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Relation	

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Habitat utilization and secondary production of the sharp-nosed sand goby *Favonigobius gymnauchen* around intertidal areas

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Declarations

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Ethics approval The laboratory experiment was conducted following the guidelines of the Hiroshima University Animal Research Committee (registration number CD001825).

Availability of data and material The authors share the data upon request.

Code availability Not applicable.

Authors' contributions All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by all authors. The first draft of the manuscript was written by Yusei Yoshida and Takeshi Tomiyama commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Abstract

The sharp-nosed sand goby *Favonigobius gymnauchen* is one of the most dominant fish species around tidal flats and sandy beaches in Japan, and plays an important role in the food web. To clarify the habitat utilization and secondary production of *F. gymnauchen* in these waters, we investigated the density, size compositions, feeding, and prey availability in sandy beaches, a muddy sand estuary, and a seagrass bed in Hiroshima Bay, central Seto Inland Sea, Japan. The density of *F. gymnauchen* was the highest in the estuarine habitat and the lowest in the sandy beaches. They mainly consumed copepods, gammarids, and polychaetes. The body sizes of *F. gymnauchen* were larger in the estuarine habitat than in the seagrass bed, although prey availability was higher in the seagrass bed than in the estuary. Secondary production of *F. gymnauchen* was the highest (>1 g wet weight m^{-2} $year^{-1}$) in the estuarine habitat. The growth rate in the estuarine habitat was estimated to be 0.2 mm d^{-1}. In a laboratory experiment in which fish were exposed to various salinity conditions and fed excess food, the feeding and growth of *F. gymnauchen* were not significantly different at salinities of 5, 15, and 30, and the maximum growth of juveniles at nearly 25 °C was estimated to be 0.2 mm d^{-1}. These results indicate that *F. gymnauchen* grows at nearly maximum rates in estuarine habitats despite their high density, thereby resulting in the high secondary production of this species.

Keywords: coastal habitats; food availability; growth; secondary production; Gobiidae

Introduction

Tidal flats are important habitats for a wide variety of animals (Kuipers et al. 1981), and intertidal and subtidal areas, including riverine estuaries, seagrass beds, and sandy beaches, are important nurseries for fishes (Reise 1985; Beyst et al. 2001; Suda et al. 2002; McLachlan and Brown 2006; Nanami and Endo 2007; De Raedemaecker et al. 2011). A wide variety of environments can provide nurseries for various marine and brackish water fish species, but species-specific habitat suitability and productivity should be well understood for the conservation of fish and ecosystems.

The sharp-nosed sand goby *Favonigobius gymnauchen* is a dominant species in and around intertidal areas in Japan (Yamamoto and Tominaga 2005; Kamimura and Shoji 2009; Shoji et al. 2017) and South Korea (Choi et al. 1996; Park et al. 2015). This species is an annual fish (Nakamura 1944b; Choi et al. 1996). *Favonigobius gymnauchen* spawn eggs from May to September in bivalve shells after covering the shell with sand (Nakamura 1944a, b). Males are the nest-holders (Nakamura 1944a). Their nests were found at sites with average salinities of 3.8–10.2, within 1 km of the mouth of the Ikisan River, western Japan, from June to October (Inui et al. 2010). Yet, its feeding habits, growth rate, and secondary production are crucially lacking for understanding the role of this species in the ecosystem. *Favonigobius gymnauchen* has been recognized as a predator of fishery resources such as the larval swimming crab *Portunus trituberculatus* (Imada and Namba 1981), larval kuruma prawn *Marsupenaeus japonicus* (Harada et al. 2015), and newly settled Japanese flounder *Paralichthys olivaceus* (Noichi et al. 1993), whereas it is consumed by the Japanese sea bass *Lateolabrax japonicus* (Miyahara et al. 1995), Japanese flounder (Yamamoto and Tominaga 2014), and fat greenling *Hexagrammos otakii* (Kwak et al. 2005). Thus, this species seems to play an important role in the food web around tidal flats. In Hiroshima Bay, western Japan, *F. gymnauchen* was the most dominant species in all habitats (estuary, seagrass bed, and sandy beaches), although the species composition greatly varied between the studied sites (Yoshida et al. 2019). To elucidate the function of these habitats for *F. gymnauchen*, it is essential to investigate the food utilization, growth, and secondary production of this species in each habitat.

The aim of this study was to elucidate the feeding habits, growth, and secondary production of *F. gymnauchen* in different habitats, such as estuarine, seagrass, and sandy beach habitats, to better understand the dynamics of the fish or the roles of habitats on dwellers. We investigated the density, size distribution, and gut contents of this species, along with the prey availability in each of the studied habitats. Salinity is considered a potential factor affecting growth rates (Bœuf and Payan 2001). Because *F. gymnauchen* was most abundant in riverine estuaries with large salinity fluctuations (Yoshida et al. 2019), we hypothesized that its growth is greater under intermediate salinities of approximately 50% seawater, as observed in other euryhaline species (Imsland et al. 2001; Wada et al. 2004; Mont'Alverne et al. 2016). To test this hypothesis, we conducted a laboratory experiment in which *F. gymnauchen* was reared with excess food under various salinity conditions. The maximum growth rate determined in this experiment was used to evaluate the observed growth rate in the habitat utilized by this species during its life cycle.

Materials and Methods

Study sites

We selected two sandy beaches in Ujina Island (Sites B1 and B2), a muddysand site in the Ota River estuary (Site MS), and a seagrass (*Zostera marina*) bed in Misuji River estuary (Site SG) in Hiroshima Bay, Japan as the study sites (Fig. 1). The water temperature during the ebb tide changed seasonally with a range of 10–29 °C (Table 1). The maximum tidal range was approximately 4 m. Sites B1, B2, and SG were usually polyhaline, whereas Site MS was polyhaline or mesohaline. The median grain diameter of the sediment was the smallest at Site MS, followed by that at Site SG (Table 1). The silt-clay content was the highest at Site MS.

Field survey

Monthly fish collections were conducted at each site from February 2015 to January 2016. At each site, a small beach seine (1 m high and 2 m wide net mouth: 3 mm mesh) was towed by two people at depths of <1 m for a distance of 30 m at a speed of 0.3 m s^{-1} around the ebb tide in the daytime. A single tickler chain was attached in front of the net mouth to increase the catch efficiency of demersal fishes, including *F. gymnauchen*. The water temperature and salinity in the bottom layer were measured using a portable multimeter (WTW Multi 3420, Germany). Fish samples were brought to the laboratory in a cooler box.

To assess the prey availability for *F. gymnauchen* in each season, macrobenthos near the beach seine towing location were collected every three months (March, June, September, and December) using a core sampler (5 cm inner diameter) and a 1 mm mesh sieve. The core sampling to a 5 cm sediment depth was randomly repeated six times to cover wider areas. The samples were immediately fixed in 10% formalin.

Measurement and analyses

The standard length (SL, mm) of the collected *F. gymnauchen* was measured to the nearest 0.01 mm in the laboratory. The data from Sites B1 and B2 were pooled because the sample sizes at these sites were small and the environmental characteristics at these sites were similar (Table 1). The gut contents of 10 individuals randomly selected from each season were then extracted and preserved in 10% formalin for later observation. The samples collected in March, June, September, and December were primarily used as seasonal representatives, and samples in other months were secondarily used to satisfy the sample sizes.

To assess prey availability in each habitat investigated, the macrobenthic animals were identified and classified into six categories: polychaetes, gammarids, other malacostracans, copepods, bivalves, and others. The density (N m^{-2}) was calculated using the number of individuals in each category, and the density of each prey category was compared between habitats using the Friedman test.

The gut contents of *F. gymnauchen* were observed under a microscope. The index of relative importance (IRI) was calculated for the six prey categories at each site in each season. The IRI was calculated as follows:

$$IRI_i = (\%N_i + \%W_i) \times \%F_i$$

$$\%IRI_i = IRI_i / \sum_{i=1} IRI_i \times 100$$

where $\%N_i$ is the percentage number of prey item i, $\%W_i$ is the percentage wet weight (WW) of prey item i, and $\%F_i$ is the frequency of occurrence of prey item i. Unidentified gut contents were not included in the calculation of the IRI. The %IRI was used to evaluate the principal diet.

To test whether the prey varied with body size and habitat, we constructed a generalized linear model (GLM) with a binomial family and logit-link function. The presence or absence of each prey category was used as a response variable. The initial explanatory variables were the SL, site, and season. The model was selected based on the Akaike information criterion (AIC).

To assess the growth pattern in each habitat, two analyses were performed. First, the SL of *F. gymnauchen* was compared between habitats. Because *F. gymnauchen* showed single cohorts in most months and their recruitment was observed in August (Kamimura and Shoji 2009), we divided the specimens into year classes 2014 and 2015 from their size distribution. To test whether the body size differed between habitats, a linear model for the SL was constructed for each year class. The initial explanatory variables were habitat and days from February 1. The model was selected based on the AIC. Second, the growth rate of the young-of-the-year *F. gymnauchen* was estimated from the length-frequency distributions. Because a large sample size was obtained only at Site MS (see results), the linear model for the SL was constructed for the data at this site from August to October, during which the water temperatures were >20 °C (28.4 °C, 24.9 °C, and 21.6 °C in August, September, and October, respectively). The initial explanatory variable was days from February 1, and the model was selected based on the AIC. The coefficient of days can be regarded as the growth rate (mm d^{-1}).

Annual secondary production (*SP*) was estimated using the size-frequency method (Krueger and Martin 1980), as follows:

$$SP = a \times \left[\sum_{j=1}^{a-1} \left(\bar{Y}_j - \bar{Y}_{J+1} \right) \times \left(W_j \times W_{J+1} \right)^{0.5} + \left(\bar{Y}_a \times W_a \right) \right]$$

$$\bar{Y}_j = 0.5 \times \sum_{i=1}^{12} \left(\bar{Y}_{i,j} + \bar{Y}_{i+1,j} \right)$$

where *a* is the number of size classes, W_j is the mean weight per individual in size class *j*, and $\bar{Y}_{i,j}$ is the density (N m^{-2}) in the *i*th month in the *j*th size class. The data for January 2015 were assumed to be equivalent to those of January 2016 and used for the estimation of annual production.

Laboratory experiment and analyses

To evaluate the effects of salinity on the feeding and growth of *F. gymnauchen* and to assess the maximum growth under excess food conditions, an individual-based laboratory experiment (Kusakabe et al. 2017) was conducted in September 2016. A total of 30 wild *F. gymnauchen* (approximately 28 mm SL) were collected with a scoop net (35 cm width and 2 mm mesh) from depths of <1 m in the Kamo River estuary (34° 19′ N, 132° 54′ E; Fig. 1), Japan, around ebb tide during the daytime. The fish were transferred to the laboratory and accommodated in a 100 L tank filled with running seawater for acclimation to commercial pellets for 5 d.

For the experiment, seven 100 L tanks were used with different salinity regimes; two tanks were filled with water with a salinity of 5, another two tanks were filled with water with a salinity of 15, and the remaining three were filled with seawater with a salinity of 30. Three plastic cages (27 cm long, 16 cm wide, and 11 cm high; same as Kusakabe et al. 2017) were floated in each tank, and each cage was partitioned into two compartments to accommodate two fish per cage. Six individuals were used per group, and five groups with different salinity regimes were set. Groups A, B, and C were treated with constant salinities of 5, 15, and 30, respectively, whereas Groups D and E were treated with salinities fluctuating between 5 and 30 or between 15 and 30, respectively (Online Resource Table S1, Fig. S1). Groups D and E mimicked the tidal salinity fluctuation in estuaries. All the cages were moved between the tanks irrespective of the groups at 8:00 and 14:00 to minimize the differences in the handling effects between groups (Fig. S1).

Prior to the experiment, the fish were measured (SL and body wet weight [BW, g]) and placed randomly in cages for 24 h without feeding. The fish were then fed for 7 d. Excess amounts of commercial pellets (Otohime S1, 0.62 mg dry weight per particle, Marubeni Nisshin Feed Co. Ltd., Tokyo, Japan) were fed to the fish twice per day during the daytime (10:00 and 16:00). The remaining pellets were removed after 1 h. The number of pellets given to the fish and those remaining in each compartment were recorded so that the food intake (number of consumed pellets × average weight of pellets) could be assessed. Twenty four hours after the last feeding on the seventh day, all the individuals were collected and measured again. Specimens were then dried at 80 °C for ≥24 h to determine the body dry weight (BDW, mg). The water temperature was measured twice per day and was 25.2 ± 1.0 °C (mean ± SD, $N = 90$).

To evaluate the feeding and growth of *F. gymnauchen*, the absolute growth rate (AGR, mm d^{-1}), specific growth rate (SGR), daily food intake (DFI, mg d^{-1}), and feed conversion efficiency (FCE) were determined as follows:

$$AGR = (SL_{end} - SL_{start})/t$$

$$SGR = (\ln BW_{end} - \ln BW_{start})/t \times 100$$

$$DFI = \frac{1}{t} \times TFI$$

$$FCE = (BDW_{end} - BDW_{start})/TFI \times 100$$

where SL_{end} and SL_{start} are SL at the end and start of the experiment, respectively, t is the period (7 d) in the experiment, and TFI is the total food intake (mg). Because the commercial pellets were almost dried, the FCE was calculated on a dry weight basis. BDW_{start} was calculated using the BW, obtained from the specimens at the end of the experiment: BDW (mg) = 238.53 × BW (g) + 9.87 ($N = 30$, $r = 0.95$).

To test whether feeding and growth were affected by the salinity or the body size of the fish, linear models were constructed for the AGR, SGR, DFI, and FCE. The initial explanatory variables were group and SL_{start}. Models were selected based on the Akaike information criterion for small sample sizes (AICc). All statistical procedures were performed using the software R version 3.5.1 (www.r-project.org).

Results

Field survey

A total of 572 individuals of *F. gymnauchen* were collected. The number and total weight of *F. gymnauchen* were the greatest at Site MS, although the number of individuals and biomass of all fish species were the greatest at Site SG (Table 1). Secondary production of *F. gymnauchen* was estimated to be 0.082 g WW m^{-2} $year^{-1}$ at Sites B1 and B2, 1.976 g WW m^{-2} $year^{-1}$ at Site MS, and 0.107 g WW m^{-2} $year^{-1}$ at Site SG.

Recruitment of small individuals around 20 mm SL was observed mainly in August–September (Fig. 2). A rapid increase in SL was observed at Site MS from August to October. Selected linear models showed that the SL was larger at Sites B1, B2, and MS than at Site SG in year class 2014, whereas the SL was larger at Site MS than at Sites B1 and B2 in year class 2015 (Table 2). The SL growth rates were estimated to be 0.12 mm d^{-1} and 0.13 mm d^{-1} for year classes 2014 and 2015, respectively, whereas the growth rate was high at 0.215 mm d^{-1} for year class 2015 at Site MS from August to October (Table 2; Online Resource Fig. S2).

The diet composition varied between sites, but polychaetes, gammarids, and copepods were commonly consumed at all the sites (Fig. 3). In the GLM used to determine the presence or absence of each prey in the diet of *F. gymnauchen*, the SL was adopted as an explanatory variable only for polychaetes and copepods. The coefficient of the SL was positive in polychaetes ($P = 0.014$), whereas it was negative in copepods ($P = 0.012$). Site was adopted as the explanatory variable for gammarids (the highest at Sites B1 and B2, $P = 0.041$) and copepods (the highest at Site SG, $P = 0.066$). Season was not adopted for any prey category. The prey availability, especially the density of polychaetes, was the greatest at Site SG (Fig. 3). The prey density was the lowest at Sites B1 and B2. The density was significantly different between habitats for polychaetes (Friedman test, $P = 0.026$), gammarids ($P = 0.044$), copepods (*P* = 0.038), and bivalves (*P* = 0.036).

Laboratory experiment

No individuals died during the experiment. All the individuals consumed pellets and grew with an increment of >1 mm SL. Although the AGR and SGR of the individuals under the salinity of 15 (Group B) were slightly high (Fig. 4), the group was excluded from the models for the AGR, SGR, DFI, and FCE (Table 4). In contrast, SL_{start} was selected in all the models. A negative correlation with SL was observed for the AGR and SGR, whereas positive relationships were observed for the DFI and FCE (Fig. 4).

Using the selected model for the AGR, the maximum growth rates of *F. gymnauchen* were estimated to be 0.25, 0.23, and 0.20 mm d^{-1} for individuals with SLs of 25, 30, and 35 mm, respectively.

Discussion

This study illustrated that secondary production of *F. gymnauchen* was greater in the estuarine habitat than in the sandy beach and seagrass habitats, although this species dominated in all habitats (Yoshida et al. 2019). The secondary production of *F. gymnauchen* at Site MS (2.0 g m^{-2} $year^{-1}$) was smaller than that of the common goby *Pomatoschistus microps* in an estuary in Portugal (3.8 g m^{-2} $year^{-1}$; Souza et al. 2014), but was greater than that of the sand goby *Pomatoschistus minutus* in the same estuary (0.2 g m^{-2} $year^{-1}$; Souza et al. 2015). Spawning events occur twice or thrice each year in *P. microps* with its lifespan of ≤16 months (Leitão et al. 2006; Souza et al. 2014), whereas *P. minutus* lives for two years with a much lower abundance than *P. microps* (Souza et al. 2015), thereby indicating their large or small secondary production. Considering the lifespan of one year, the production of *F. gymnauchen* is relatively large, and this species has a secondary production typical of a short-living organism. The high productivity of *F. gymnauchen*, especially in estuaries, would contribute to the diet of higher trophic levels, such as Japanese sea bass *Lateolabrax japonicus* (Miyahara et al. 1995), which is a common species in estuaries (Yoshida et al. 2019).

By comparing data from an experiment designed to study the effect of salinity on the feeding and growth of *F. gymnauchen* to the observed data collected in the field, the present study demonstrated that salinities ranging from 5 to 30 did not affect the feeding efficiency and growth rate of *F. gymnauchen*. Therefore, our hypothesis of the advantage of intermediate salinities for *F. gymnauchen* was not demonstrated. Thus, salinity fluctuation in estuaries did not seem to be a limiting factor for this species, although it is unclear whether it prefers mesohaline areas. In general, euryhaline species exhibit the highest growth rates under intermediate salinity conditions (Wada et al. 2004; Mont'Alverne et al. 2016). The congeneric species *Favonigobius lateralis* inhabits lower estuaries with relatively high salinities despite being highly euryhaline (Gill and Potter 1993), thereby indicating that *Favonigobius* species might prefer polyhaline areas.

In this experiment, food consumption and feeding efficiency increased as body size increased (Table 4). This is expected because the metabolic rate would decrease with an increase in size (Fonds et al. 1992) and energy allocation to production would increase.

High growth rates of 0.22 mm d^{-1} of young-of-the-year *F. gymnauchen* were observed from August to October (Table 3), which is the growing season for this species (Kamimura and Shoji 2009). The growth rate in the field was similar to the maximum growth under excess food conditions at temperatures around 25 °C (AGR in Fig. 4), thereby indicating that fish grew at nearly maximum rates without being affected by any density-dependent effect (van der Veer and Witte 1993) in estuarine habitats. Such high growth rates without food limitations were observed in juvenile marbled flounder in nearby estuaries (Tomiyama et al. 2018) and in the sand goby *P. minutus* in Europe (Freitas et al. 2011).

The high growth rates and high productivity of *F. gymnauchen* in estuaries, despite their high densities, should be supported by the high prey availability. However, prey abundance was greater in the seagrass bed than in the estuarine site (Fig. 3). The relatively low abundance of *F. gymnauchen* despite the high prey availability in seagrass habitats may reflect the preference of this species in bare sand areas. The mean SL of *F. gymnauchen* was approximately 20–40 mm at a bare sand site, whereas it was approximately 20 mm at a *Zostera japonica* bed throughout the year (Uede et al. 2012), thereby suggesting that *F. gymnauchen* might utilize seagrass beds as a habitat only in early juvenile stages to avoid predation. An experimental study suggested that gobies residing in eelgrass beds would sacrifice growth and precede survival (Sogard 1992). Thus, seagrass beds function as areas of high prey availability and refuge from predators in general (Adams 1976; Heck et al. 2000), but the former function may not be important for *F. gymnauchen*. Sandy beaches have less prey, which might result in the low abundance of *F. gymnauchen*. However, sandy beaches may have a higher density of bivalve shells for nesting, and these habitats may function as spawning grounds for this species. In contrast, bivalve shells are found only rarely at Site MS. This site does not seem to be appropriate as a spawning ground because of the small grain size and high silt-clay content (Table 1). We found another sandy area with relatively abundant clam shells near Site MS in the estuary, indicating that *F. gymnauchen* can move to other microhabitats for spawning.

This study did not investigate the sex ratio of *F. gymnauchen*. Although the sex ratio was almost 1:1, even during the spawning season in a past study (Nakamura 1944b), the large body size of males might affect size distribution because nest-holder males would be less catchable. Other observations found that size distribution was similar between sexes at sandy beaches (34° 19′ N, 132° 56′ E), even during the spawning season from June to August, as estimated from the seasonal gonad development (Sakamiya K, unpubl. data, 1999; Hidaka K, unpubl. data, 2012). Furthermore, the feeding activity of guarding male gobies generally decreases during the spawning season (Magnhagen 1993; Skolbekken and Utne-Palm 2001). Further investigation is required to determine the effects of sex ratio on size distribution or feeding during the spawning season.

Habitat function would differ between the studied sites. During the spawning season from June to August, *F. gymnauchen* was scarcely collected at sites B or SG (Fig. 2). This result might indicate that they migrate to other sites that are appropriate for spawning. For *F. gymnauchen*, sites B and SG would function as complementary feeding grounds or shelters from predation except during the spawning season. The highest density of this species at Site MS may indicate their preference for estuarine habitats, although this species is known to dominate in fish communities of sandy beaches throughout a year (Watanabe and Shimizu 2015).

The diet of *F. gymnauchen* mainly comprised polychaetes, gammarids, and copepods (Fig. 3), as suggested in a previous estuarine study (Aoki et al. 2014). In another sandy beach with depths of 1–5 m in the Seto Inland Sea, this species fed mainly on mysids and decapod shrimps (Yamamoto and Tominaga 2005). Congeneric species fed mainly on polychaetes and crustaceans (Gill and Potter 1993) or copepods and decapods (Chargulaf et al. 2011), thereby indicating that *Favonigobius* species are opportunistic carnivores. In addition, the presence of copepods in the diet was greater in smaller individuals, whereas the presence of polychaetes in the diet was greater in larger individuals, as suggested by the GLM, thereby demonstrating an ontogenetic diet shift from small to large prey in *F. gymnauchen*, similar to that observed in the round goby *Neogobius melanostomus* (Henseler et al. 2020). Such size-related feeding habits may explain the differences in body size distribution between habitats.

This study suggests that the growth rates and productivity of *F. gymnauchen* are high in estuarine habitats with large salinity fluctuation. Further studies are necessary to reveal the function of each habitat, including the reproduction of *F. gymnauchen* because bivalve shells were not abundant at any of the sites in this study.

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Table 1 Abiotic conditions and total number of fish species, total number of individuals, and total biomass collected by a beach seine net at each site from February 2015 to January 2016

	Site B1	Site B2	Site MS	Site SG
Water temperature*	18.7 ± 5.2 (11.8–27.2)	18.5 ± 5.2 (11.1–26.9)	18.5 ± 5.8 (10.5–28.4)	19.2 ± 5.7 (11.9–29.0)
Salinity*	29.8 ± 1.3 (27.8–31.6)	29.6 ± 1.4 (27.5–31.3)	20.3 ± 3.8 (12.8–23.9)	28.5 ± 1.9 (24.6–30.8)
Median grain diameter (mm)**	2.76	1.13	0.09	0.34
Silt-clay (%)**	0.09	0.06	22.12	2.56
Fish (all species)***				
Number of species	12	9	24	32
Number of individuals	67	84	947	1822
Biomass (g)	422.3	70.0	852.2	6022.5
Gobiidae				
Number of species	2	2	9	7
Number of individuals	34	55	760	237
Biomass (g)	20.5	28.6	669.9	183.1
Favonigobius gymnauchen				
Number of individuals	24	29	443	75
Biomass (g)	18.2	24.2	361.6	21.2

* Water temperature and salinity are shown as mean ± SD (range).

** Sediment samples (97–131 g) were collected from the bottom surface to a depth of 5 cm at each site in June 2015 (one sample per site). The samples were dried at 80 °C for 48 h after removing organic matter with hydrogen peroxide solution and were then sieved through 4, 2, 1, 0.5, 0.025, 0.0125, and 0.0625 mm meshes.

*** Detailed information on the collected fish species is shown in Yoshida et al. (2019).

Table 2 Results of linear models for the standard length (SL) of *Favonigobius gymnauchen* collected in the field surveys

Analysis of variance				Coefficients			
Error source	df	Sum sq	*P*	Parameter	Estimate	SE	*P*
Year class 2014 (adjusted $R^2 = 0.42$, $P < 0.001$)							
Error	276	16238.8		Intercept	21.68	2.07	<0.001
Habitat	2	1029.8	<0.001	Site MS	−0.28	1.50	0.85
				Site SG	−6.19	1.91	0.0014
Days	1	5736.5	<0.001	Days	0.12	0.012	<0.001
Year class 2015 (adjusted $R^2 = 0.49$, $P < 0.001$)							
Error	288	12246.4		Intercept	−9.11	3.16	0.004
Habitat	2	6482.2	<0.001	Site MS	7.55	1.41	<0.001
				Site SG	−7.37	1.79	<0.001
Days	1	7709.1	<0.001	Days	0.14	0.010	<0.001
Growth of young-of-the-year at Site MS (adjusted $R^2 = 0.69$, $P < 0.001$)							
Error	158	3754.5		Intercept	−20.14	3.00	<0.001
Days	1	7627.5	<0.001	Days	0.215	0.012	<0.001

Analysis of variance was performed using the Type II test. Sum sq indicates the sum of squares. For year classes 2014 and 2015, the initial explanatory variables were habitat and days from February 1. No variables were excluded from the models. The final models were selected based on the Akaike information criterion (Online Resource Table S2). The effect of habitat was assessed based on Site B (pooled data from Sites B1 and B2).

Table 3 Results of generalized linear models for the presence or absence of each prey in the diet of *Favonigobius gymnauchen* collected in the field surveys

Analysis of variance				Coefficients			
Error source	df	LR Chisq	*P*	Parameter	Estimate	SE	*P*
Polychaetes							
				Intercept	−5.31	1.67	0.001
SL	1	7.31	0.007	SL	0.10	0.042	0.014
Gammarids							
				Intercept	−0.25	0.50	0.62
Habitat	2	6.40	0.041	Site MS	−0.67	0.78	0.39
				Site SG	−2.05	0.90	0.022
Other malacostracans							
				Intercept	−1.44	0.35	<0.001
Copepods							
				Intercept	2.92	1.43	0.042
SL	1	7.22	0.007	SL	−0.098	0.039	0.012
Habitat	2	5.45	0.066	Site MS	−0.13	0.82	0.87
				Site SG	1.71	0.89	0.054

Analysis of variance was performed using the Type II likelihood ratio chi-square (LR Chisq) test. The prey category of bivalves was not analyzed because it occurred in the gut of only one *F. gymnauchen* throughout the study. The initial explanatory variables were standard length (SL), habitat, and season. The final models were selected based on the Akaike information criterion (Online Resource Table S3). The effect of habitat was assessed based on Site B (pooled data from Sites B1 and B2).

Table 4 Results of linear models for the feeding and growth of *Favonigobius gymnauchen* in the laboratory experiment

Analysis of variance				Coefficients			
Error source	df	Sum sq	*P*	Parameter	Estimate	SE	*P*
Absolute growth rate (adjusted $R^2 = 0.076$, $P = 0.077$)							
Error	28	0.043		Intercept	0.39	0.084	<0.001
SL_{start}	1	0.005	0.077	SL_{start}	−0.0055	0.0030	0.077
Specific growth rate (adjusted $R^2 = 0.26$, $P = 0.002$)							
Error	28	4.83		Intercept	7.35	0.897	<0.001
SL_{start}	1	1.97	0.002	SL_{start}	−0.11	0.032	0.002
Daily food intake (adjusted $R^2 = 0.27$, $P = 0.002$)							
Error	28	147.7		Intercept	−3.29	4.96	0.51
SL_{start}	1	61.3	0.002	SL_{start}	0.60	0.18	0.002
Feed conversion efficiency (adjusted $R^2 = 0.28$, $P = 0.002$)							
Error	28	532.4		Intercept	−6.96	9.42	0.47
SL_{start}	1	233.1	0.002	SL_{start}	1.16	0.33	0.002

Sum sq indicates the sum of squares. The initial explanatory variables were the group and SL_{start}, and the group was excluded from all the models. The final models were selected based on the Akaike information criterion for small sample sizes (Online Resource Table S4).

Figure legends

Fig. 1 Map of the study sites. Area A shows the sites of the field surveys and area B shows the collection site of *Favonigobius gymnauchen* for the laboratory experiment. Sites B1 and B2 were sandy beach sites, Site MS was a muddy sand estuary site, and Site SG was a seagrass bed in Hiroshima Bay, western Japan

Fig. 2 Seasonal changes in length-frequency distributions of *Favonigobius gymnauchen* in each habitat. The dark (blue in online version) and light (orange) bars indicate year classes 2014 and 2015, respectively. The triangles show the average standard length (SL) of each year class. The numerals indicate the sample sizes

Fig. 3 Seasonal changes in the diet of *Favonigobius gymnauchen* (left panels) and prey availability (right panels) in each habitat. The %IRI is the index of relative importance of the gut contents. The numerals above the bars indicate the number of individuals with identified prey items, although 10 samples were examined for each site in each season

Fig. 4 Absolute growth rate (AGR), specific growth rate (SGR), daily food intake (DFI), and feed conversion efficiency (FCE) of *Favonigobius gymnauchen* in the laboratory experiment. Details of the treatment groups are shown in Fig. 2. In the left panels, the boxes show the 25% and 75% quartiles and the median, the dashed vertical bars show the maximum and minimum values, and the open circles show the outliers. In the right panels, the solid and dashed lines show the linear regression and the 95% confidence interval, respectively

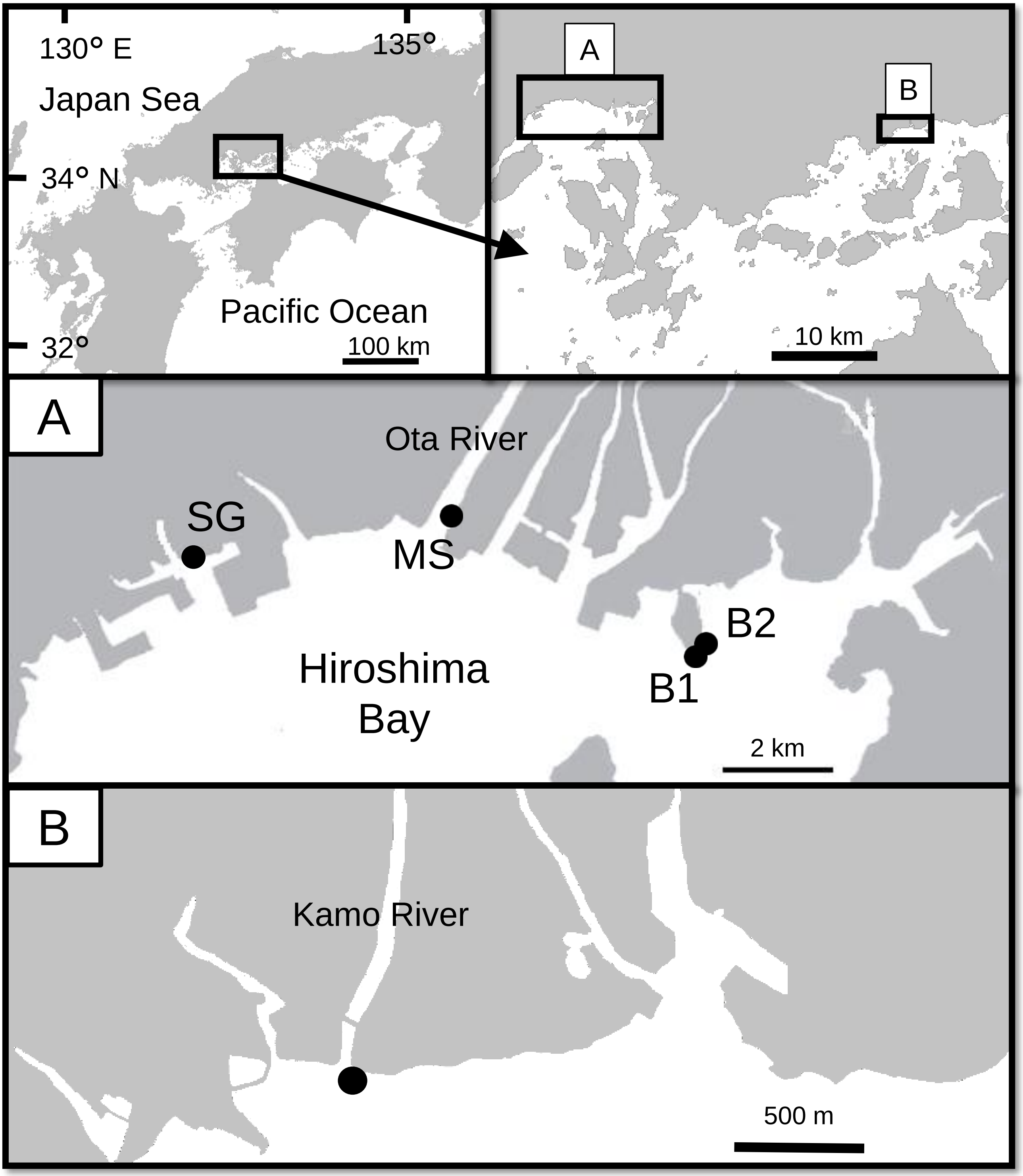
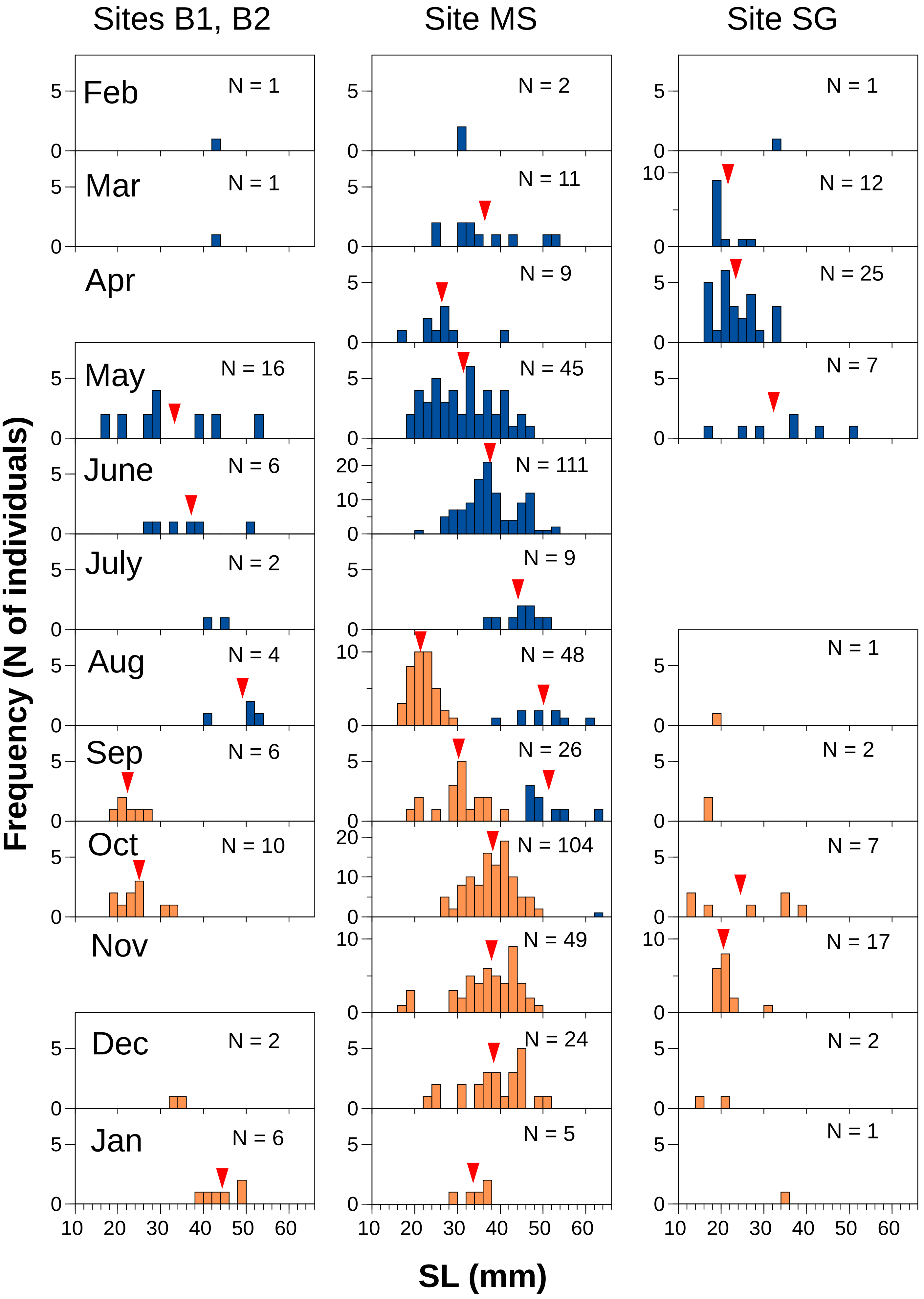

130° E
135°
Japan Sea
34° N
32°
Pacific Ocean
100 km
A
B
10 km
A
Ota River
SG
MS
B2
B1
Hiroshima
Bay
2 km
B
Kamo River
500 m

Fig2


Sites B1, B2
Site MS
Site SG
Frequency (N of individuals)
SL (mm)
Feb
N = 1
N = 2
N = 1
Mar
N = 1
N = 11
N = 12
Apr
N = 9
N = 25
May
N = 16
N = 45
N = 7
June
N = 6
N = 111
July
N = 2
N = 9
Aug
N = 4
N = 48
N = 1
Sep
N = 6
N = 26
N = 2
Oct
N = 10
N = 104
N = 7
Nov
N = 49
N = 17
Dec
N = 2
N = 24
N = 2
Jan
N = 6
N = 5
N = 1
0
5
10
20
10
20
30
40
50
60

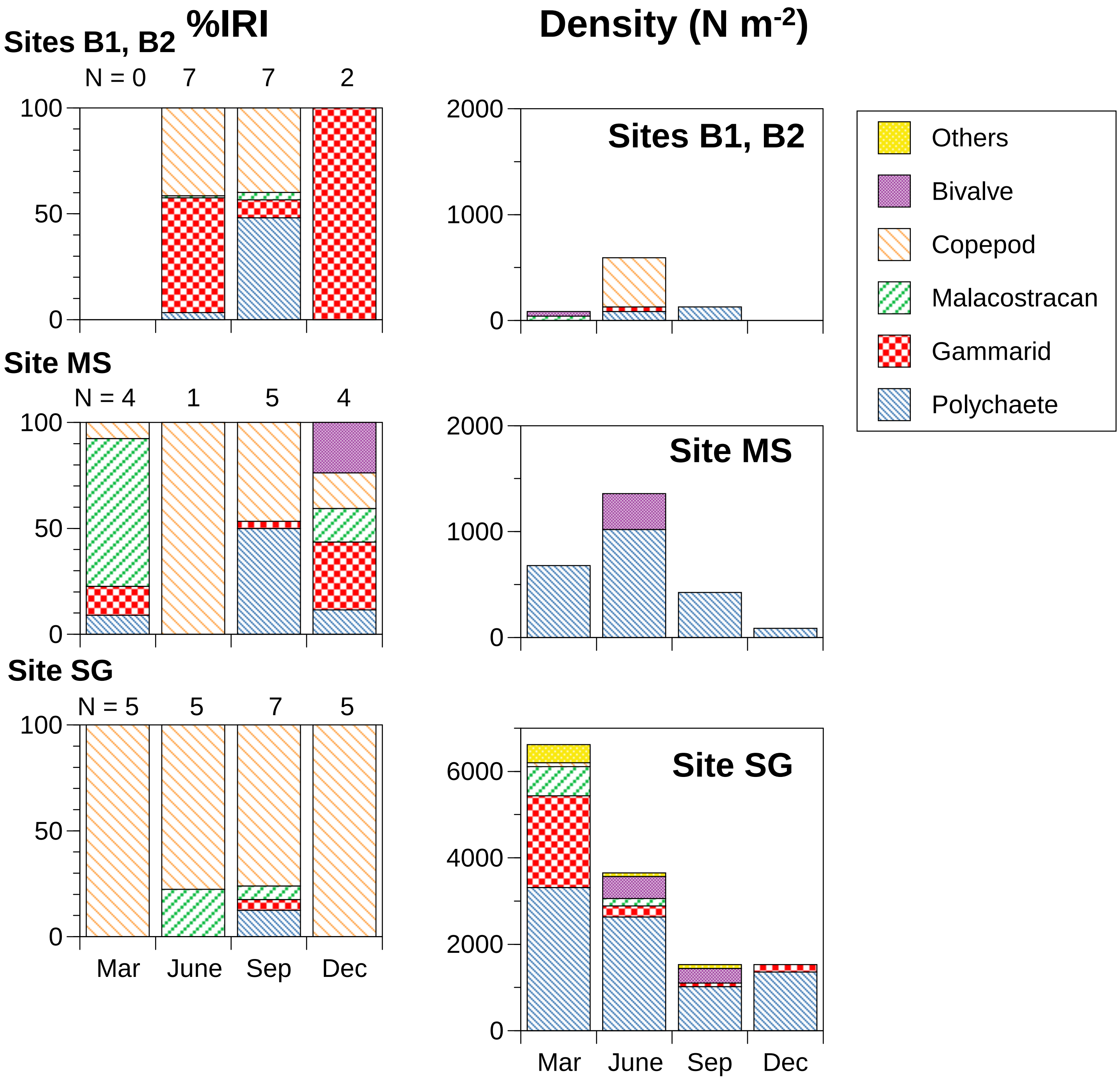
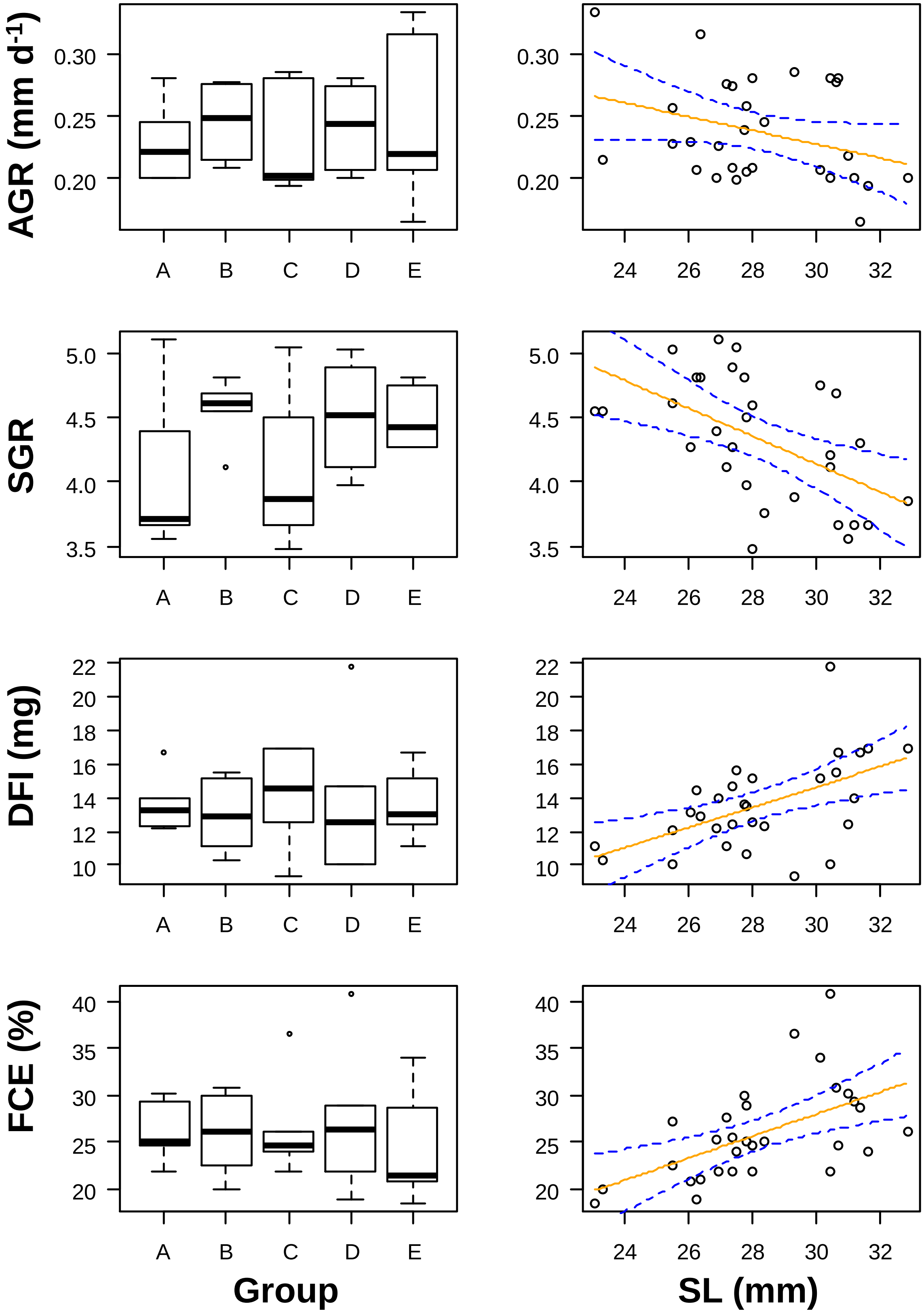

%IRI
Density (N m⁻²)
Sites B1, B2
N = 0
7
7
2
100
50
0
Site MS
N = 4
1
5
4
100
50
0
Site SG
N = 5
5
7
5
100
50
0
Mar
June
Sep
Dec
2000
1000
0
Sites B1, B2
2000
1000
0
Site MS
6000
4000
2000
0
Site SG
Mar
June
Sep
Dec
Others
Bivalve
Copepod
Malacostracan
Gammarid
Polychaete

Fig4


AGR (mm d^{-1})
0.20
0.25
0.30
SGR
3.5
4.0
4.5
5.0
DFI (mg)
10
12
14
16
18
20
22
FCE (%)
20
25
30
35
40
A
B
C
D
E
Group
24
26
28
30
32
SL (mm)