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Occurrence patterns and ontogenetic intervals based on osteological and morphometric characters of larval and juvenile gluttonous goby (*Chaenogobius gulosus*) in Furuhama Park, innermost Tokyo Bay, central Japan

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Abstract: The occurrence patterns of the larval and juvenile gluttonous goby, *Chaenogobius gulosus* in Omori Furusato-no-Hamabe Park in the innermost portion of Tokyo Bay were investigated by monthly sampling. Four types of gear were used: a small seine net towed off the sandy beach and over the tidal flat between January 2015 and December 2018; basket nets placed at a wharf with a vertical seawall between January 2016 and December 2018; a hand net used at the wharf between January 2016 and December 2016; and a set net placed on the tidal flat and in the waterway from the tidal flat to a tidepool between January 2016 and December 2018. Ontogenetic intervals were determined from the morphometric characters of 274 specimens (3.93–41.7 mm body length [BL]) and the osteological characters of 92 cleared and stained specimens (3.93–25.5 mm BL). In total, 124 individuals (3.78–30.3 mm BL) were collected from the sandy beach, 447 (3.98–72.9 mm BL) from the tidal flat, 239 (22.8–107 mm BL) from the wharf using basket nets, 221 (6.30–45.2 mm BL) from the wharf using a hand net, two (17.3 and 30.4 mm BL) from the tidal flat using a set net, and one (4.50 mm BL) from the waterway. Based on morphological development, the developmental stages of the larvae and juveniles were divided into four phases each of swimming and feeding functions and five phases of relative growth. The occurrence patterns and ontogenetic intervals imply that hatched larvae are transferred to the sandy beach or tidal flat by flow, occupy these habitats while their swimming and feeding functions develop, then begin migrating to the wharf at 8–9 mm BL. Subsequently, juveniles settle on the seafloor; they then migrate and settle at the wharf until ~35 mm BL. *C. gulosus* utilizes different habitats in this artificially established seaside zone depending on the developmental phase from hatching to immature individuals, although the distribution of mature individuals remains unclear.

Keywords : *Gobiidae, early life history, artificially constructed environment, ontogenetic development*

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1. Introduction

For hundreds of years, the development of human society has caused environmental destruction; interest is currently increasing in the environmental conservation and preservation of ecosystems. In Japan, approximately 80–90% of tidal flats and shoals have disappeared as a result of land reclamation during the period of high economic growth (KOARAI and NAKANO, 2013); in Tokyo Bay, tidal flat areas decreased by 89.2% over the period of approximately 35 years after 1945, from 9449 ha to 1016 ha (Toyo Koku Jigyo Co., Ltd., 1980). In 1982, the Cabinet of Japan released a comprehensive national development plan that included extensive conservation and aggressive utilization of coastal zones; since then, preparations for artificial beaches on reclaimed land have been conducted in various regions (KOARAI and NAKANO, 2013).

However, according to KOHNO (2012), who compared fish fauna among tidal flats in Tokyo Bay while considering the reconstruction of ruined shallow waters and tidal flats, there is a need to identify the habitat that the artificial environment provides for fishes at each location. Although many surveys have been conducted in developed coastal areas, no study is yet available regarding the long-term usage patterns of such artificial environments by certain species.

The gluttonous goby, *Chaenogobius gulosus*, is distributed from Hokkaido southward to Kyushu in Japan; around the Korean Peninsula and Jeju Island; and in the Pohai Sea, Yellow Sea, and Qingdao City in Shandong, China (AKIHITO *et al.*, 2013). Despite several studies investigating the traits of this species, such as the period until eggs hatch, growth rate, feeding habits, and spawning areas (NAKAMURA, 1936; SASAKI and HATTORI, 1969; HARADA, 2014; BEACK *et al.*, 2010; PARK *et al.*, 2020), their ecology in inner Tokyo Bay has remained unexplained because they are rarely collected there. However, many samples have been caught in Omori Furusato-no-Hamabe Park (hereinafter referred to as Furuhama Park). Therefore, we decided to investigate this species.

Here, we aimed to define the ontogenetic intervals during the early life history of *C. gulosus* in terms of functional improvement of its swimming and feeding abilities, as well as the relative growth rate. In addition, we investigated the relationships of these ontogenetic intervals with the occurrence patterns of larvae and juveniles at various sites in Furuhama Park, which was artificially constructed in the northwestern area of the inner Tokyo Bay in 2007, to elucidate how this species utilizes its habitat. This study clarifies where larvae and juveniles of *C. gulosus* acquire the abilities to swim and feed; it also describes how artificial coastal-zone environments can provide habitats for this species.

2. Materials and methods

The specimens used in this study were collected from four sites, including a sandy beach, tidal flat, wharf with vertical walls, and waterway in Furuhama Park (Fig. 1). There are no *Sargassum* or *Zostera* beds in the park. Water temperature fluctuates between approximately 10℃ and 30℃ in the sandy beach, the tidal flat and the wharf; the annual mean salinity is approximately 18 in the sandy beach and the tidal flat, approximately 17 at sea surface of the wharf, and 27 on the sea bottom of the wharf (MARUYAMA *et al.*, 2021; ONODERA *et al.*, 2020). All samples were collected using one of four types of sampling gear (i.e., a small seine net, basket nets, hand net, or set net) during daytime at low tide around the spring tide of each month. An 0.8-mm mesh small seine net (cf., KANOU *et al.*, 2002) was deployed monthly between January 2015 and December 2018, with two tows of approximately 100 m^2 at a depth of approximately 1 m along the sandy beach and over the tidal flat. Three 40-mm mesh basket nets (0.4 m in length and width, 0.5 m in height) were deployed at the sea surface and an additional three were placed on

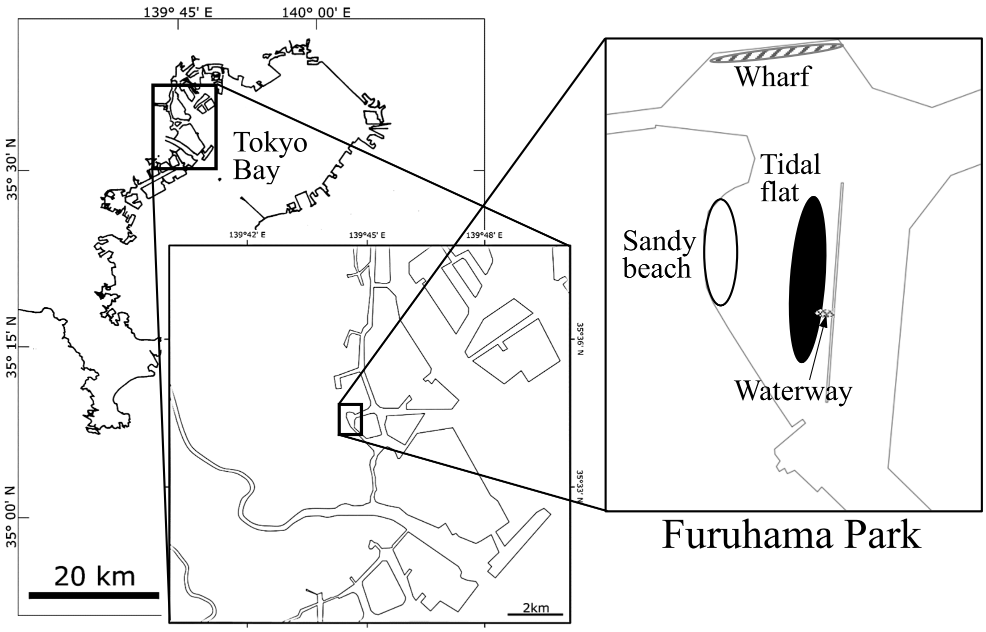

Fig. 1 Map showing the sampling sites in Furuhama Park located in the innermost Tokyo Bay. Fish were caught with a small seine net in the sandy beach and the tidal flat, with a hand net and basket nets in the wharf of vertical wall and with a set net in the tidal flat and the waterway.

the seafloor of the wharf; each basket net included a fishing gut net, several pieces of bamboo brooms or oyster shells to provide shelter for fishes, and the nets were collected after specific intervals (cf., ONODERA *et al.*, 2020). Withdrawal was conducted twice monthly from January 2016 to December 2018, at 1 month after placement and on the following day. A 1-mm mesh hand net (0.35 m in width) was also used for sampling at the wharf monthly from January to December 2016; the hand net was pushed into the water as deeply as possible and fishes were gathered while the net was rubbed against the wall for 30 min. A set net was placed monthly from January 2016 to December 2018 at the tidal flat and the waterway sites between the area of tide pools and the tidal flat. Captured fishes were collected at 24 h after placement of the net.

Collected specimens were fixed in seawater containing 5% formalin, then preserved in 70% ethanol. Identification of the species was performed in accordance with the approach used by NAKABO (2013) and OKIYAMA (2014). The body length (BL; notochord length until notochord flexion and standard length after post-flexion), of each specimen was measured to three significant digits using a micrometer attached to a binocular stereomicroscope for specimens of up to 16 mm; a digital caliper was used for specimens larger than 16 mm.

Of 571 specimens collected with the seine net from the sandy beach and tidal flat during the 3-year period, 274 individuals (3.93–41.7 mm BL) were randomly selected for morphometric measurement to establish the ontogenetic intervals. The following morphometric characters were measured: swimming-related characters of body depth at the base of the pectoral fins, body depth

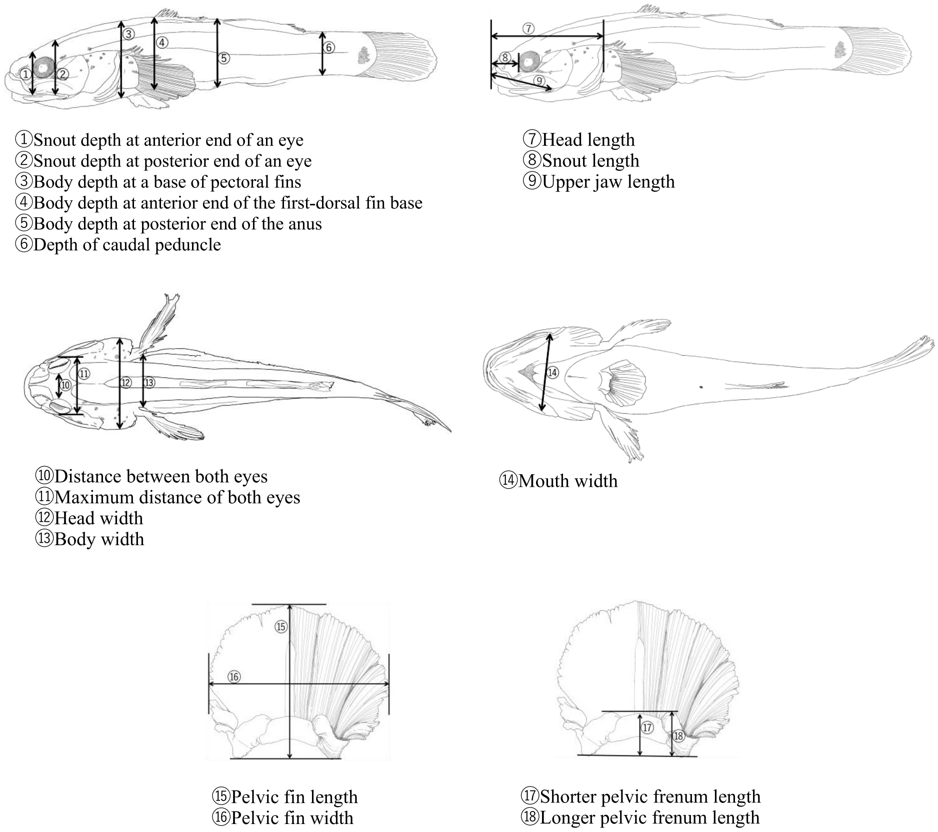

Fig. 2 Morphometric characters for relative growth in which 18 characters out of 25 measured characters are shown. Seven remains are the maximum body depth, the position of the maximum body depth, gut shape, the area of pelvic fin, the volume of swimbladder, wet weight and the condition factor.

at the anterior end of the first dorsal-fin base, body depth at the posterior end of the anus, depth of the caudal peduncle, maximum body depth, and the position of the maximum body depth; feeding-related characters of mouth width, upper-jaw length, snout length, gut shape, and body width; eyesight-related characters of distance between the eyes and maximum distance between the eyes; settlement-related characters of pelvic fin length, pelvic fin width, area of the pelvic fin, shorter and longer pelvic frenum lengths, and the volume of the swimbladder; head-shape-related characters of snout depth at the anterior and posterior ends of the eye, head length, and head width; and body-condition-related characters of wet weight and condition factor (Fig. 2). Each character was measured with a micrometer attached to a binocular stereomicroscope or digital caliper using the same criterion applied for BL. The volume of the swimbladder was calculated using the following equations: $V=\frac{4}{3}\pi r^3$ for spherical swimbladders and $V=\frac{\pi}{6}lh^2$ (Blaxter and Hampel, 1963) for oval-shaped swimbladders (V, r, l, and h indicate volume, radius, length, and width, respectively). The condition factor, CF, was computed with the following equation: $CF = \frac{BL^3}{W} \times 10^4$, where W is wet weight. The gut shape was separated into the following four stages: straight in stage 1; bending at a right angle in stage 2; slightly folding back in stage 3; and completely folding back in stage 4 (Fig. 3).

Of the 274 individuals used for morphometrics, 92 (3.93–25.5 mm BL) were selected for osteological measurement to assess functional development. These specimens were cleared and stained using the method of POTTHOFF (1984), and the following characters were observed: swimming-related characters of fin supports and rays, the angle of notochord flexion, the vertebral centra, and hemal and neural spines; and feeding-related characters of the upper-jaw structure (premaxilla and maxilla), lower-jaw structure (Meckel's cartilage; dentary, angular and retroarticular processes), jaw teeth, and the ratio of premaxilla to gape, as well as the suspensorium, hyoid arch, branchiostegal rays, opercular bones, and pharyngeal teeth. Developmental phases were determined in accordance with the method established by KOHNO and SOTA (1998), which combines the histogram method of identifying developmental events by 0.5-mm body-length intervals employed by SAKAI (1990) and the key characters method.

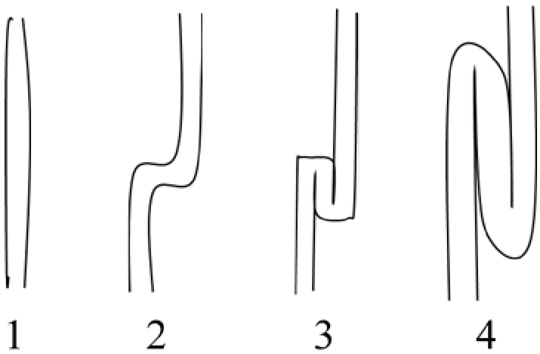

Fig. 3 Developmental stages of gut shape.

3. Results

3.1 Occurrence patterns

The total number of *C. gulosus* collected from the sandy beach was 124 individuals ranging from 3.78 mm to 30.3 mm BL (Fig. 4), with no discernable yolk in the smallest larvae. The months of occurrence ranged from February to May. The number of samples and size range in each month was 22 individuals in February (range, 3.93–10.7 mm BL; mode, 4.00–5.99 mm BL), 29 individuals in March (range, 3.78–13.1 mm BL; mode, 4.00–5.99 mm BL), 72 individuals in April (range, 7.18–19.0 mm BL; mode, 12.0–13.9 mm BL), and 1 individual in May (30.3 mm BL)

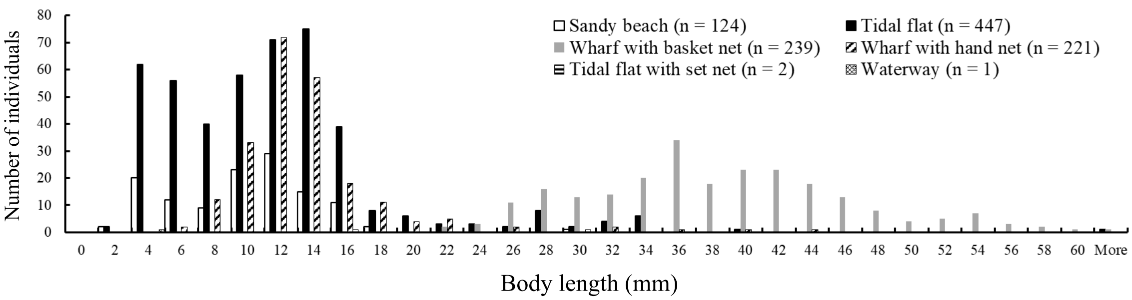

Fig. 4 Occurrences of all the gluttonous gobies collected at all the sampling sites or methods during the four-year period from 2015 to 2018 in Furuhama Park.

(Fig. 5).

The total number of specimens caught on the tidal flat was 447 individuals, ranging from 3.98 mm to 72.9 mm BL (Fig. 4). *C. gulosus* occurred from January to July; its monthly occurrence was 2 individuals in January (range, 4.08–4.54 mm BL), 26 in February (range, 3.98–8.67 mm BL; mode, 4.00–5.99 mm BL), 121 in March (range, 3.93–13.4 mm BL; mode, 6.00–7.99 mm BL), 267 in April (range, 5.92–21.5 mm BL; mode, 14.0–15.9 mm BL), 27 in May (range, 18.6–34.9 mm BL; mode, 28.0–29.9 mm BL), 3 in June (range, 35.5–41.6 mm BL), and 1 in July (72.9 mm BL) (Fig. 5).

The total number of specimens collected from the wharf with basket nets was 239, ranging from 22.8 mm to 107 mm BL (Fig. 4). Occurrence was observed between May and August; the monthly occurrence was 71 individuals in May (range, 22.8–40.8 mm BL; mode, 28.0–29.9 mm BL), 108 in June (range, 29.4–54.7 mm BL; mode, 36.0–37.9 mm BL), 53 in July (range, 34.1–61.5 mm BL; mode, 46.0–47.9 mm BL), and 7 in August (range, 53.2–107 mm BL; modes, 54.0–55.9 and 56.0–57.9 mm BL) (Fig. 5). At the same site, the total number of *C. gulosus* sampled with a hand net was 221 individuals ranging from 6.30 mm to 45.2 mm BL (Fig. 4). The period of occurrence ranged from April to July; the monthly occurrence was 211 individuals in April (range, 6.3–27.5 mm BL; mode, 12.0–13.9 mm BL), 5 in May (range, 10.9–27.9 mm BL), 3 in June (range, 32.5–40.5 mm BL), and 2 in July (range, 37.4–45.2 mm BL) (Fig. 5).

The total number of specimens collected from the tidal flat with the set net was two individuals (Fig. 4): one in April 2016 (17.3 mm BL) and the other in May 2016 (30.4 mm BL) (Fig. 5). Only one individual (4.50 mm BL) was caught in the waterway in April 2016. At these sites, no specimens were collected in 2017 or 2018.

3.2 Morphological development

3.2.1 Developmental phases of swimming function in terms of osteological development

Based on the skeletal development of the swimming-related characters illustrated in Fig. 6, *C. gulosus* larvae and juveniles were divided into the following four phases.

SF-I, the phase of less active swimming (*up to ~5 mm BL*): No swimming-related characters appeared, with the exception of pectoral fin elements such as the cleithrum, coraco-scapular cartilage, and cartilaginous blade, which later developed into actinosts and postcleithrum. No fin rays appeared, and all fins were composed of fin folds.

SF-II, the phase of caudal fin and whole-body propulsion (*from ~5 mm to ~8–9 mm BL*): Caudal fin supports and rays began appearing and notochord end bending commenced at ~5 mm BL. At ~7.5–8 mm BL, all bony elements of the caudal fin supports were discernable; ossification of the caudal fin supports began; the caudal, dorsal, and anal fins attained their adult complements of rays; notochord flexion was completed; and all cartilaginous elements of the vertebrae began ossifying.

SF-III, the phase of upgraded propulsion using the caudal fin and whole body with maneuverability (*from ~8–9 mm to ~17 mm BL*): All cartilaginous elements of each fin support had begun to ossify by ~14 mm BL.

SF-IV, the phase of functional, juvenile swimming (*> 17 mm BL*): All fin rays were completed in number at ~17 mm BL, and thus all characters concerning swimming function were completed and began to ossify.

3.2.2 Developmental phases of feeding function in terms of osteological development

Based on the skeletal development of feeding-

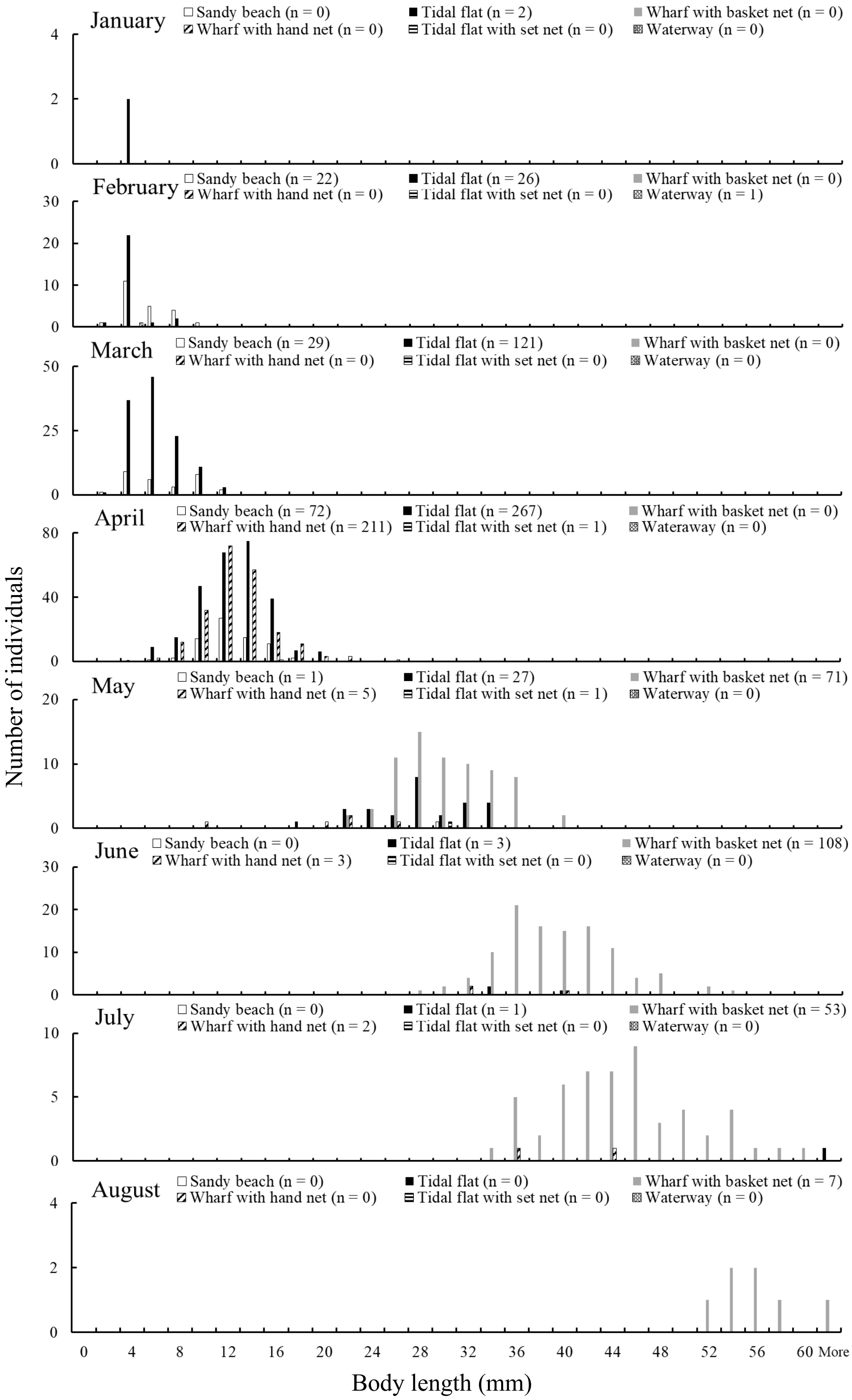

Fig. 5 Occurrences of all the gluttonous gobies collected at all the sampling sites or methods during the four-year period from 2015 to 2018 in Furuhama Park, shown by months.

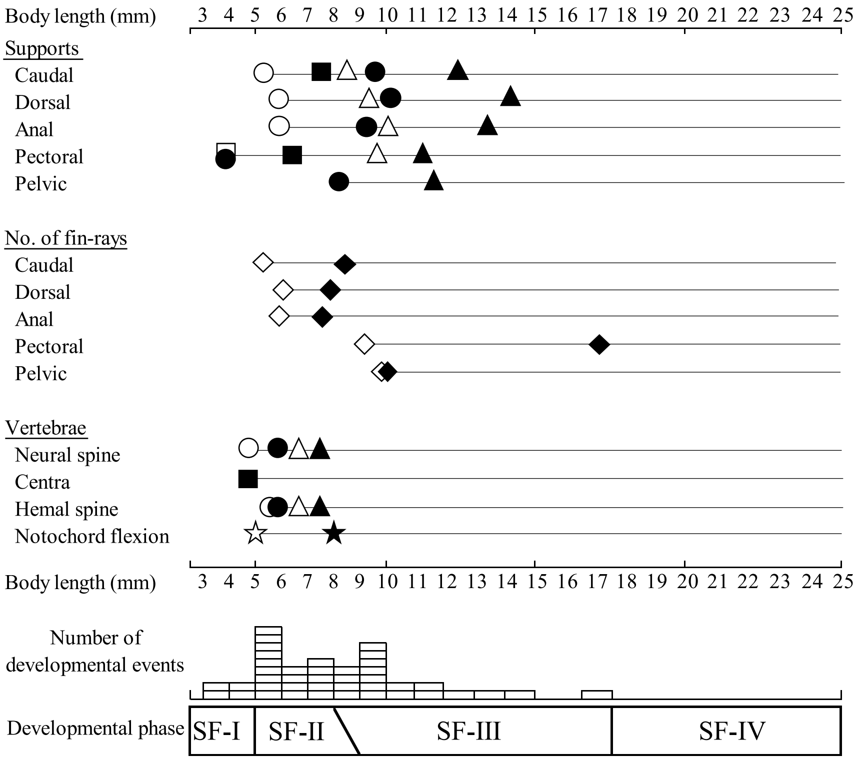

Fig. 6 Schematic representation of the development of swimming-related characters with osteological growth, showing the developmental phases in the gluttonous goby, *Chaenogobius gulosus*, collected from the sandy beach or the tidal flat in Furuhama Park. ○: cartilaginous elements start appearing; ●: cartilaginous elements become complete in number; □: bony elements start appearing; ■: bony elements become complete in number; △: cartilaginous elements start ossifying; ▲: all cartilaginous elements start ossifying; ◇: fin rays start appearing; ◆: fin rays become complete in number; ☆: notochords start flexing; ★: notochord flexions become complete. Developmental events are shown by boxes, and developmental phases are also shown in the bottom.

related characters, *C. gulosus* larvae and juveniles were divided into the following five phases (Fig. 7).

FF-I, the phase of primordial sucking (*up to ~6 mm BL*): Characters comprising the oral cavity (e.g., the premaxilla, maxilla, Meckel's cartilage, dentary, angular, several parts of the suspensorium, hyoid arch, and branchiostegal rays) developed rapidly.

FF-II, the phase of enhanced sucking (*from ~6 mm to ~9–10 mm BL*): All elements comprising the oral cavity were completed in number and began to ossify.

FF-III, the phase of sucking and biting (*from ~9–10 mm to ~18 mm BL*): After completion of the oral cavity, the numbers of both upper- and lower-jaw teeth plateaued at ~17.5 mm BL.

FF-IV, the phase for completion of feeding functions (*from ~18 mm to ~23–24 mm BL*): The number of upper pharyngeal teeth sharply in-

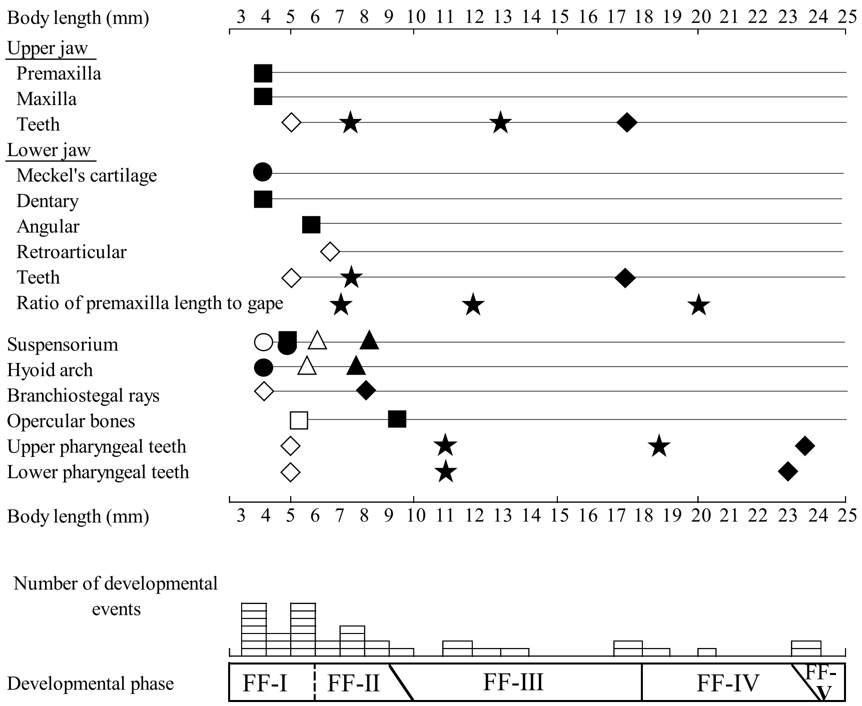

Fig. 7 Schematic representation of the development of feeding-related characters with osteological growth, showing the developmental phases in the gluttonous goby, *Chaenogobius gulosus*, collected from the sandy beach or the tidal flat in Furuhama Park. ○: cartilaginous elements start appearing; ●: cartilaginous elements become complete in number; □: bony elements start appearing; ■: bony elements become complete in number; △: cartilaginous elements start ossifying; ▲: all cartilaginous elements start ossifying; ◇: teeth, branchial rays and retroarticular start appearing; ◆: teeth and branchial rays become complete in number; ★: changing points of developmental speed. Developmental events are shown by boxes, and developmental phases are also shown in the bottom.

creased again and the number of lower pharyngeal teeth maintained constant growth during this period. In addition, the ratio of premaxillary length to gape reached a plateau at ~20 mm BL.

FF-V, the phase of functional juvenile feeding (*greater than ~23–24 mm BL*): No developmental alterations were observed in this period because the growth of both upper and lower pharyngeal teeth was complete.

3.2.3 Developmental phases in terms of relative growth of morphometric characters

Based on the relative growth of morphometric characters related to swimming, feeding, eyesight, settlement, head shape and body condition, *C. gulosus* larvae and juveniles were divided into the following five phases (Fig. 8).

RG-I, floating phase with general growth of the body and rapid development of swimming and feeding functions (*from 3.78 mm to ~10–11 mm BL*): In total, 12 flection points were detected

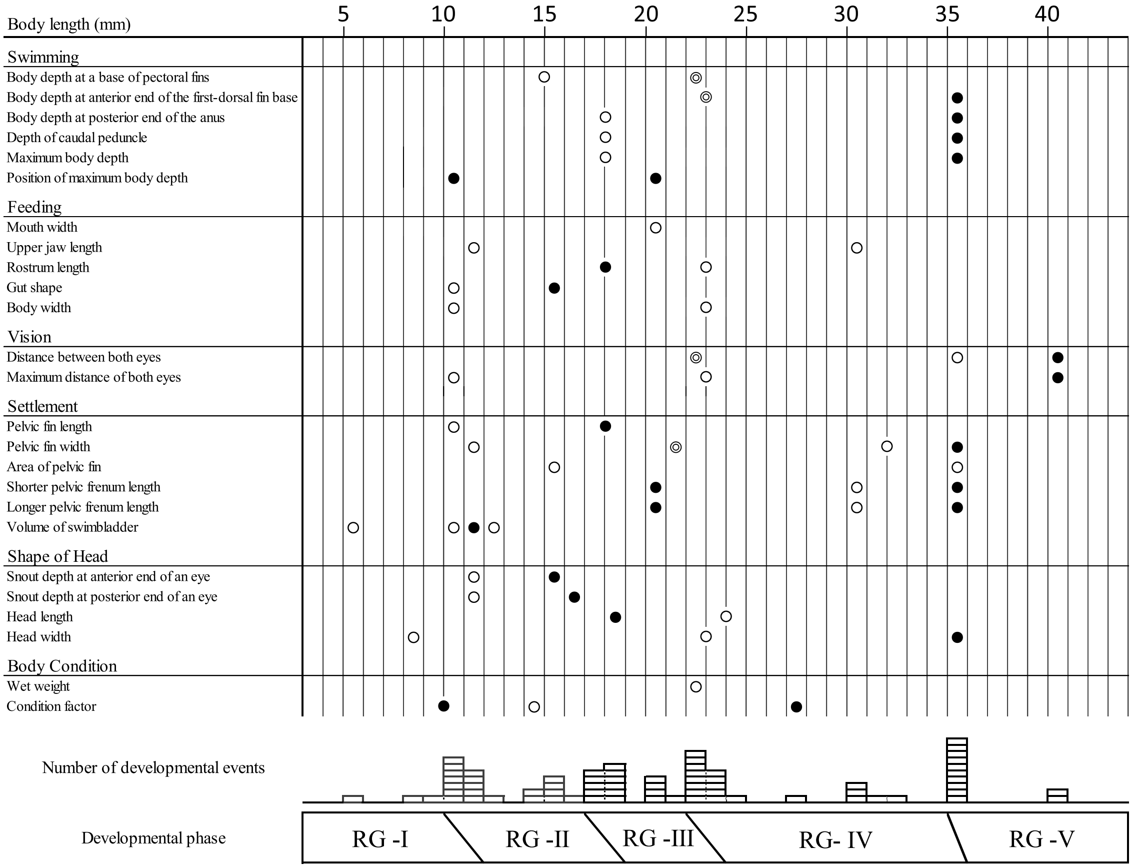

Fig. 8 Schematic representation of the development of morphometric characters with relative growth, showing the developmental phases in the gluttonous goby, *Chaenogobius gulosus*, collected from the sandy beach or the tidal flat in Furuhama Park. ○: increasing points of gradients; ●: decreasing points of gradients; ◎: leaping points of graphs. Developmental events are shown by boxes, and developmental phases are also shown in the bottom.

from various sections of the body at 10–11 mm BL. Among swimming-related characters, the position of the maximum body depth shifted significantly backwards until 10 mm BL; the volume of the swimbladder began to increase at ~5 mm BL, then exhibited extremely rapid growth between 10 mm BL and 11 mm BL. The pelvic fin became measurable from 6–7 mm BL; it grew slowly until ~10 mm BL. Among feeding-related characters, upper-jaw length and body width increased gradually between BLs of ~4 mm and 10–11 mm. This phase nearly overlapped with the respective periods of rapid osteological development of swimming and feeding functions: SF-I and -II (Fig. 6), and FF-I and -II (Fig. 7).

RG-II, the initial phase of settlement (from ~10–11 mm to ~17–18 mm BL): The changes in this phase mainly affected characters related to swimming, feeding, and settlement. The swimbladder, which was significantly enlarged during RG-I, suddenly disappeared at 12 mm BL. The ratio of the caudal peduncle to the maximum body depth sharply increased from 15% to 50% at ~18 mm BL. Pelvic fin length increased sharply between ~10 mm and ~18 mm BL, and the ratio of pelvic fin width to length rapidly shifted after ~10 mm BL. Moreover, pelvic fin area rapidly expanded beginning at ~15 mm BL. Among feeding-related characters, the gut folded back fully at 15 mm BL; this phase overlapped with the period of FF-III, when larvae acquired the feeding function of biting (Fig. 7).

RG-III, the completion phase of settlement (from ~17–18 mm to ~22–23 mm BL): The growth rate of the maximum body depth, body depth at the posterior end of the anus, and caudal peduncle increased at the beginning of this phase. Additionally, the pelvic fin was rapidly transformed from elongated to circular in shape during this period. In terms of feeding-related characters, the growth of mouth width increased at ~20 mm BL; wet weight significantly increased after ~22 mm BL. This period corresponded to FF-IV (Fig. 7), when the development of feeding functions approached completion.

RG-IV, settlement and reaching final body proportions (from ~22–23 mm to ~35 mm BL): The flection points at the beginning of this phase were increases in the gradients, with a shift to decreasing gradients concentrated at the border with the next phase, ~35 mm BL.

RG-V, immature stage (greater than ~35 mm BL): This phase is equivalent to the post-RG-IV period. The growth rates of all morphometric characters significantly decreased; some reached plateaus after ~35 mm BL.

4. Discussion

4.1 Usage pattern of Furuhama Park by C. gulosus

4.1.1 Size of newly hatched larvae

In this study, many individuals of less than 5 mm BL were observed; four individuals were less than 4 mm BL, including the smallest larva of 3.78 mm BL, which lacked a yolk, while 51 individuals were between 4.00 mm and 4.99 mm BL. Nakamura (1936), who observed and studied the habits of *C. gulosus* in captivity, reported that *C. gulosus* hatched at ~5.5–6.1 mm total length; on the basis of that study, Harada (2014) forecasted that the size of fixed newly hatched larvae would be ~4.4–5.0 mm BL, after the application of a reduction ratio for 4% formalin. However, all specimens sampled in this study lacked a yolk-sac, implying that the size at hatching is smaller than 3.78 mm BL. Additionally, our samples may have shrunk more than HARADA (2014) predicted, because we employed seawater containing 5% formalin for fixation and 70% ethanol for preservation.

4.1.2 Larvae of SF-I and -II, FF-I and -II, and RG-I (< 8–10 mm BL)

Individuals of less than 4 mm BL occurred at the sandy beach and tidal flat sites from January to March, when most individuals were up to ~10.0 mm BL. The period during which specimens are smaller than ~10 mm BL corresponds to RG-I; it includes SF-I and -II, as well as FF-I and -II.

Based on the findings in Fig. 9, larvae in SF-I are presumed to drift passively, rather than actively swim. During SF-II, caudal fin propulsion (Kohno *et al.*, 1983) and whole-body propulsion are enhanced. As stated in previous reports, the vertebrae efficiently conduct the oscillation of the caudal fin forward (Gosline, 1971; Omori *et al.*, 1996); the dorsal and anal fins regulate the sway that accompanies forward swimming (Gosline, 1971). Thus, the larvae likely acquire swimming ability using both the caudal fin and the whole body during this period. In FF-I, individuals can apply negative pressure to the inside of their

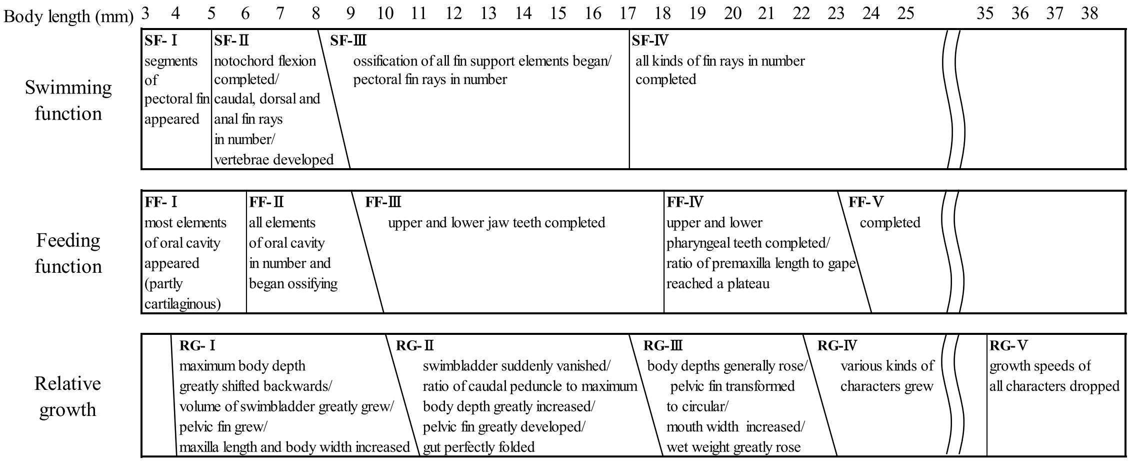

Fig. 9 Summary of developmental phases on swimming function, feeding function and relative growth, shown with developmental events happened in each phase.

mouth (GOSLINE, 1971), but this negative pressure is presumably weak because of the cartilaginous parts of the oral cavity (Fig. 9). Therefore, the larvae appear to achieve an initial sucking type of feeding in this phase. During FF-II, more powerful sucking becomes possible (Fig. 9). During RG-I, growth of the whole body and rapid improvement of both swimming and feeding functions occur (Fig. 9).

Therefore, *C. gulosus* larvae occurring during the 3 months from January to March are likely transferred by tidal flow after hatching; they then migrate between the sandy beach and tidal flat with physical and functional growth. According to OMORI and TSURUTA (1988), the nursery site (where many fishes spend the period of initial development) improves survival rates during early life stages, compared with other locations; thus, the nursery site has the ideal inorganic environment, low predation danger, and suitable food availability. The sandy beach and tidal flat in Furuhama Park constitute an appropriate nursery area for larvae of *C. gulosus*.

4.1.3 Larvae of SF-III, FF-III, and RG-II (between 8 mm and 16 mm BL)

In April, collection of *C. gulosus* at the wharf with the hand net began, in addition to collection from the sandy beach and the tidal flat. The BLs of fishes collected at these three sites were similar, ranging mainly from 8–16 mm BL; these lengths corresponded to SF-III, FF-III, and RG-II.

On the basis of the findings in Fig. 9, during SF-III, propulsion by the caudal fin and the whole body is enhanced and maneuverability is acquired, consistent with the report by TANIGUCHI (1987), indicating that the pectoral fins have roles in propulsion, stopping, and buoyancy. *C. gulosus* individuals also obtain the ability to bite, in addition to sucking, for feeding, in FF-III (Fig. 9). In addition, the pelvic fin function of adhesion and the instantaneous power for swimming markedly intensify at this stage; food composition can change during the period of RG-II (Fig. 9). The sucker-shaped pelvic fin of fish in the family Gobiidae adheres to surfaces using a hydraulic gap between the inside and outside of the fin, which is produced by extruding water from inside the sucker. Additionally, the caudal peduncle is associated with instantaneous swimming ability, rather than the ability for cruising, implying that prey-ambushing species possess sturdier caudal peduncles (WEBB, 1994).

According to NAKAMURA (1936), *C. gulosus* becomes an omnivore after settlement, feeding on various organisms including green algae, polychaetes, small crustaceans, snails, small insects, and fish eggs. Furthermore, SASAKI and HATTORI (1969) reported that the main diet of the *C. gulosus* included crabs, polychaetes, algae, hermit crabs, isopods, and shrimp, implying that modification of food composition occurs after settlement. Considering that RG-II overlaps with the period of improved swimming and feeding functions, *C. gulosus* likely commences preparing for settlement during RG-II. Hence, the larvae expand their habitat to the wharf from ~8 mm BL, when the larvae began to appear at the wharf.

4.1.4 Juveniles of SF-IV, FF-IV and -V, and RG-III (between 18 mm and 26 mm BL)

The greatest month-to-month difference in the distributions of BL was between April and May; in that period, samples of 18–26 mm BL (corresponding to SF-IV, FF-IV and -V, and RG-III) were rarely collected.

According to the findings in Fig. 9, the juvenile stage of swimming commences at SF-IV. Furthermore, FF-IV is the time of feeding ability enhancement, which is initiated in the previous phase; the juvenile feeding mode becomes fully functional in juveniles during FF-V. The swimming speed of *C. gulosus* improves after acquiring the functional juvenile swimming mode during RG-III (Fig. 9), as described by FISHER *et al.* (2005); their study showed that body depth is associated with the amount of muscle, which is related to fishes' swimming speed. Furthermore, from the discussion above and the findings in Fig. 9, *C. gulosus* settles on the seafloor at 22–25 mm BL, around the transition between RG-III and RG-IV; HARADA (2014) estimated that the settlement period of this species was between ~20 mm and ~40 mm BL. *C. gulosus* settles more slowly than do other gobioid fishes, such as *Acanthogobius flavimanus* (KANOU *et al.*, 2004) and *Eutaeniichthys gilli* (ANGMALISANG *et al.*, 2020). Moreover, according to DOTSU (1988), the *C. gulosus* habitat preference shifts to the seafloor at sizes greater than 30 mm BL. HARADA (2005) caught juveniles, which were up to ~33 mm BL, near the sea surface. Some individuals over 25 mm BL were also caught with a hand net at the surface in this survey. However, we were unable to determine whether these individuals remained at the surface after the acquisition of settlement ability or physically were unable to migrate to the bottom because of environmental factors. The sampling site of our research exhibits hypoxic conditions in summer, particularly between June and October; animals disappear from the seafloor during this period (ONODERA *et al.*, 2020). Thus, from an ontogenetic perspective, RG-III constitutes the period of settlement completion and the time of the greatest physical growth. In addition, a discussion of settlement that combines ontogenetic information with behavioral patterns should be conducted in the future.

Although larvae were present at the wharf, they were not caught with basket nets in April. The largest individual sampled with the hand net in April was 27.5 mm BL, while the smallest individual caught with basket nets in May was 22.8 mm BL. The period between these two sizes is generally equivalent to the settling period. Furthermore, regarding to lost swimbladders at ~12 mm BL, additional studies in this species should be conducted to reveal how they acquire buoyancy without swimbladders until settlement from ~12 mm BL to ~22 mm BL, because swimbladders of hemiplanktonic fishes in related *Gymnogobius* such as *Gymnogobius urotaenia*, *Gymnogobius breunigii*, *Gymnogobius isaza* and *Gymnogobius heptacanthus* do not undergo involution after being mature (Dotsu, 1961).

4.1.5 Juveniles of RG-IV and RG-V (> 35 mm BL)

After May, *C. gulosus* individuals were sampled almost exclusively with basket nets. Observations in this period were limited to individuals larger than ~35 mm BL, which is the border between RG-IV and RG-V.

Fig. 8 and Fig. 9 indicate that *C. gulosus* exhibits accelerated quantitative growth in RG-IV after the completion of qualitative development; this phase is the period when body proportions are adjusted to the dimensions observed in adults. Our results also imply that RG-V is the immature stage of *C. gulosus*. Moreover, a survey conducted beginning in 2000 in Furuhama Park by Ota City showed that numerous individuals over 35–36 mm BL were collected in the region of the vertical seawall, which is near the wharf sampled in this study and the mouth of the Uchikawa River (Ota City, 2001–2015). Therefore, this species presumably completes its migration from the tidal flat to the wharf by RG-V when its adult body proportions are reached. As a reference, no *Chaenogobius annularis*, which is the most closely related species to *C. gulosus* and often occupies the same habitat as *C. gulosus*, has ever been found in the park (Ota City, 2001–2015).

4.1.6 Spawning period and ground

The occurrence period of *C. gulosus* lasted until August in this study; no specimens were caught after that month. The size range of individuals sampled in August was from ~52 mm to 107 mm BL. Conversely, in autumn, an individual of ~90 mm BL was sampled at the vertical seawall site near the wharf during the survey conducted by Ota City (Ota City, 2001–2015). These findings imply that *C. gulosus* continues to utilize the vertical seawall area after the last occurrence in August.

This species begins to mature sexually in November (Kim *et al.*, 2004); the 50% maturity size for females is reportedly 79 mm standard length (Beack *et al.*, 2011). Additionally, Kim *et al.* (2004) reported that the gonad somatic index of *C. gulosus* changed most between December and March.

The spawning ground of this species has been suggested to occur near the low-tide line in inner areas of inlets or small bays with sand or shingle sediments and scattered appropriately sized stones (Sasaki and Hattori, 1969). Furthermore, Nakamura (1936) noted that *C. gulosus* eggs are deposited on the undersides of stones or small rocks in shallow water. Sasaki and Hattori (1969) reported that one spawning site was a small stone, while two others were large rocks that could not easily be displaced by two people. A rocky area is present at the west end of Furuhama Park, and fish larvae or juveniles are unlikely to enter Furuhama Park from outside because the park is situated in the innermost part of Tokyo Bay (Murai *et al.*, 2016). Thus, *C. gulosus* probably spawns in the park.

Regarding the spawning period, Nakamura (1936) indicated a range from January to May, with a peak between February and April. Beack *et al.* (2011) and Park *et al.* (2020) reported that the spawning season of this species is from December to April in Korea. Murase *et al.* (2007) suggested that the spawning period in the innermost portion of Tokyo Bay is during winter and spring. In addition, eggs hatch at approximately 1 month after spawning (Nakamura, 1936). Considering these reports, the spawning period in Furuhama Park is presumably between December and February.

4.2 Artificial environment

In this study, we investigated three types of environments in an artificial seaside park: a sandy beach, a tidal flat, and a wharf. We discovered that *C. gulosus* occupied the artificial environment and individuals utilized various habitats throughout development.

Many fish surveys have been conducted in artificial environments other than Furuhama Park, and *C. gulosus* has been sampled in such surveys. According to the Bureau of Environment of Tokyo Metropolitan Government (1992–2018), this species has been collected at an artificial sandy beach and two tidal flats; all collected individuals were less than ~20 mm BL. In surveys conducted by Yokohama City (1974, 1978, 1981, 1986, 1989, 1992, 1995, 1996, 2001, 2004, 2007, 2010, 2014, and 2018), most samples between ~50 mm and ~100 mm BL were collected at revetments or wharfs. However, existing evidence is fragmentary, although these surveys indicate which fishes occupy specific habitats at specific times each year in an artificial environment. Furthermore, each study conducted in a different area is considered discrete, although several survey areas have included multiple types of environments. This inconsistency limits the understanding of successive use of adjacent habitats by fishes. Thus, synchronous investigations in adjacent but differing environments, rather than in only one type of habitat, are crucial to elucidate the role of each environment for fishes. Furthermore, artificial locations are presumably capable of providing fishes with habitats where they can spend longer periods or their entire life histories because they contain diverse environments, in contrast to the simple environments created when beaches, tidal flats, or shoals are rebuilt.

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