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Spatial variations in tidepool fish assemblages related to environmental variables in the Tama River estuary, Japan

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Abstract: Spatial variations in fish assemblages in soft-substrata estuarine tidepools (n = 55, 0.6–6.4 m^2) were investigated on tidal flats 0–4 km from the mouth of the Tama River estuary, central Honshu, Japan in early June 2003. A total of 1,838 individuals, representing 2 families and 11 species, were collected during the study period. All fishes collected were less than 50 mm SL, being mostly gobiid juveniles and adults. *Acanthogobius flavimanus* was the most abundant species, comprising 52.2% of the total individual number, followed by *Pseudogobius masago* (24.6%), *Gymnogobius macrognathos* (12.7%), *G. breunigii* (7.0%), *Mugil cephalus cephalus* (1.0%), *Favonigobius gymnauchen* (0.9%), *Mugilogobius abei* (0.7%) and *Eutaeniichthys gilli* (0.5%). Of these, six benthic gobies except for *G. breunigii* and *M. cephalus cephalus* occurred at different densities in the lower, middle and upper estuarine areas. The canonical correspondence analysis using densities of abundant species in each tidepool revealed that spatial variations in the fish assemblage structures were largely associated with environmental variables, including mud shrimp-burrow density, median grain size, salinity, height above low tide level, water temperature, pool size and water depth.

Keywords : *fish assemblage, Tama River, estuarine tidepools, environmental variables*

1. Introduction

Estuarine tidal flats in temperate regions play important roles as nurseries and foraging grounds for many fishes, including target species of local fisheries (KANOU *et al*., 2000; MORRISON *et al*., 2002; HAMPEL *et al*., 2003; KANOU *et al*., 2004b), as well as providing essential habitat for various species, including threatened gobies (OKAZAKI *et al*., 2012; INUI and KOYAMA, 2014; KOYAMA *et al*., 2016; INUI *et al*., 2018). Movements of coastal and estuarine fishes between subtidal and intertidal zones in response to daily tidal rhythms have been investigated in several coastal habitats (e.g., tidal flat, salt marsh and sandy beach), such movements with rising tides being directly associated with benefits such as foraging of intertidal prey items and/or avoidance of potential predators (GIBSON *et al*., 1996; HAMPEL *et al*., 2003; MORRISON *et al*., 2002; KANOU *et al*., 2005a, 2005b).

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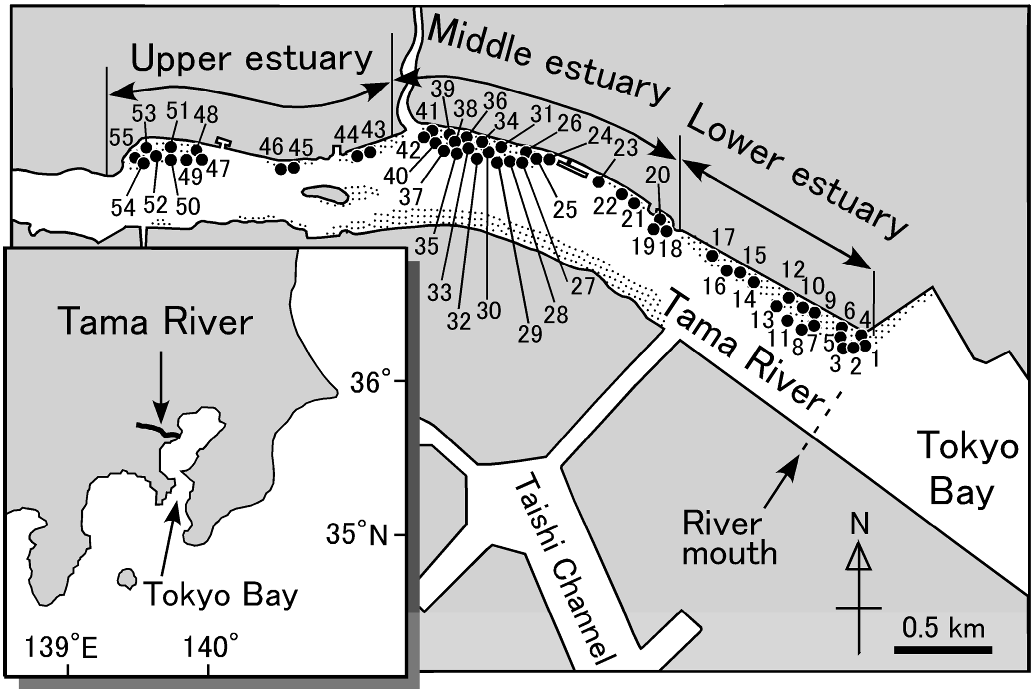

Fig. 1 Map showing the sampling sites (solid circles) in the Tama River estuary, central Japan. Dotted areas indicate tidal flats.

On the other hand, as extensive tidal flat areas are exposed with ebbing tides, most fishes move to the subtidal zone (MORRISON *et al*., 2002; KANOU *et al*. 2005a), although some species stay in invertebrate burrows, tidepools and small creeks in the intertidal zone (MEAGER *et al*., 2005; UCHIDA *et al*., 2008; OKAZAKI *et al*., 2012; HERMOSILLA *et al*., 2012; INUI and KOYAMA, 2014). Recent studies have demonstrated that the occurrence patterns of fish species remaining in the intertidal zone on tidal flats during low tide were partly related to a variety of environmental factors, such as water temperature, salinity, pool size, pool depth, elevation and sediment particle size, and the availability of invertebrate burrows and cobbles (GIBSON *et al*., 2002; MEAGER *et al*., 2005; UCHIDA *et al*., 2008; KRÜCK *et al*., 2009; OKAZAKI *et al*., 2012; KUNISHIMA *et al*., 2014; KOYAMA *et al*., 2016; INUI *et al*., 2018). However, very little information is available on the spatial variation of fish assemblages in relation to environmental gradients in soft-substrata tidepools on estuarine tidal flats (MEAGER *et al*., 2005).

The objectives of the present study were to describe fish assemblage structures in soft-substrata tidepools on selected tidal flats throughout the Tama River estuary, central Japan, and to identify relationships between spatial variations of fish assemblages and environmental variables.

2. Materials and methods

Study site

The study was conducted in the Tama River estuary (35° 32′N, 139° 46′E), located in western Tokyo Bay, central Japan (Fig. 1) and characterized by a relatively well conserved, typical estuarine shoreline, despite the history of significant landfill in the bay. The estuary is subject to semidiurnal tides (tidal range up to ca. 2 m) and has long narrow tidal flats (0.95 km^2) along the shoreline. Fish survey areas were established at the lower (0–1 km from the river mouth), middle (1–2.5 km) and upper-parts (2.5–4.0 km) of the estuary (hereafter referred to as lower, middle and upper estuary, respectively). The intertidal zones of the survey areas were about 55–105 m wide during spring tide. The high-tide zones (> 50 cm above the low water level at ordinary spring tide) of the tidal flats had numerous tidepools (about 50–350 pools ha^{-1}), being naturally occurring depressions due to tidal currents or the result of burrowing activity by large crustaceans (e.g., mud shrimp *Upogebia major*), foraging behavior of elasmobranch rays or human disturbance (including activities such as bait collection and clam gathering). Numerous cobbles (10–25 cm in diameter) were found in tidepools in the middle estuary and burrow entrances of the mud shrimp in the lower estuary. Rooted macrophyte vegetation was absent in the survey areas.

Fish sampling

Because greater species richness and abundance of tidepool fishes in early summer had been previously recorded on tidal flats in the Tama River estuary and adjacent waters (Kanou, 2003; Uchida *et al.*, 2008), sampling was conducted on four consecutive days during spring tide in early June 2003. A total of 55 tidepools (0.6–6.4 m^2) were randomly selected on tidal flats in the lower (n = 17), middle (n = 25) and upper (n = 13) estuaries. In each tidepool, all visible fish were caught by dip net (15 cm wide × 12 cm deep, mesh size 1 mm) at low tide in daytime; the net was then used to sweep the entire area of the pool until no more fish were taken in three consecutive sweeps, as subsequently described by Okazaki *et al.* (2012). All samples were fixed in 10% formalin in the field.

Fishes were identified to species [see also Nakabo (2013) and Okiyama (2014)], and categorized as juvenile or adult following examination of gonads or observation of body coloration and genital papilla morphology. Juvenile gobiid developmental stages followed Kanou *et al.* (2004a). The standard length (SL) of each specimen was measured to the nearest 0.1 mm with digital calipers.

Environmental variables

Immediately after fish sampling, water temperature in each pool was measured with a standard mercury thermometer and salinity with a salinity refractometer (S/Mill-E, Atago, Tokyo, Japan). The surface area of each pool (defined as pool size) was measured to the nearest 0.1 m^2 with folding scales. Mean water depth in each pool at low tide was estimated from five random depth measurements. The height of each pool above low tide level was determined each day by measuring the water depth on a pole placed vertically on the low tide line, when the subsequent incoming tide reached each pool. A sediment sample (7.5 cm diameter and 3 cm depth) was collected with a cylindrical core sampler from the point of maximum depth in each pool. Dry sediment samples, except for organic material, were sieved through seven mesh trays (1000, 500, 250, 180, 125, 63, 45 μm) using a vibratory sieve shaker (AS200 basic, Retsch Co.). After the sediment retained in each sieve was weighed to the nearest 0.001 g, median grain size and mud content (%) (defined as proportion of particles < 63 μm of total weight of sediment) were calculated. Because several fishes inhabiting tidal flat pools may prefer the structural complexity of cobbles or mud shrimp burrows (Okazaki *et al.*, 2012; Inui and Koyama, 2014;

Table 1. Mean values ± standard deviation of environmental variables in tidal flat tidepools in the Tama River estuary

Environmental variables	Lower estuary	Middle estuary	Upper estuary
Pool size (m^2)	4.6 ± 2.9^a	1.6 ± 0.8^b	2.2 ± 1.5^b
Water depth (cm)	5.4 ± 5.7	4.8 ± 2.6	6.0 ± 2.5
Height above low tide level (cm)	34.1 ± 24.7^a	89.8 ± 4.9^b	88.2 ± 10.9^b
Water temperature (°C)	27.8 ± 1.3^a	30.2 ± 3.4^{ab}	31.5 ± 2.8^b
Salinity	18.3 ± 2.2^a	13.9 ± 1.7^b	8.9 ± 3.2^c
Mud content (%)	9.1 ± 6.2^a	13.8 ± 8.3^a	39.3 ± 12.1^b
Median grain size (μm)	221.9 ± 39.3^a	144.9 ± 32.9^b	78.2 ± 22.9^c
Cobble-cover rate (%)	1.8 ± 6.1^a	8.4 ± 9.7^b	0.8 ± 1.9^a
Mud shrimp-burrow density (/0.1 m^2)	7.9 ± 4.8^a	0.5 ± 1.6^b	0.0 ± 0.0^b

^{abc} Significant differences found between groups with different superscripts at $p < 0.05$ by Scheffé or Steel-Dwass test.

HENMI *et al*., 2018; INUI *et al*., 2018), the area occupied by cobbles relative to the surface area of each pool was measured, and the entrances of mud shrimp burrows within a quadrat (30 cm × 30 cm) in each pool were identified following the morphological characteristics described in KINOSHITA (2002) and counted.

Data analysis

A one-way analysis of variance (ANOVA) was used to test whether total numbers of species per pool, total number of individuals per 1 m^2 and environmental variables (water temperature, salinity, pool size, water depth, height above low tide level, median grain size and mud content) differed among the survey areas. The Scheffé test was used for a posteriori multiple comparison. Before the analysis for total number of individuals, homogeneity of variances was improved by transformation of the data to $\log_{10}(x + 1)$ (ZAR, 2010). Because the data variance for density (number of individuals per 1 m^2) of each abundant species, cobble-cover rate and mud shrimp-burrow density were heterogeneous (even for transformed data), the non-parametric Kruskal-Wallis test and Steel-Dwass post hoc test were employed to detect differences among the survey areas. To assess relationships between abundant fish distributions and environmental variables, a canonical correspondence analysis (CCA) was performed using CANOCO software (ter BRAAK and SMILAUER, 2002). Prior to the CCA, mud content strongly correlated (Pearson's $r = -0.91$) to median grain size was excluded from explanatory variables.

3. Results and discussion

Mean values of each environmental variable measured in tidal flat tidepools in the lower, middle and upper estuaries are shown in Table 1. Of the 9 environmental variables, 8 (except water depth) differed significantly among survey areas (One way ANOVA: salinity, $F_{2, 52} = 63.0$, $P < 0.001$; median grain size, $F_{2, 52} = 69.9$, $P < 0.001$; mud content, $F_{2, 52} = 46.4$, $P < 0.001$; water temperature, $F_{2, 52} = 7.52$, $P < 0.002$; height above low tide level, $F_{2, 52} = 79.0$, $P < 0.001$; pool size, $F_{2, 52} = 14.2$, $P < 0.001$; water depth, $F_{2, 52} = 0.42$, $P = 0.66$; Kruskal-Wallis test: cobbles-cover rate, $H = 13.7$, $P < 0.002$; mud shrimp-burrow density, $H = 43.2$, $P < 0.001$). Water temperature and mud content increased gradually, and salinity and median grain size decreased gradually, from the lower to upper estuary (Table 1). Pool size

Table 2. Number of individuals, size ranges and developmental stages of fishes collected by dip net in tidal flat tidepools in the Tama River estuary

Family and Species (abbreviation)	Number of individuals	Ratio (%)	SL (mm)	Developmental stage
Mugilidae				
Mugil cephalus cephalus (Mc)	19	1.0	27–40	J
Gobiidae				
Acanthogobius flavimanus (Af)	959	52.2	13–45	J_3
A. lactipes	2	0.1	36–37	A
Eutaeniichthys gilli (Eg)	9	0.5	34–40	A
Favonigobius gymnauchen (Fg)	16	0.9	19–47	J_3, A
Gymnogobius breunigii (Gb)	129	7.0	19–29	J_3
G. macrognathos (Gm)	233	12.7	18–25	J_3
Luciogobius guttatus	2	0.1	19–22	J_3
Mugilogobius abei (Ma)	13	0.7	22–35	A
Pseudogobius masago (Pm)	453	24.6	16–23	A
Tridentiger bifasciatus	3	0.2	32–37	A
Total	1838			

Developmental stage: A, adult; J, juvenile; J_3, juvenile with same pigmentation pattern as adult.

and mud shrimp-burrow density were larger and much more abundant in the lower estuary than in the middle and upper estuaries, the opposite being true for height above low tide level. Cobble-cover rate was much higher in the middle estuary.

A total of 1,838 individuals (all $<$ 50 mm SL, including both juveniles and adults), representing 2 families and 11 species, were collected during the study period (Table 2). *Acanthogobius flavimanus* was the most abundant species, comprising 52.2% of the total individual number of fishes, followed by *Pseudogobius masago* (24.6%), *Gymnogobius macrognathos* (12.7%), *G. breunigii* (7.0%), *Mugil cephalus cephalus* (1.0%), *Favonigobius gymnauchen* (0.9%), *Mugilogobius abei* (0.7%) and *Eutaeniichthys gilli* (0.5%) (Table 2). With the exception of the marine fish *M. cephalus cephalus* (all juveniles), all of the abundant species were estuarine gobiids known to remain on tidal flats during their juvenile and adult stages (Kanou *et al.*, 2000). Similar gobiid fish assemblages have been reported in other estuarine soft-substrata tidepools and small tidal creeks (Meager *et al.*, 2005; Nanjo *et al.*, 2010; Hermosilla *et al.*, 2012).

Mean total numbers of species and individuals, and mean density of each abundant species collected in tidal flat tidepools in the lower, middle and upper estuaries are shown in Table 3. Mean total numbers of species and individuals differed significantly among survey areas (One way ANOVA: total number of species, $F_{2, 52} = 5.06$, $P < 0.01$; total number of individuals, $F_{2, 52} = 5.79$, $P < 0.01$), the total number of species being higher in the lower estuary than in the middle and upper estuaries, although the opposite was found for total number of individuals (Table 3). Marked changes for species and individual numbers with increasing distance from the estuarine mouth have been reported in ichthyofaunal studies of other estuaries, possibly due in part to estuarine or marine species occurring abundantly within a particular area of each estuary (e.g.,

Table 3. Mean values ± standard deviation of total number of species per pool, total number of individuals and densities of the eight most abundant species per 1 m^2 in tidal flat tidepools in the Tama River estuary

	Lower estuary	Middle estuary	Upper estuary
Total no. of species	3.29 ± 1.21^a	2.32 ± 0.99^b	2.31 ± 0.95^b
Total no. of individuals	5.84 ± 3.52^a	17.95 ± 20.96^b	22.39 ± 17.69^b
Density of abundant species			
Acanthogobius flavimanus	2.18 ± 1.44^a	10.33 ± 10.11^b	13.21 ± 10.88^b
Eutaeniichthys gilli	0.16 ± 0.26^a	0.00 ± 0.00^b	0.00 ± 0.00^b
Favonigobius gymnauchen	0.21 ± 0.27^a	0.03 ± 0.17^b	0.00 ± 0.00^b
Gymnogobius breunigii	0.09 ± 0.22	1.12 ± 3.47	1.52 ± 2.64
G. macrognathos	3.02 ± 2.55^a	0.04 ± 0.15^b	0.00 ± 0.00^b
Mugilogobius abei	0.00 ± 0.00^a	0.32 ± 0.57^b	0.19 ± 0.69^{ab}
Pseudogobius masago	0.00 ± 0.00^a	5.91 ± 10.04^b	7.41 ± 8.49^c
Mugil cephalus cephalus	0.18 ± 0.69	0.10 ± 0.51	0.06 ± 0.21

[abc] Significant differences found between groups with different superscripts at $p < 0.05$ by Scheffé or Steel-Dwass test.

NEIRA *et al*., 1992; YOKOO *et al*., 2012).

Of the 8 most abundant species, the densities of 6 benthic gobies (*A. flavimanus*, *E. gilli*, *F. gymnauchen*, *G. macrognathos*, *M. abei* and *P. masago*) differed significantly among survey areas (Kruskal-Wallis test: *A. flavimanus*, $H = 19.2$, $P < 0.001$; *E. gilli*, $H = 14.7$, $P < 0.001$; *F. gymnauchen*, $H = 15.7$, $P < 0.001$; *G. macrognathos*, $H = 48.2$, $P < 0.001$; *M. abei*, $H = 6.45$, $P < 0.05$; *P. masago*, $H = 20.6$, $P < 0.001$), although no significant differences in densities of nektonic *Gymnogobius breunigii* and *Mugil cephalus cephalus* were found among the areas (*G. breunigii*, $H = 3.95$, $P = 0.18$; *M. cephalus cephalus*, $H = 0.87$, $P = 0.65$). Of the aforementioned six benthic gobies, *E. gilli*, *F. gymnauchen* and *G. macrognathos* were more abundant in the lower estuary, whereas much greater abundances of *A. flavimanus*, *P. masago* and *M. abei* were found in the middle and/or upper estuary.

The first two axes of the CCA ordination explained 42.5% of the variances of site- or species-explanatory variable biplots (axis 1, 33.2%; axis 2, 9.3%) (Fig. 2a, b). The vectors of mud shrimp-burrow density, median grain size, salinity and pool size with all of the lower estuary stations were on the right (positive) side of axis 1, whereas the vectors of other factors, including height above low tide level, water temperature, water depth and cobble-cover rate with almost all of the middle and upper estuary stations were on the left (negative) side of axis 1 (Fig. 2a). Mud shrimp-burrow density (correlation coefficient, $r = 0.94$), median grain size ($r = 0.71$), salinity ($r = 0.61$), height above low tide level ($r = -0.78$), water temperature ($r = -0.52$) and pool size ($r = 0.52$) were highly correlated with axis 1, whereas water depth ($r = 0.87$) was highly correlated with axis 2. These results suggested that spatial variations in the fish assemblage structure in tidepools within the present survey areas were largely associated with the seven environmental variables. MEAGER *et al.* (2005), who investigated relationships between fish assemblage structure and environmental variables in soft-substrata tidepools on tidal flats in Moreton Bay, Australia, also indicated that the abundance and/or species richness of fishes were partly affected by pool size, water depth, vertical elevation in the intertidal zone and invertebrate bur-

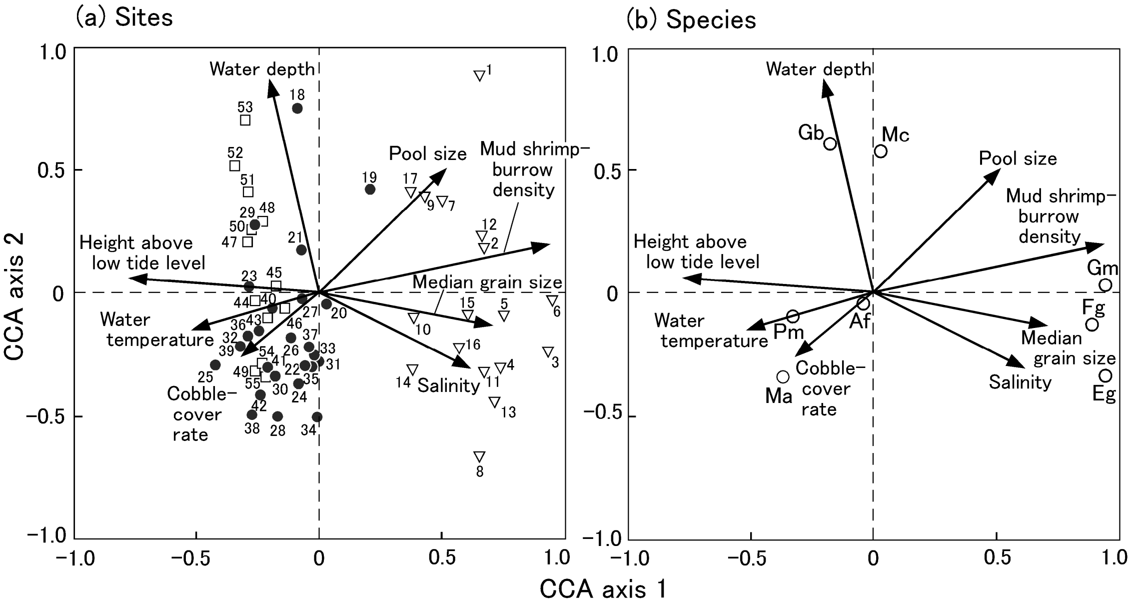

Fig. 2 Canonical correspondence analysis (CCA) ordination diagrams based on the densities of eight abundant fish species in tidepools on tidal flats in the Tama River estuary: sites scores (a) and species scores (b). CCA axis 1 and CCA axis 2 had eigenvalues of 0.464 and 0.130, respectively. Environmental variables represented by vectors. Open triangles, lower estuary stations (St. 1–17); solid circles, middle estuary stations (St. 18–42), open squares, upper estuary stations (St. 43–55). Species abbreviations given in Table 2.

rows.

The CCA also revealed relationships among the eight most abundant fish species and environmental variables (Fig. 2b). Of 3 benthic gobies occurring mainly in the lower estuary, *G. macrognathos* was associated with higher mud shrimp-burrow density, and *E. gilli* and *F. gymnauchen* with larger median grain size and higher salinity. *Gymnogobius macrognathos* spawns on the inner wall of mud shrimp burrows (Henmi *et al.*, 2018), and utilizes such burrows as an important microhabitat during benthic juvenile and adult stages (Kanou, 2003; Inui *et al.*, 2018). Although similar spawning behavior and microhabitat usage is known in *E. gilli* (Dotu, 1955; Henmi and Itani, 2014), a strong relationship between this species and burrow abundance was not apparent during the present study, probably due to their low densities. *Favonigobius gymnauchen* were frequently observed buried in the sandy bottom. Such behavior in several species belonging to *Favonigobius* suggests a preference for relatively coarser sediment (Horinouchi *et al.*, 2016).

Of the 3 benthic gobies occurring abundantly in the middle and upper estuaries, the most abundant species (*A. flavimanus* juveniles) failed to show any clear environmental factor-related tendency, probably because it inhabited a broad range throughout the survey area. In fact, the species utilizes a wide variety of shallow estuarine habitats, including tidal flats (Kanou *et al.*, 2007), cobble areas (Uchida *et al.*, 2008) and eelgrass (*Zostera japonica*) beds (Fujita *et al.*, 2002), as nurseries. *Mugilogobius abei* was frequently found in tidepools with a greater proportion of cobble cover, and *P. masago* in tidepools of greater elevation above low tide level and higher water temperature. OKAZAKI *et al.* (2012) also pointed out that *M. abei* occurred mainly in tidepools with cobbles, whereas *P. masago* almost evenly occurred in tidepools with and without cobbles during spring and early summer. The conspicuously-colored *M. abei* may utilize cobbles as both a refuge from predation and hard substrata on which to lay their eggs (KANABASHIRA *et al.*, 1980; OKAZAKI *et al.*, 2012). In contrast, *P. masago* may rely on other forms of predator avoidance, such as crypsis (OKAZAKI *et al.*, 2012) or burying in the bottom sediments (KUNISHIMA *et al.*, 2014). The spawning substratum of this species has not been found to date (ITOH and MUKAI, 2007). In any case, the adaptation of *P. masago* to tidepools of greater elevation above low tide level and higher water temperature may be useful for temporally extended access to intertidal food under reduced predation risk from larger fish, as mentioned for other temperate tidal flat species (van der VEER and BERGMAN, 1986; GIBSON *et al.*, 2002; KRÜCK *et al.*, 2009).

Unlike the above benthic gobies, the two nektonic species, *G. breunigii* and *M. cephalus cephalus*, were strongly associated with deeper pools. Juveniles of these species, moving frequently to the intertidal zone with rising tides (KANOU *et al.*, 2005a), may become stranded in intertidal pools with the ebbing tide. Such pools may require a certain water depth to enable frequent swimming during the low tide period.

The present study demonstrated that spatial variations in the tidepool fish assemblages on estuarine tidal flats could be partly explained by various environmental gradients related to species-specific ecological characteristics. Similar findings were reported by KOYAMA *et al.* (2016) and INUI *et al.* (2018), who investigated relationships between the distributions of threatened goby species and several environmental variables (elevation, sediment particle size, salinity and large crustacean burrows) on tidal flats in southern Japanese estuaries. KOYAMA *et al.* (2016) suggested that maintenance of various environmental conditions, such as elevation, sediment and salinity, on estuarine tidal flats are necessary for the conservation of threatened gobies, such as *E. gilli*, *G. macrognathos* and *P. masago*. Since the same species were collected during the present study, a similar caution seems applicable to tidepool fish assemblages. It is highly likely that intertidal habitats, such as tidepools and small tidal creeks with various environmental gradients, normally available for intertidal fish inhabitants, have been greatly reduced by extensive reclamation and establishment of artificial structures in the Tama River estuary and adjacent bay waters (KANOU and KOHNO, 2014; MURASE *et al.*, 2014). Accordingly, deliberate restoration of tidal flats, including essential fish assemblage habitats, should be included in future development plans (TAKEYAMA *et al.*, 2013; KANOU and KOHNO, 2014).

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