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FULL PAPER

Abiotic and biotic factors influence the habitat use of four species of *Gymnogobius* (Gobiidae) in riverine estuaries in the Seto Inland Sea

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Abstract Gobies that are phylogenetically related or coexist in the same marine and estuarine systems often exhibit abiotic and/or biotic habitat segregation. Thus, it is possible that species of *Gymnogobius* inhabiting the same riverine estuaries also exhibit abiotic and/or biotic habitat segregation. The goal of this study was to determine the differences in abiotic and biotic habitat use between these species by sampling goby and host shrimps, and by examining the physical environments of the rivers where these species are found. The surveys of goby and host shrimps were conducted in the estuaries of the Saba and Ibo rivers, which drain into the Seto Inland Sea, a body of water that separates three of the four main islands of Japan. We used hand nets and shovels to collect goby and host shrimps, and measured median sediment particle size, elevation, and salinity at each site. Generalized linear models (GLMs) were used to assess the preferences in abiotic and biotic habitat use by the goby species. Median particle size, salinity, and elevation were used as the abiotic environmental predictors, whereas the presence/absence of host shrimps were re-organized into four categories consisting of "*Upogebia major*" only, "*Nihonotrypaea japonica*" only, "*Upogebia major* & *Nihonotrypaea japonica*," and "*Upogebia yokoyai*," which were used as the biotic environmental predictors. The GLMs demonstrated that median particle size had the largest influence of the abiotic variables, with goby species segregating according to differences in sediments; moreover, there was some evidence suggesting that the host and symbiont do not always correlate at the species level. Our results indicated that although there is some overlap in abiotic and biotic habitat use among the four species of *Gymnogobius*, the differences were broad enough to provide an explanatory mechanism as to how these species can coexist in the same river systems.

Keywords Estuary · Endangered species · Shrimp · Symbiosis · Tidal flat

Introduction

The gobiid fish species *Gymnogobius cylindricus*, *Gymnogobius scrobiculatus*, *Gymnogobius macrognathos*, and *Gymnogobius uchidai*, which are inhabitants of the tidal flats of brackish water, reside in the burrows of mud shrimp and/or ghost shrimp, which are also used as spawning sites (Dôtu 1957; Suzuki and Shibukawa 2004; Inui and Koyama 2014; Ministry of the Environment 2015; Koyama et al. 2016b). The ranges of these species largely overlap, and all the four species are known to occur in the area between Ise Bay and Kyushu; moreover, they often can be found in the same river (Inui and Koyama 2014; River Environment Database 2007).

Phylogenetically related or ecologically similar gobies often exhibit abiotic habitat segregation; for example, segregation based on the abiotic factors, such as water depth, salinity, and sediment type in the same genus is known to occur in *Acentrogobius* and *Pseudogobius* (Horinouchi 2008; Inui et al. 2011a; Matsui et al. 2012; Kunishima et al. 2014). On the other hand, several gobies

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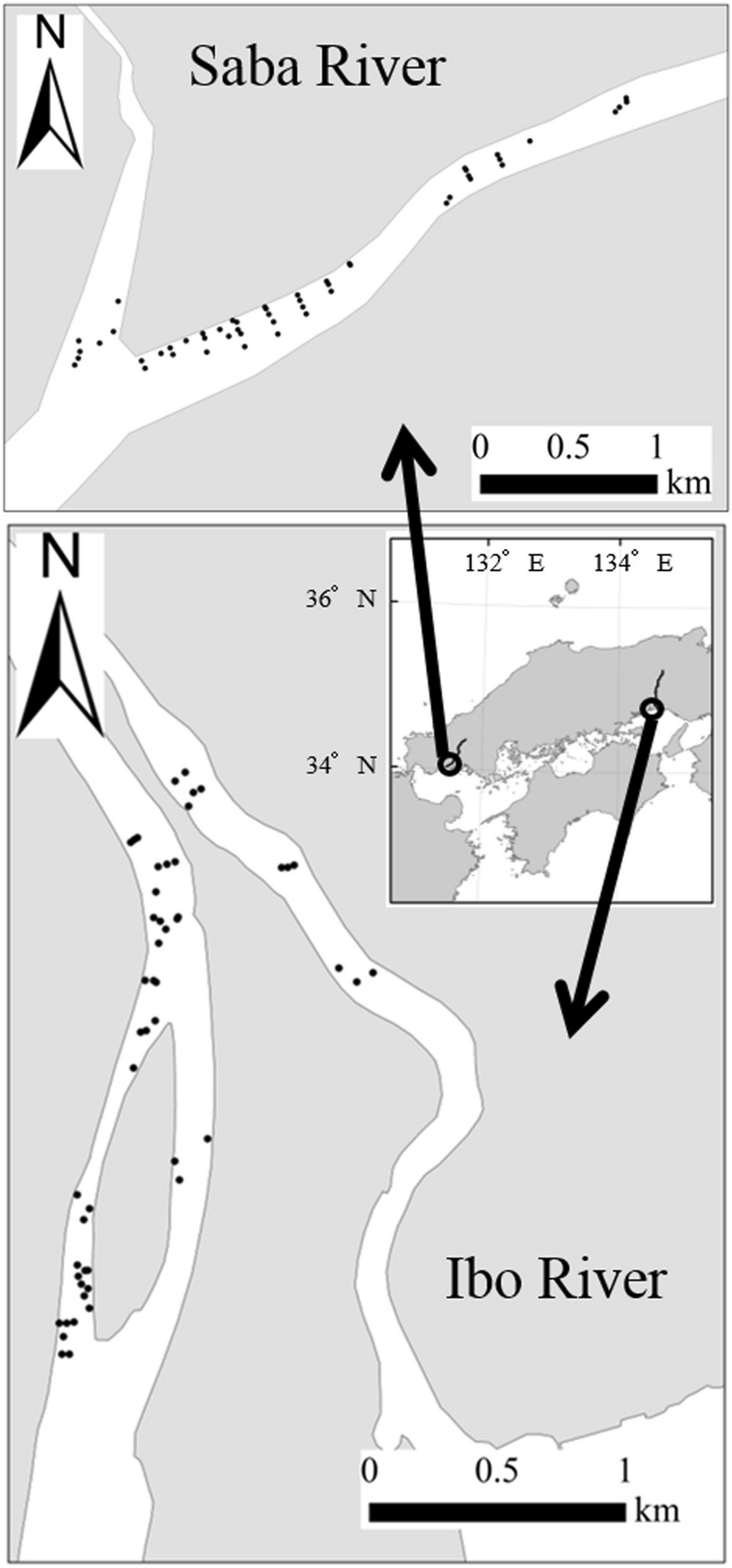


Fig. 1 Map of the survey sites along the Saba and Ibo rivers, which flow into the Seto Inland Sea. *Plots* show the survey sites along each river

are reported to use the burrow of a specific snapping shrimp (Karplus et al. 1981; Karplus and Thompson, 2011). Thus, these gobies segregate based on the biotic habitat. Goto and Kato (2012) suggested that the high degree of variability observed among symbiotic communities of invertebrates that were associated with the same burrowing host species was due to differences in local sediments. Thus, it is possible that the four species of *Gymnogobius* are capable of coexisting in the same river systems because of abiotic and/or biotic habitat segregation; moreover, because these species are listed in the Red Data Book of the Ministry of the Environment (2015), determining the mechanisms that drive habitat segregation of these gobies is important for the formulation of conservation strategies.

The differences in the habitats of the four species of *Gymnogobius* are as follows: *G. cylindricus*, *G. macrognathos*, and *G. uchidai* inhabit sandy and/or muddy flats, *G. scrobiculatus* prefer gravel flats (Inui and Koyama 2014; Ministry of the Environment 2015; Koyama et al. 2016a), *G. cylindricus* and *G. scrobiculatus* use the burrows of both mud shrimp and ghost shrimp as spawning nests (Dôtu 1957; Koyama et al. 2016b), *G. macrognathos* use the burrows of ghost shrimp as spawning nests (Koyama et al. 2016b), and *G. uchidai* use the burrows of both mud shrimp and ghost shrimp as spawning nests (Dôtu 1957; Inui et al. 2011b). However, direct comparisons of their abiotic and/or biotic habitat preferences are yet to be made. Thus, the goal of this study was to determine the differences in abiotic and biotic habitat use between these four species by sampling gobies and their host shrimps, and by examining the physical environments of the rivers where these species coexist.

Materials and methods

Field survey. We selected Saba and Ibo rivers as the study sites (Fig. 1) because all four goby species are known to inhabit these rivers. Saba River, which has a mainstream length of 56 km and a catchment area of 460 km^2, flows into Suonada Bay, located in the western part of the Seto Inland Sea, in south-central Japan. Ibo River, which has a mainstream length of 70 km and a catchment area of 810 km^2, flows into Harimanada Bay, located in the eastern part of the Seto Inland Sea (Ministry of Land, Infrastructure, Transport and Tourism 2008).

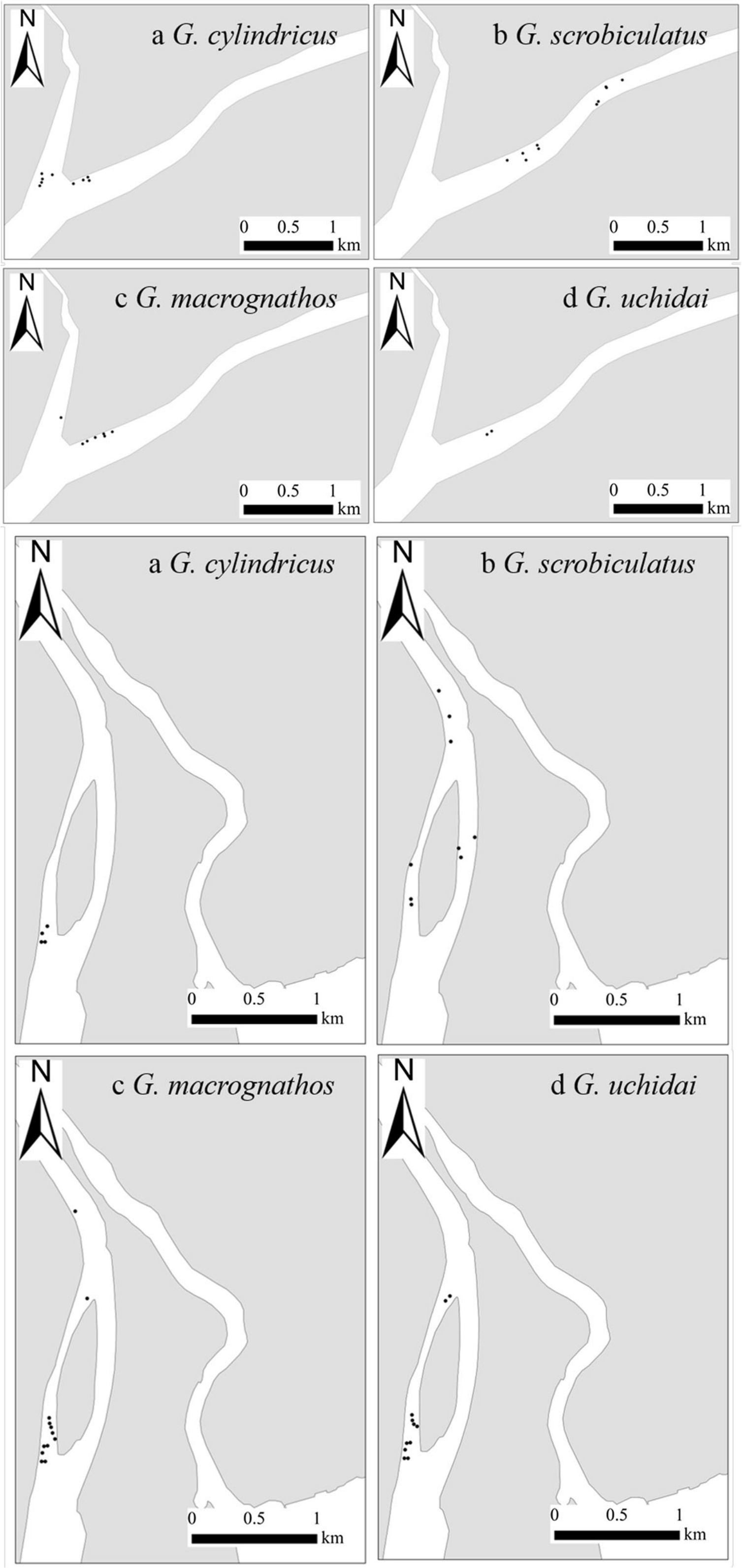
Surveys of goby and host shrimps were conducted at 44 sites in the Saba River and 49 sites in the Ibo River from June to July 2013, and at 47 sites in the Saba River and 51 sites in the Ibo River from February to March 2014 (Fig. 1). Survey points covering the entire zone of intertidal brackish water were established in both rivers. Goby and host shrimps were collected from an area of 30 m^2 at each site for 10 min by two people using hand nets and shovels. Sampling was conducted during spring tide, for a period of 3 h before and after the low tide during daytime. We dug at least two 30 cm or deeper holes at all sites to collect enough host shrimps. Species identification was made primarily in the field and followed the criteria of Akihito et al. (2002), Asakura (1995), and Tamaki et al. (1999). Most fish were released at their site of capture following identification.

In addition to the sampling of gobies and host shrimps, sediment samples were collected from depths of up to 3 cm from each site with a cylindrical corer that had a diameter of 8 cm. All sediment samples were dried and sieved into eight distinct groups based on particle size (<0.063 mm, 0.063–0.125 mm, 0.125–0.25 mm, 0.25–0.5 mm, 0.5–1 mm, 1–2 mm, 2–4 mm, and >4 mm), in accordance with the procedure described by Matsumoto (1986). The sediment attributes were expressed in terms of median particle size (mm), which corresponded to the 50 % ordinate value in the cumulative curve for each size category (McLachlan and Brown 2006). The elevation at each site was measured using a GNSS (Trimble R4, Nikon-Trimble Co., Ltd., Tokyo), a DGPS (Sokkia GIR1600, Topcon Corp., Tokyo), and a level planer (Sokkia LP410, Topcon Corp., Tokyo). In addition, groundwater salinity (ppt) was measured at a depth of 30 cm in the holes that were dug with shovels at each site with a handheld salinity meter (SCT Meter 30, YSI/Nanotech Japan, Kanagawa).

Table 1 Results of field surveys of goby and host shrimps in the Saba and Ibo rivers

The number of sites	Saba River		Ibo River	
	June–July	February–March	June–July	February–March
Gymnogobius cylindricus	2	8	3	3
G. scrobiculatus	8	5	5	7
G. macrognathos	3	5	9	11
G. uchidai	2	0	8	7
Upogebia major	3	6	7	4
U. yokoyai	5	9	4	6
Nihonotrypaea japonica	4	13	7	4

Fig. 2 Distribution patterns of **a** *Gymnogobius cylindricus*, **b** *G. scrobiculatus*, **c** *G. macrognathos*, and **d** *G. uchidai* in the Saba and Ibo rivers. *Plots* show the sites where each species was present



Data analysis. A generalized linear model (GLM) was used to elucidate the abiotic and biotic habitat preferences of the gobies. The presence/absence (1/0) of target gobies were used as the dependent variable, and abiotic and biotic environmental predictors were used as the independent variables. Median particle size (MPS, mm), salinity (SAL,

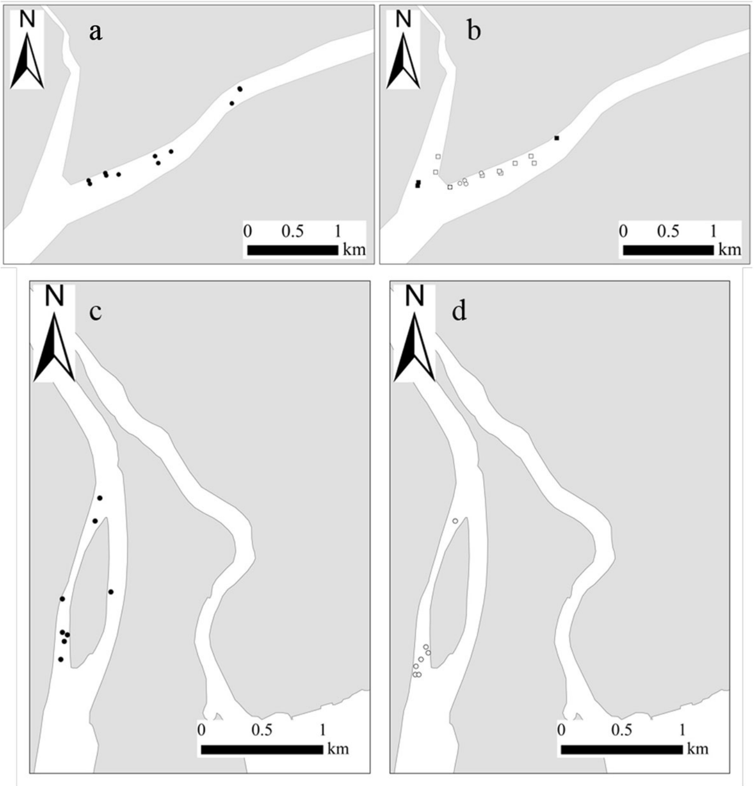


Fig. 3 Distribution patterns of host shrimps **a** *Upogebia yokoyai*, **b** *U. major* and *Nihonotrypaea japonica* in the Saba River, **c** *U. yokoyai*, **d** *U. major* and *N. japonica* in the Ibo rivers. *Solid circles* show *U. yokoyai*, *open circles* show *U. major* & *N. japonica*, *solid squares* show "*U. major*" only, and *open squares* show "*N. japonica*" only

ppt), elevation (ELEV, cm) and their square values were used as the abiotic environmental predictors, and the presence/absence (1/0) of host shrimps were used as the biotic environmental predictors. Because *Upogebia major* and *Nihonotrypaea japonica* were found to be highly sympatric, the presence/absence (1/0) of host shrimps were re-organized into four categories consisting of "*Upogebia major*" only, "*Nihonotrypaea japonica*" only, "*Upogebia major* & *Nihonotrypaea japonica*," and "*Upogebia yokoyai*" to minimize multicollinearity. Finally, time of year (June to July or February to March) and site (Saba or Ibo River) were used as dummy variables.

A logistic regression was conducted for all possible sets of independent variables, followed by an Akaike information criterion (AIC; Akaike 1974). To evaluate model performance, a receiver operating characteristic (ROC) analysis was conducted between the predicted and actual fish distributions (Akobeng 2007).

Variables that affect the habitat of each goby species were determined on the basis of the number of times they were selected in the top 20 model runs, based on AIC; more than half (11 or more) of the selected variables were defined as such. Furthermore, response curves of variables that were determined to affect multiple goby species were constructed in order to visualize and compare the results of the model for each goby species.

Results

Fish and host shrimp survey. The results of the goby and host shrimp surveys are summarized in Table 1, and collection sites for goby and host shrimps are shown in Fig. 2 and Fig. 3. All four of the goby species were found in both the Saba and Ibo rivers. *Gymnogobius macrognathos* was the most common goby species (collected from 28 sites) and *Gymnogobius cylindricus* the least common (collected from 16 sites) in the two rivers. The host shrimp species *Upogebia major*, *Nihonotrypaea japonica*, and *Upogebia yokoyai* were found to inhabit both rivers (Table 1).

Differences in abiotic and biotic factors. Ranges of the abiotic factors measured at the sites are summarized in Table 2. Median particle size ranged from mud (<0.063 mm) to gravel (>2 mm) and salinity levels (ppt) ranged

Table 2 Min–max (mean) of abiotic factors collected during a series of surveys of the Saba and Ibo rivers

	Saba River	Ibo River
MPS (μm)	63–4000 (1472)	63–4000 (1792)
SAL (ppt)	0.1–28.7 (17.9)	0.1–29.8 (17.1)
ELEV (cm)	-113–164 (-6)	-70–100 (-17)

MPS Median particle size; *SAL* Salinity; *ELEV* Elevation

Table 3 Statistical results of the three top models based on Akaike information criterion and the area under the receiver operating characteristic curve of each best model of *Gymnogobius cylindricus*, *G. scrobiculatus*, *G. macrognathos*, and *G. uchidai*

Species	Model	AIC	ΔAIC	AUC	Sensitivity	Specificity	Estimate (SE) Intercept
G. cylindricus	1	38.42	0	0.992	0.938	0.944	-8.57 (3.58)
	2	38.83	0.42				-7.89 (3.61)
	3	38.91	0.49				-13.04 (6.62)
G. scrobiculatus	1	84.90	0	0.951	0.880	0.882	-17.93 (6.82)
	2	86.40	1.50				-17.73 (6.72)
	3	86.50	1.60				-17.82 (6.77)
G. macrognathos	1	90.81	0	0.934	0.821	0.900	-5.66 (1.68)
	2	91.34	0.53				-5.07 (1.80)
	3	91.60	0.79				-5.76 (1.66)
G. uchidai	1	74.32	0	0.937	0.824	0.876	-4.78 (1.35)
	2	75.35	1.04				-5.04 (1.32)
	3	75.49	1.17				-4.60 (1.35)
Species	Model	Estimate (SE)					
		MPS	MPS^2	ELEV	$ELEV^2$	SAL	SAL^2
G. cylindricus	1	0.0310 (0.0189)	-6.17×10^{-5} (3.48×10^{-5})	-0.065 (0.031)			
	2	0.0335 (0.0181)	-6.88×10^{-5} (3.34×10^{-5})	-0.075 (0.032)			
	3	0.0253 (0.0177)	-4.80×10^{-5} (3.14×10^{-5})	-0.210 (0.146)	-0.00111 (0.00100)		
No. of variables in top 20 models		18	20	20	3	2	2
G. scrobiculatus	1	0.0052 (0.0015)	-1.01×10^{-6} (3.17×10^{-7})	-0.071 (0.030)	-0.00052 (0.00030)	1.13 (0.632)	-0.027 (0.015)
	2	0.0051 (0.0015)	-9.79×10^{-7} (3.23×10^{-7})	-0.072 (0.031)	-0.00052 (0.00031)	1.10 (0.623)	-0.026 (0.015)
	3	0.0051 (0.0015)	-9.81 × 10-7 (3.18 × 10-7)	-0.071 (0.030)	-0.00051 (0.00030)	1.13 (0.627)	-0.027 (0.015)
No. of variables in top 20 models		20	20	20	15	20	20
G. macrognathos	1		-2.88×10^{-6} (1.74×10^{-6})			0.16 (0.067)	
	2		-2.55×10^{-6} (1.69×10^{-6})		-0.00020 (0.00018)	0.15 (0.071)	
	3		-2.64×10^{-6} (1.58×10^{-6})			0.17 (0.066)	

Table 3 continued

Species	Model	AIC	ΔAIC	AUC	Sensitivity	Specificity	Estimate (SE) Intercept
No. of variables in top 20 models		7	14	1	7	14	7
G. uchidai	1	0.0083 (0.0035)	-5.08 × 10^{-6} (2.44 × 10^{-6})	-0.032 (0.023)	-0.00102 (0.00044)		
	2	0.0090 (0.0036)	-5.33 × 10^{-6} (2.52 × 10^{-6})		-0.00058 (0.00026)		
	3	0.0085 (0.0036)	-5.17 × 10^{-6} (2.47 × 10^{-6})	-0.032 (0.023)	-0.00102 (0.00044)		
No. of variables in top 20 models		20	20	13	20	4	3
Species	Model	Estimate (SE)					
		Only *U. major*	Only *N. japonica*	*U. major* & *N. japonica*	*U. yokoyai*	River	Season
G. cylindricus	1			20.90 (3184.30)	-20.49 (3184.30)	-18.52 (3184.30)	1.97 (1.35)
	2			20.12 (3183.08)	-18.86 (3183.08)	-18.27 (3183.08)	
	3			21.61 (3071.02)	-21.64 (3071.02)	-18.70 (3071.02)	2.77 (1.70)
No. of variables in top 20 models		1	4	20	16	14	10
G. scrobiculatus	1			-17.99 (2258.89)	1.65 (0.76)		
	2			-18.11 (2254.47)	1.68 (0.78)		-0.49 (0.69)
	3	-16.89 (5945.14)		-18.02 (2266.84)	1.62 (0.76)		
No. of variables in top 20 models		5	7	18	18	6	5
G. macrognathos	1			2.18 (0.69)	1.17 (0.70)	1.48 (0.60)	
	2			2.41 (0.74)	1.10 (0.70)	1.18 (0.64)	
	3			2.27 (0.69)		1.43 (0.58)	
No. of variables in top 20 models		1	1	20	14	20	1
G. uchidai	1			1.92 (0.92)		2.03 (0.84)	
	2			2.24 (0.89)		2.19 (0.83)	
	3		-15.28 (1783.29)	1.86 (0.91)		1.81 (0.85)	
No. of variables in top 20 models		3	6	19	3	20	3

AIC Akaike information criterion; *ΔAIC* Difference of Akaike information criterion from top model; *AUC* The area under the receiver operating characteristic curve; *MPS* Median particle size; *MPS^2* The square values of Median particle size; *ELEV* Elevation *$ELEV^2$* The square values of Elevation; *SAL* Salinity; *SAL^2* The square values of Salinity from freshwater to near-seawater in both rivers, whereas the elevation range was slightly broader for sites in the Saba River than in the Ibo River.

The results of the GLMs for the four gobies are summarized in Table 3. Areas under the curve (AUC) of the best model for each species, as determined by the lowest AIC, were above 0.9 for all species, indicating a high degree of accuracy (Akobeng 2007). The models used in this study were therefore deemed to have performed satisfactorily. Variables that affect habitat use by each species are described below. We defined the number of variables selected in the top 20 model runs as indicators of the strength of the effect, and variables that were selected more than half the time (i.e., 11 or more model runs) were defined as effective variables.

For *G. cylindricus*, MPS was selected 18 times and showed a positive relationship, whereas the square value of MPS was selected 20 times and showed a negative relationship. ELEV was selected 20 times and showed a negative relationship. In terms of the biotic environment variables, "*Upogebia major* & *Nihonotrypaea japonica*" was selected 20 times and showed a positive relationship, and "*Upogebia yokoyai*" was selected 16 times and showed a negative relationship. Site (Saba or Ibo River) was selected 14 times and showed a negative relationship (i.e., *G. cylindricus* is more likely to inhabit the Saba River than the Ibo River). In addition, these variables were selected in the best (i.e., AIC-based top) model.

For *Gymnogobius scrobiculatus,* MPS was selected 20 times and showed a positive relationship, whereas the square value of MPS was selected 20 times and showed a negative relationship. ELEV was selected 20 times and showed a negative relationship, and the square value of ELEV was selected 15 times and showed negative relationship. SAL was selected 20 times and showed a positive relationship, and the square value of SAL was selected 20 times and showed a negative relationship. For the biotic environment, "*Upogebia major* & *Nihonotrypaea japonica*" was selected 18 times and showed a negative relationship, and "*Upogebia yokoyai*" was selected 18 times and showed a positive relationship. In addition, these variables were selected in the best (i.e., AIC-based top) model.

For *G. macrognathos*, the square value of MPS was selected 14 times and showed a negative relationship. SAL was selected 14 times and showed a positive relationship. For the biotic environment, "*Upogebia major* & *Nihonotrypaea japonica*" was selected 20 times and showed a positive relationship, and "*Upogebia yokoyai*" was selected 14 times and showed a positive relationship. Site (Saba or Ibo River) was selected 20 times and showed a positive relationship (i.e., *G. macrognathos* is more likely to inhabit the Ibo River than the Saba River). In addition, these variables were selected in the best (i.e., AIC-based top) model.

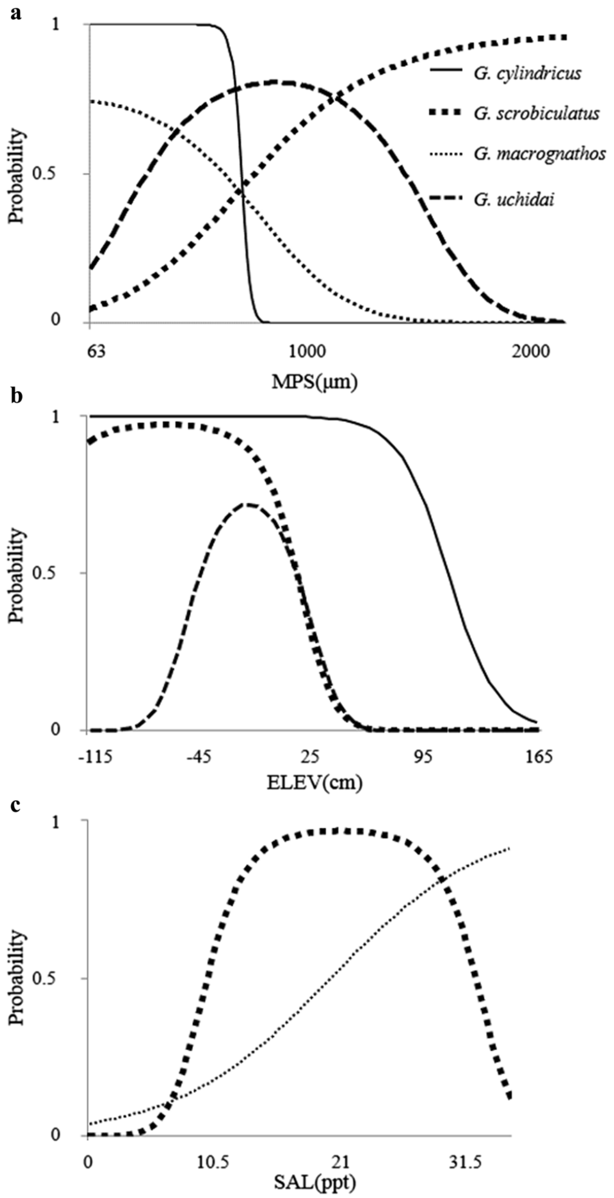


Fig. 4 Habitat suitability curves of several *Gymnogobius* species on the basis of the best-generalized linear models for **a** median particle size (*MPS*), **b** elevation (*ELE*), and **c** salinity (*SAL*)

For *Gymnogobius uchidai*, MPS was selected 20 times and showed a positive relationship, whereas the square value of MPS was selected 20 times and showed a negative relationship. ELEV was selected 13 times and showed a negative relationship, and the square value of ELEV was selected 20 times and showed a negative relationship. For the biotic environment, "*Upogebia major* & *Nihonotrypaea japonica*" was selected 19 times and showed a positive relationship. Site (Saba or Ibo River) was selected 20 times and showed a positive relationship (i.e., *G. uchidai* is more likely to inhabit the Ibo River than the Saba River). In addition, these variables were selected in the best (i.e. AIC-based top) model.

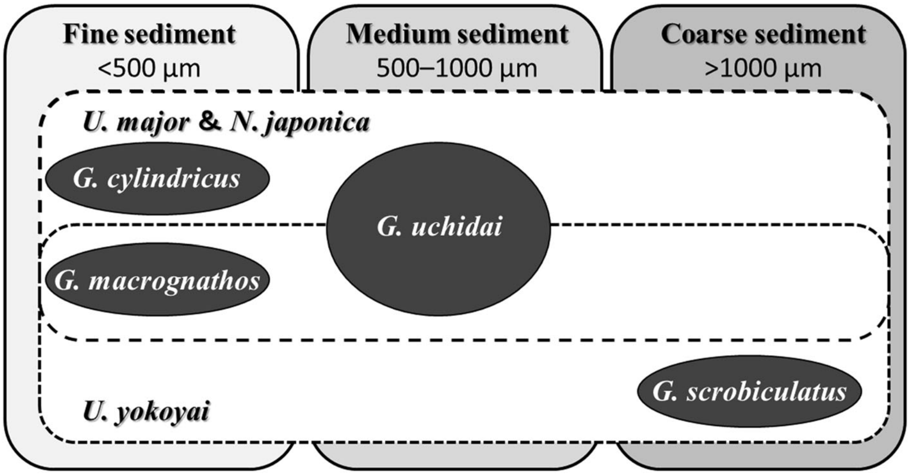


Fig. 5 Schematic of the differences in the abiotic and biotic habitats of the four species of *Gymnogobius*

All abiotic variables affected habitat selection of more than one goby species; MPS, ELEV, and SAL influenced four, three species, and two species, respectively. The response curves of each species with respect to MPS are shown in Fig. 4a; the curves were convex in shape for *G. cylindricus*, *G. uchidai*, and *G. scrobiculatus*. The shape of the response curve of *G. cylindricus* was similar to that of *G. macrognathos*, which showed negative correlation. *G. cylindricus* and *G. macrognathos* were most likely to be found at sites where sediments consisted of finer than medium sand (<500 µm), *G. uchidai* tended to occur at sites where sediments consisted of medium sand (500–1000 µm), and *G. scrobiculatus* preferred sediments that were considerably coarser, i.e., were larger than 1000 µm. The response curves of each species, except for *G. macrognathos* for ELEV, are shown in Fig. 4b. Although the inflection points of the response curves differ for each species, there is some overlap of the high-probability areas for three gobies. The response curves of each species to SAL are shown in Fig. 4c. *G. macrognathos* appeared to prefer areas where salinity levels were relatively high, whereas *G. scrobiculatus* was more likely to occur at sites with moderate salinity levels.

Discussion

The GLM outputs indicated that of all the abiotic variables, sediment MPS had the largest effect on goby distribution. *Gymnogobius cylindricus* and *Gymnogobius macrognathos* preferred finer than medium sand (<500 µm), *Gymnogobius uchidai* preferred medium sand (500–1000 µm), and *Gymnogobius scrobiculatus* preferred more coarse sediment (>1000 µm). Thus, (a) *G. cylindricus* and *G. macrognathos*, (b) *G. uchidai*, and (c) *G. scrobiculatus* tend to segregate according to sediment type. Koyama et al. (2016a) showed that *G. cylindricus* and *G. macrognathos* preferred monotonous sandy sediment, while *G. scrobiculatus* preferred sandy and gravelly sediment. The trends observed in the preference of sediment by these species were similar to those observed in our present study.

The results of the GLMs show that ELEV was the second most effective predictor. With the exception of *G. macrognathos*, gobies were mainly found at lower elevations, and the response curves indicated substantial overlap in the suitable elevation for the three species other than *G. macrognathos*, suggesting that elevation is not a factor in species segregation. However, the GLMs demonstrated that SAL is also an effective segregation parameter, as *G. macrognathos* species were more frequently found in waters with high salinity and *G. scrobiculatus* in waters of medium salinity.

Previous research has shown that closely related marine and/or estuarine gobies—for example, *Acentrogobius* (Horinouchi 2008; Inui et al. 2011a; Matsui et al. 2012) and *Pseudogobius* (Kunishima et al. 2014)—segregate based on abiotic habitat factors, including salinity, water depth, and sediment type. The results of this study suggested that estuarine species of *Gymnogobius* segregate in response to abiotic cues as well, with sediment type the most prominent mechanism.

In terms of the biotic habitat, *G. cylindricus* tended to coexist with "*Upogebia major* & *Nihonotrypaea japonica*" and were not found with "*Upogebia yokoyai*," whereas *G. scrobiculatus* tended to coexist with "*Upogebia yokoyai*" but not with "*Upogebia major* & *Nihonotrypaea japonica*." *G. macrognathos* tended to coexist with "*Upogebia yokoyai*" and "*Upogebia major* & *Nihonotrypaea japonica*," and *G. uchidai* tended to coexist with "*Upogebia major* & *Nihonotrypaea japonica*." Thus, it would appear that "*Upogebia major* & *Nihonotrypaea japonica*" burrows are used as habitat by *G. cylindricus*, *G. macrognathos*, and *G. uchidai*, whereas "*Upogebia yokoyai*" burrows are used by *G. scrobiculatus* and *G. macrognathos*. In this study, each goby tended to coexist with the host that was used for spawning (Dôtu 1957; Dôtu 1961; Inui et al. 2011b; Koyama et al. 2016b). Most previous studies have been conducted in a single site (Dôtu 1957; Dôtu 1961; Inui et al. 2011b; Koyama et al. 2016b) and have focused on a single species (Dôtu 1957; Dôtu 1961). It is new finding that host preference of each goby was the same trend as previous studies focusing on a single site and/or a single species even in rivers where four gobies coexist. Although distinguishing between *U. major* and *N. japonica* habitats was difficult, there is a possibility that hosts and symbionts do not coexist in a one-to-one correlation at the species level in the case of estuarine *Gymnogobius*, as Goto and Kato (2012) demonstrated for invertebrates, in which symbiotic communities of invertebrates associated with the same burrowing host species were highly variable due to differences in sediments. Given the abiotic and biotic habitat differences of the four species of *Gymnogobius*, it is very likely that goby species that use the same host segregate based on differences in the abiotic environment, especially sediment type, similar to the observations of Goto and Kato (2012).

The results of this study indicated that estuarine species of *Gymnogobius* segregate in response to differences in abiotic and biotic conditions (Fig. 5), and that the lack of complete overlap among the four species in terms of abiotic and biotic habitat preferences allows for their coexistence in the same river systems. Because detailed fieldwork—for example, direct observations made via snorkeling—is extremely difficult in the brackish waters of estuarine intertidal zones, experimental rearing, like that done by Henmi and Itani (2014), will help to further our understanding of these systems. In addition, to protect these species of *Gymnogobius*, it is important to conserve not only the host shrimp species but also sediment diversity as well. As such, ecological engineering approaches, such as ecohydraulics (Inui et al. 2015), are needed for expanding our understanding of the mechanisms that support sediment diversity in areas of brackish water.

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