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Comparing ichthyofaunal composition between *Zostera japonica* beds (Plantae, Alismatales, Zosteraceae) and adjacent bare ground within a small temperate estuary in southern Japan

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Abstract

Zostera japonica Ascherson et Graebner, 1907 is a dominant seagrass species that forms coastal habitats in the northwestern Pacific. Bare areas adjacent to these seagrass beds are also recognized as fish habitat. However, few studies have comparatively evaluated the ecological importance of *Z. japonica* beds and adjacent bare ground within estuarine environments. We conducted seine net sampling to compare ichthyofaunal composition between *Z. japonica* beds and adjacent bare ground in a small temperate estuary in Kyushu, southern Japan, during three summer seasons (2015, 2016, and 2019), when seagrass growth is at its peak. Fish species richness and the abundance of the predominant species, *Redigobius bikolanus* (Herre, 1927), were significantly higher in the seagrass beds than over bare ground. Additionally, the size distribution of *R. bikolanus* was broader in seagrass beds. PERMANOVA analysis revealed a significant difference in abundance-based species composition between the two habitats, and SIMPER analysis identified three species that contributed most to this distinction: *R. bikolanus* and *Gerres japonicus* Bleeker, 1854 (both more abundant in seagrass beds), and *Gymnogobius breunigii* (Steindachner, 1880) (more abundant over bare ground). These findings imply that *Z. japonica* beds enhance fish diversity and serve as key habitats for dominant fish species, while adjacent bare ground also supports specific fish communities. The results underscore the importance of conservation efforts within estuaries that account for the ecological roles of both seagrass and bare substrates.

Keywords

Fish assemblages, fish diversity, sand/mud habitats, seagrass

Introduction

Seagrass beds are a vital component of coastal ecosystems worldwide, playing a key role in structuring biotic habitats and providing indirect benefits such as supplies of organic matter to a wide range of fish species, including those of commercial importance (Pollard 1984; Jackson et al. 2001; Hogarth 2007; Hyndes et al. 2018). In estuarine environments, seagrasses are among the most important macrophytes in terms of supporting

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fish communities (Whitfield 2017). Recent research has demonstrated that fish diversity and density in seagrass beds and over adjacent sand or mud bare ground vary depending on environmental conditions and the specific seagrass species present (Hyndes et al. 2018).

Moreover, unique fish species, including those targeted by fisheries, are often found over bare ground surrounding seagrass beds, highlighting the need for further investigation into the ecological roles of the two habitat types (Horinouchi et al. 2016, 2025). Notably, fragmented seagrass beds have been shown to support higher species diversity than continuous beds, with several species exhibiting greater densities in these fragmented habitats (Horinouchi et al. 2009; Horinouchi 2022). These findings imply that seagrass beds and adjacent bare ground fulfill distinct ecological functions within the same spatial context.

Therefore, elucidating differences in fish community structure between these two habitat types, across varying environmental conditions and seagrass species, is crucial for advancing our understanding of seagrass ecosystem dynamics and for informing effective conservation strategies (Horinouchi et al. 2025).

In East Asia and the northwestern Pacific, *Zostera japonica* Ascherson et Graebner, 1907 is a key species that forms seagrass beds in intertidal zones, including estuarine environments (Lee 1997; Huong et al. 2003; Taino 2004; Uede 2007). Its role in shaping complex coastal and estuarine habitats, coupled with its vulnerability to habitat loss, underscores the urgent need to conserve this species and its associated ecosystems (Hanawa 1996; Lee 1997; Taino 2004). To support effective policy development and conservation efforts, it is essential to understand the local ecological significance of estuarine seagrass beds and adjacent environments for fish communities.

Despite this need, few studies have examined the relationship between *Z. japonica* beds and fish communities (but see Fujita et al. 2002; Uede et al. 2012). In particular, variation in ichthyofaunal composition between *Z. japonica* beds and adjacent bare ground within estuaries is still poorly understood. Regional declines in *Z. japonica* populations (e.g., Hanawa 1996; Miyazaki Prefecture 2020) have further complicated direct sampling efforts in some areas. However, during environmental assessment surveys in Nobeoka City, Miyazaki Prefecture, southern Japan, the authors were able to conduct quantitative fish sampling in a small temperate estuary where *Z. japonica* remains present.

This study compared the fish community structure between *Z. japonica* beds and adjacent bare ground within the estuary, and evaluated the ecological roles of these habitats in supporting fish diversity and abundance.

Materials and methods

Study site. Quantitative fish surveys were undertaken in the Tomouchi River estuary, Nobeoka City, northern Miyazaki Prefecture, Kyushu, southern Japan (Fig. 1). This small estuary is a branch of the lower Kita River (mainstream) that is approximately 1.6 km long and 15 to 100 m wide, and rejoins the mainstream near the mouth. It is known for its large colonies of *Z. japonica* (Nobeoka City 2021). The targeted area (between 32°36′25.1″N, 131°41′40.3″E and 32°36′33.1″N, 131°41′42.0″E) is in the upper reaches of the estuary, covering an area of

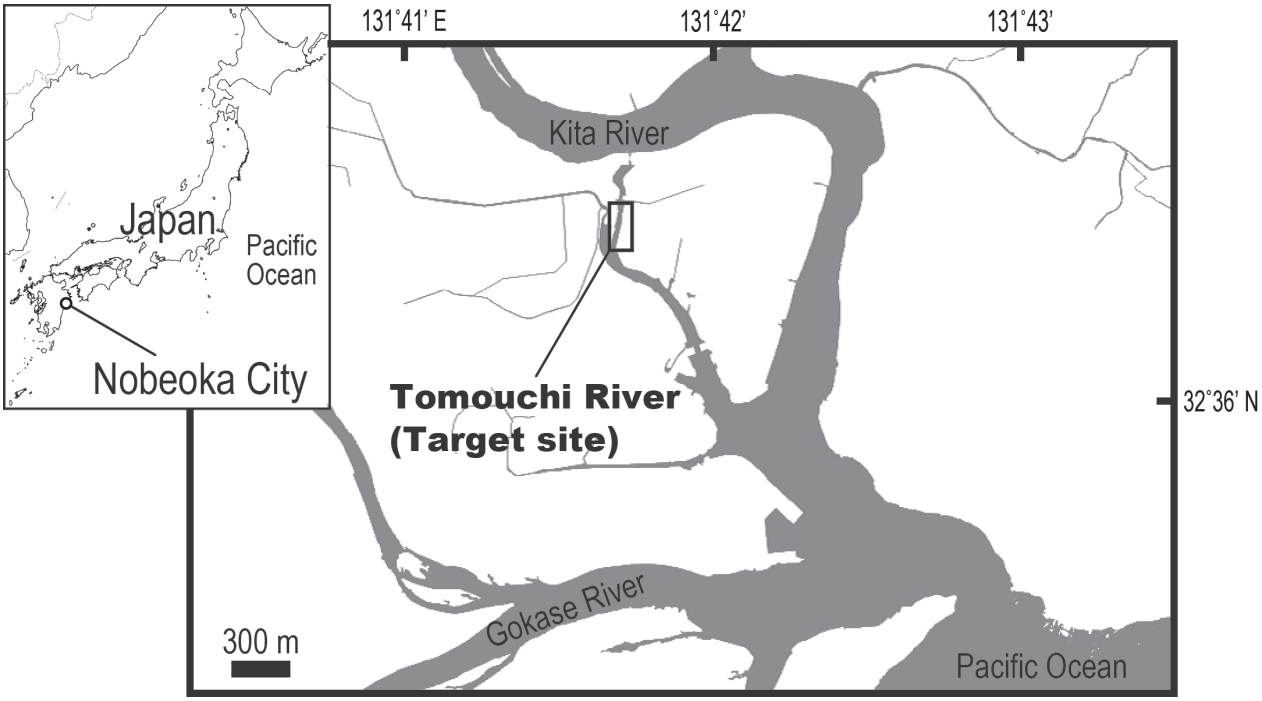


Figure 1. Map showing location of the study site in the Tomouchi River estuary, Nobeoka City, Miyazaki Prefecture, Kyushu, southern Japan. Maps of the Japanese mainland and sampling sites were modified from free maps (https://www.freemap.jp/) and a topographic map from the Geospatial Information Authority of Japan, respectively.

approximately 5500 m^2, about half of which is covered by relatively dense colonies of *Z. japonica*. The substrate consists of *Z. japonica* beds of various sizes and sand/mud bare areas. The maximum tidal range at the study site is nearly 2 m, and the *Z. japonica* bed is submerged at high tide and partially exposed to the air at low tide.

Sampling. From the perspective of conserving *Z. japonica*, which is a near-threatened (NT) species in Miyazaki Prefecture that has declined significantly due to habitat and water-quality degradation (Miyazaki Prefecture 2020), ichthyofaunal surveys should be conducted using non-destructive methods (e.g., visual census); however, the target site where this seagrass species grows is extremely shallow and can become turbid under certain conditions. Considering these issues, we used a relatively small seine net to survey the fish fauna. Consistent with the general seasonal growth patterns of seagrasses (Whitfield 2017), the density of *Z. japonica* in southern Japan is relatively high during the summer months (June to September) (Taino 2004; Uede 2007). Therefore, the survey period was scheduled for July or August, when precipitation levels are relatively low and environmental conditions are more stable. To minimize ecological disturbance during sampling, the number of surveys conducted per year was kept to a minimum. However, to ensure sufficient data collection, fish sampling was carried out three times over multiple years: August 2015, July 2016, and August 2019.

Fish were sampled using a small seine net (2-mm mesh), consisting of two 2.3-m-long/0.78-m-high wings and a 2.55-m-long/0.92-m-wide bunt (Murase et al. 2025). For each sampling, the net was towed for a distance of 10 m, with the net held open at a width of 3 m (covering an area of 30 m^2 per haul). This procedure was performed several times (n = 4) per year in each habitat (seagrass beds and adjacent bare ground), resulting in 40 m of seining per habitat annually. Sampling was conducted during daylight hours (around low tide during spring or neap tides) at a depth of approximately 0.5 m. Water temperature and salinity were measured once per haul, following Murase et al. (2025). For salinity measurements in 2015 and 2016, a YK-31SA device (Sato Shouji Inc., Kawasaki, Japan) was used but it was carried out by sampling water from the middle layer with a 2-mL tube using a digital salinity meter (PAL-06S, Atago, Co., Ltd., Osaka, Japan) in 2019.

Laboratory procedure. All sampled fish were euthanized immediately after collection and subsequently fixed and preserved in the laboratory following Murase et al. (2025). The fish were identified in the laboratory based on Nakabo (2013) and Okiyama (2014), while scientific names followed the taxonomy of Motomura (2025). The standard length (SL) of each specimen was measured according to Murase et al. (2025). To estimate fish biomass per seine haul, the wet weight (g) of each specimen lot (corresponding to each museum collection number) was measured using an electronic analytical balance (ATX124, Shimadzu Co., Ltd., Tokyo, Japan).

To ensure traceability of the materials examined, voucher specimens were deposited in the fish collection of the Kanagawa Prefectural Museum of Natural History, Odawara, Japan (KPM-NI). A complete list of these specimens, including measurements and wet weights, is provided in Suppl. material 1. Registration numbers in the KPM database consist of seven digits, including leading zeros (e.g., KPM-NI0089914), but leading zeros are omitted in this manuscript.

An unidentified specimen of Gobiidae (KPM-NI 90207) was treated as a species distinct from any identified Gobiidae species in this study. Additionally, because species of *Mugilogobius* other than *Mugilogobius abei* (Jordan et Snyder, 1901) are extremely rare in Miyazaki Prefecture (Murase et al. 2015), an unidentified specimen of the genus (KPM-NI 90161) that could not be identified due to its small size was treated as *M. abei* for the purposes of the following analysis.

Statistical analysis. All statistical analyses were conducted using R version 4.3.3 (R Core Team 2024). For paired comparisons, tests were performed matching the year of sampling and the order of seine net. Variation in water temperature between seagrass beds and bare ground was tested using the Wilcoxon signed-rank test, as the normality assumption was violated even after log10 (x + 1.0) transformation. Paired Student's t-tests were used to compare salinity, fish abundance, biomass, and the diversity index (Simpson's D: Krebs 1999) between the two habitats. Fish species richness was analyzed using Welch's t-test because the data were normally distributed but exhibited unequal variance between habitats. Among these variables, abundance and biomass were tested after log10 (x + 1.0) transformation.

The size distribution of the predominant fish species was compared using the Wilcoxon rank-sum test, as the data did not meet the assumption of normality. To assess differences in fish species composition between habitats, the similarity index of Chao et al. (2005) (an extension of the Jaccard index that accounts for unseen species and abundance data; Doi and Okamura 2011) was calculated. Non-metric multidimensional scaling (NMDS) was used to generate ordination plots based on the Chao similarity values.

To test for variation in species composition between habitats, permutation multivariate analysis of variance (PERMANOVA) was performed using the adonis2 function in the R package "vegan," based on abundance per seine of each fish species, with 999 permutations and the Chao method. Similarity percentages analysis (SIMPER) was also conducted to identify the individual species contributing most to the dissimilarity in species composition between the habitats.

Results

Environmental data are presented in Suppl. material 2. Physical conditions did not significantly differ between the two habitats, with mean water temperature and salinity showing no notable variation. In all, 24 seine samplings

conducted in the upper reaches of the Tomouchi River estuary over three summers yielded 1288 individuals (317.0 g in biomass), representing 32 species (including two unidentified taxa) from 11 families. A detailed list of the fish species collected each year in each habitat is provided in Suppl. material 3.

The gobiid species *Redigobius bikolanus* (Herre, 1927) was consistently present in both habitats across all years and accounted for more than 50% of the total catch in each habitat in 2015 and 2019. Due to its dominance in the catch, *R. bikolanus* was selected for further comparisons of abundance and body size between the two habitats. Overall, fish assemblage metrics tended to be higher in seagrass beds than over bare ground (Fig. 2), although most comparisons were not statistically significant, except for species richness ($P < 0.001$) and the abundance of the predominant species ($P < 0.01$).

The SL of *R. bikolanus* did not differ significantly between habitats (analysis for 2016 was omitted due to a limited sample size). However, within each year, the individuals from seagrass beds exhibited a broader size range, including larger specimens, compared to those from bare ground (Fig. 3).

The NMDS ordination (stress value = 0.214; Fig. 4) indicated a weak tendency to separate fish community structures between habitats. Nonetheless, PERMANOVA revealed significant differences in species composition ($P < 0.01$). SIMPER analysis identified three species as contributing most to the dissimilarity between habitats, with the following contribution values: *R. bikolanus* (0.50), *Gymnogobius breunigii* (Steindachner, 1880) (0.20), and *Gerres japonicus* Bleeker, 1854 (0.07). These species were consistently dominant (first or second in percent abundance) in at least one habitat each year, and their abundance was strongly biased toward the habitat they dominated. Specifically, *R. bikolanus* was markedly more abundant in seagrass beds than over bare ground (306 vs. 30 in 2015; 22 vs. 2 in 2016; 294 vs. 110 in 2019). The pattern for *Ge. japonicus* was similar (118 vs. 3 in 2015; absent in 2016 and 2019), whereas *Gy. breunigii* exhibited the opposite trend (2 vs. 15 in 2015; 0 vs. 195 in 2016; absent in 2019).

Discussion

Although previous studies have documented the occurrence patterns of several fish species in *Z. japonica* beds within temperate estuaries (Fujita et al. 2002), no research to date has compared ichthyofaunal composition between these vegetated habitats and adjacent bare ground. The presently reported study is the first to demonstrate structural differences in summer fish assemblages between *Z. japonica* beds and nearby unvegetated areas in a small temperate estuary. Specifically, fish species richness and the abundance of the predominant species were significantly higher in seagrass beds, and species composition differed markedly between the two habitats, with three representative species contributing to this distinction.

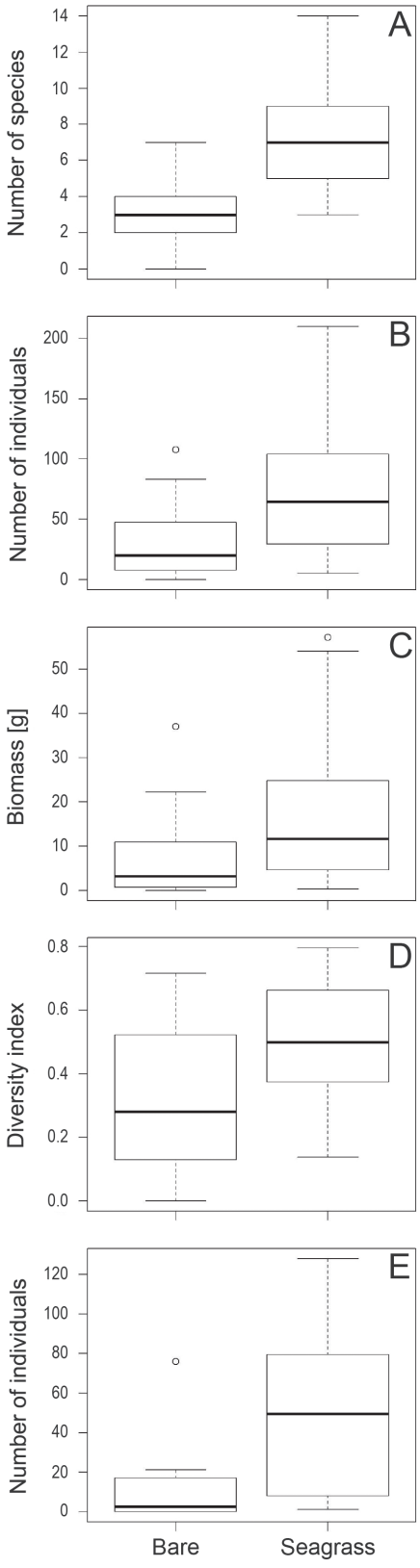


Figure 2. Boxplots showing differences in variation in five parameters of fish assemblages between bare ground (left, $n = 12$) and seagrass beds (right, $n = 12$) within the estuary: **A**, species richness; **B**, fish abundance; **C**, fish biomass; **D**, diversity index (Simpson's D); **E**, abundance of predominant species (*Redigobius bikolanus*). Horizontal lines indicate the minimum, 25th percentile, median, 75th percentile, and maximum of the data, and open circles show outliers.

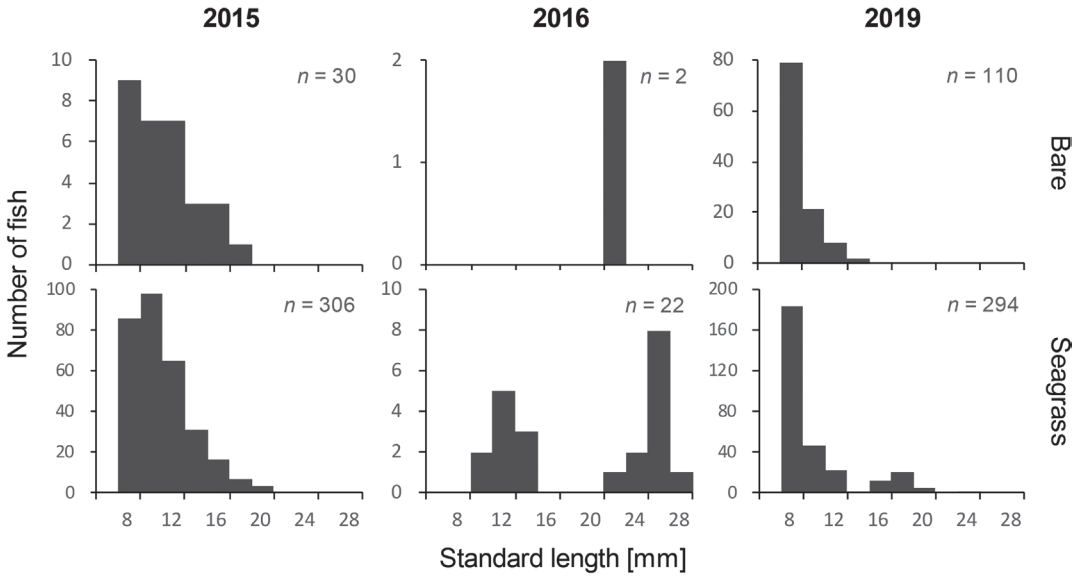


Figure 3. Histogram of the standard lengths of the predominant fish species *Redigobius bikolanus* collected from seagrass beds (lower) and adjacent bare ground (upper) in the Tomouchi River estuary showing similar size distributions among habitats with a wider size class range in the seagrass beds than over the bare ground sites each year.

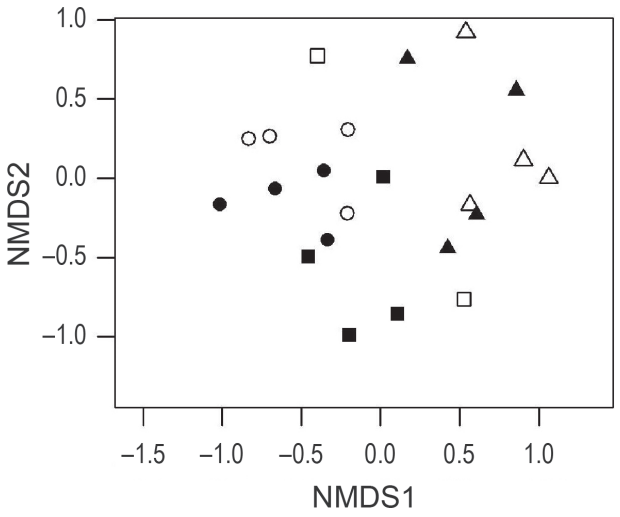


Figure 4. NMDS plots showing weak discrimination of abundance-based fish species composition between seagrass beds (solid symbols) and bare ground (open symbols) in the Tomouchi River estuary, southern Japan: circle, 2015; triangle, 2016; square, 2019. Four samples were collected from each habitat in each year, but for bare ground in 2019, either no fish were collected or there were samples with similar species composition, resulting in only two plots.

Previous research in similar temperate estuaries has shown that seagrass beds support greater fish species diversity than adjacent unvegetated areas (Beckley 1983; Connolly 1994), and the current findings are consistent with this pattern. The significantly higher species richness observed in seagrass beds may be attributable to the presence of multiple low-dominance species (<3.0%) that were found exclusively in seagrass habitats each year (Suppl. material 3). Many of these species—e.g., *Hippichthys heptagonus* Bleeker, 1849, *Lates japonicus* Katayama et Taki, 1984, *Nuchequula nuchalis* (Temminck et Schlegel, 1845), *Gerres equulus* Temminck et Schlegel, 1844, and *Rhynchopelates oxyrhynchus* (Temminck et Schlegel, 1843)—are associated with seagrass habitats during their life cycles (Kinoshita et al. 1988; Fujita et al. 2002; Sato et al. 2016; Kurihara et al. 2021), implying that when seagrass beds and bare ground coexist within an estuarine system, these species preferentially occupy the vegetated environment.

Notably, several species that occurred only in seagrass beds during this study, such as *Gymnogobius uchidai* (Takagi, 1957) and *Pseudogobius masago* (Tomiyama, 1936), are typically found in tidal flats or over sand/mud bottoms. In areas where seagrass beds and bare ground coexist, it is possible that these species utilize different habitats seasonally. Clarifying these patterns will require further seasonal surveys. This study demonstrates that fish species richness is higher within seagrass beds than over adjacent bare ground, at least during the summer when *Z. japonica* is at peak growth. These findings imply that *Z. japonica* beds contribute to enhancing fish diversity in the temperate estuaries of the western Pacific Ocean. Several factors may influence fish habitat selection of seagrass beds, including predator avoidance and food availability (Horinouchi 2007), and further research is needed to elucidate the mechanisms by which *Z. japonica* beds support fish diversity in estuarine environments.

In this study, *Redigobius bikolanus* was identified as the predominant species both in seagrass beds and over bare ground, with significantly higher abundance observed in the former habitat. Additionally, individuals from seagrass beds exhibited a broader size range, implying that these habitats may support a wider range of developmental stages. This pattern of abundance and size distribution aligns with findings from a previous study conducted in another estuary (Fujita et al. 2002). *R. bikolanus* is primarily an estuarine species, typically found near or beneath structures such as leaves and macrophytes (Dotsu et al. 2008;

Takeuchi 2019). Collectively, the present and past studies imply that *Z. japonica* beds serve as a preferred habitat for this goby compared to adjacent bare ground.

Fish species composition was statistically differentiated between seagrass beds and bare ground, primarily due to the presence of three representative species that dominated either habitat in specific years. These findings highlight the distinct ecological roles that each habitat plays in supporting the fish communities within an estuary. Among the species that were more abundant in seagrass beds were *R. bikolanus* and the gerreid *Gerres japonicus*. Although *Ge. japonicus* can reach up to 15 cm in SL (Nakabo 2013), all specimens collected in this study (8.1–23.0 mm SL) were immature, implying that *Z. japonica* beds may function as nursery habitat for this species. While confirmation of the nursery function requires comparative studies across multiple habitats, including marine environments, the present findings indicate that *Ge. japonicus* is a key species characterizing the fish community in seagrass beds during the peak growth period of *Z. japonica*, and that these beds provide an important habitat within the estuary.

In contrast, *Gymnogobius breunigii*, another gobiid species contributing to the differentiation of fish communities, was almost exclusively found over bare ground habitats. This species inhabits and breeds in sand/mud flats of estuaries (Inui et al. 2011), and its distribution in this study implies a strong preference for unvegetated substrates, even when seagrass beds are present. These results underscore that bare ground habitats can be more critical than seagrass beds for certain fish species.

Overall, the results of PERMANOVA and SIMPER analyses reflect the ecological importance of both *Z. japonica* beds and adjacent bare ground for different fish species within a small estuary. This study demonstrated clear differences in ichthyofaunal composition between coexisting seagrass and bare ground habitats during summer, when *Z. japonica* is most abundant. These differences were driven by variation in species abundance and the presence of distinct dominant species in each habitat. The findings are consistent with previous studies conducted along the tropical coast of Thailand, which examined fish assemblages in seagrass beds and over bare sand/mud ground (Horinouchi et al. 2016, 2025). Those studies concluded that conservation and restoration policies should account for the ecological value of both habitat types. In line with these recommendations, the present study emphasizes that seagrass restoration projects in temperate estuaries where *Z. japonica* occurs should identify original seagrass distribution areas and incorporate conservation strategies that also recognize the ecological functions of adjacent bare sand/mud ground, as advocated by Horinouchi et al. (2025).

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Supplementary material 1

Voucher specimen list

Authors: Yoi Ota, Ryuya Sakamoto, Yukiya Ogata, Takumi Kurihara, Atsunobu Murase

Data type: xlsx

Explanation note: All of examined specimens data (collection number, species, size, weight, etc.) are listed here.

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Link: https://doi.org/10.3897/aiep.55.168507.suppl1

Supplementary material 2

Environmental data

Authors: Yoi Ota, Ryuya Sakamoto, Yukiya Ogata, Takumi Kurihara, Atsunobu Murase
Data type: xlsx
Explanation note: Environmental data (water temperature and salinity) collected during the survey are shown here.
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Link: https://doi.org/10.3897/aiep.55.168507.suppl2

Supplementary material 3

Species list

Authors: Yoi Ota, Ryuya Sakamoto, Yukiya Ogata, Takumi Kurihara, Atsunobu Murase
Data type: xlsx
Explanation note: Fish species and abundance recorded in the present study are listed here.
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