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Habitat Shifts of Larval and Juvenile Konoshiro Gizzard Shad, *Konosirus punctatus*, in Relation to the Functional Development in Tokyo Bay, Central Japan

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Abstract:　Occurrence patterns of konoshiro gizzard shad *Konosirus punctatus* larvae and juveniles were examined in Tokyo Bay by monthly samplings using the following two types of gear: a small seine net towed at three tidal flats in the inner bay from June 2006 to August 2008 and at three surf zones in the outer bay from April 1998 to March 1999 except July 1998; and a ring net towed at five sites in offshore waters of the outer bay from April 1996 to March 1997 except August 1996. Their ontogenetic intervals were also determined by the development of swimming- and feeding-related characters based on 129 cleared and stained specimens of 3.6-25.1 mm in body length, BL. In the outer Tokyo Bay, specimens collected from offshore waters were 1,114 individuals ranging from 3.0 to 7.2 mm BL, while those from surf zones being 4,991 ranging from 7.8 to 34.1 mm BL. Specimens collected from the tidal flats of inner Tokyo Bay was 1,800 individuals ranging from 5.2 to 18.3 mm BL. Four developmental phases were detected on both the swimming and feeding functions. Spawning grounds of *K. punctatus* are suggested to be formed in offshore waters, lower reaches of rivers and a brackish lagoon of the inner Tokyo Bay as well as offshore waters of outer Tokyo Bay. The surf zones and tidal flats of Tokyo Bay were clarified to be a nursery ground for *K. punctatus* larvae/juveniles. However, the larval body size when the number of individuals starts decreasing was different between the tidal flats, > ca. 10 mm BL and the surf zone, > ca. 18 mm BL. Based on the developmental phases, *K. punctatus* larvae/juveniles would acquire the functional, juvenile swimming and feeding abilities at about 18 mm BL, and thus the decrease in the surf zones are considered to be an active behaviour to shift their habitats for more adequate growth. However in the tidal flats of inner bay, the decrease in number is not accounted by habitat shifts but supposed to be caused by such other factors as the water quality, extent of tidal flats and/or any other unknown causes.

Key words:　konoshiro gizzard shad, early life history, occurrence patterns, functional development

Introduction

The konoshiro gizzard shad *Konosirus punctatus* is widely distributed in the northwestern Pacific, coasts of Japan southward from about 37 °N, i.e. not Hokkaido, Yellow Sea and East China Sea south to Taiwan and Hong Kong (Whitehead, 1985). This species inhabits rivers and coastal waters, especially relatively shallow bays, and is commonly known as *kohada*, a popular *sushi* fish in Japan. This species occupies an important position in the fisheries in Ariake Sound (Takita, 1978a) and in Tokyo Bay (Kuroda et al., 2002). Various studies have been conducted as follows: the description and development of eggs (Matsushita and Nose, 1974; Takita, 1978a, b; Kong et al., 1998), age and growth (Kuwatani, 1958), artificial insemination (Kuwatani et al., 1956, 1958), and larval and juvenile morphologies (Yoshida, 1937; Kuroda et al., 1983; Takita, 1988; Noichi, 2014). Occurrence patterns of eggs, larvae and/or juveniles have also been studied in offshore waters (Takita, 1980; Mori, 1995; Kimura et al., 1999; Yamamoto et al., 2001; Kanou et al., 2002a; Koshikawa, 2003; Kusaka et al., 2013) and shoreline waters (Kinoshita, 1998; Kanou et al., 2000; Arayama et al., 2002).

However, no information is available on the development of swimming- and feeding-related characters nor on the ontogenetic intervals of *K. punctatus* larvae. Although occurrence patterns of larvae and juveniles have been investigated by habitats such as offshore and nearshore waters, no integrated studies are available to consider both the results of offshore and coastal samplings. The present study was thus conducted to clarify the ontogenetic intervals during the early life history of *K. punctatus* based on the development of swimming- and feeding-related characters. The occurrence patterns of larvae/juveniles were also investigated in the offshore and coastal waters in Tokyo Bay, and the relationships between the ontogenetic intervals and occurrence patterns were clarified to elucidate how each area of Tokyo Bay works as habitats for this species.

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Materials and methods

The specimens used in this study were collected from both the outer and inner Tokyo bays. Tokyo Bay is the northern area of an imaginary line between Sunosaki of Boso Peninsula and Tsurugisaki of Miura Peninsula. The inner and outer Tokyo bays are divided by an imaginary line between Futtsumisaki of Boso Peninsula and Kannonzaki of Miura Peninsula, where the northern area being the inner and the southern area the outer Tokyo bays.

In the outer Tokyo Bay, specimens were collected from five sites in offshore waters and from three surf zones (Fig. 1). A 1.3 m diameter ring net with 0.33-mm mesh opening towed monthly for 15 minutes by two knots through the surface layer during day time from April 1996 to March 1997 except August 1996 in the offshore water sampling sites (St. 1-5: Fig. 1). A small seine-net with 0.8-mm mesh opening (cf., Kanou et al., 2002b) was towed monthly for about 100 m^2 at about 1m depth during day time from April 1998 to March 1999 except July 1998 in three surf zones, Kazusaminato, Tomiyama and Hojo (Fig. 1). In the inner Tokyo Bay, on the other hand, no samplings were carried out in the offshore waters, but the seine-net samplings in the same manner as in the outer Tokyo Bay were conducted at three tidal flats, Haneda, Keihin and Ebitori (Fig. 1) from June 2006 to August 2008. Data of water temperature and salinities were recorded after each sampling using a salinity refractometer and a mercury-in-glass thermometer in the outer Tokyo Bay sampling stations and a portable CTD (YSI/Nanotech, EC-300) in those of the inner Tokyo Bay.

Specimens were fixed in 5% seawater formalin and later preserved in 70% ethanol. The 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 for larvae smaller than 15 mm BL, and a digital caliper for larvae of 15 mm and larger. Specimens were measured at most 100 individuals by each sampling station/month.

Of the specimens collected, 129 individuals (3.6-25.1 mm BL) were randomly selected for the morphological study to determine the functional development. These specimens were cleared and stained by the method of Potthoff (1984), and the following characters were observed: fin supports and rays, the angle of notochord flexion, the vertebral centra, hemal and neural spines and the greatest body depth (GBD) and its position from the snout as the swimming-related characters; and the structure of upper jaw (maxilla, premaxilla and supramaxilla), the structure of lower jaw (Meckel's cartilage, dentary, angular and retroarticular), jaw teeth, mouth width, the ratio of premaxilla to gape, pharyngeal teeth, suspensorium, opercular bones, hyoid arch and branchiostegal rays 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 characters method were applied. In the present 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.

Results

1. Water temperature and salinity

The water temperature in three surf zones of outer Tokyo Bay during the period from May to July, when *K. punctatus* specimens collected, ranged from 17.0 to 26.5 °C and salinities from 22.5 to 34.5. In offshore waters of outer Tokyo Bay, water temperature ranged from 13.0 to 23.0 °C and salinities from 29.2 to 34.2 in the period from May to July. In three tidal flats of inner Tokyo Bay, water temperature ranged from 13.9-29.1 °C and salinities from 3.3-25.4 in the period from April to August.

2. Occurrence patterns

The total number of *K. punctatus* larvae collected from offshore waters of outer Tokyo Bay was 1,114 individuals ranging from 3.0 to 7.2 mm BL with a mode of 4.0-4.9 mm BL (Fig. 2). These specimens occurred from April to July.

Specimens collected from the surf zones of outer Tokyo Bay numbered 4,991 individuals ranging from 7.8 to 34.1 mm BL and showed a bimodality with two size-class peaks at 11.0-11.9 and 18.0-18.9 mm BL (Fig. 2). These specimens were collected from May to July.

The total number of specimens collected from the tidal flats of inner Tokyo Bay was 1,800 individuals ranging from 5.2 to 18.3 mm BL with a mode of 10.0-10.9 mm BL (Fig. 2). These specimens were collected from April to August.

3. Functional development

1) Swimming-related characters

Flexion of the notochord end: Flexion of the notochord end was first evident in 7.4 mm BL specimen with the angle of 14.0° (Fig. 3A). The notochord flexion became complete at an angle about 45 to 55° and more in specimens larger than about 11 mm BL.

Caudal fin supports and fin rays: No elements of caudal skeleton were detected until 7.4 mm BL, when three cartilaginous buds of parhypural and hypurals 1 and 2 were observed. The cartilaginous buds of hemal arch and spine of the future preural centrum 2 were observed at 7.7 mm BL. Thereafter, hypurals 3 and 4 were observed at 7.8 mm BL, followed by hypural 5 at 9.3 mm BL. In the specimen of 10.0 mm BL, hypural 6, cartilaginous buds of hemal arch and spine of the future preural centrum 3, as well as the cartilaginous bud of neural arch of the future preural centrum 1 were perceived, and then the neural arch of the future preural centrum 2 and 3 appeared at 10.2 mm BL. The cartilaginous buds of epurals 1 and 2 were observed at 10.5 mm BL, while neural spine of the future preural centra 2 at 10.6 mm BL. The cartilaginous epural 3 and neural spine of future preural centra 3 were observed at 12.3 mm BL, followed by that of preural centra 1 at 12.6 mm BL, when all the cartilaginous elements became complete in number.

The ossification was first perceived on the hypurals 1-3 and parhypural at 10.0 mm BL. Hypurals 4 and 5 started ossifying at 10.4 mm BL, followed by hypural 6 at 11.2 mm BL. Cartilaginous buds of hemal/neural spines of preural centra started ossifying before those of the hemal/neural arches. Hemal spines of preural centra 2 and 3 started ossifying at 12.5 mm BL and 12.6 mm BL, respectively. The cartilaginous buds of neural spine of preural

centra 1, 2 and 3 started ossifying at 17.3 mm BL, 12.5 mm BL, and 12.6 mm BL, respectively. Epurals 1 and 2 started ossifying at 17.5 mm BL, while epural 3 at 17.7 mm BL, when all the cartilaginous elements started ossifying.

The first bony element appeared at 10.0 mm BL when the uroneural 1 was observed, followed by uroneurals 2 and 3 being evident at 11.2 mm BL and 16.1 mm BL, respectively. With the appearance of uroneural 3, the bony elements became complete in number.

The caudal fin rays started appearing at 7.7 mm BL (Fig. 3B). The adult complement of 10 + 9 principal caudal fin rays attained at 10.2 mm BL.

Dorsal fin supports and fin rays: Six cartilaginous buds of proximal pterygiophores were first observed at 7.4 mm BL. Nine distal pterygiophores were first discerned at 7.7 mm BL, and the adult complement of 16 – 18 pterygiophores was first observed at 12.9 mm BL. The ossification was first discerned at 15.2 mm BL specimen in which 5 proximal pterygiophores ossifying.

Dorsal fin rays were first discerned at 7.7 mm BL, when 7 soft fin rays were observed (Fig. 3C). The adult complement of 16-20 rays was attained at 12.9 mm BL.

Anal fin supports and fin rays: The smallest specimen possessing the cartilaginous buds of proximal pterygiophores, 4 in number, was 11.2 mm BL. The adult complement of 19–27 pterygiophores was attained at 15.5 mm BL. The ossification was first discerned at 17.5 mm BL, in which 3 proximal pterygiophores ossifying.

Anal fin rays were first evident at 12.3 mm BL, when 7 soft fin rays were observed. The adult complement of 19-27 rays was attained at 15.5 mm BL (Fig. 3D).

Pectoral fin supports and fin rays: All the specimens examined in this study possessed a rod-shaped bony cleithrum. A cartilaginous coraco-scapular and a cartilaginous plate, which later grew into actinosts, were first observed at 4.0 and 5.2 mm BL, respectively. The blade-like cartilaginous plate was divided into four actinosts at 18.0 mm BL, when all the cartilaginous elements became complete in number. The bony elements of supracleithrum and posttemporal were first evident at 12.3 and 13.5 mm BL, respectively, followed by postcleithrum 1, supratemporal and postcleithrum 2 at 18.0 mm BL, 18.8 mm BL and 19.2 mm BL, respectively, and all the bony elements became complete in number. The ossification was first observed at 16.1 mm BL, when the center of coraco-scapular cartilage started ossifying. The ossification of actinosts 1 and 2 started at 20.5 mm BL, while those of 3 and 4 at 23.3 mm BL, when all the cartilaginous elements started ossifying.

The pectoral fin rays were first discerned at 15.8 mm BL, when four were observed (Fig. 3E). The fin rays increased in number and attained the adult complement in number at 19.2 mm BL, when the developmental stage changed from a larva to a juvenile.

Pelvic fin supports and fin rays: The pelvic fin support, basipterygium, was first observed at 12.5 mm BL, and the ossification started at 17.1 mm BL.

The pelvic fin rays were first discerned at 12.8 mm BL, when three rays were observed (Fig. 3F). The adult complement of eight rays was attained at 15.8 mm BL.

Vertebra: The smallest specimen possessing vertebral elements was 10.1 mm BL, in which 48 cartilaginous hemal and neural

arches were observed. The hemal and neural spines and 18 centra were observed at 12.5 mm BL. The adult complement of 49 centra was attained at 13.0 mm BL, and hemal spines and arches became complete in number at 13.2 mm BL, while those of neural at 17.2 mm BL. The ossification of the hemal and neural spines and arches were first observed at 13.0 mm BL. All hemal spines and arches started ossifying at 17.5 mm BL, while those of neural at 18.5 mm BL.

Greatest body depth (GBD) and its position: The ratio of GBD to BL was 8.7% in the smallest specimen examined of 3.6 mm BL, then slightly decreased to 7.1% at about 9 mm BL. The ratios increased exponentially thereafter, with the ratio of 23.8% at the largest specimen of 25.1 mm BL (Fig. 3G).

The position of GBD was around the head, and the ratios to the BL varied from about 10 to 30% up to about 10 mm BL (Fig. 3H). The position shifted to around dorsal fin in the specimens larger than about 10 mm BL, the ratios varying from about 50 to 70%. In the specimens larger than 17.7 mm BL, the ratios more or less decreased to 25-45% to BL.

2) Feeding-related characters

Upper jaw length: The mouth opened first at 4.4 mm BL, with the length of upper jaw being 0.26 mm (Fig. 4A). The growth of upper jaw length was more or less slow until about 11.9 mm BL and then became rapid thereafter to reach 3.9 mm at 25.1 mm BL.

Jaw structure: The smallest specimen of 3.6 mm BL possessed a Meckel's cartilage. The maxilla was first observed at 4.8 mm BL. Both the dentary and retroarticular appeared at 9.3 mm BL and the angular at 12.8 mm BL, premaxilla at 15.5 mm BL and supramaxilla at 15.8 mm BL.

Jaw teeth: An upper jaw tooth was first observed at 7.4 mm BL (Fig. 4B). The number of upper jaw teeth increased rapidly from about 9.5 mm BL to about 19.5 mm BL and somehow decreased thereafter. The maximum number of upper jaw teeth was 19 at 19.3 mm BL, and the largest specimen of 25.1 mm BL possessed nine upper jaw teeth.

The lower jaw teeth were first observed at 9.3 mm BL with two in number (Fig. 4C). Thereafter, the number of lower jaw teeth varied from 0 to 4, except five of 15.8 mm BL specimen.

Suspensorium: The palatoquadrate and hyomandibular-sympletic cartilages were first discerned at the smallest specimen of 3.6 mm BL. The bony endopterygoid and ectopterygoid were observed at 12.6 mm BL and 12.8 mm BL, respectively. The ossficiation started at 12.8 mm BL in the sympletic, followed by the hyomandibular and quadrate at 17.2 mm BL. The metapterygoid started ossifying at 17.7 mm BL.

Hyoid arch and branchiostegal rays: The hypohyal, cerato-epihyal, and interhyal cartilages were first observed at 4.8 mm BL. The ceratohyal, hypohyal, epihyal and interhyal started ossifying at 16.3 mm BL, 17.5 mm BL, 17.7 mm BL and 18.3 mm BL, respectively.

Three branchiostegal rays were first noted at 15.8 mm BL, and the adult complement of 6 rays was attained at 18.0 mm BL (Fig. 4D).

Opercular bones: A bony opercle appeared first at 12.2 mm BL, followed by the preopercle at 12.6 mm BL, subopercle at 13.4 mm BL and interopercle at 13.7 mm BL.

Pharyngeal teeth: One upper pharyngeal tooth was first

observed at 9.3 mm BL (Fig. 4E). The number tended to increase and then decrease, and no tooth was found finally in the largest specimen of 25.1 mm BL. One lower pharyngeal tooth was first discerned at 6.0 mm BL (Fig. 4F). The number of teeth increased to about 12.5 mm BL and varied from three to 11 thereafter.

Discussion

1. Developmental phases of *K. punctatus* larvae and juveniles

1) Developmental phases of swimming function

Based on the development of swimming-related characters shown in Figure 5, the *K. punctatus* larvae and juveniles were divided into the following four developmental phases.

The phase of less active swimming (from 3.6 mm BL to 7-8 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. According to Kuwatani et al. (1956), reared larvae at this phase tended to spend most of their time on the bottom of the rearing tank.   Therefore, the larvae in this phase are considered to have little swimming ability and thus drift passively rather than to swim actively.

The phase of caudal fin propulsion (from 7-8 mm BL to 12-13 mm BL): In this phase, notochord end flexion started and became completed and caudal fin supports and rays started appearing, indicating that the larvae attaining the ability of propulsion (Kohno et al., 1983) at this stage.

During this phase, the caudal fin rays reached the adult complement in number as well as the ossification on the caudal fin support was first observed during this phase. Hemal and neural arches and spines and the dorsal fin supports and rays started appearing. Such development of swimming-related characters indicate that, as suggested by Kohno (1998), the larvae start preparing whole body propulsion by strongly vibrating their long body with tail-beats.

The phase of whole body propulsion (from 12-13 mm BL to 17-19 mm BL): The vertebral centra started appearing and became completed in number, and the dorsal and anal fin supports were also reached to the adult complement in number; therefore, the strong body axis and completed dorsal and anal fins allow the larvae to swim powerfully by propagating the beat of the whole body posterior to generate propulsion (Omori et al., 1996). 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 the whole-body beating (Gosline, 1971).

The ossification was observed on the pectoral fin supports, and the pelvic fin support and rays appeared and were completed during this phase. The development of paired fins indicates the improvement of maneuverability (Lagler et al., 1977; Matsuoka, 1987; Narisawa et al., 1997). Position of the greatest body depth also shifted during this phase, indicating an improvement of swimming ability (Aleev, 1963).

The phase of functional, juvenile swimming (over 17-19 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 17.7 mm BL were considered to have acquired the functional, juvenile swimming mode although the full count of fin rays was attained at 19.2 mm BL.

2) Developmental phases of feeding function

Based on the development of feeding-related characters shown in Figure 6, the *K. punctatus* larvae and juveniles were divided into the following four developmental phases.

The phase of primordial feeding (from 3.6 mm BL to 9-10 mm BL): Mouth opened at 4.4 mm BL. The oral cavity was enclosed by the small bony maxilla and dentary, Meckel's cartilage and cartilaginous suspensorium and hyoid arch, indicating that the feeding mode is considered to be primordial. (e.g., Kohno et al., 1996, 1997).

The phase of increasing capturing ability (from 9-10 mm BL to 12-13 mm BL): The lower jaw and upper pharyngeal teeth started appearing, and the upper jaw and lower pharyngeal teeth increased in number during this phase. The functions of the jaw and pharyngeal teeth are to capture and to propel acquired food organisms to the digestive tract, respectively (Gosline, 1971). The initial feeding mode of *K. punctatus* having the longer shirasu-type body is considered to be a 'straining' (cf., Kohno et al., 1996; Kohno, 1998).

The phase of increasing straining ability (from 12-13 mm BL to 18-19 mm BL): The angular, retroarticular and opercular bones started appearing and the suspensorium ossifying at the beginning of this phase, and the premaxilla appeared and the hyoid arch started ossifying during this phase. The appearance of gape elements of the premaxilla and angular indicates that gape opening and closing abilities increased (Shinagawa et al., 2002). Moreover, the ossification of some elements enclosing the oral cavity indicates that the feeding ability increased (Tamura et al., 2013). Therefore, this phase is considered as the phase when the straining ability increased. Kohno (1998) mentioned that the shirasu-type larvae improved their feeding ability without a change in the feeding mode.

The phase of functional, juvenile feeding (over 18-19 mm BL): All the elements enclosing the oral cavity started ossifying, and the branchiostegal rays reached the adult complement in number. The number of teeth also decreased during this phase, indicating the change of food habits, and thus the larvae/juvenile are considered as having acquired juvenile feeding ability.

2. Spawning ground of *K. punctatus* in Tokyo Bay

1) Offshore waters of outer Tokyo Bay

K. punctatus specimens collected from offshore waters in the present study ranged from 3.0 to 7.2 mm BL with a dominant size class of 4.0-4.9 mm BL (Fig. 2). Kuwatani et al. (1956) reported that a newly hatched larva of *K. punctatus* was 3.06 mm in total length, TL, and the yolk including the oil globule was completely absorbed at 5.0 mm TL of 3.5 days after hatching. Considering the sizes of newly hatched and yolk-absorbed larvae, the larvae collected in this study would be newly hatched and of several days after hatching. These results in the present study lead to the

conclusion that *K. punctatus* would spawn in offshore waters of outer Tokyo Bay.

This conclusion is in accordance with the result of Kawasaki et al. (2006) in which *K. punctatus* eggs of early developmental stages were collected from the eastern part of the mouth of Sagami Bay, bordering the west of Tokyo Bay, and advanced-stage eggs and early larvae were collected from the inner bay near the mouth of Sagami River. Nakata (1983) reported the appearance of *K. punctatus* eggs in Sagami Bay and outer and inner Tokyo Bay, and Kong et al. (2004) also reported that *K. punctatus* spawned in the offshore waters from the eastern Sagami Bay to southern inner Tokyo Bay.

2) Offshore waters of inner Tokyo Bay

We did not operate ring-net samplings in the offshore waters of inner Tokyo Bay in this study; however, *K. punctatus* larvae have been collected by a ring net there as below. Kouhara and Kohno (1999) reported the appearance of yolk-sac – postflexion larvae of 2.8-17.6 mm BL. Nagaiwa et al. (2005) collected 3.8-5.9 mm BL *K. punctatus* larvae from five offshore stations in Tokyo Bay, and *K. punctatus* larvae collected from the inner bay stations occupied 30.2 and 34.1% of total fish number collected in summer and 87.8% in spring; however, the number of *K. punctatus* larvae collected were almost equal in both the bays in each season. Kanou et al. (2002a) conducted ring-net samplings at five offshore stations from the inner to outer Tokyo Bay and collected 1,646 individuals (10.2% of total fish number) of 2.7-9.9 mm BL of *K. punctatus* larvae mainly from the outer Tokyo Bay.

Although Kanou et al. (2002a) classified *K. punctatus* into 'bay-mouth type' in which pelagic larvae appeared mainly in the outer Tokyo Bay, they showed that the spawning ground could be formed in the inner Tokyo Bay on the basis of the results in other areas such as Ariake Sound (Takita, 1980), Yuya Bay (Mori, 1995), Nagara River Estuary (Kimura et al., 1999) and Osaka Bay (Yamamoto et al., 2001), where the eggs and early stage larvae were collected from the innermost bay and/or the river mouth. Furthermore, Kusaka et al. (2013) reported in Harima-nada, Seto Inland Sea, that *K. punctatus* eggs were collected from lower salinity areas such as a river mouth, and that the larvae of 2.0-8.3 mm BL were collected from such higher salinity as offshore waters.

These results suggest that there seems to be a possibility of the *K. punctatus* spawning ground being formed in offshore waters of the inner Tokyo Bay. Kong et al. (2004) indicated that the main spawning peak-period and ground of *K. punctatus* moved from eastern Sagami Bay in April to inner Tokyo Bay in June and July via outer Tokyo Bay in May.

3) A brackish water lagoon in the innermost Tokyo Bay

During spring and early summer in 1976 and 1978, *K. punctatus* eggs were collected from a brackish water lagoon *Shinhama-ko* located at the innermost Tokyo Bay, and 104,434 *K. punctatus* eggs were collected by a ring-net with 0.45 mm mesh opening on 29 May 1980 (Takeuchi and Yasuda, 1980). Takeuchi and Yasuda (1980) summarized that *K. punctatus* spawned from April to June, hatched larvae were collected from May to June, and 5-25 mm BL larvae/juveniles appeared from June to July in *Shinhama-ko*. Furthermore, *K. punctatus* juveniles of 20-65 mm BL were also

collected by a bottom trawl with a net of 2 mm mesh opening in the tidal flat. On the other hand by using a small seine-net with 0.8 mm mesh opening at a tidal flat in *Shinhama-ko*, Kanou et al. (2000) collected only three *K. punctatus* larvae, which occupied 0.02% of total fish collected, of 9.8-18.0 mm BL and Kohno et al. (2008) 12 larvae/juveniles, 0.05%, of 9.5-30.9 mm BL. Recently, monthly samplings from April 2018 to March 2019 conducted by the Laboratory of Ichthyology, Tokyo University of Marine Science and Technology, showed that ripen *K. punctatus* adults appeared (Mr. R. Sawai: personal comm.) and many larvae were collected (Mr. K. Nakano: pers. comm.) in *Shinhama-ko*.

These results suggest that, as summarized by Takeuchi and Yasuda (1980), the spawning ground of *K. punctatus* is likely to be formed at the brackish lagoon, *Shinhama-ko*, in the innermost Tokyo Bay, although the intensity of spawning would vary with the years. In addition to the brackish water lagoon, there would be a possibility of lower reaches of rivers flowing into the innermost Tokyo Bay such as *Tama-gawa*, *Sumida-gawa*, *Ara-kawa* and *Edo-gawa* rivers to be a spawning ground of *K. punctatus*, although no definite evidences are available. In our laboratory work, many *K. punctatus* eggs and early larvae were collected by a ring net in the river mouths of *Sumida-gawa* and *Ara-kawa* during the summer of 2018 (Mr. T. Mori: pers. comm.).

In two coupled brackish water lakes in the Sea of Japan, *Naka-umi* and *Shinji-ko*, many *K. punctatus* individuals ascending from *Naka-umi* to *Shinji-ko*, the latter lake being lower salinity than the former, possessed matured gonads, indicating the spawning being conducted in the lower salinity area, *Shinji-ko* (Koshikawa, 2003). Kimura et al. (1999) investigated the eggs, larvae and juveniles in the lower reaches of *Nagara-gawa* River running into Ise Bay, central Japan, and pointed out that the lower estuary would play an important role as a spawning and nursery ground for *K. punctatus*.

3. Nursery ground for K. punctatus in Tokyo Bay

1) Surf zones in the outer Tokyo Bay

In the present study *K. punctatus* specimens collected from surf zones in the outer Tokyo Bay ranged from 7.8 to 34.1 mm BL with bimodal peaks at size classes of 11.0-11.9 and 18.0-18.9 mm BL (Fig. 2). As mentioned above, the larvae collected from offshore waters of outer Tokyo Bay ranged from 3.0 to 7.2 mm BL, and, based on the functional development revealed in this study, their swimming mode changed from less active to caudal propulsion at about 7-8 mm BL (Fig. 5). Therefore, hatched and drifting *K. punctatus* larvae in the offshore waters of outer Tokyo Bay are considered to perform passive and then active shoreward migration to the surf zones at about 7-8 mm BL and larger. Nakata and Mitani (1980) reported that the largest *K. punctatus* larva collected by a ring net from the offshore waters in Kaneda Bay located on Miura Peninsula and opened to the outer Tokyo Bay was 12 mm in total length, TL, with an average of about 5 mm TL.

Although the number of larvae collected from the surf zones decreased to the size class of 13.0-13.9 mm BL, the number increased thereafter to the peak of 18.0-18.9 mm BL. At the former size class, the swimming mode would change from 'caudal' to 'whole body' propulsions and the feeding from 'capturing ability increased' to 'straining ability increased', and at the latter

size class the *K. punctatus* juveniles would acquire the juvenile swimming and feeding modes. Therefore, the surf zones of outer Tokyo Bay may be a good nursery ground for *K. punctatus* from larvae of weak swimming to juveniles of substantially strong swimming and feeding. *K. punctatus* is a second dominant species following to the icefish *Salangichthys ishikawae* at surf zones in the outer Tokyo Bay (Arayama et al., 2002). Kinoshita (1998) classified *K. punctatus* larvae/juveniles into the WPR (wading depth, pelagic and resident) type of life style categories among major larvae/juveniles using a surf zone, and showed that *K. punctatus* is a second dominant species at a surf zone in Tosa Bay, Shikoku of southern Japan, and that all the specimens dissected possess foods in the digestive tract.

The number of *K. punctatus* at the surf zones decreased after reaching 18.0-18.9 mm BL, which corresponds to the time when *K. punctatus* juveniles acquire the substantial abilities to swimming and feeding. Therefore, this phenomenon of decrease and disappearance from the surf zones is considered to be an active behaviour to shift their habitats for more adequate growth.

2) Tidal flats in the inner Tokyo Bay

On the other hand in the tidal flats of inner Tokyo Bay, *K. punctatus* collected in this study ranged from 5.2 to 18.3 mm BL with a peak at the size class of 10.0-10.9 mm BL (Fig. 2). As in the surf zones of outer Tokyo Bay, *K. punctatus* larvae collected from the tidal flats were drifted and then swim weakly to the shorelines. The result that the smaller larvae were collected from the tidal flats, 5.2 mm BL, than from the surf zones, 7.8 mm BL, suggests a possibility of spawning ground of *K. punctatus* being formed in the inner Tokyo Bay as discussed above.

The peak size class was observed at 10.0-10.9 mm BL in the tidal flats and 11.0-11.9 mm BL in the surf zones; however, the number of specimens was continued to decrease in the tidal flats, while another peak was observed at 18.0-18.9 mm BL in the surf zones. In the inner Tokyo Bay, the size of *K. punctatus* collected by a seine net in the tidal flats ranged from 4.5 to 19.6 mm BL (Kohno et al., 2014: three stations around *Tama-gawa* river mouth) and from 5.6 to 14.1 mm BL (Murai et al., 2016: *Furuhama* Park). These results suggest that the phenomena of *K. punctatus* larvae decreasing in number and disappearance from the tidal flats of inner Tokyo Bay could not be accounted by an active behaviour to shift their habitats as in the surf zones of outer Tokyo Bay but supposed to be caused by the water quality, size of tidal flats and/or any other unknown factors.

Acknowledgments

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Figure Legend

Fig. 1. Map showing the sampling stations at offshore waters and surf zones in the outer Tokyo Bay and at tidal flats in the inner Tokyo Bay.

Fig. 2. Size composition of Konosirus punctatus collected from the offshore waters, surf zones and tidal flats in Tokyo Bay.

Fig. 3. Changes in swimming-related characters with growth in Konosirus punctatus.

Fig. 4. Changes in feeding-related characters with growth in Konosirus punctatus.

Fig. 5. Schematic representation of the development of swimming-related characters with growth in Konosirus punctatus collected from Tokyo Bay. ○ : cartilaginous elements start appearing; ● : all cartilaginous elements start appearing; □ : bony elements start appearing; ■: all bony elements start appearing; △: cartilaginous elements start ossifying; ▲: all cartilaginous elements start ossifying; ◇: fin rays start appearing; ◆: fin rays become complete in number; ☆: notochord end starts to flex; ★: flexion points of morphometric characters are observed, notochord flexion become complete.

Fig. 6. Schematic representation of the development of feeding-related characters with growth in Konosirus punctatus collected from Tokyo Bay. ○ : cartilaginous elements start appearing; ● : all cartilaginous elements start appearing; □ : bony elements start appearing; ■: all bony elements start appearing; △: cartilaginous elements start ossifying; ▲ : all cartilaginous elements start ossifying; ◇ : teeth and branchial rays start appearing; ◆ : branchial rays become complete in number; ☆: mouth opens and premaxilla start appearing; ★: flexion points of teeth number and upper jaw length are observed.

東京湾におけるコノシロ仔稚魚の出現様式と発育段階

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　東京湾外湾の沖合 5 地点（稚魚ネット：1996 年 4 月〜1997 年 3 月）と砕波帯 3 地点（地曳網：1998 年 4 月〜1999 年 3 月）および内湾の干潟域 3 地点（地曳網：2006 年 6 月〜2008 年 8 月）で採集したコノシロの仔稚魚について、その出現状況を明らかにした。さらに 129 個体（体長 3.6〜25.1mm）を透明骨格標本にし、遊泳・摂餌機能に関する形質の発達を観察した。外湾の沖合では 1,114 個体（体長 3.0〜7.2mm）が、砕波帯では 4,991 個体（7.8〜34.1mm）が、さらに内湾の干潟域では 1,800 個体（5.2〜18.3mm）が出現した。関連形質の発達に基づいて、遊泳・摂餌機能別の発育段階をそれぞれ 4 段階設定した。産卵場は外湾の沖合だけではなく、内湾の沖合や河川下流域、あるいは汽水の潟湖などに形成されることが示唆された。外湾の砕波帯と内湾の干潟域はコノシロ仔稚魚の成育場であるが、採集された個体数は干潟域では体長 10mm 以上、砕波帯では 18mm 以上になると減少しはじめた。体長 18mm で稚魚としての遊泳・摂餌能力が獲得されるため、砕波帯での個体数の減少は、より良い成長をするために積極的な生息場の移動をおこなった結果だと考えられた。しかし内湾の干潟域における個体数の減少は、生息場の移動では説明できないため、水質や干潟域の規模、あるいは何らかの他の要因に起因すると推定された。
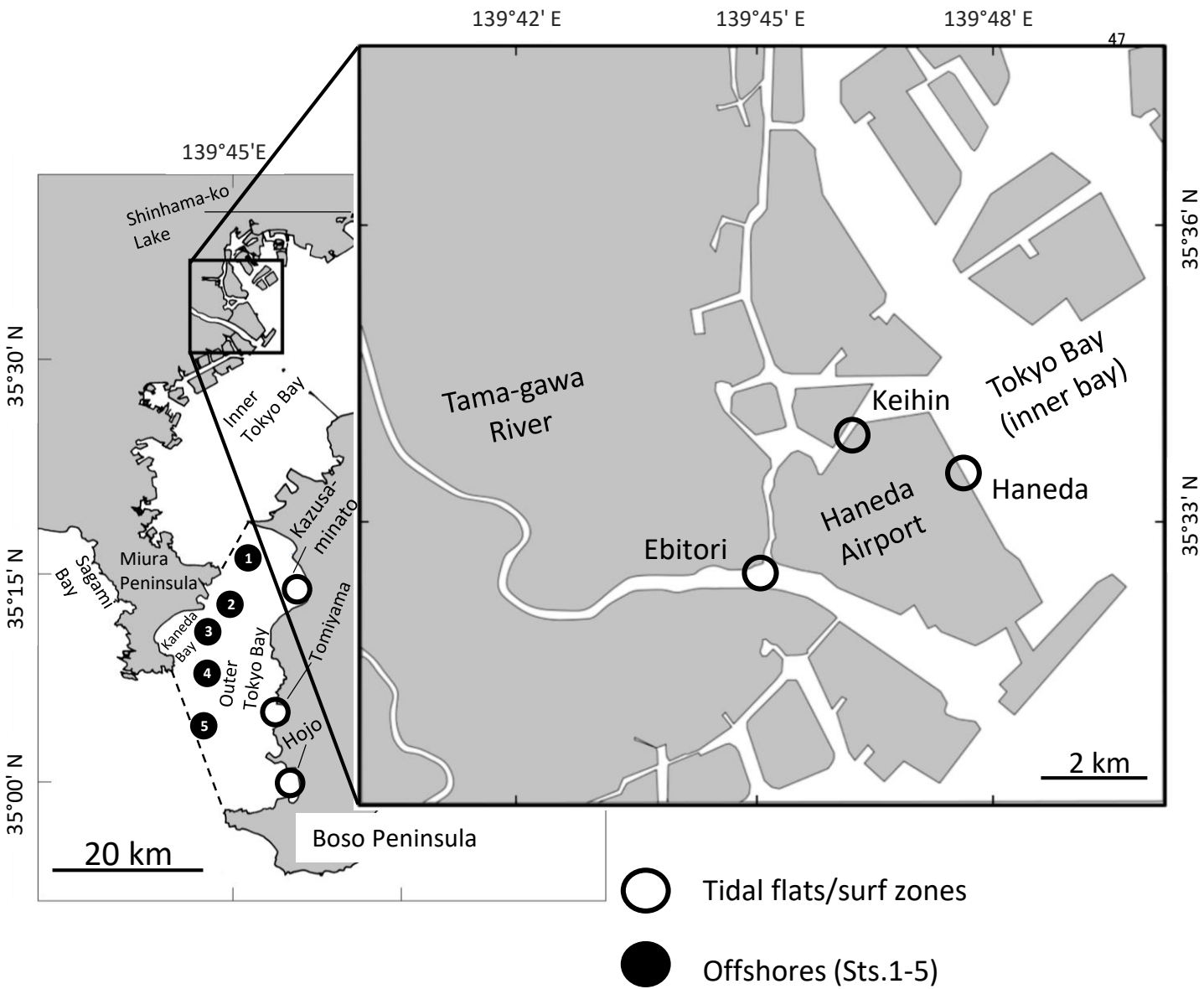
キーワード：　コノシロ、初期生活史、出現様式、機能的発育

Fig. 1 Map showing the locations of offshores, and tidal flat/surf zone sampling stations in both inner and outer of Tokyo Bay, central Japan.
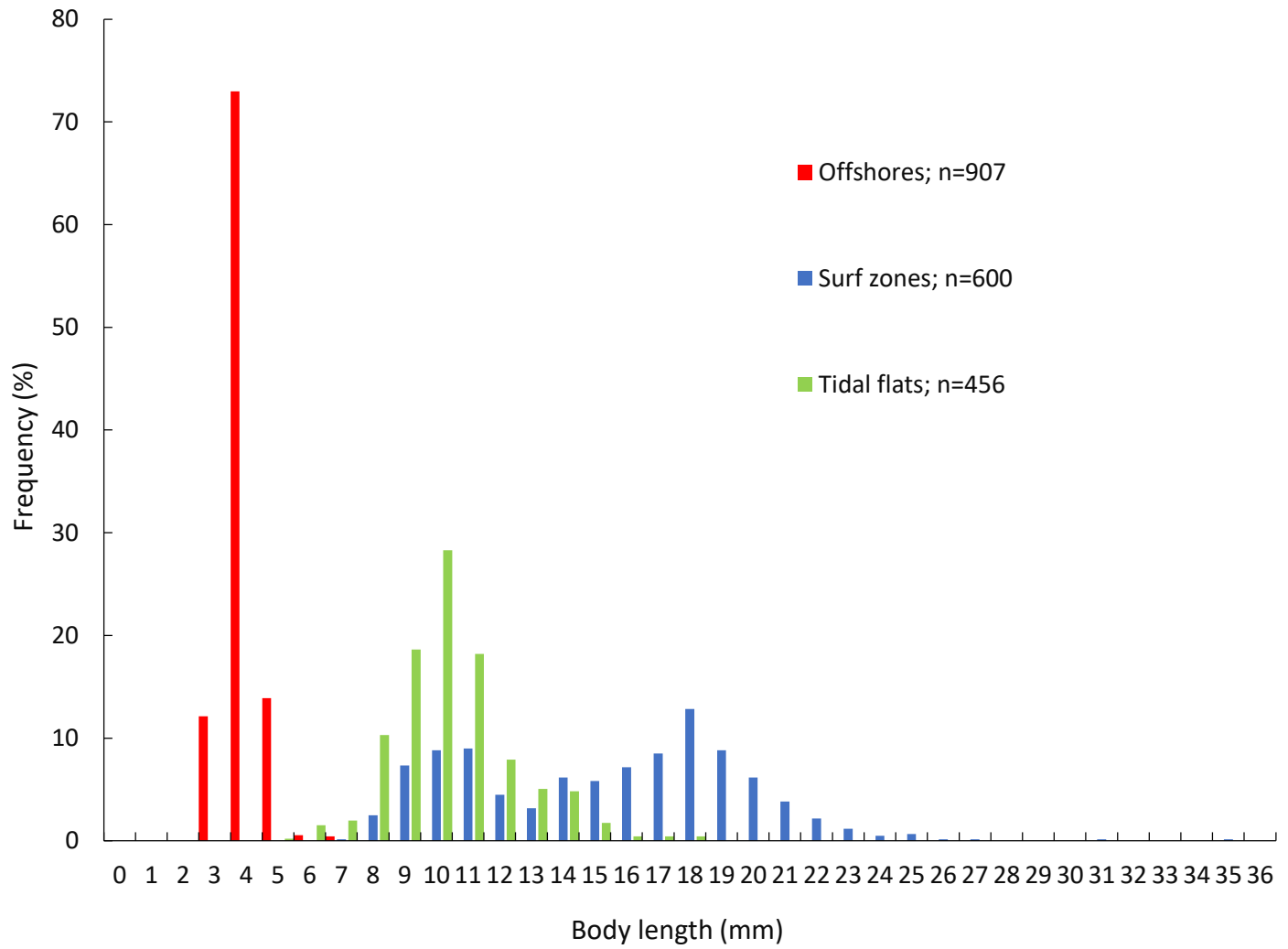
Fig. 2 Size composition of the Konoshiro gizzard shad, *Konosirus punctatus*, collected from the offshore, tidal flat and surf zone sampling stations in Tokyo Bay.
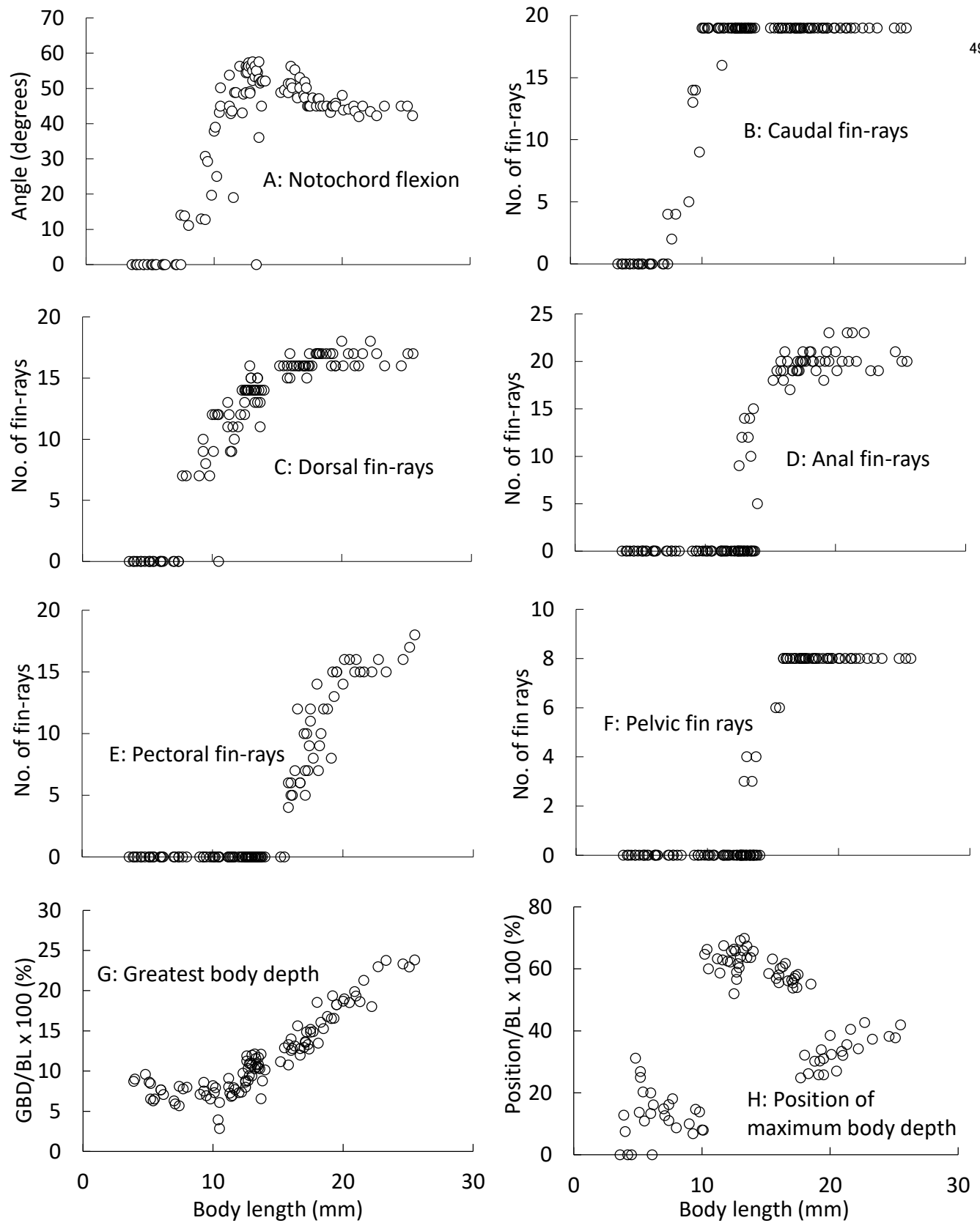
Fig. 3 Changes in swimming-related characters with growth in the Konoshiro gizzard shad *Konosirus punctatus*.
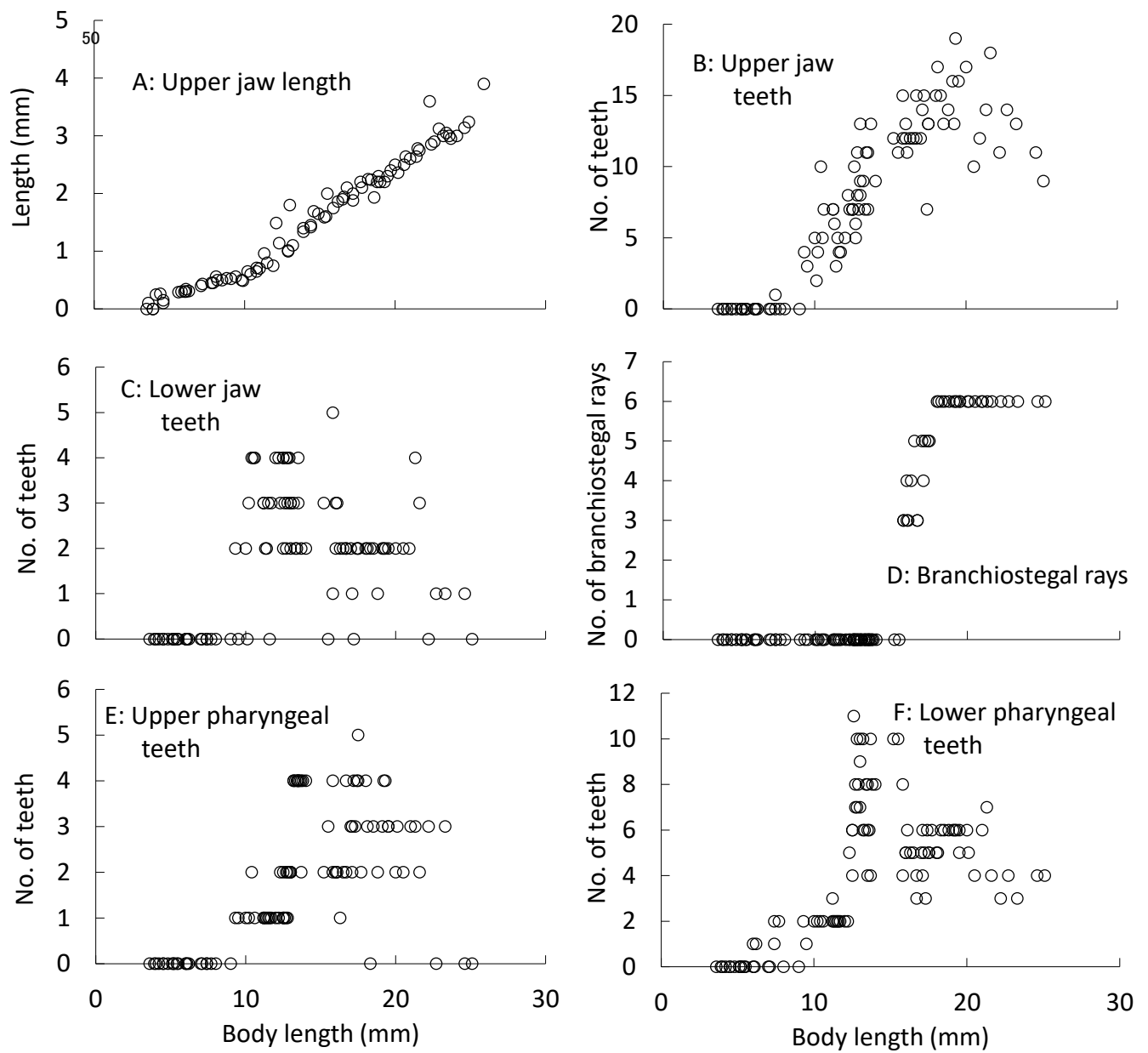
Fig. 4 Changes in feeding-related characters with growth in the Konoshiro gizzard shad *Konosirus punctatus*.
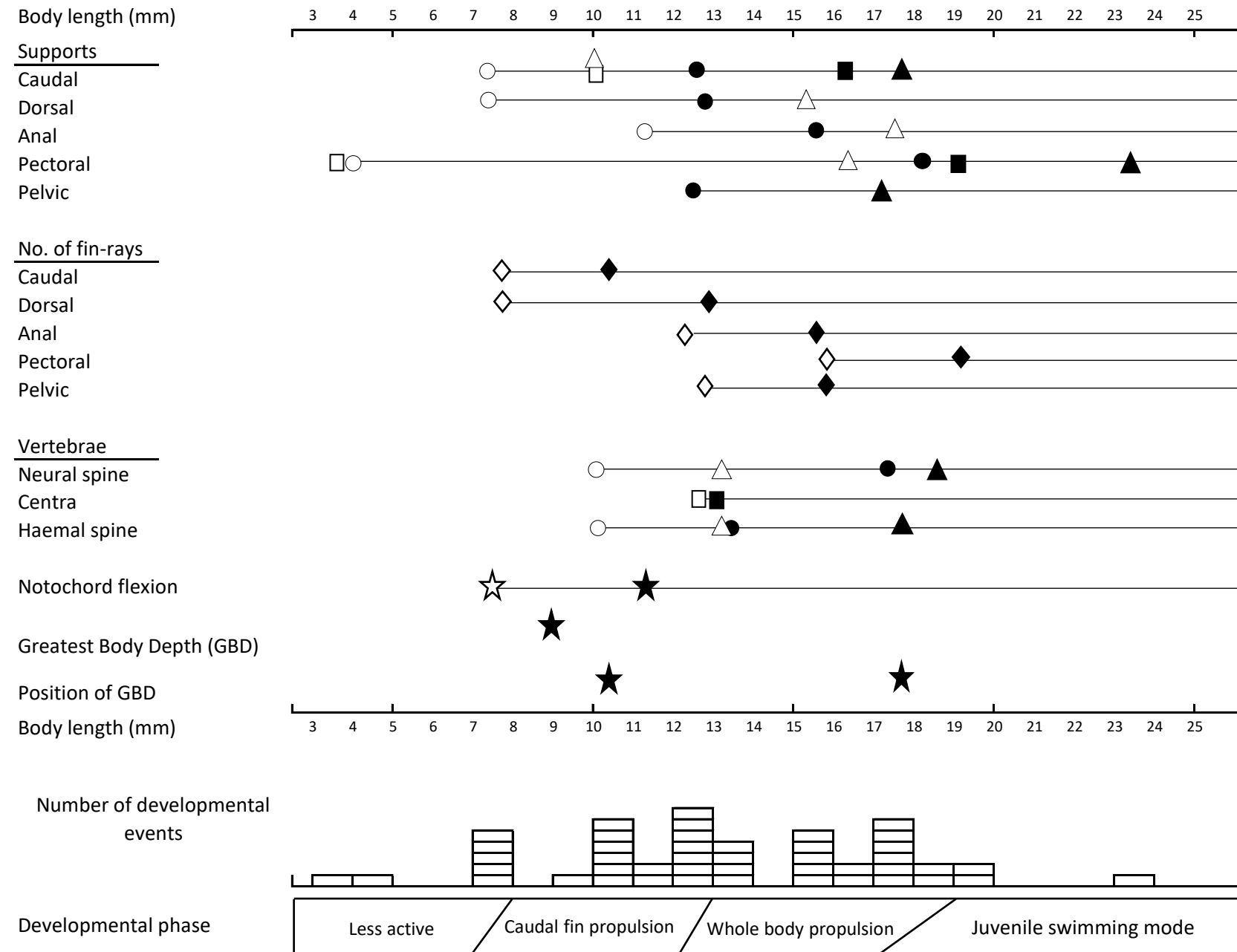
Fig. 5   Schematic representation of the development of swimming-related characters with growth in *Konosirus punctatus* collected from Tokyo Bay. ○: cartilaginous elements start appearing; ●: all cartilaginous elements start appearing; □ : bony elements start appearing; ■ : all bony elements start appearing; △ : cartilaginous elements start ossifying; ▲ : all cartilaginous elements start ossifying; ◇ : fin rays start appearing; ◆ : fin rays become complete in number; ☆ : notochord end starts to flex; ★ : flexion points of morphometric characters are observed, notochord flexion become complete.

Body length (mm)   3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25

Upper Jaw
Maxilla
Premaxilla
Supramaxilla
Teeth

Lower jaw
Meckel's cartilage
Dentary
Angular
Retroarticular
Teeth

Pharyngeal teeth
Upper pharyngeal teeth
Lower pharyngeal teeth

Suspensorium
Hyoid arch
Branchiostegal rays
Opercular bones
Upper jaw length

Body length (mm)   3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25

Number of developmental events

Developmental phase

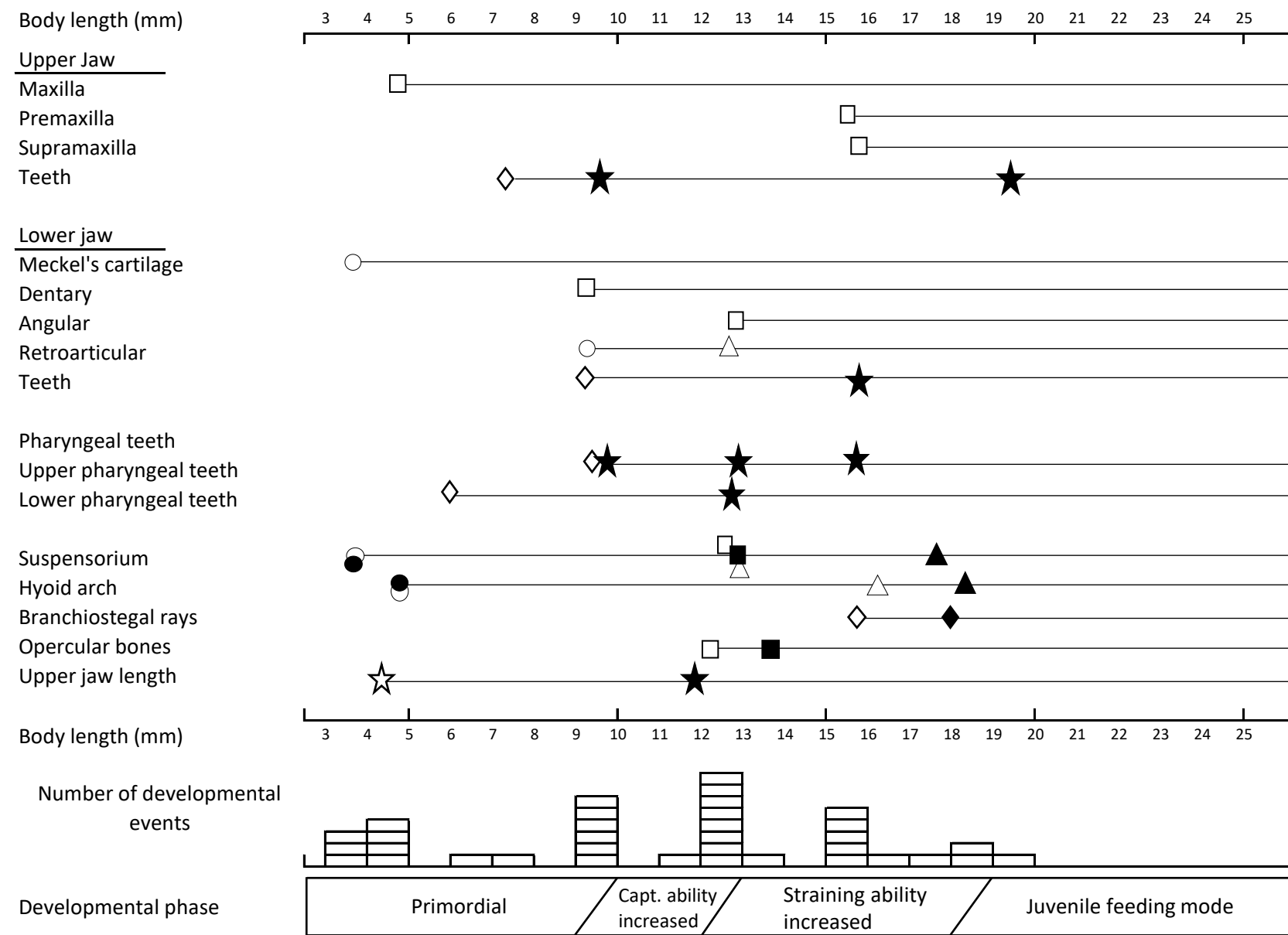| Primordial | Capt. ability increased | Straining ability increased | Juvenile feeding mode |

Fig. 6 Schematic representation of the development of feeding-related characters with growth in *Konosirus punctatus* collected from Tokyo Bay. ○ : cartilaginous elements start appearing; ● : all cartilaginous elements start appearing; □ : bony elements start appearing; ■ : all bony elements start appearing; △ : cartilaginous elements start ossifying; ▲ : all cartilaginous elements start ossifying; ◇ : teeth and branchial rays start appearing; ◆ : branchial rays become complete in number; ☆ : mouth opens and premaxilla start appearing; ★ : flexion points of teeth number and upper jaw length are observed.