.

No serious environmental problems affect the sea bass spawning ground at the mouth of Tokyo Bay. However, the distance from the spawning ground at the mouth of Tokyo Bay to the innermost tidal flats is about 50 km, and the avenue to the nursery ground including the spawning ground is narrow and experiences heavy maritime traffic, with the giant ports of Yokohama, Tokyo and Chiba being located in the inner bay. Therefore, the challenging migration of the sea bass to the nursery ground could likely be disturbed by anthropogenic impacts, although the details of the mechanisms of transport for eggs and early larvae to the nursery grounds are unknown.

Many studies have pointed out that sea bass nursery grounds are diversified, including surf zones in open waters and tidal flats, shallow areas, seagrass beds and rivers in embayments (HIBINO, 2002; KINOSHITA, 2002; FUJITA *et al.*, 2007), and the adaptability of sea bass to these diversified environments would increase the stability of their population dynamics. However, these nursery grounds in innermost Tokyo Bay have been destroyed by factors such as reclamation, dredging and the construction of ports and estuarine dams.

To properly maintain the Tokyo Bay sea bass population, further studies are needed to demonstrate the mechanisms of shoreward migrations and the variety of embayment nurseries used, and the environments of the habitats required during the early life history of the sea bass should be protected from any sort of destruction.

Acknowledgments

The authors are grateful to staff of the Laboratory of Ichthyology and Laboratory of Planktology, Tokyo University of Marine Science and Technology (TUMSAT), for assistance in fieldwork. We thank the crews of T/S *Hiyodori* and TR/V *Seiyo-maru* of TUMSAT for their support during the samplings in offshore waters. This study was supported in part by JSPS KAKENHI Grant Number 24310028.

References

- ARAYAMA, K., H. Imai, K. KANOU and H. KOHNO (2002): Ichthyofauna of surf zones in the outer Tokyo Bay. *La mer*, **40**, 59–70. (in Japanese with English abstract)
- FISHERIES AGENCY (2011): Catch volumes per sea region/prefecture for major types of fish: <http://www.e-stat.go.jp/SG1/estat/List.do?lid=000001076424> (cited in October 2012).
- FUJITA, S., I. KINOSHITA, Y. KAWAMURA and D. AOYAMA (2007): The diversity in the early life history of *Lateolabrax japonicus* in the Ariake Bay. *Aquabiology*, **29** (1), 47–54. (in Japanese)
- GOSLINE, W. A. (1971): Functional morphology and classification of teleostean fishes. University Press of Hawaii, Honolulu, 208 pp.
- HATOOKA, K. (2002): Moronidae. In: T. NAKABO (ed). *Fishes of Japan with pictorial keys to the species*. English edition. Tokai Univ. Press, Tokyo, 1435.
- HIBINO, M. (2002): Early life history diversity of the Ariake population. In: M. TANAKA and I. KINOSHITA, eds. *Temperate bass and biodiversity: new perspective for fisheries biology*. Koseisha-Koseikaku, Tokyo, 65–78. (in Japanese)
- HIBINO, M., T. OHTA, T. ISODA, K. NAKAYAMA and M. TANAKA (2006): Diel and tidal changes in the distribution and feeding habits of Japanese temperate bass *Lateolabrax japonicus* juveniles in the surf zone of Ariake Bay. *Ichthyol. Res.*, **53**, 1062–1068.
- HIBINO, M., T. OHTA, T. ISODA, K. NAKAYAMA and M. TANAKA (2007): Distribution of Japanese temperate bass, *Lateolabrax japonicus*, eggs and pelagic larvae in Ariake Bay. *Ichthyol. Res.*, **54**, 367–373.
- HIBINO, M., T. OHTA, I. KINOSHITA and M. TANAKA (2002): Fish larvae and juveniles occurring in the littoral zone of a tidal flat, in the bottom of Ariake Bay. *Japan. J. Ichthyol.*, **49**, 109–120. (in Japanese with English abstract)
- HOUDE, E. D. (1987): Fish early life dynamics and recruitment variability. *Am. Fish. Soc. Symp.*, **2**, 17–29.
- ISLAM, M. and M. TANAKA (2005): Nutritional condition, starvation status and growth of early juvenile Japanese sea bass (*Lateolabrax japonicus*) related to prey distribution and feeding in the nursery ground. *J. Exp. Mar. Biol. Ecol.*, **323**, 172–183.
- ISLAM, M., Y. YAMASHITA and M. TANAKA (2011): A review on the early life history and ecology of Japanese sea bass and implication for recruitment. *Env. Biol. Fishes*, **91**, 389–405.
- KANOU, K., K. ARAYAMA, H. IMAI, K. KANAZAWA, T.

- KOIKE and H. KOHNO (2002a): Seasonal and spatial changes in the larval and juvenile fish fauna in surface waters of Tokyo Bay, central Japan. *La mer*, **40**, 11–27. (in Japanese with English abstract)
- KANOU, K., H. KOHNO, P. TONGNUNUI and H. KUROKURA (2002b): Larvae and juveniles of two engraulid species, *Thryssa setirostris* and *T. hamiltoni*, occurring in the surf zone at Trang, southern Thailand. *Ichthyol. Res.*, **49**, 401–405.
- KANOU, K., T. KOIKE and H. KOHNO (2000): Ichthyofauna of tidelands in the inner Tokyo Bay, and its diversity. *Japan. J. Ichthyol.*, **47**, 115–129. (in Japanese with English abstract)
- KENDALL, A. W., Jr., E. H. AHLSTROM and H. G. MOSER (1984): Early life history stages of fishes and their characters. In: H.G. MOSER, W.J. RICHARDS, D.M. COHEN, M.P. FAHAY, A.W. KENDALL, Jr. and S.L. RICHARDSON, eds. *Ontogeny and systematics of fishes*. *Am. Soc. Ichthyol. Herpetol., Spec. Pub.*, **1**, 11–22.
- KINOSHITA, I. (2002): Diversity of the early life history. In: M. TANAKA and I. KINOSHITA, eds. *Temperate bass and biodiversity: new perspective for fisheries biology*. Koseisha-Koseikaku, Tokyo, 79–90. (in Japanese)
- KINOSHITA, I. and S. FUJITA (1988): Larvae and juveniles of temperate bass, *Lateolabrax latus*, occurring in the surf zone of Tosa Bay, Japan. *Japan. J. Ichthyol.*, **34**, 468–475.
- KOHNO, H., Y. KURITA and T. SEIKAI (2000): Ontogenetic intervals based on the development of swimming- and feeding-related characters in the hexagrammid, *Hexagrammos agrammus*, larvae and juveniles. *La mer*, **38**, 77–86. (in Japanese with English abstract)
- KOHNO, H., R. ORDONIO-AGUILAR, A. OHNO and Y. TAKI (1997): Why is grouper larval rearing difficult?: an approach from the development of the feeding apparatus in early stage larvae of the grouper, *Epinephelus coioides*. *Ichthyol. Res.*, **44**, 267–274.
- KOHNO, H. and K. SOTA (1998): Ontogenetic intervals based on the development of swimming- and feeding-related characters in larvae and juveniles of the lumpfish, *Inimicus japonicus*. *SUISANZOSHOKU*, **46**, 333–342. (in Japanese with English abstract)
- KOHNO, H., T. YOKOO, M. MOTTEKI and K. KANOU (2008): Ichthyofauna of the artificial lagoon, Shinhama-ko, located along the northernmost shore of Tokyo Bay. *Biogeography*, **63**, 133–142. (in Japanese with English abstract)
- LEIS, J.M. and T. TRNSKI (1989): *The larvae of Indo-Pacific shorefishes*. Univ. Hawaii Press, Honolulu, 371 pp.
- MATSUMIYA, Y., T. MITANI and M. TANAKA (1985): Ecology of ascending larval and early juvenile Japanese sea bass in the Chikugo estuary. *Nippon Suisan Gakkaishi*, **51**, 1955–1961.
- MOTTEKI, M., K. YASUDA, K. YAMAMOTO, T. YOKOO, H. KOHNO, K. MOROHOSHI, N. SUZUKI, S. MATSUZAKA and R. ARIZI (2009): Seasonal changes of fish fauna at the Keihin-jima artificial tidal flat in the inner Tokyo Bay, with special reference to the necessity of long-term biological monitoring. *La mer*, **46**, 121–134. (in Japanese with English abstract)
- NAGAIWA, R., M. MOTTEKI and H. KOHNO (2005): Larval and juvenile fish assemblages in surface waters at the mouth of Tokyo Bay. *La mer*, **43**, 97–104. (in Japanese with English abstract)
- NAKATA, H. and T. IWATSUKI (1991): Reproduction of *Lateolabrax* observed in the relation with transport process of substances. *The monthly KAIYOU*, **23**, 199–203. (in Japanese)
- NARISAWA, Y., H. KOHNO and K. FUJITA (1997): Development of swimming- and feeding-related characters in the grouper, *Epinephelus coioides*, larvae. *J. Tokyo Univ. Fish.*, **84**, 75–92. (in Japanese with English abstract)
- NIP, T.H.M., W.-Y. HO and C.K. WONG (2003): Feeding ecology of larval and juvenile black seabream (*Acanthopagrus schlegeli*) and Japanese sea-perch (*Lateolabrax japonicus*) in Tolo Harbour, Hong Kong. *Env. Biol. Fishes*, **66**, 197–209.
- OHMI, H. (2002): Juvenile ecology in Yura river estuary in Wakasa Bay. In: M. TANAKA and I. KINOSHITA, eds. *Temperate bass and biodiversity: new perspective for fisheries biology*. Koseisha-Koseikaku, Tokyo, 44–53. (in Japanese)
- OMORI, M., Y. SUGAWARA and H. HONDA (1996): Morphogenesis in hatchery-reared larvae of the black rockfish, *Sebastes schlegeli*, and its relationship to the development of swimming and feeding functions. *Ichthyol. Res.*, **43**, 267–282.
- POTTHOFF, T. (1984): Clearing and staining techniques. In: H.G. MOSER, W.J. RICHARDS, D.M. COHEN, M.P. FAHAY, A.W. KENDALL, Jr. and S.L. RICHARDSON, eds. *Ontogeny and systematics of fishes*. *Am. Soc. Ichthyol. Herpetol., Spec. Pub.*, **1**, 35–37.
- SAKAI, H. (1990): Larval development intervals in *Tribolodon hakonensis* (Cyprinidae). *Japan. J. Ichthyol.*, **37**, 17–28.
- SHINAGAWA, J., K. KAJI, H. KOHNO and K. FUJITA (2002): Ontogenetic intervals based on the development of swimming- and feeding-functions in the amphidromous *Cottus pollux* larvae and juveniles. *J. Tokyo Univ. Fish.*, **88**, 25–32. (in Japanese with English abstract)
- SHOJI, N., K. SATO and M. OZAKI (2002): Distribution and utilization of the stock. In: M. TANAKA and I. KINOSHITA (eds.) *Temperate bass and bio-*

- diversity: new perspective for fisheries biology. Koseisha-Koseikaku, Tokyo, 9–20. (in Japanese)
- SUZUKI, H. (1982): 1) Morphology and distribution of eggs. *In*: 2. Ecology, I Ecology and Resources of the Japanese sea bass, Report of polluted waters with materials such as mercury No. 3, Department of Research, Fisheries Agency, 16–21. (in Japanese)
- SUZUKI, H. and Y. ITOH (1982): Distribution and ecology of the Japanese sea bass in Tokyo Bay. *In*: II Ecology of the Japanese sea bass in specific marine waters, Report of polluted waters with materials such as mercury No. 3, Department of Research, Fisheries Agency, 75–89. (in Japanese)
- WATANABE, T. (1965): Ecological distribution of eggs of common sea bass, *Lateolabrax japonicus* (Cuvier) in Tokyo Bay. Bull. Japan. Soc. Sci. Fish., **31**, 585–590. (in Japanese with English abstract)

Received: October 22, 2012
Accepted: January 15, 2013