

Size distribution and growth patterns of gobies in habitats associated with a natural estuary of inner Tokyo Bay, central Japan

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Abstract. Size distribution and growth patterns of *Gymnogobius breunigii*, *G. macrognathos* and *G. uchidai* in habitats associated with the natural estuary of Obitsu-gawa River of inner Tokyo Bay, central Japan were studied from specimens collected from May to December 2005 and March to April 2006 and specimens from the shallow tidal creek and soft sediment pools from July 2009 to June 2010. The gobies showed preference for a particular estuarine habitat at a given stage of ontogenetic development and habitat shift corresponded with change in body shape implying the level of competence exhibited by these species during ontogeny. The occurrence of larva and the early J1 in the lower estuary around May was timed with spring bloom that was attributed to increase in the secondary production of estuaries in the bay particularly the zooplankton, which was the main prey item of gobies during the pelagic phase. The movement in the tidal creek from late J1 to J2 was related with shift to benthic lifestyle with preference for benthic prey but it could also be attributed to refuge from predators as well as temperature-mediated growth and morphogenesis in the shallow habitat. Relevant changes in body shape was a prelude to benthic life particularly the narrowing of the head, reduction in the angle of the mouth on the ventral surface bringing the mouth closer to the substrate, deformation at the anterior trunk region that resulted to a tumescent appearance on the dorsal region of the trunk as well as a relatively elongated and ventrally displaced tail. All these characters were attained at J3. The gobies gained competence when they reached J3 having the ability to explore "high-risked" habitats such as the middle estuary and a specialized habitat like the soft sediment pools. The J3 of *G. breunigii* on the other hand corresponded with upstream movement to preferred adult habitats. Changes during the adult stage was primarily associated with the elaboration of the morphological form inherent at J3. The study proposed that the estuarine habitats associated with the lower region of Obitsu-gawa River are important for gobies during the transition from pelagic to benthic life that would likely increase their survival and subsequent recruitment into the estuary.

Key Words: Tidal creek, soft sediment pool, morphometry, allometry.

Introduction. Estuaries are complex system of habitats (Selleslagh & Amara 2008; França et al 2009; Inui et al 2010b) that are often associated with estuarine fish communities with species-specific differences in habitat use (Rakocinski et al 1992; Whitfield 1999; Ramos et al 2006). In a study conducted by Hermosilla et al (2012a) in Obitsu-gawa River Estuary, family Gobiidae had the most number of taxa with at least 10 identified species and the distribution of a particular ontogenetic stage in this natural system was largely influenced by changes in monthly water temperature, station and their interaction. Estuarine gobies were also the most dominant fishes in the tidal creek of the said estuary representing 98% of the fish community and the occurrence of a particular ontogenetic stage also showed strong association with month and water temperature that led to a conclusion that very shallow habitats like the tidal creek and soft sediment pools associated with estuaries can also function as habitats for fishes and the prevalence of certain life history stages at a given time suggest the importance of these habitats at certain stage in the life history of fish particularly for the resident gobies of inner Tokyo Bay (Hermosilla et al 2012b). Having established that gobies that inhabit the Obitsu-gawa River Estuary vary in time and space in terms of ontogenetic development (Hermosilla et al 2012a; 2012b), the current study attempted to establish the relationship among these estuarine habitats based on the size distribution of the

resident species such as *Gymnogobius breunigii* (Steindachner, 1879), *Gymnogobius macrognathos* (Bleeker, 1860) and *Gymnogobius uchidai* (Takagi, 1957). Additionally, fishes experience changes in shape with growth in order to effectively perform vital biological functions and the development of morphological characteristics generally corroborates with the importance of these characters at a given stage during the early stages of ontogenetic development (Loy et al 1998, 2001; Osse & van den Boogaart 1999; Simonović et al 1999, Russo et al 2007) and that shape modifications during development are closely linked with ontogenetic changes in habitat and resource use (Webb 1978, 1984). Therefore, an attempt to describe the morphological growth patterns will also give some valuable insights about the priorities during the early stages of ontogenetic development of fishes that can be an interesting topic for research in the field of fish ecology and behavior. It was for these reasons that the current study also attempted to describe changes in the morphological characteristics associated with the specific ontogenetic development of the three gobies as they moved from one habitat to another in the natural estuary of Obitsu-gawa River. Specifically, the objectives were to identify distinguishable morphological changes during ontogenesis and explore the correspondence between morphological development and habitat preference.

Material and Method. Fish sampling was performed along the saline reaches of Obitsu-gawa River from May to December 2005 and March to April 2006 including the shallow tidal creek and soft sediment pools from July 2009 to June 2010 (Figure 1). The estuary is situated in Chiba Prefecture as part of the Boso Peninsula of Tokyo Bay, Japan. There were three stations along the river. The lower station was situated adjacent to the river mouth fronting Tokyo Bay while the middle station with an approximate distance of 0.5 km inner to the previous station. The upper station was located further upstream at a distance of 2 km from the middle station. Sampling was not made possible in these stations from January and February including the lower station in March and April. In addition, fish samples were also collected in a nearby creek situated west of the river mouth. It has an average depth of 20 cm and width of 4 m at low tide with soft sediment pools along its edges that are fringe by reed vegetation.

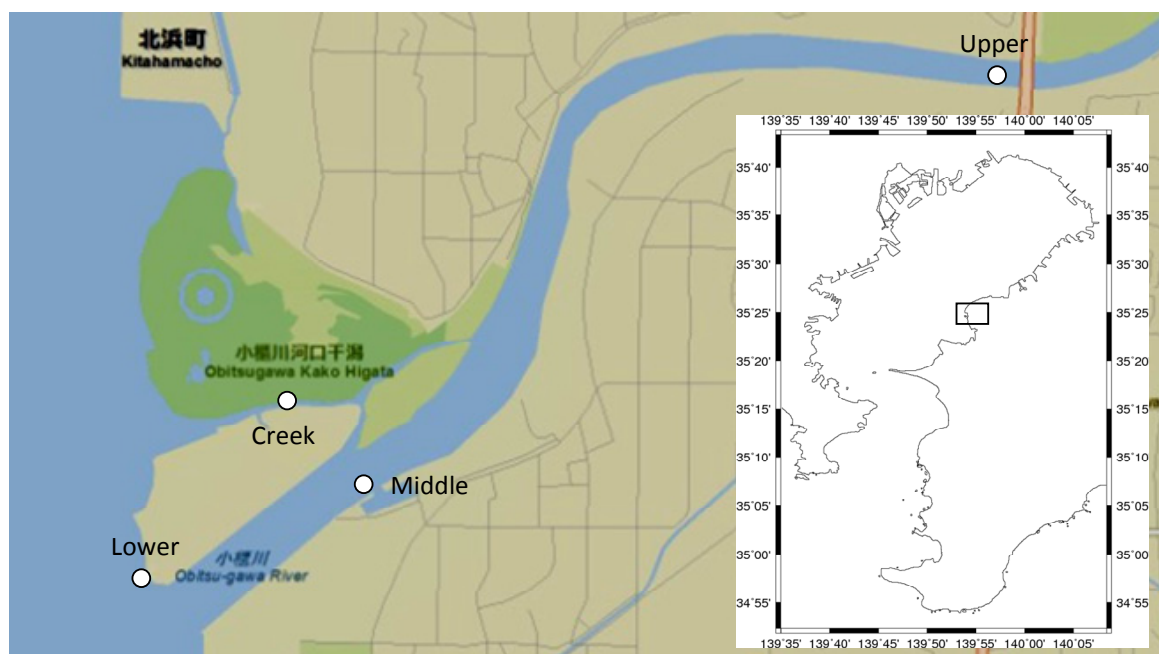


Figure 1. Map of Tokyo Bay and the location of Obitsu-gawa River Estuary (□) and the stations where the fish sampling was conducted (○). [Maps courtesy of the National Geophysical Data Center (<http://www.ngdc.noaa.gov/mgg/coast/>) and Environmental Sciences Research Institute (<http://www.esri.com/>)].

Fishes in the lower, middle and upper estuary were sampled using a seine net (Figure 2A) while a customized trap nets were installed at two points along the tidal creek with one net blocked the incoming water while the other was fixed 2 m away that was designed to trap fishes (Figure 2B). The net design and the actual procedure of the fish collection were described in detail by Hermosilla et al (2012a) for the lower, middle and upper river while Hermosilla et al (2012b) for the tidal creek and soft sediment pool sampling. Fishes were placed in pre-labelled, plastic containers with 10% formaldehyde as the initial fixative. Water temperature and salinity were also recorded from these habitats.

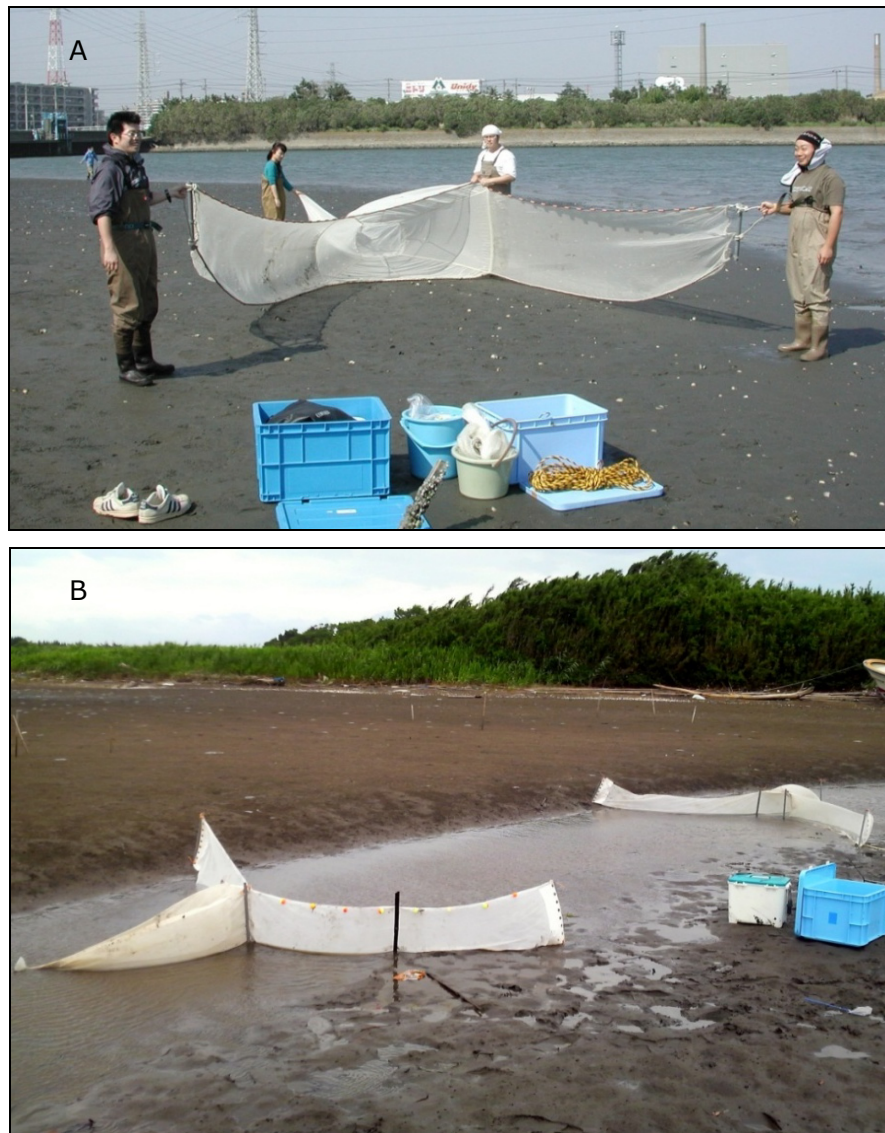


Figure 2. The seine net (A) used in the actual fish sampling in the lower, middle and upper estuary and the installation of customized trap nets (B) in the tidal creek that covered an area of 10 m² of the habitat.

Fish samples were placed in a clean tray for removal of debris, sorting and counting. Taxonomic identification was made to species level as possible. Standard length (SL) of *G. breunigii*, *G. macrognathos* and *G. uchidai* were measured to the nearest 0.01 mm using a digital caliper. Fish specimens were transferred in storage bottles or vials with 70% ethanol as the final preservative. Each was labeled with species name with corresponding date and habitat. In addition, developmental stages were identified based on the descriptions made by Kendall Jr et al (1984). Juveniles were further divided into three

distinct groups based on their body pigmentation patterns with juvenile one (J1) having pigmentation patterns similar to post flexion larvae (L) while juvenile two (J2) corresponds to the transition period between J1 and J3. Juvenile three (J3) has similar pigmentation pattern as adults (A) (Kanou et al 2004, 2005).

Clearing of tissues and staining of cartilages and bones were performed on the three species of gobies according to the method described by Potthoff (1984). The cleared and stained specimens were studied for morphometry and allometry based on a series of digital images taken for each specimen. A total of 188 specimens of *G. breunigii* (10.20 mm – 46.68 mm SL), 148 specimens of *G. macrognathos* (11.99 mm – 39.78 mm SL) and 175 specimens of *G. uchidai* (12.13 mm – 30.38 mm SL) were cleared and stained. Geometric approach for within species variation in morphometric characteristics associated with ontogenetic development was the method of choice. Specifically, the landmark method was used to quantify shape deformations based on the 12 landmarks on the lateral axis of the fish encompassing the cephalic to caudal regions (Figure 3A). These homologous landmarks were situated at the proximal end of the premaxilla (1), the supraoccipital (2), the base of the first spine of the first dorsal fin (3), the base of the first spine of the second dorsal fin (4), the base of the last ray of the second dorsal fin (5), the anterior part of the hypural 3+4 (6), the posterior part of the hypural 1+2 (7), the base of the last ray of the anal fin (8), the base of the first spine of the anal fin (9), at the region of the pelvic fin (10), the cleithral symphysis (11) and the junction between the angular and quadrate bones (12).

Acquisition of raw data and superimposition procedure were performed using Jim Rohlf's tps suite software package (<http://life.bio.sunysb.edu/morph/>). Assignment of landmarks was done by building a TopSpeed data (TPS) file from digital images using the "tpsUtil" program and utilized the "tpsDig2" program to assign landmarks for each image, record the scale factors and saving these data into a tps format. Digital images were then matched in shape space by removing differences in location size and orientation from the data through superimposition in the "CoordGen6f" program. Resistant-Fit Theta-Rho analysis (RFTRA) was the superimposition method of choice. Coordinates that were generated after the superimposition were then used for geometric morphometric analysis using the MorphoJ software package (Klingenberg 2011). Initially, the canonical variate analysis (CVA) was used to find the shape features that best distinguish among the stages of development (e.g., larva, J1, J2, J3 and adult) followed by a permutation test of pairwise distances (9,999 iterations per comparison) between groups. Test proceeded with discriminant function analysis (DFA) to further examine the difference between two developmental stages particularly between the larva (or J1) and another stage of ontogenetic development. The reliability of the test was assessed by leave-one-out cross-validation with 9,999 permutation runs. In addition, a diagram of the 12 landmarks implying the shape difference between the two group means was generated for visualizing the results.

For allometric study, traditional morphometric distances were extracted from the calibrated coordinates of the landmark's endpoints thereby resulting to a box-truss network between landmarks (Strauss & Bookstein 1982). A total of 26 truss distances were obtained from the 12 landmarks (Figure 3B). Archiving of truss distances was performed in the "tmorphgen6" program of Jim Rohlf's tps suite (<http://life.bio.sunysb.edu/morph/>). In order to understand how a given truss distance scaled against SL throughout the course of ontogenetic development, values for truss distances were grouped according to stages of ontogenetic development and each truss distance was subjected to a standardized major axis (SMA) test for estimation and inference about allometric lines associated with ontogeny. Values for truss dimensions and SL were log-transformed prior to analysis, and were approximately linearly related on the transformed scale approximately following a power law, $y = ax^b$ wherein y is the dependent variable (e.g., truss dimension) and x is the independent variable (e.g., SL). The "scaling exponent" b is the slope on log-transformed axes while the "proportionality coefficient" a relates to the elevation on log-log axes. Of particular interest in the current study was the value for parameter b , which described how steep the relationship between a given truss distance and SL was. In isometric growth, the value of b is 1, whereas

smaller values are interpreted as negative allometry while larger values are interpreted as positive allometry. SMA was performed using the "smatr" package developed by Warton et al (2012) under the statistical computing language R (version 2.12.0).

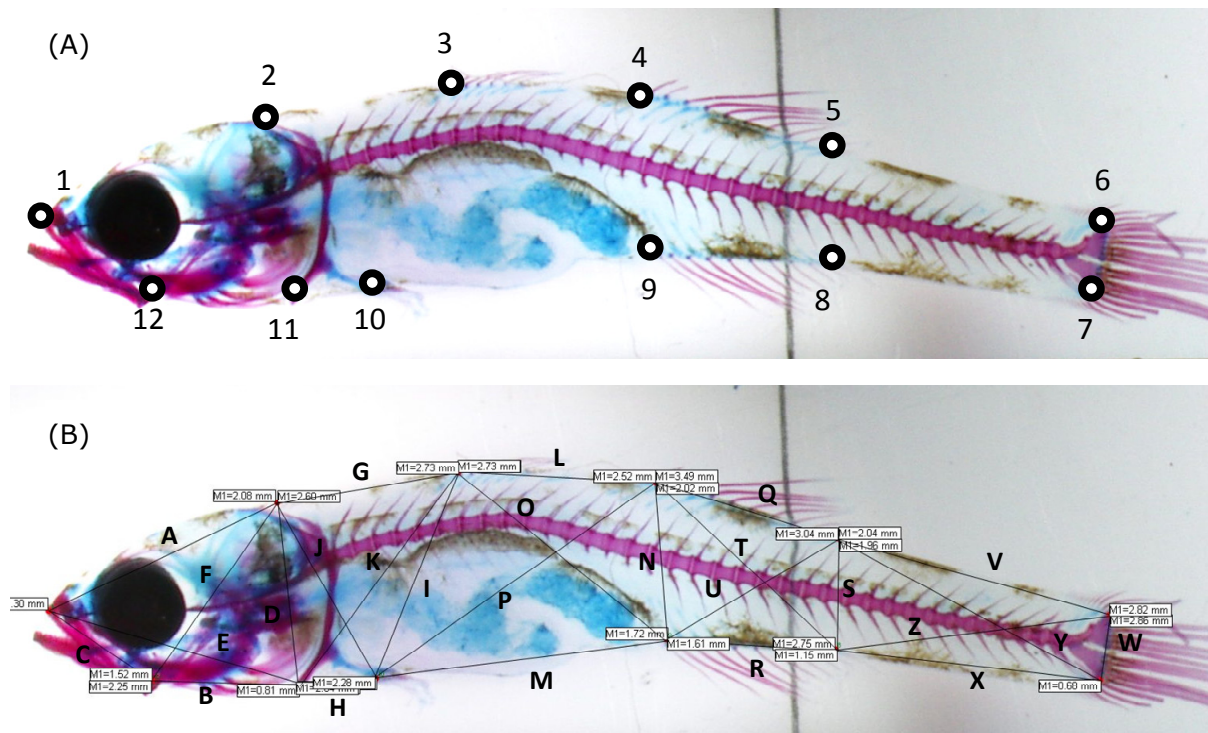


Figure 3. A calibrated digital image of a cleared and stained *G. breunigii* larva (SL=11 mm) with 12 landmark configurations (A) that formed the basis for geometric morphometric analysis and a network of box-truss dimensions (B) of the same specimen for allometric studies.

Statistical test was performed using the maximum likelihood approach based on the SL of the three estuarine gobies to explore variation in size in response to several environmental predictors. To do this, the SL for each species was initially fitted to at least 13 feasible statistical distribution families capable of handling a continuous response variable ranging from 0 to $+\infty$. Thirteen models for SL were integrated into a generalized additive models for location, scale and shape (GAMLSS) framework by Stasinopoulos and Rigby (2007), which is a semi-parametric regression type of model. The Generalized Akaike Information Criterion (GAIC) with a maximum penalty of 2.5 was used to determine which of the 13 distribution families best described the variation in the SL for a given species. Model with the lowest GAIC score was considered as the "best" approximating model for the response variable SL (Figure 4). To build a model for the predictors, environmental variables such as habitat type, month, water temperature, water salinity and their interactions were considered in the model-fitting process. These predictors were fitted to the SL data of a given species with the appropriate distribution family. However, to simplify and hasten the computing time for the model selection process, the "dropterm" function of the "MASS" package (Venables & Ripley 2002) was used to remove the least important predictor and a new model was built on the most relevant predictor variables. The "addterm" function was used to explore any possible two-way interaction in the new model. Test proceeded with the stepwise selection of the model in GAMLSS. If a continuous variable (e.g., water temperature or water salinity) was retained in the final model, test proceeded in determining if a smoothing additive term was necessary for the said variable. The polynomial (surface) curve was the smoothing additive term of choice. Any two-way interactions were further subjected to a recursive partitioning and regression tree analysis by modeling the SL variable with the relevant environmental variable as the predictor. The "rpart" package by Therneau et al

(2010) was used for this analysis. Since the expected endpoint of the regression tree was a continuous variable (e.g., mean SL), analysis of variance was the statistics used to discriminate these size classes and subsequently associate these size classes with the predictor.

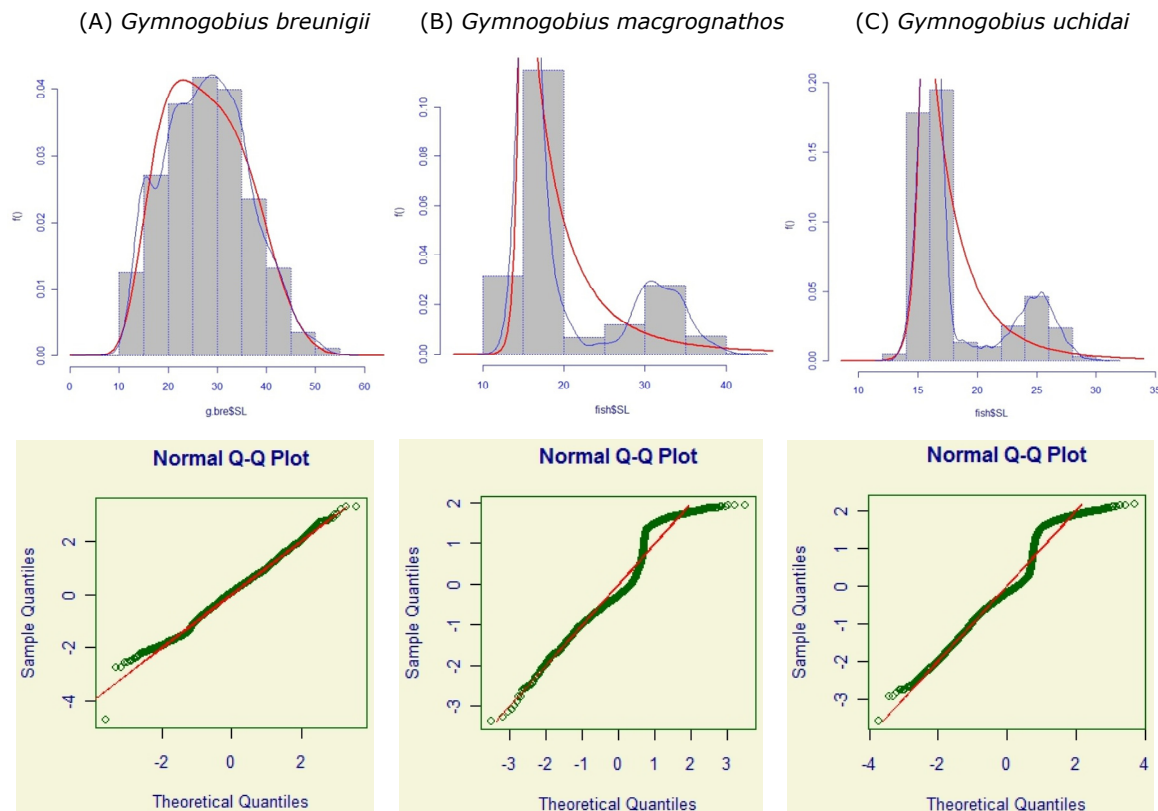


Figure 4. Standard length data (bars) for the three species of gobies with Kernel density estimate (blue line) and the fitted Box-Cox Power Exponential (A) and Generalized Beta type 2 (B and C) distributions (red line). A Q-Q plot below shows how the SL data (green points) were fitted with the statistical distribution family (red line).

Results and Discussion. *G. breunigii* was observed in all the estuarine habitats of Obitsu-gawa River but very few individuals were sampled from the soft sediment pools, which were primarily adults (median SL = 40.9 mm; $n = 9$) indicating that the said estuarine habitat was less likely favored by the said species. Nevertheless, the result showed that there was a difference in SL in these habitats (Figure 5). Early J1 was prevalent in the lower station (median SL = 15.85 mm; $n = 612$) and was present in the tidal creek as J2 (median SL = 25.85 mm; $n = 838$). Early J3 was prevalent in the middle estuary (median SL = 30.34 mm; $n = 579$) and upper estuary (median SL = 31.61 mm; $n = 1,197$). *G. breunigii* is known to inhabit both brackish water and freshwater habitats (Stevenson 2002). However, the current study had shown that the larvae and early juveniles (e.g., J1 and J2) were prevalent in habitats associated with the lower region of the estuary such as the lower estuary and tidal creek. They began to move upstream when they reached J3. The preference for the upstream habitat can also be attributed to the preference for the shelving and calm water conditions (Inui et al 2010a). Size distribution also showed significant association with month and water temperature interaction (Figure 7A). J1 and J2 were prevalent in May but their occurrences varied with water temperature. While J1 (mean SL = 16.53 mm; $n = 602$) was prevalent when water temperature was between 15.65-18.15°C, the early J2 (mean SL = 23.74 mm; $n = 472$) was evident when water temperature was $\geq 18.15^\circ\text{C}$. The late J2 (mean SL = 27.05 mm; $n = 307$) was observed when water temperature was $<15.65^\circ\text{C}$. The J3 stage

(mean SL = 29.98 mm; n = 1,366) was noticeable from June to August when water temperature was $\geq 24.75^{\circ}\text{C}$ while adult (mean SL = 40.55 mm; n = 488) was prevalent when water temperature was $< 24.75^{\circ}\text{C}$ from September to April. It was likely that the larva and J1 preferred the relatively cold waters of the lower estuary while the J2 preferred the very shallow but warmer waters of the tidal creek in May. J3 was prevalent in the middle estuary during the warm months and moved upstream in months when the water temperature was decreasing.

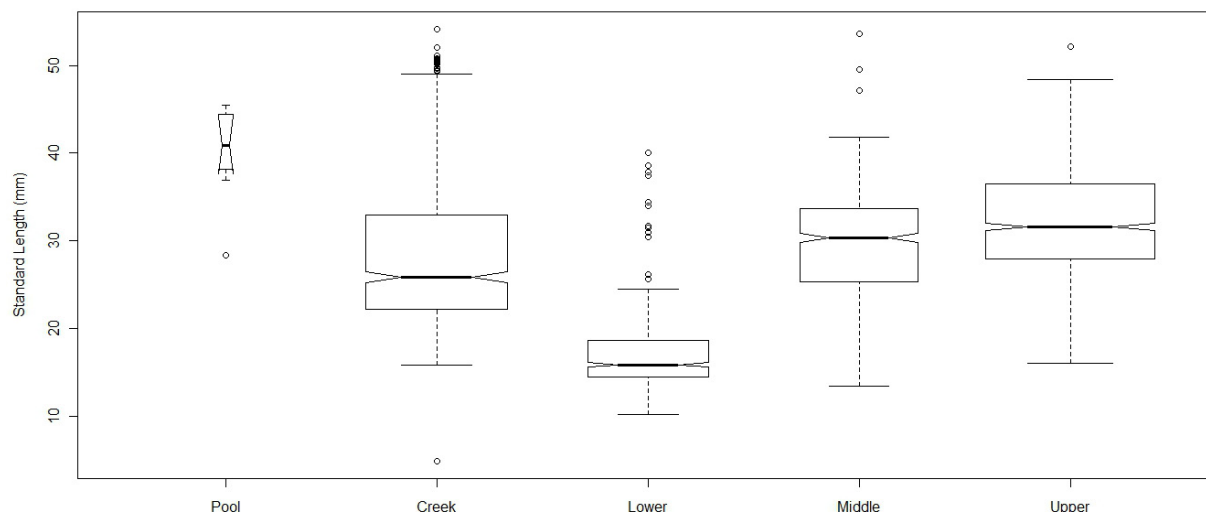


Figure 5. Standard length distribution of *G. breunigii* in the five estuarine habitats. Each box was drawn with the width proportional to the square-root of the number of observations in a given station and the notches on each side of the box corresponded to the confidence interval of the median SL for that station. The lack of overlap of the notches between stations indicated that their median SL was different.

G. macrognathos was observed in habitats in the lower region of the estuary. Month (Figure 6) as well as station and water temperature interaction (Figure 7B) best explained the size distribution of this species. Generally, adult was prevalent in January (median SL = 32.32 mm; n = 88), February (median SL = 30.24 mm; n = 134), March (median SL = 32.31 mm; n = 96) and April (median SL = 32.17 mm; n = 65). J1 was prominent in May (median SL = 15.93 mm; n = 1,661) and June (median SL = 19.48 mm; n = 25). J2 was prevalent in July (median SL = 23.45 mm; n = 21), August (median SL = 23.70 mm; n = 7), September (median SL = 22.84 mm; n = 4), October (median SL = 22.69 mm; n = 2) and November (median SL = 24.23 mm; n = 5). A few J3 were observed in December (median SL = 28.98 mm; n = 5) (Figure 6). Station and temperature interaction also played a significant part in explaining the size distribution of *G. macrognathos* in the lower region of the estuary. Early J1 stage (mean SL = 15.97 mm; n = 1,464) was observed in the lower estuary but a considerable number of late J1 (mean SL = 18.85 mm; n = 49) was found in the soft sediment pools when the water temperature was $\geq 28.12^{\circ}\text{C}$ and was replaced by J3 (mean SL = 28.50 mm; n = 31) when the water temperature was $< 28.12^{\circ}\text{C}$. Tidal pools can be a potential refuge for young-of-the-year fishes because of its characteristic warm water (Smith & Able 1994) in addition to being the source of prey items and therefore act as a trophic support function for fishes (Larkin et al 2008, 2009), which in this case for the juveniles of *G. macrognathos*. Water temperature was also a significant factor in the variation in size observed in the tidal creek and middle estuary. Early J3 (mean SL = 25.81 mm; n = 173) was prevalent in these habitats when water temperature was $\geq 20.40^{\circ}\text{C}$ and was replaced by the adult (mean SL = 31.34 mm; n = 400) when the water temperature was $< 20.40^{\circ}\text{C}$ (Figure 7B). It was likely that adult was prevalent in the tidal creek and middle estuary during the cold months around January to April and were completely

overwhelmed by the influx of larva and J1 in the lower estuary around May. Some of the late J1 and early J2 moved to the soft sediment pools particularly during the warm month of July and preferred the tidal creek and the middle estuary with further growth.

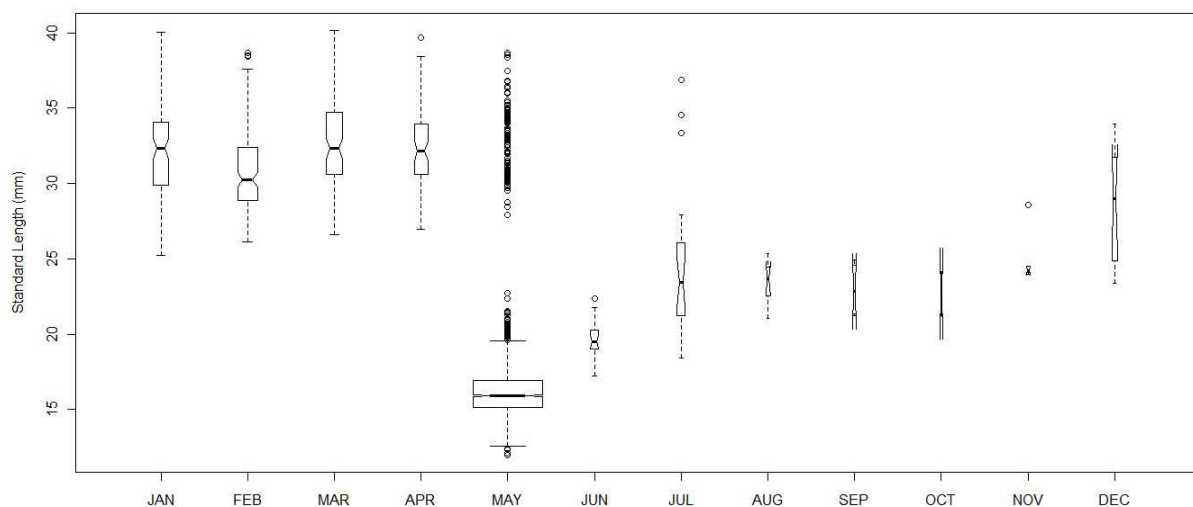


Figure 6. Standard length distribution of *G. macrognathos* across months. Each box was drawn with the width proportional to the square-root of the number of observations in a given month and the notches along each side of the box corresponded to the confidence interval of the median SL for that month. The lack of overlap of the notches between months indicated that their median SL was different.

G. uchidai generally had a narrow habitat range with the preference for the lower region of the estuary. The adult inhabited the river mouths (Masuda et al 1984) and its dominance in the tidal creek further indicated the importance of the tidal creek habitat to the said species (Hermosilla et al 2012b). Month and station interaction best described the variation in the SL distribution of this species (Figure 7C). Early J2 (mean SL = 15.98 mm; n = 3,627) was concentrated in the lower estuary in May and moved to shallower habitats with growth. Specifically, some J2 (mean SL = 17.98 mm; n = 147) were observed in the soft sediment pools during the warm months from June to September while the late J2 (mean SL = 19.54 mm; n = 151) preferred the tidal creek and the middle estuary from June to November and inhabited these habitats until adult (mean SL = 25.04 mm; n = 920) particularly from December to May. Few J3 were present in the soft sediment pools (mean SL = 23.55 mm; n = 62) and lower estuary (mean SL = 23.24 mm; n = 20) from October to August.

The occurrence of larva and the early J1 gobies in the lower estuary around May was timed with the spring bloom in inner Tokyo Bay. A more or less similar result was observed by Kanou et al (2007) wherein metamorphosing newly settled juveniles of the yellowfin goby, *Acanthogobius flavimanus* (Temminck & Schlegel, 1845) in Tama-gawa River Estuary of inner Tokyo Bay was prominent from mid-March to late May with a sharp peak in density in early May.

Recruitment of estuarine gobies around spring can be attributed to increase primary productivity of the coastal system of inner Tokyo Bay in spring (Ogawa & Ogura 1997; Nakane et al 2008; Bouman et al 2010) considering that the eutrophic estuaries located east of inner Tokyo Bay, where Obitsu-gawa River Estuary is situated, were considered as areas with notable phytoplankton growth and high chlorophyll a concentration during the warm months (Ogawa & Ogura 1997; Suzumura et al 2004). However, this contention is meaningful only if the utilization of the shallow habitats by epibenthic fishes is related to feeding (Cattrijse et al 1994; Kneib & Wagner 1994; Kneib 1997; Laffaille et al 2000; Nemerson & Able 2003).

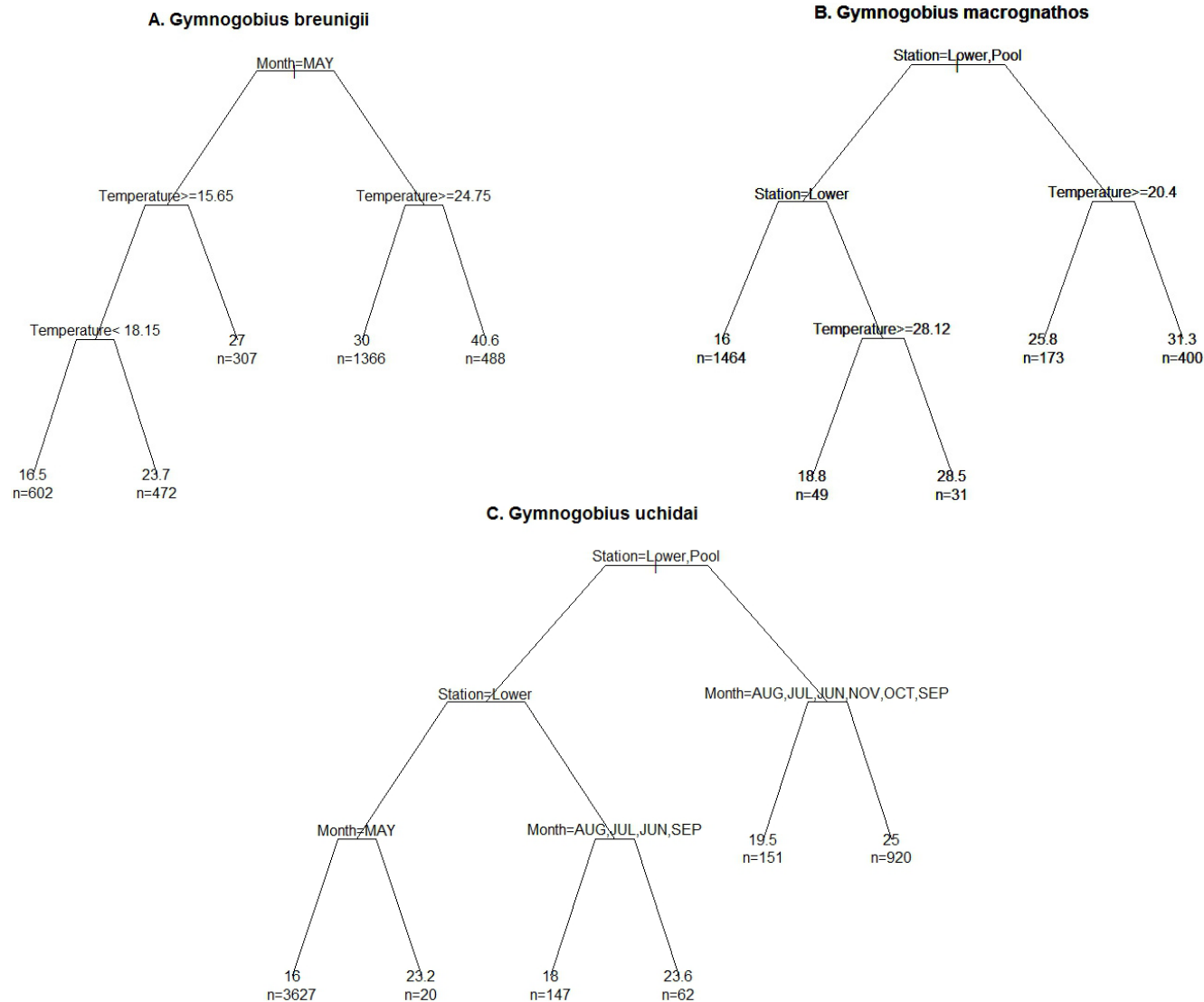


Figure 7. Regression trees for the standard length distribution of *G. breunigii* (A), *G. macrognathos* (B) and *G. uchidai* (C) in Obitsu-gawa River Estuary in relation with the relevant explanatory variables. The trees were presented in a manner in which relevant explanatory variables with the lowest deviance scores were positioned on the left hand of the branch. Terminal nodes corresponded to the mean SL and below were the actual number of samples (n) that were assigned to the group.

Phytoplankton that intrude the estuary can be a food source assimilated by benthic consumers (Antonio et al 2010) and the high primary productivity in spring was likely the key factor that fueled the secondary production of the estuary with cascading effect on the lower trophic level consumers such as the zooplankton and the immature gobies that feed on them. Gut content analysis of gobies in the tidal mudflats of Tama-gawa River estuary showed that the larva and J1 of *G. breunigii* subsisted on cladocerans and planktonic copepods while the J1 of *G. macrognathos* subsisted on calanoid and cyclopoid copepods (Kanou et al 2004). It was likely that similar prey items were consumed by these gobies in Obitsu-gawa River Estuary and was likely true also for *G. uchidai*. The movement of these gobies in the tidal creek from late J1 to J2 can be attributed to shift to benthic prey items with growth (Kanou et al 2004). However, the hyperbenthic fauna of marsh habitats is most often comparable to the hyperbenthos in the adjacent subtidal habitat (Cattrijsse et al 1994) and the preference for the tidal creek cannot be exclusively attributed to feeding alone but by other relevant factor such as refuge from predators (Paterson & Whitfield 2000; Kimball & Able 2007). With their small size and considerable adaptability to very shallow waters of the tidal creek at low tide, these gobies can extend their foraging time while reduce the risk of predation considering that the tidal creek of Obitsu-gawa River Estuary was observed to be devoid of large predators primarily due to its very shallow nature and the gobies were noticeable in the said habitat at low tide (Hermosilla et al 2012b). Moreover, the prevalence of high temperature waters from May to October can also promote temperature-mediated growth that can be further enhanced when these gobies moved in the tidal creek after the larval phase and take advantage of the tidal creek resources. Temperature-mediated growth during the early stages of ontogenetic life had been reported for the goby (Gill et al 1996) and other fish species (Boehlert & Yoklavich 1983; Polo et al 1991; Fuiman et al 1998; Klimogianni et al 2004; Niklitschek & Secor 2009) with the common contention that ontogenic growth rate increased with increasing temperature. The results of the standard major axis test for the three species of gobies were shown in Tables 1-3. In the current study, negative allometry was an inherent characteristic observed for the J3 of *G. macrognathos* (Table 2) and *G. uchidai* (Table 3) during the cold months and growth resumed only during the adult stage most likely around spring time with consistent prey availability and the water temperature was increasing. Nevertheless, these gobies became more competent when they reached J3 and explored other habitats such as the middle estuary and to a certain extent, the soft sediment pools. Gobies are important component of the tidepool fish assemblage (Meager et al 2005; Krück et al 2009; Chargulaf et al 2011) including inner Tokyo Bay (Okazaki et al 2011) and it was likely that the soft sediment pools of Obitsu-gawa River Estuary function as a refuge as well as trophic support function specially for J3 during the cold months when food resources were likely limited. The J3 of *G. breunigii* on the other hand corresponded to the stage wherein movement to upstream adult habitats was observed.

The results of canonical variate analysis for the three species of gobies were shown in Figures 8-10. A difference in shape between the larva and adult *G. breunigii* was observed (Figure 8). The J1 and J2 had close affinity to the larval shape rather than the adult. The J3 had intermediate characters that were shared with J1, J2 and adult but less likely for the larva. Deformation grid and a histogram for the discriminant function analysis comparing the change in shape between the larva and the later stages of ontogenetic development was presented in figure 11 as well as a series of images corresponding to the different stages of development was shown in figure 12 for *G. breunigii*. Much of the distinguishing features between the larva and adult were evident in the cephalic region as shown by the deformation of the landmarks of the head. Minor deformations were also observed in the upper trunk, upper tail and lower tail. Deformations at the base of the first spine of the first dorsal fin (3), supraoccipital (2), proximal end of the premaxilla (1) and at the junction between the angular and quadrate bones (12) assumed a counterclockwise displacement while the region of the pelvic fin (10) was opposing. These deformations slightly positioned the mouth closer

to the substrate. The upper caudal region was characterized by the caudally directed deformation at the base of the last ray of the second dorsal fin (5) and the base of the last ray of the anal fin (8) while the anterior part of the hypural 3+4 (6) as well as the posterior part of the hypural 1+2 (7) were slightly ventrally positioned. Deformations of the said landmarks were evident at J3 (Figure 11 & 12). Deformations in the head region were likely attributed to positive allometry on the dorsal region of the head (dimension A) from J1 to J3 combined with negative allometry on the ventral surface of the mouth (dimension C) from J1 to adult (Table 1). Deformation on the caudal region initially started with ventral displacement around the base of the last ray of the anal fin (8) and base of the first spine of the anal fin (9) from J1 to J2. However, it changed its course with growth together with the rest of the landmarks associated with the caudal region (except the hypurals), which became prominent through positive allometry between the base of the last ray of the second dorsal fin (5) and the anterior part of the hypural 3+4 (6) (dimension V), isometric growth between the base of the last ray of the anal fin and the posterior part of the hypural 1+2 (dimension X), positive allometric growth between the last ray of the second dorsal fin (5) and the posterior part of the hypural 1+2 (7) (dimension Y) and isometric growth between the base of the last ray of the anal fin (8) and the anterior part of the hypural 3+4 (6) (dimension Z) at J2. The same growth patterns were likely responsible for the slight ventral displacement of the hypurals. Sixteen out of the 26 dimensions along the lateral axis of *G. breunigii* shared no common slope ($P\text{-value} \leq 0.05$), which was an indication of the prevalence of allometric growth pattern during the development from larva to adult. Generally, negative allometry in almost all truss dimensions was prominent in the adult as compared to the earlier stages of ontogenetic development.

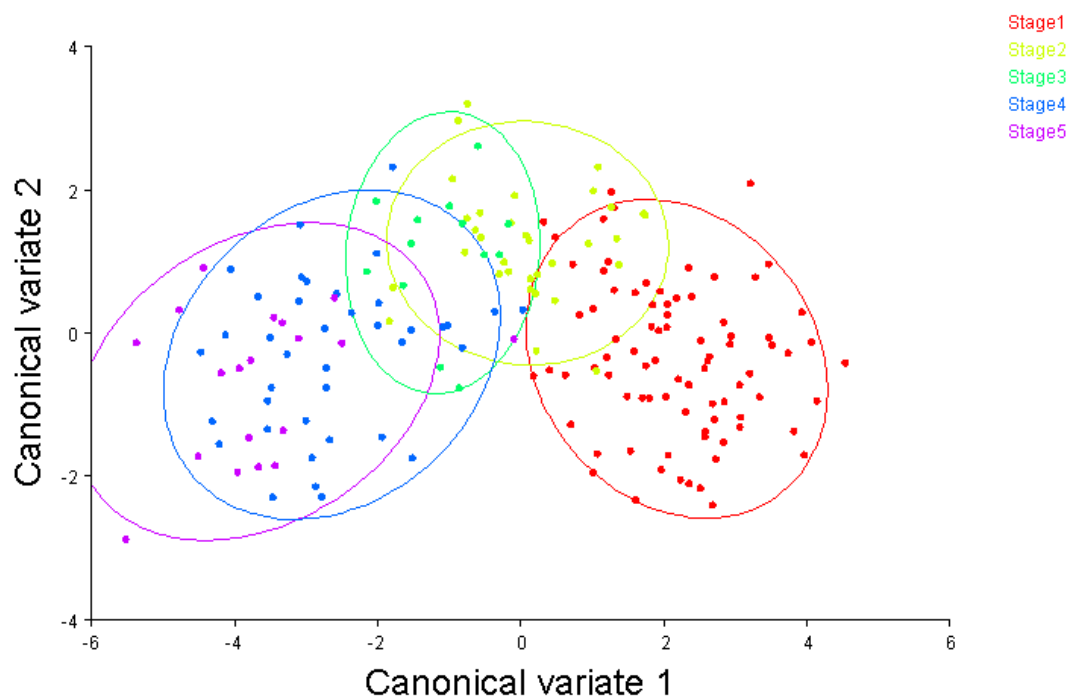


Figure 8. Canonical variate analysis for the larva (Stage1), J1 (Stage 2), J2 (Stage 3), J3 (Stage 4) and adult (Stage 5) stage of *G. breunigii*. The equal frequency ellipse contains 90% of randomly drawn data points for a given stage of ontogenetic development. CVA 1 explains 85.67% of the variance while CVA 2 explains 8.32% of the variance.

Table 1

Results of the standard major axis test that showed how a given truss dimension scaled against the SL of *G. breunigii* at a given stage of ontogenetic development. The *a* is the intercept, *b* for slope, R^2 for the strength of the linear relationship between variables at a given stage while the P-value corresponds to the level of significance of the linear relationship. Test for a common slope was also performed to determine how a given truss dimension changed throughout the course of ontogenetic development

Region	Dimension	Common slope	Larva				Juvenile 1				Juvenile 2				Juvenile 3				Adult			
		P-value*	<i>a</i>	<i>b</i>	R^2	P-value	<i>a</i>	<i>b</i>	R^2	P-value	<i>a</i>	<i>b</i>	R^2	P-value	<i>a</i>	<i>b</i>	R^2	P-value	<i>a</i>	<i>b</i>	R^2	P-value
Head	A	0.41	0.63	0.99	0.91	0.00	0.56	1.13	0.87	0.00	0.60	1.08	0.91	0.00	0.62	1.07	0.77	0.00	0.73	0.96	0.57	0.01
	B	0.00	0.91	0.84	0.72	0.00	0.92	0.93	0.09	0.04	1.05	0.73	0.57	0.00	1.29	0.48	0.00	0.99	1.45	0.28	0.44	0.03
	C	0.00	0.95	1.10	0.76	0.00	1.05	0.74	0.51	0.00	1.04	0.86	0.72	0.00	1.24	0.54	0.61	0.00	1.91	-0.46	0.00	0.92
	D	0.06	0.78	0.99	0.93	0.00	0.76	1.04	0.78	0.00	0.82	0.96	0.92	0.00	0.88	0.90	0.67	0.00	1.27	0.43	0.37	0.05
	E	0.01	0.64	0.97	0.90	0.00	0.48	1.27	0.62	0.00	0.73	0.89	0.81	0.00	0.77	0.90	0.40	0.00	1.12	0.54	0.40	0.04
Upper trunk	F	0.08	0.65	1.14	0.88	0.00	0.68	1.08	0.75	0.00	0.74	1.02	0.92	0.00	0.75	1.04	0.68	0.00	1.14	0.58	0.56	0.01
	G	0.01	0.83	0.92	0.81	0.00	0.91	0.78	0.88	0.00	0.84	0.93	0.94	0.00	0.95	0.77	0.89	0.00	1.08	0.63	0.65	0.00
	H	0.00	1.09	0.67	0.75	0.00	1.13	0.58	0.81	0.00	1.09	0.84	0.84	0.00	1.18	0.69	0.66	0.00	1.36	0.41	0.14	0.26
	I	0.00	0.71	0.96	0.90	0.00	0.76	0.90	0.84	0.00	0.72	1.00	0.91	0.00	0.92	0.75	0.79	0.00	1.29	0.36	0.50	0.02
	J	0.00	0.76	0.97	0.88	0.00	0.79	0.90	0.78	0.00	0.82	0.88	0.95	0.00	0.85	0.87	0.82	0.00	1.38	0.27	0.39	0.04
Lower trunk	K	0.01	0.65	0.91	0.92	0.00	0.70	0.85	0.88	0.00	0.60	1.02	0.94	0.00	0.76	0.84	0.92	0.00	0.85	0.76	0.75	0.00
	L	0.10	0.80	0.83	0.90	0.00	0.78	0.89	0.84	0.00	0.81	0.86	0.95	0.00	0.86	0.81	0.84	0.00	1.16	0.49	0.69	0.00
	M	0.05	0.61	0.84	0.88	0.00	0.59	0.89	0.82	0.00	0.59	0.92	0.91	0.00	0.85	0.67	0.75	0.00	0.80	0.73	0.13	0.29
	N	0.03	0.86	0.93	0.83	0.00	0.90	0.81	0.87	0.00	0.82	0.99	0.92	0.00	0.85	0.99	0.61	0.00	1.20	0.53	0.14	0.26
	O	0.50	0.65	0.90	0.96	0.00	0.67	0.86	0.93	0.00	0.61	0.94	0.96	0.00	0.66	0.90	0.88	0.00	0.65	0.91	0.63	0.00
Upper tail	P	0.02	0.54	0.91	0.94	0.00	0.53	0.94	0.85	0.00	0.56	0.93	0.94	0.00	0.75	0.75	0.85	0.00	0.94	0.59	0.66	0.00
	Q	0.03	0.77	1.07	0.87	0.00	0.84	0.85	0.78	0.00	0.83	0.89	0.94	0.00	0.82	0.92	0.66	0.00	2.23	-0.72	0.01	0.72
	R	0.51	0.82	0.95	0.78	0.00	0.84	0.89	0.72	0.00	0.85	0.91	0.87	0.00	0.92	0.83	0.62	0.00	1.15	0.56	0.06	0.48
	S	0.01	1.01	0.89	0.87	0.00	1.03	0.77	0.85	0.00	0.98	0.94	0.92	0.00	1.01	0.97	0.47	0.00	1.32	0.46	0.27	0.10
	T	0.12	0.65	1.01	0.89	0.00	0.73	0.86	0.91	0.00	0.67	0.96	0.95	0.00	0.67	0.98	0.78	0.00	0.77	0.87	0.14	0.26
Lower tail	U	0.36	0.75	0.98	0.88	0.00	0.78	0.90	0.79	0.00	0.78	0.91	0.95	0.00	0.67	1.07	0.75	0.00	0.92	0.78	0.07	0.44
	V	0.01	0.61	0.94	0.93	0.00	0.66	0.89	0.79	0.00	0.54	1.06	0.94	0.00	0.73	0.87	0.71	0.00	1.02	0.58	0.55	0.01
	W	0.02	1.20	0.84	0.83	0.00	1.21	0.73	0.72	0.00	1.23	0.91	0.89	0.00	1.27	0.93	0.58	0.00	1.48	0.38	0.00	0.95
	X	0.13	0.65	0.92	0.90	0.00	0.68	0.91	0.78	0.00	0.61	1.02	0.94	0.00	0.72	0.92	0.55	0.00	1.09	0.53	0.28	0.09
	Y	0.00	0.60	0.93	0.94	0.00	0.66	0.87	0.82	0.00	0.53	1.06	0.95	0.00	0.67	0.92	0.74	0.00	1.03	0.57	0.61	0.00
	Z	0.36	0.62	0.94	0.92	0.00	0.64	0.93	0.82	0.00	0.58	1.01	0.94	0.00	0.67	0.94	0.59	0.00	0.99	0.62	0.23	0.13

*P-value ≤ 0.05 indicates that a given truss dimension did not share a common slope in the course of ontogenetic development

Table 2

Results of the standard major axis test that showed how a given truss dimension scaled against the SL of *G. macrognathos* at a given stage of ontogenetic development. The *a* is the intercept, *b* for slope, R^2 for the strength of the linear relationship between variables at a given stage while the P-value corresponds to the level of significance of the linear relationship. Test for a common slope was also performed to determine how a given truss dimension changed throughout the course of ontogenetic development

Region	Dimension	Common slope	Larva				Juvenile 1				Juvenile 2				Juvenile 3				Adult			
		P-value*	<i>a</i>	<i>b</i>	R^2	P-value	<i>a</i>	<i>b</i>	R^2	P-value	<i>a</i>	<i>b</i>	R^2	P-value	<i>a</i>	<i>b</i>	R^2	P-value	<i>a</i>	<i>b</i>	R^2	P-value
Head	A	0.61	0.70	0.90	0.79	0.00	0.69	0.95	0.87	0.00	0.62	1.06	0.91	0.00	0.56	1.15	0.41	0.00	0.70	0.98	0.79	0.00
	B	0.01	1.01	0.78	0.25	0.00	1.11	0.56	0.19	0.00	1.21	0.50	0.04	0.55	1.35	0.31	0.09	0.24	1.36	0.40	0.31	0.00
	C	0.11	0.97	0.89	0.55	0.00	1.05	0.63	0.76	0.00	1.02	0.72	0.76	0.00	1.12	0.57	0.08	0.26	1.03	0.76	0.68	0.00
	D	0.23	0.88	0.92	0.68	0.00	0.88	1.03	0.71	0.00	1.03	0.70	0.76	0.00	1.02	0.76	0.21	0.06	0.99	0.85	0.67	0.00
	E	0.11	0.68	0.97	0.71	0.00	0.81	0.75	0.73	0.00	0.70	0.96	0.68	0.00	0.88	0.74	0.25	0.04	0.93	0.70	0.69	0.00
Upper trunk	F	0.00	0.69	1.26	0.69	0.00	0.62	1.51	0.65	0.00	0.84	1.08	0.73	0.00	1.07	0.70	0.09	0.21	0.99	0.87	0.63	0.00
	G	0.02	0.82	0.91	0.85	0.00	0.85	0.84	0.87	0.00	0.55	1.39	0.75	0.00	1.01	0.64	0.76	0.00	0.90	0.84	0.82	0.00
	H	0.85	1.12	0.65	0.55	0.00	1.14	0.71	0.55	0.00	1.16	0.74	0.50	0.01	1.24	0.62	0.04	0.43	1.21	0.80	0.13	0.05
	I	0.01	0.86	0.71	0.60	0.00	0.78	0.99	0.83	0.00	0.90	0.79	0.68	0.00	0.99	0.66	0.53	0.00	0.96	0.73	0.69	0.00
	J	0.55	0.87	0.85	0.76	0.00	0.85	0.94	0.73	0.00	0.94	0.78	0.84	0.00	1.01	0.70	0.29	0.02	0.92	0.84	0.78	0.00
Lower trunk	K	0.80	0.71	0.86	0.77	0.00	0.69	0.95	0.85	0.00	0.64	1.02	0.86	0.00	0.76	0.86	0.68	0.00	0.73	0.92	0.69	0.00
	L	0.26	0.77	0.88	0.91	0.00	0.80	0.83	0.89	0.00	0.86	0.73	0.93	0.00	0.95	0.64	0.52	0.00	0.84	0.79	0.81	0.00
	M	0.05	0.57	0.85	0.71	0.00	0.67	0.74	0.88	0.00	0.37	1.10	0.54	0.01	0.86	0.58	0.70	0.00	0.58	0.87	0.74	0.00
	N	0.03	0.94	0.79	0.79	0.00	0.92	0.90	0.86	0.00	1.03	0.69	0.96	0.00	1.10	0.60	0.43	0.00	0.99	0.79	0.63	0.00
	O	0.33	0.66	0.84	0.92	0.00	0.70	0.78	0.97	0.00	0.66	0.85	0.89	0.00	0.85	0.64	0.62	0.00	0.66	0.84	0.85	0.00
Upper tail	P	0.32	0.53	0.94	0.85	0.00	0.57	0.90	0.89	0.00	0.55	0.93	0.86	0.00	0.80	0.67	0.70	0.00	0.60	0.87	0.82	0.00
	Q	0.68	0.72	0.91	0.76	0.00	0.77	0.84	0.92	0.00	0.84	0.75	0.88	0.00	0.86	0.76	0.78	0.00	0.79	0.85	0.76	0.00
	R	0.05	0.81	0.87	0.66	0.00	0.74	1.08	0.72	0.00	0.90	0.80	0.76	0.00	0.99	0.71	0.32	0.02	0.99	0.74	0.50	0.00
	S	0.00	1.09	0.68	0.81	0.00	1.07	1.02	0.78	0.00	1.12	0.88	0.83	0.00	1.19	0.69	0.25	0.03	1.05	1.08	0.27	0.00
	T	0.60	0.68	0.87	0.87	0.00	0.65	0.94	0.92	0.00	0.74	0.83	0.96	0.00	0.71	0.87	0.68	0.00	0.68	0.91	0.84	0.00
Lower tail	U	0.13	0.75	0.96	0.76	0.00	0.72	1.04	0.81	0.00	0.90	0.75	0.81	0.00	0.94	0.72	0.56	0.00	0.85	0.88	0.49	0.00
	V	0.20	0.71	0.91	0.77	0.00	0.57	1.19	0.64	0.00	0.73	0.98	0.64	0.00	0.81	0.87	0.55	0.00	0.73	1.00	0.73	0.00
	W	0.20	1.21	0.69	0.55	0.00	1.27	0.95	0.58	0.00	1.29	0.79	0.75	0.00	1.32	0.85	0.06	0.31	1.37	0.71	0.55	0.00
	X	0.08	0.69	1.00	0.70	0.00	0.64	1.14	0.68	0.00	0.77	0.96	0.61	0.00	0.99	0.67	0.54	0.00	0.64	1.16	0.70	0.00
	Y	0.12	0.69	0.92	0.78	0.00	0.52	1.23	0.69	0.00	0.70	0.99	0.66	0.00	0.75	0.93	0.52	0.00	0.62	1.11	0.73	0.00
	Z	0.13	0.68	0.98	0.76	0.00	0.60	1.14	0.73	0.00	0.72	0.99	0.72	0.00	0.91	0.74	0.62	0.00	0.65	1.10	0.77	0.00

*P-value ≤ 0.05 indicates that a given truss dimension did not share a common slope in the course of ontogenetic development

Table 3

Results of the standard major axis test that showed how a given truss dimension scaled against the SL of *G. uchidai* at a given stage of ontogenetic development. The *a* is the intercept, *b* for slope, R^2 for the strength of the linear relationship between variables at a given stage while the P-value corresponds to the level of significance of the linear relationship. Test for a common slope was also performed to determine how a given truss dimension changed throughout the course of ontogenetic development

Region	Dimension	Common slope	Juvenile 1				Juvenile 2				Juvenile 3				Adult			
		P-value*	<i>a</i>	<i>b</i>	R^2	P-value	<i>a</i>	<i>b</i>	R^2	P-value	<i>a</i>	<i>b</i>	R^2	P-value	<i>a</i>	<i>b</i>	R^2	P-value
Head	A	0.08	0.63	1.08	0.80	0.00	0.61	1.10	0.95	0.00	0.89	0.71	0.11	0.11	0.74	0.95	0.69	0.00
	B	0.00	0.99	0.85	0.21	0.00	1.07	0.70	0.50	0.00	1.43	-0.16	0.00	0.87	1.31	0.27	0.07	0.10
	C	0.00	1.00	0.84	0.40	0.00	1.02	0.75	0.94	0.00	1.17	0.47	0.01	0.68	1.16	0.52	0.36	0.00
	D	0.00	0.84	1.14	0.76	0.00	0.94	0.83	0.89	0.00	1.17	0.41	0.12	0.10	1.06	0.68	0.42	0.00
	E	0.00	0.59	1.17	0.69	0.00	0.79	0.79	0.86	0.00	1.13	0.34	0.00	0.90	0.99	0.57	0.36	0.00
Upper trunk	F	0.00	0.63	1.50	0.67	0.00	0.67	1.41	0.85	0.00	1.12	0.52	0.22	0.02	1.04	0.73	0.21	0.00
	G	0.00	0.88	0.75	0.80	0.00	0.78	0.99	0.94	0.00	1.08	0.49	0.36	0.00	0.96	0.70	0.57	0.00
	H	0.00	1.12	0.63	0.55	0.00	1.08	1.14	0.65	0.00	1.28	0.40	0.09	0.15	1.32	0.33	0.06	0.12
	I	0.01	0.78	0.93	0.61	0.00	0.84	0.86	0.95	0.00	1.05	0.52	0.42	0.00	0.90	0.75	0.66	0.00
	J	0.00	0.82	1.01	0.75	0.00	0.91	0.79	0.92	0.00	1.12	0.45	0.23	0.02	0.97	0.73	0.51	0.00
Lower trunk	K	0.00	0.68	0.93	0.83	0.00	0.63	1.03	0.94	0.00	0.96	0.57	0.36	0.00	0.91	0.67	0.46	0.00
	L	0.02	0.78	0.80	0.82	0.00	0.80	0.78	0.97	0.00	1.00	0.51	0.63	0.00	0.79	0.79	0.65	0.00
	M	0.00	0.56	0.88	0.86	0.00	0.51	0.96	0.94	0.00	1.01	0.40	0.41	0.00	0.86	0.57	0.60	0.00
	N	0.00	0.92	0.93	0.67	0.00	0.94	0.94	0.92	0.00	1.15	0.49	0.49	0.00	1.07	0.66	0.62	0.00
	O	0.00	0.62	0.93	0.92	0.00	0.67	0.85	0.98	0.00	0.98	0.48	0.60	0.00	0.79	0.70	0.70	0.00
Upper tail	P	0.00	0.55	0.89	0.83	0.00	0.55	0.91	0.97	0.00	0.86	0.57	0.67	0.00	0.68	0.76	0.79	0.00
	Q	0.00	0.74	0.93	0.68	0.00	0.77	0.89	0.93	0.00	1.08	0.44	0.18	0.04	0.95	0.66	0.42	0.00
	R	0.00	0.78	0.94	0.68	0.00	0.71	1.13	0.90	0.00	1.08	0.51	0.10	0.13	0.96	0.75	0.21	0.00
	S	0.00	1.08	0.83	0.73	0.00	1.08	0.99	0.87	0.00	1.23	0.49	0.19	0.03	1.22	0.59	0.36	0.00
	T	0.01	0.60	1.07	0.75	0.00	0.66	0.98	0.96	0.00	0.96	0.57	0.25	0.01	0.80	0.79	0.56	0.00
Lower tail	U	0.00	0.78	0.86	0.78	0.00	0.72	1.03	0.93	0.00	1.10	0.43	0.15	0.06	0.95	0.71	0.33	0.00
	V	0.00	0.71	0.87	0.76	0.00	0.56	1.20	0.90	0.00	0.98	0.58	0.17	0.05	0.94	0.67	0.51	0.00
	W	0.00	1.25	0.93	0.70	0.00	1.27	1.16	0.83	0.00	1.34	0.46	0.26	0.01	1.33	0.77	0.17	0.01
	X	0.00	0.75	0.82	0.78	0.00	0.60	1.17	0.94	0.00	0.95	0.65	0.38	0.00	0.98	0.64	0.53	0.00
	Y	0.00	0.68	0.91	0.78	0.00	0.54	1.20	0.91	0.00	0.92	0.65	0.35	0.00	0.90	0.70	0.54	0.00
	Z	0.00	0.74	0.82	0.80	0.00	0.58	1.16	0.95	0.00	0.83	0.80	0.39	0.00	0.91	0.70	0.59	0.00

*P-value ≤ 0.05 indicates that a given truss dimension did not share a common slope in the course of ontogenetic development

Result of the canonical variate analysis indicated a difference in shape between the larva and adult of *G. macrognathos* (Figure 9). The larva and J1 shared similar morphology. However, J2 considerably deviated from the larval shape and somewhat more similar to J3 and adult, which further suggest that the transition stages in attaining the final adult shape were relatively shorter in *G. macrognathos* than for *G. breunigii*. Deformation grid and a histogram for the discriminant function analysis comparing the change in shape between the larva and the later stages of ontogenetic development was presented in figure 13 as well as a series of images corresponding to the different stages of development was shown in figure 14 for *G. macrognathos*. Morphological deformations were evident from the cephalic to caudal region but most importantly in the former as compared to the latter and were already prominent at J2. The head exhibited similar deformation pattern with that of *G. breunigii* including the landmarks involved in the process. However, the region at the junction between the angular and quadrate bones (12) moved deeper starting at J2. The head landmarks showed a counterclockwise displacement but with no apparent deformation in the region of the cleithral symphysis (11). Nevertheless, the result was more or less the same by reducing the angle at the ventral surface of the mouth making it closer to the substrate. Deformation in the caudal region particularly at the base of the last ray of the second dorsal fin (5), the base of the last ray of the anal fin (8) and the base of the first spine of the anal fin (9) were caudally directed and were evident at J3. Ventral displacement of the anterior part of the hypural 3+4 (6) and the posterior part of the hypural 1+2 (7) was also evident at J3 but was more prominent in *G. macrognathos* than in *G. breunigii*. Deformation between the base of the first spine of the first dorsal fin (3), the base of the first spine of the second dorsal fin (4) was divergent being anteriorly inclined for the former and caudally inclined for the latter (Figure 13 & 14). Change in shape of the cephalic region was likely attributed to positive allometry on the dorsal aspect of the head (dimension A) from J2 to J3 coupled with negative allometry on the mouth region (dimension C) that started from J1 and a consistent negative allometric growth at the region between the junction between the angular and quadrate bones and the cleithral symphysis (dimension B) from larva to adult (Table 2). Interestingly, positive allometry was prevalent between the supraoccipital (2) and at the junction between the angular and quadrate bones (12) (dimension F) from larva to J2 that resulted to a much narrower head. This process was compromised by negative allometric growth at J3 but the dorsal aspect of the head (dimension A) continues to exhibit positive allometry. Deformation at the anterior trunk region resulted to a tumescent appearance on the dorsal region that was likely due to positive allometry around the region between the supraoccipital (2) and the base of the first spine of the first dorsal fin (3) (dimension G), an isometric growth between at the region of the pelvic fin (10) and the base of the first spine of the first dorsal fin (3) (dimension I) as well as between the cleithral symphysis (11) and the base of the first spine of the first dorsal fin (3) (dimension K) at J2. In addition, positive allometry was also observed at the ventral abdominal region (dimension M) at J2, which likely resulted to the shape deformation at the base of the first spine of the anal fin (9). Deformation at the caudal region was prevalent at J1 and secondarily during the adult. Positive allometry was evident at J1 particularly between the base of the first spine of the anal fin (9) and the base of the last ray of the anal fin (8) (dimension R), between the base of the last ray of the anal fin (8) and the posterior part of the hypural 1+2 (7) (dimension X) and between the last ray of the second dorsal fin (5) and the anterior part of the hypural 3+4 (6) (dimension V). Positive allometry during the adult was observed between the base of last ray of the second dorsal fin (5) and the posterior part of the hypural 1+2 (7) (dimension Y), between the base of the last ray of the anal fin (8) and the anterior part of the hypural 3+4 (6) (dimension Z) including dimension X. Eight out of the 26 truss dimensions shared no common slope ($P\text{-value} \leq 0.05$) indicating that isometric growth was a peculiar characteristic in almost all truss dimensions on the lateral axis of *G. macrognathos* throughout the course of ontogenetic development. Except on the dorsal aspect of the head, negative allometry in all truss dimensions was prominent at J3 when compared with the other stages of ontogenetic development.

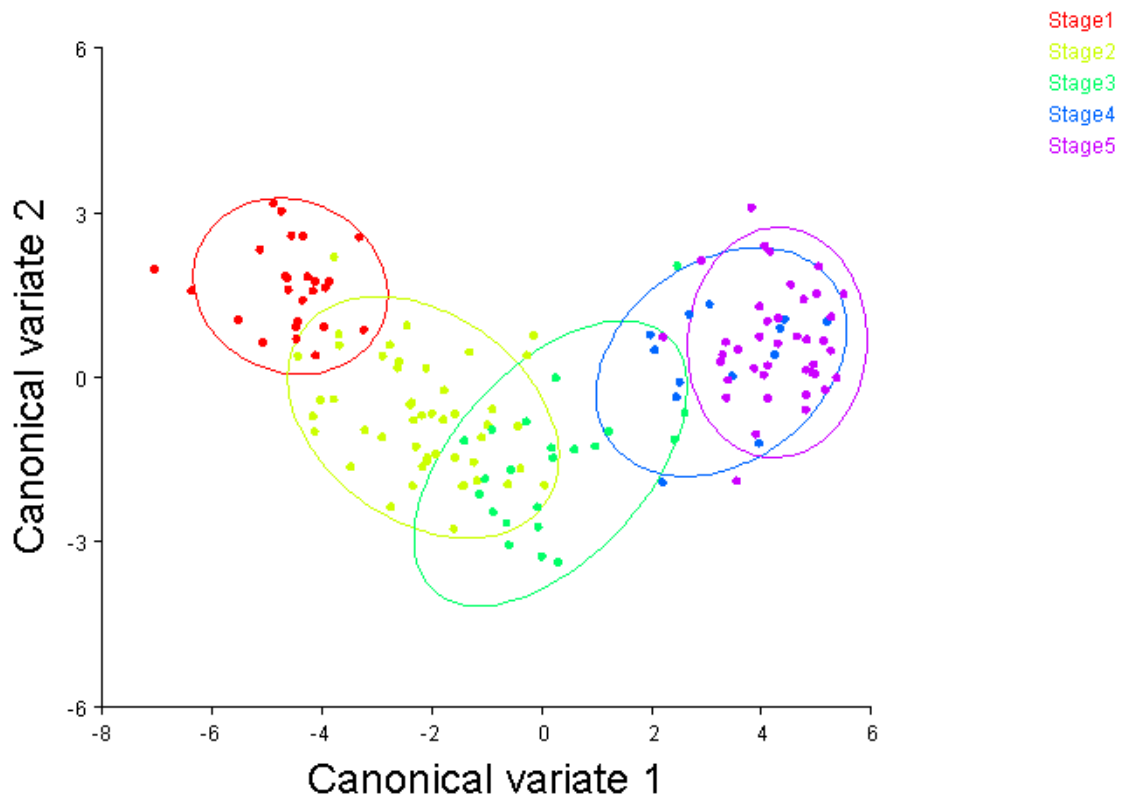


Figure 9. Canonical variate analysis for the larva (Stage1), J1 (Stage 2), J2 (Stage 3), J3 (Stage 4) and adult (Stage 5) stage of *G. macrognathos*. The equal frequency ellipse contains 90% of randomly drawn data points for a given stage of ontogenetic development. CVA 1 explains 87.49% of the variance while CVA 2 explains 8.96% of the variance.

Similar to the previous gobies, the morphology of *G. uchidai* at J1 was different from the adult (Figure 10). However, unlike *G. macrognathos*, J2 shared similar shape with J1 indicating that the transition stages in achieving the final adult shape was relatively longer for this species as compared to *G. macrognathos* and that *G. uchidai* was more similar to *G. breunigii* in terms of pattern in shape development. The J3 closely resembled the adult. Deformation grid and a histogram for the discriminant function analysis comparing the change in shape between J1 and the later stages of ontogenetic development was presented in figure 15 as well as a series of images corresponding to the different stages of development was shown in figure 16 for *G. uchidai*. Deformations in almost all landmarks were evident from the cephalic to caudal region at J3. The head had similar deformation pattern with the previous two species with the same landmarks moving in almost similar direction assuming a counterclockwise displacement without any apparent change in the region of the cleithral symphysis thereby resulting to a reduced angle on the ventral surface of the mouth bringing it closer to the substrate. In the trunk region, deformation between the base of the first spine of the first dorsal fin (3), the base of the first spine of the second dorsal fin (4) was divergent with the former being anteriorly inclined while the latter being caudally inclined. Deformation in the caudal region particularly at the base of the last ray of the second dorsal fin (5) was caudally directed. Ventral displacement of the anterior part of the hypural 3+4 (6) and the posterior part of the hypural 1+2 (7) was also evident. On the contrary, the region at base of the last ray of the anal fin (8) did not exhibit any form of deformation. A conspicuous dorsal displacement at the region around the base of the first spine of the anal fin (9) was also noticeable. Deformation at the cephalic region was likely attributed to the positive allometry on the dorsal aspect of the head (dimension A) at J1 and J2

coupled with negative allometry on the ventral surface of the mouth (dimension C) and at the region between the junction between the angular and quadrate bones and the cleithral symphysis (dimension B) throughout the ontogenetic development (Table 3). Positive allometry was evident at J1 between the proximal end of the premaxilla (1) and the region of the pelvic fin (10) (dimension E) and between the supraoccipital (2) and the region of the pelvic fin (10) (dimension D). Similar to *G. macrognathos*, positive allometry was prevalent between the supraoccipital (2) and at the junction between the angular and quadrate bones (12) (dimension F) from larva to J2 but this process slowed down at J3 stage when it underwent negative allometry. Such change in shape resulted to a narrower head. Deformation at the anterior trunk region was likely attributed to isometric growth between the supraoccipital (2) and the base of the first spine of the first dorsal fin (3) (dimension G) and positive allometry between the cleithral symphysis (11) and the base of the first spine of the first dorsal fin (3) (dimension K) at J2. Positive allometry was evident between the base of the first spine of the second dorsal fin (4) and the base of the last ray of the anal fin (8) (dimension T) at J1 that remained isometric at J2. These growth patterns were likely responsible for the tumescent appearance on the dorsal region of the trunk. Caudal deformation was evident at J2 by positive allometry between the region of the pelvic fin (10) and at the base of the first spine of the anal fin (9) (dimension R), between the base of the first spine of the anal fin (9) and the posterior part of the hypural 1+2 (7) (dimension X), between the posterior part of the hypural 1+2 (7) and the anterior part of the hypural 3+4 (6) (dimension W), between the last ray of the second dorsal fin (5) and the anterior part of the hypural 3+4 (6) (dimension V), between the last ray of the second dorsal fin (5) and the posterior part of the hypural 1+2 (7) (dimension Y) and between the base of the last ray of the anal fin (8) and the anterior part of the hypural 3+4 (6) (dimension Z). Twenty-five out of the 26 truss dimensions on the lateral axis of *G. uchidai* shared no common slope ($P\text{-value} \leq 0.05$) suggesting the prevalence of allometric growth pattern during ontogeny. Negative allometry in all truss dimensions was also evident at J3.

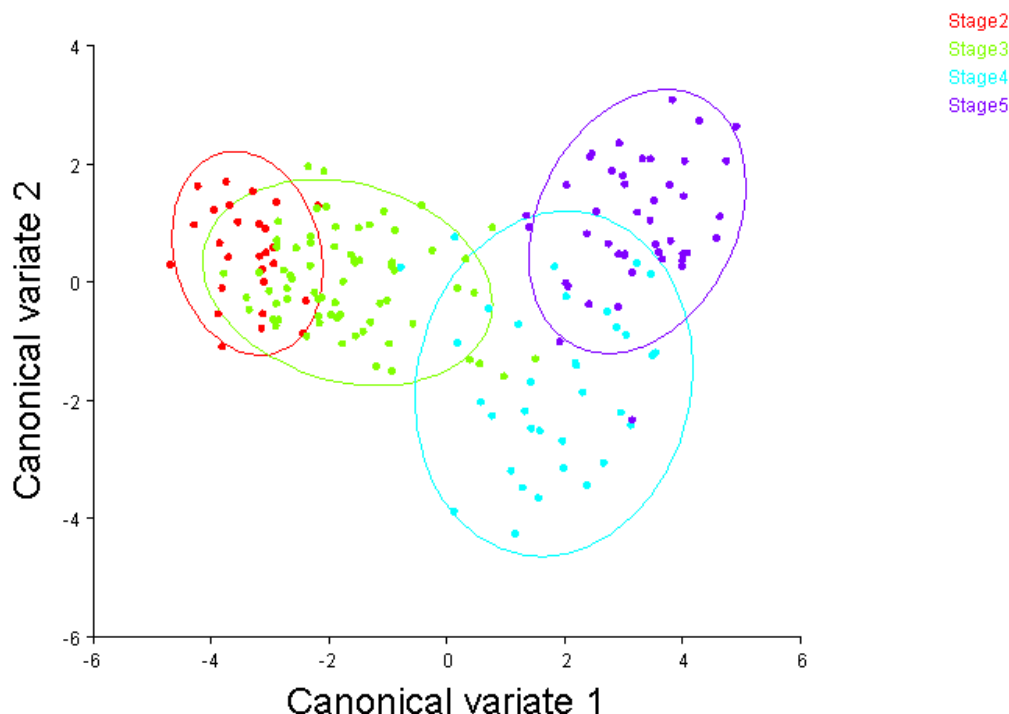


Figure 10. Canonical variate analysis for the J1 (Stage 2), J2 (Stage 3), J3 (Stage 4) and adult (Stage 5) stage of *G. uchidai*. The equal frequency ellipse contains 90% of randomly drawn data points for a given stage of ontogenetic development. CVA 1 explains 80.87% of the variance while CVA 2 explains 11.49% of the variance.

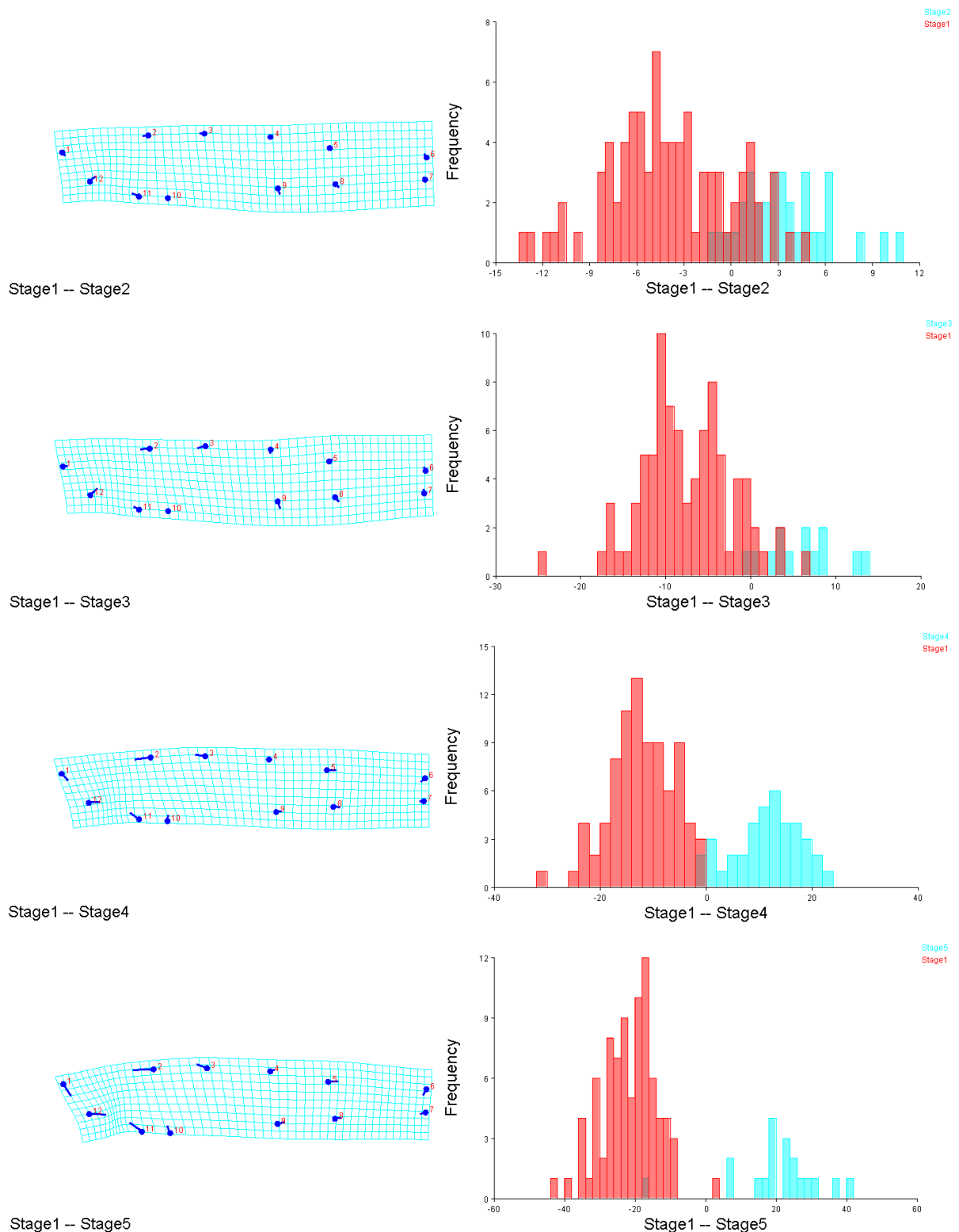


Figure 11. Deformation grid comparing the change in shape between the larva (Stage 1) and the rest of the stages of ontogenetic development (e.g., Stage 2 = J1, Stage 3 = J2, Stage 4 = J3 and Stage 5 = adult) of *G. breunigii* (left) with corresponding histogram for the result of the discriminant function analysis between two stages assessed by leave-one-out cross-validation method with 9,999 permutation runs (right).

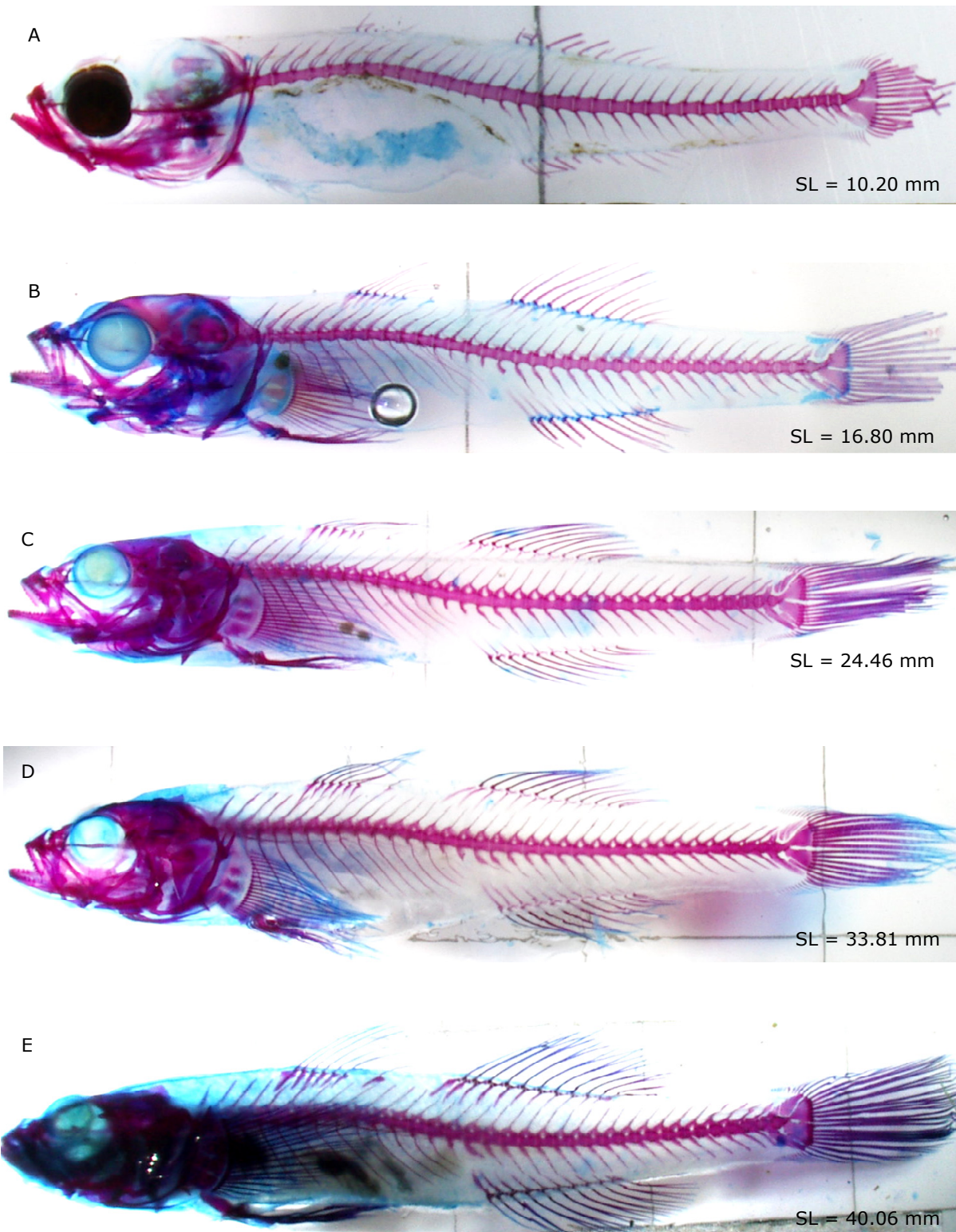


Figure 12. Cleared and stained specimens of the larva (A), J1 (B), J2 (C), J3 (D) and adult (E) *G. breunigii* from Obitsu-gawa River Estuary of inner Tokyo Bay, central Japan.

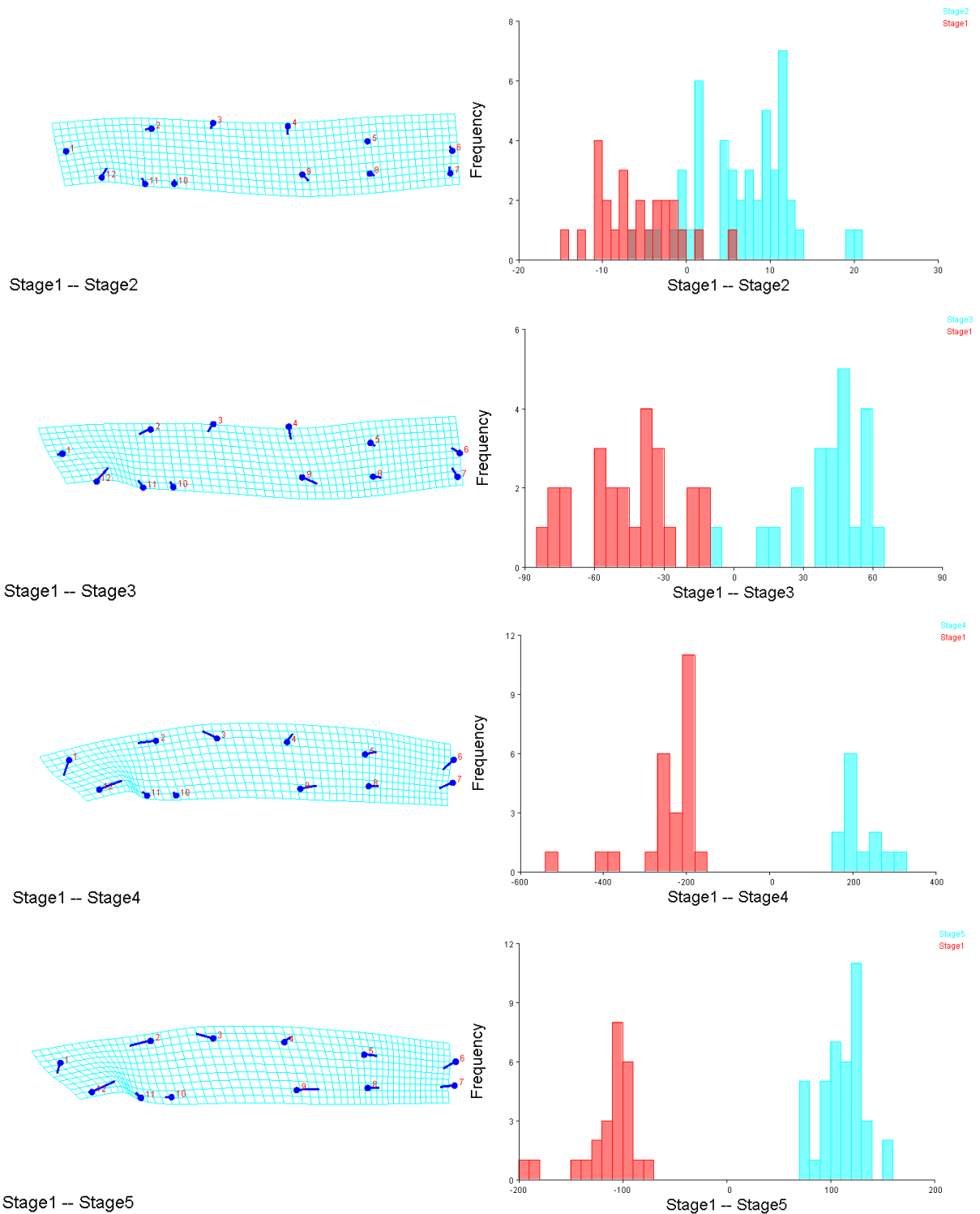


Figure 13. Deformation grid comparing the change in shape between the larva (Stage 1) and the rest of the stages of ontogenetic development (e.g., Stage 2 = J1, Stage 3 = J2, Stage 4 = J3 and Stage 5 = adult) of *G. macrognathos* (left) with corresponding histogram for the result of the discriminant function analysis between two stages assessed by leave-one-out cross-validation method with 9,999 permutation runs (right).

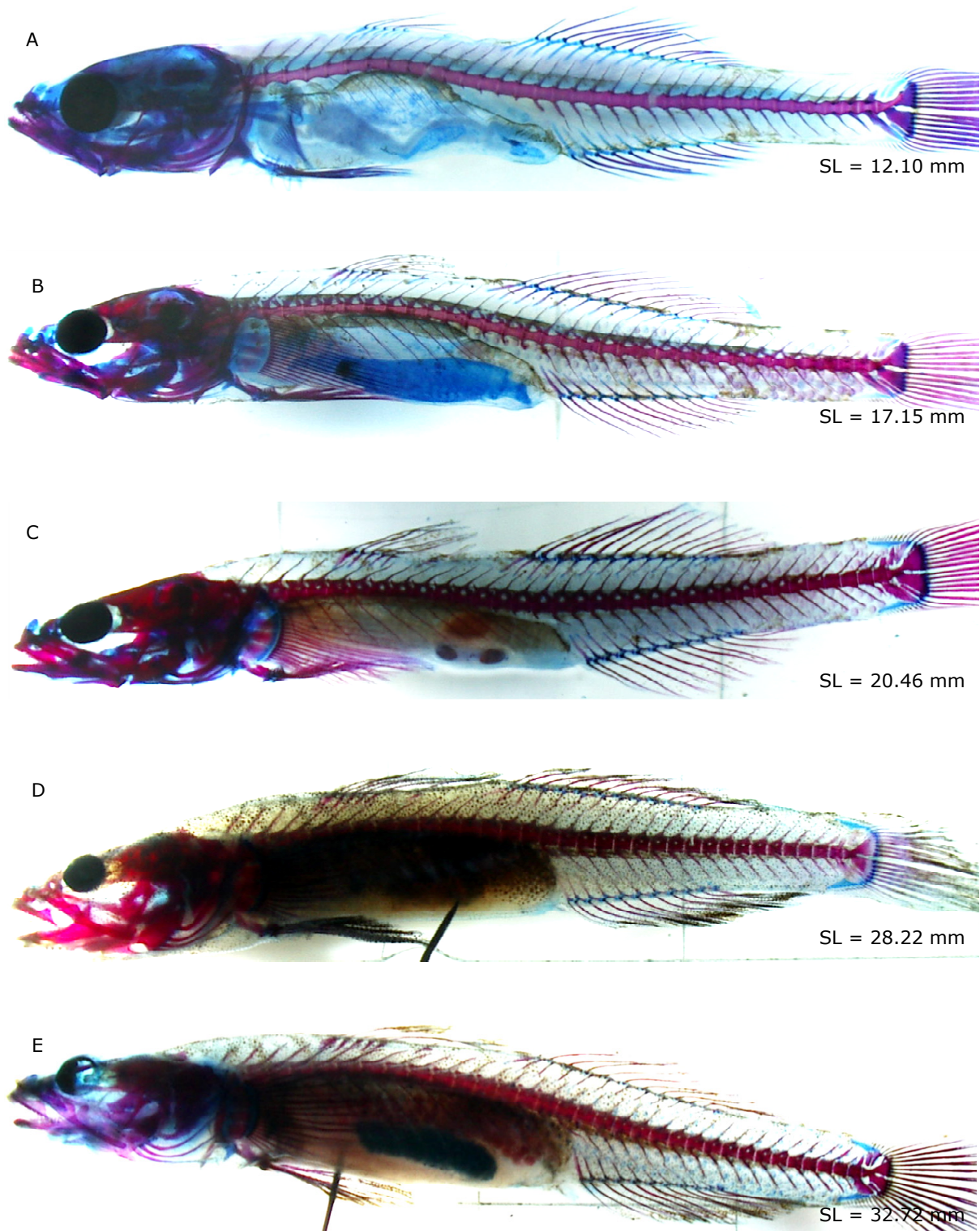


Figure 14. Cleared and stained specimens of the larvae (A), J1 (B), J2 (C), J3 (D) and adult (E) *G. macrognathos* from Obitsu-gawa River Estuary of inner Tokyo Bay, central Japan.

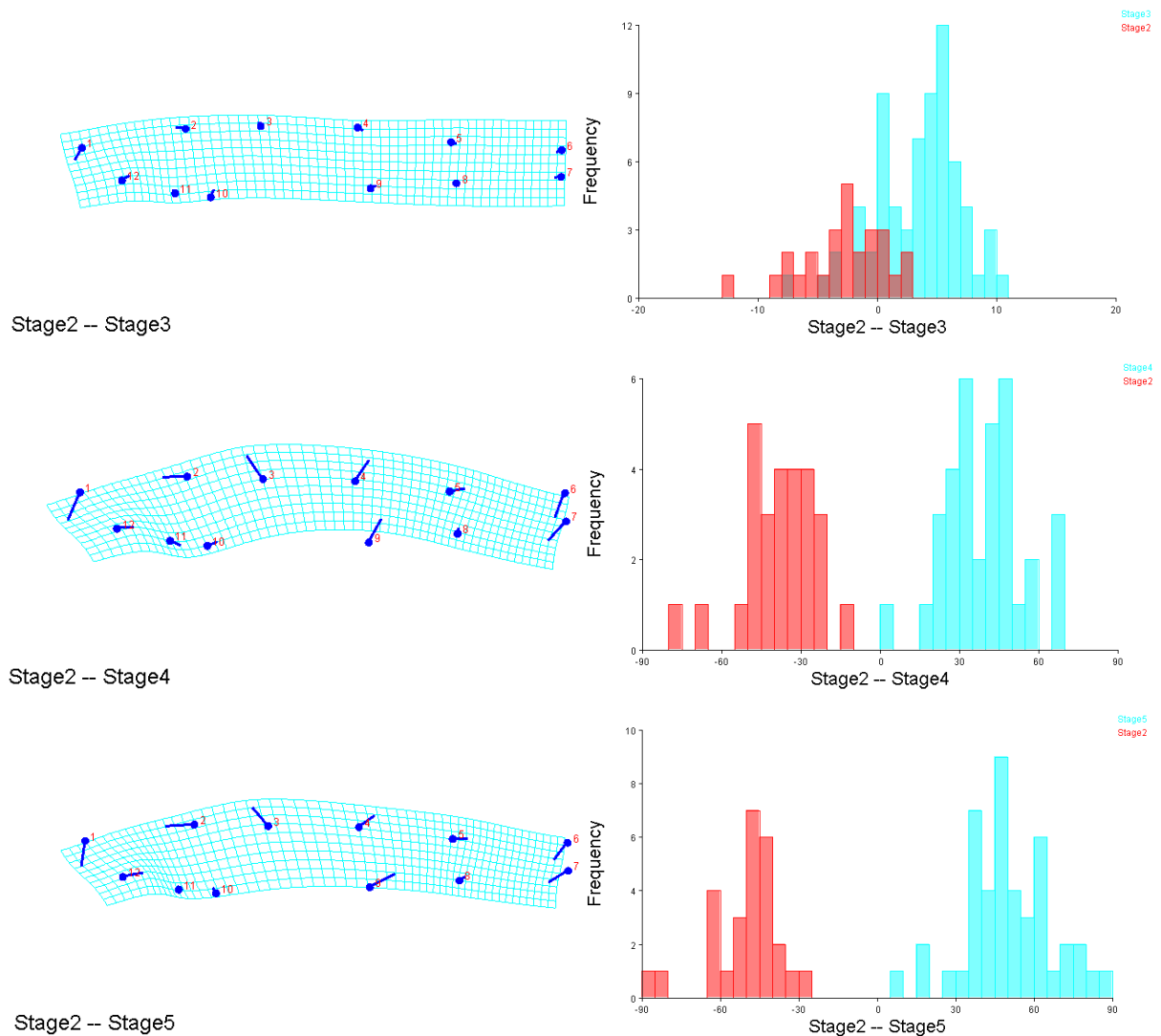


Figure 15. Deformation grid comparing the change in shape between the Juvenile 1 (Stage 2) and the rest of the stages of ontogenetic development (e.g., Stage 3 = J2, Stage 4 = J3 and Stage 5 = adult) of *G. uchidai* (left) with corresponding histogram for the result of the discriminant function analysis between two stages assessed by leave-one-out cross-validation method with 9,999 permutation runs (right).

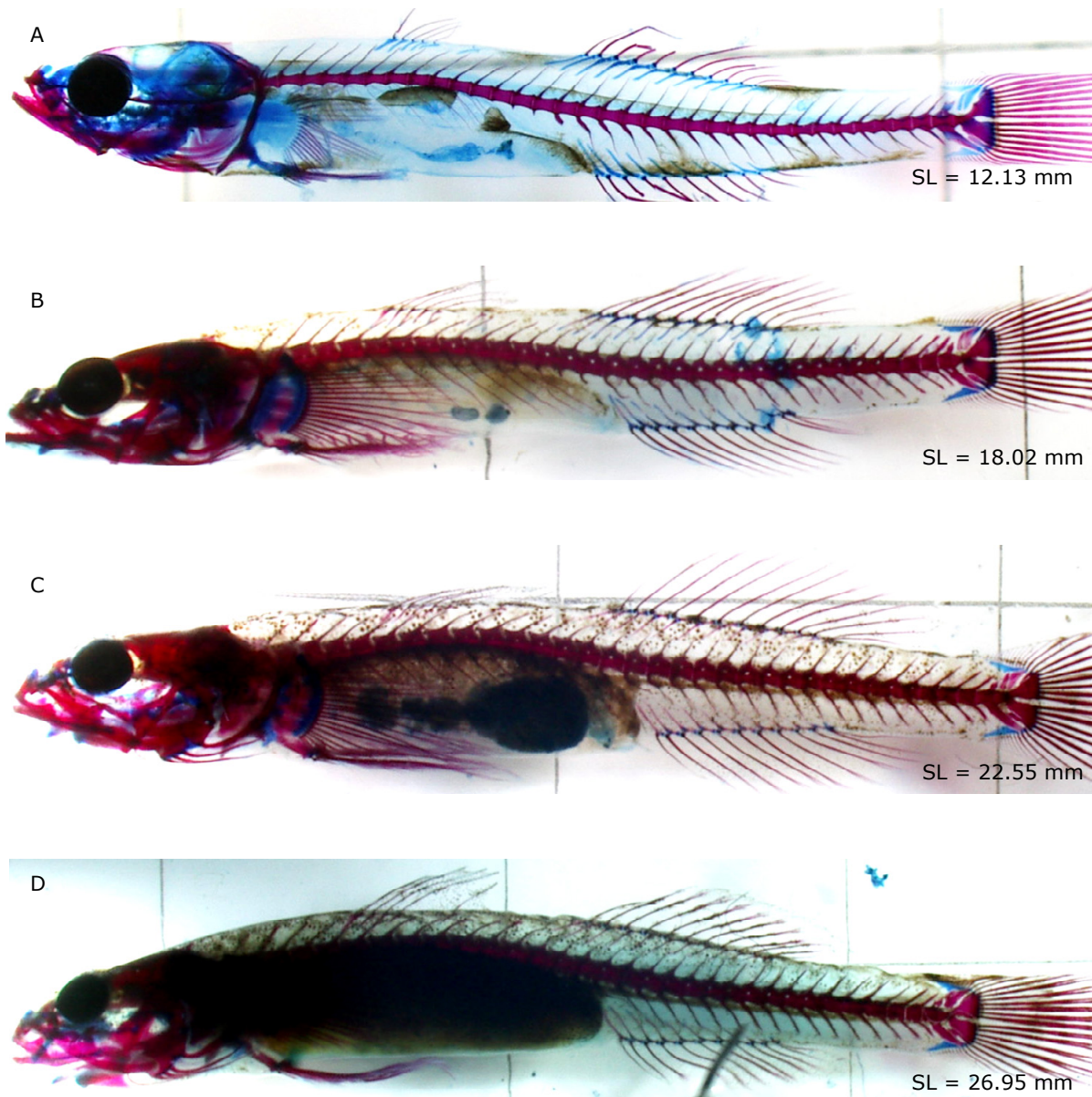


Figure 16. Cleared specimens of the J1 (A), J2 (B), J3 (C) and adult (D) *G. uchidai* from Obitsu-gawa River Estuary of inner Tokyo Bay, central Japan.

The utilization and exploitation of available resources most often rely on the competence of each stage of ontogenetic development that would later influence growth and recruitment (Garner 1996) and in the case of *G. breunigii*, *G. macrognathos* and *G. uchidai* of Obitsu-gawa River Estuary, they showed certain preference for a particular habitat at a given ontogenetic stage and habitat shift corresponded with change in body shape that was a reflection of the level of competence of these gobies. Gobies have a pelagic larval life of at least a month (Fonds 1970; Fonds & Van Buurt 1974). Generally, the larvae and J1 shared similar habitat, situated in the lower estuary most likely because of the preference for planktonic copepods (Kanou et al 2004). Other than growth, almost no apparent change in shape was observed between the larva and early J1 and both had a more or less streamlined body in which according to Webb (1984) was suitable for periodic thrusts in the water column. A streamlined body shape and a rounded head are typical of fishes that swim and feed in the water column (Winemiller 1991; Loy et al 1998, 2001). These gobies were prevalent in the shallow waters of the tidal creek at J2. Although the streamlined body was still inherent, deformation on the cephalic region had

commenced and was evident for *G. macrognathos*. Deformation on the cephalic region was characterized by the narrowing of the head and reduction in the angle of the mouth on the ventral surface bringing the mouth closer to the substrate indicating an adaptation to benthic lifestyle. It was likely that *G. macrognathos* already had the advantage in terms of exploiting the tidal creek resources at an early stage, which explained the occurrence of the late J1 and J2 in specialized habitat such as the soft sediment pools. Kanou et al (2004) observed that the importance of calanoid and cyclopoid copepods in the diet of *G. macrognathos* in Tama-gawa River Estuary significantly decreased with larger individuals (22–42 mm SL) and fed mainly on benthic or epiphytic crustaceans, including gammaridean amphipods, harpacticoid copepods and mysids. It was likely that the main priority of these gobies during the early juvenile stage was to attain the morphological features that are needed for benthic feeding in order to effectively utilize the prey resources of the estuary particularly in months when secondary productivity in the bay is prevalent. Change in shape progressed from J2 to J3 that resulted to a close resemblance between juvenile and adult. Evident at J3 was the deformation at the anterior trunk region that resulted to a tumescent appearance on the dorsal region of the trunk as well as the relatively elongated and the ventrally displaced tail. The broad profile of the trunk are shape features that allow for quick starts and rapid turns in complex environments (Loy et al 2001). Good fast-start performance is an important aspect in the normal behaviour in fish necessary to attain high speeds in traversing areas of high water flow, avoiding obstacles and determines the success of predator strikes and the success of prey escape (Webb 1978). It was proposed that having a broader trunk and a relatively elongated, ventrally displaced tail coupled with a well-developed median fins significantly improved the fast-start performance at J3 that equates to the competence of fish at this stage allowing the exploitation of “high-risked”, more exposed habitat such as the middle estuary including a highly specialized habitat like the soft sediment pools. In the case of *G. breunigii*, the J3 corresponded to the stage of movement to preferred adult habitats upstream of the river. Changes during the adult stage was primarily associated with the elaboration of the morphological form inherent at J3.

Conclusions. The large influx of larva and early J1 gobies in May in the lower estuary was likely attributed to increase primary productivity in inner Tokyo Bay that was usually followed by high secondary production of estuaries particularly the zooplankton, which is the main prey item of gobies during the pelagic phase. The larva and J1 possessed a more or less streamlined body and a round head, which are adaptations for pelagic swimming and feeding. The occurrence of late J1 and J2 in the shallow tidal creek can be attributed to preference for benthic prey items and although a streamlined body was still inherent, deformation on the cephalic region had already commenced. Deformation was characterized by the narrowing of the head and reduction in the angle of the mouth on the ventral surface bringing the mouth closer to the substrate. It was proposed that the attainment of these characteristics at an early stage had a greater advantage in exploiting the benthic resources of the tidal creek like in the case of *G. macrognathos*. As for *G. breunigii* and *G. uchidaii*, the occurrence in the tidal creek despite the prevalence of the larval shape at J2 cannot be exclusively attributed to feeding alone but could be accredited to the role of the tidal creek habitat as refuge from predators. With their small size and adaptability to very shallow waters, these gobies had the advantage of reduced risk of predation while extending their foraging period in the tidal creek. Moreover, the prevalence of high temperature waters from May to October can promote temperature-mediated growth that could hasten the processes associated with positive allometry inherent at J1 and J2 that are necessary in order to attain the necessary features for benthic life. Generally, the ideal adult shape was attained at J3 with deformation at the anterior trunk region that resulted to a tumescent appearance on the dorsal region of the trunk as well as the elongation and the ventrally displaced caudal region that would likely increase the fast-start performance of these gobies needed in attaining high speeds in traversing areas of high water flow, avoiding obstacles and determines the success of predator strikes and the success of prey escape. This would explain why the gobies

became more competent when they reached J3 exploring “high-risked” habitat such as the middle estuary and highly specialized habitat such as the soft sediment pools. This was further elaborated by *G. breunigii* whose J3 corresponded with upstream movement to preferred adult habitats. Changes during the adult stage was primarily associated with the elaboration of the morphological form inherent at J3. Moreover, the current study had shown that the estuarine habitats associated with the lower region of Obitsu-gawa River are important for gobies during the transition from pelagic to benthic life. Whenever shallow, sheltered waters such as the tidal creek and soft sediment pools are present in the estuary, such habitat most likely attracts gobies in their juvenile stages for the purpose of foraging, refuge as well as for growth enhancement and metamorphosis particularly if the larval dispersal of gobies is timed in periods wherein the estuary consistently experience warm water temperatures. Such strategy would likely increase survival and recruitment of gobies into the estuary.

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