1	Variations in epifaunal assemblages among different algal species in the coastal waters of the
2	Noto Peninsula, Japan
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4	Variations in epifauna by algal species
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22	
23	Abstract
24	Algal beds are biodiversity hotspots in coastal ecosystems, forming complex food webs based on
25	seaweeds. Epifauna serve as important indicators of algal productivity and environmental change,
26	interacting closely with their host seaweeds. This study compared the composition of epifaunal
27	assemblages associated with different seaweed species in the Noto Peninsula, Japan, to elucidate their
28	characteristics. A survey of epifaunal communities on 13 seaweed species around Tsukumo Bay
29	revealed significant differences in abundance and composition among species. Epifaunal abundance
30	was particularly high in Sargassum siliquastrum and S. patens. Differences in assemblage structures
31	were observed among seaweed species and sampling sites, with flow velocity, salinity, and water depth
32	identified as key environmental factors. Fucales seaweeds harbored more diverse epifaunal
33	communities compared to Laminariales species. Variations in epifaunal composition among taxa
34	suggest that interactions with host seaweed species play a crucial role in shaping community structure.
35	
36	Keywords: algal beds, Sargassum seaweeds, epifaunal community, Sea of Japan

Introduction

39 Algal beds serve as biodiversity hotspots in coastal ecosystems, offering habitat and food resources 40 for a wide range of marine organisms. As primary producers, seaweeds support complex food webs 41 that sustain various invertebrates and fish (Fuse, 1962; Mukai, 1978). These ecosystems also 42 contribute to carbon sequestration and water purification, enhancing coastal environmental stability 43 (Akeda et al., 2010; Filbee-Dexter et al., 2024).

44 Epifauna, small invertebrates residing on or near seaweed surfaces, act as key indicators of 45 ecosystem health and productivity. Primary composed of crustaceans and gastropods, these 46 communities are shaped by environmental conditions, seasonal changes, and structural characteristics 47 of their host seaweed (Mukai, 1978; Yamamoto et al., 1999). Factors such as structural complexity, 48 food availability, wave action and interaction with other algal species contribute to seasonal variations 49 in faunal communities (Hirst, 2007; Machado et al., 2015; Winkler et al., 2017). Epifauna benefit 50 seaweeds by controlling competitive epiphytes and facilitating fertilization, but can also negatively 51 impact hosts through direct grazing (Duffy, 1990; Mancinelli & Rossi, 2001; Kamermans et al., 2002; 52 Poore et al., 2014; Lavaut et al., 2022). These findings highlight the multifunctional role of epifaunal 53 communities in algal ecosystems. 54 Previous studies have examined the effects of specific seaweed species and their morphology on

55 epifaunal assemblages (e.g. Mukai, 1971; Imada et al., 1981; Ito et al., 2019; Kodama et al., 2020). 56 However, how different seaweed species share epifaunal communities and form distinct assemblages 57 remains unclear, with regional and environmental factors influencing outcomes (Saito et al., 2002; 58 Yatsuya et al., 2008). Understanding these interactions is particularly important in Japan's coastal 59 regions, known for their high biodiversity and complex environmental conditions. This study 60 investigates epifaunal assemblages across multiple seaweed species in the Noto Peninsula, a central 61 region of the Sea of Japan. By comparing epifaunal diversity and abundance among different host 62 seaweeds, we aim to clarify the influence of seaweed species and environmental factors on community 63 structure. These findings provide insights into coastal ecosystem dynamics and species interactions in algal beds. 64

65

#### 66 **Materials and Methods**

67 Seaweeds were randomly collected from Sargassum beds at depths shallower than 1 m around 68 Tsukumo Bay on the Noto Peninsula in February and March 2023. Sampling sites included six 69 locations: Hime port (HP), Ogi port (OP), Noto Isaribi Youth Hostel (NIYH), Hotel Notokinpura (HN), 70 Noto Marine Center (NMC), Shiromaru (S) (Fig. 1). Individual seaweeds were manually collected

- 71 from the holdfast while wearing a long body suit and stored in plastic bags. Environmental parameters,
- 72 including illuminance (lux), air temperature (°C), water temperature (°C), salinity (‰), depth (cm),

and flow velocity (cm/s; VR-401, Kenek, Japan), were measured at each site. Collected seaweeds were
 stored at -20°C.

75 Defrosted seaweeds were washed three times in a water-filled bucket by rubbing. This method 76 recovers over 99% of total epifaunal abundance in S. fusiforme (Kondo et al., 2019). Organisms 77 detached from seaweeds were collected using a 1.0 mm sieve and classified into 11 taxa, based on Ito 78 et al. (2019) and Ministry of Environment (accessed online 2 January 2025), plus three Decapoda taxa: 79 Nematoda, Mollusca, Gastropoda, Bivalvia, Annelida, Arthropoda, Gammaridea, Caprellidea, Isopoda, 80 Caridea, Anomura and Brachyura. Taxa such as Foraminifera, Acarina, Ostracoda, Tanaidacea, 81 Cumacea, and Harpacticoida were excluded as they were not found in this study. Ito et al. (2019) and 82 Ministry of Environment (accessed online 2 January 2025) included Polychaeta, but as it is now 83 considered non-monophyletic, Annelida was used instead (Kobayashi, 2021). The suborder 84 Caprellidea was reclassfied into Senticaudata along with some Gammaridea taxa, invalidating both 85 suborders (Lowry & Myers, 2013, 2017). However, following Kodama et al. (2020), we treated the historical suborders Gammaridea and Caprellidea separately. The wet weight of seaweeds, after 86 87 removing organisms, was measured using a digital scale with 0.1 g accuracy.

- 88 Epifaunal abundance was normalized to individuals per 100 g of seaweed. All subsequent analyses 89 were based on standardized abundances. Cluster analysis using Ward's method (ward.D2) grouped 90 samples at 50% similarity. PERMANOVA assessed the effects of host seaweed species, location, and 91 their interaction on community structure. Non-metric multidimensional scaling (nMDS) based on 92 Bray-Curtis distance visualized faunal community similarities. Species significantly influencing 93 community structure were identified at the 5% level, while environmental factors were analyzed at the 94 10% level. Renyi's diversity profiles were calculated for each sample and averaged for each seaweed 95 species. Community prosperity was calculated by multiplying total abundance by the number of 96 effective species as determined from Renyi's diversity profile. All statistical analyses were performed 97 in R (version 4.3.2), using the 'vegan' package (version 2.6.4) (Oksanen et al., accessed online 7 98 February 2025) for ordination and the 'adonis2' function for PERMANOVA, the 'metaMDS' function 99 for nMDS, and the 'renyi' function for Renyi's diversity profiles. These results were output by the 100 'ggplot2' package (version 3.5.1) (Wickham et al., accessed online 7 February 2025).
- 101

#### 102 **Results**

103 A total of 13 species (39 individuals) were collected from six sites around Tsukumo Bay (Table 1).

104 These included 10 species of Fucales (Myagropsis myagroides, Sargassum autumnale, S. confusum, S.

105 horneri, S. macrocarpum, S. microceratium, S. patens, S. piluliferum, S. siliquastrum, and S.

- 106 thunbergii), two Laminariales species (Ecklonia cava and Undaria pinnatifida), and one red algal
- 107 species, Gracilariales (*Gracilaria textorii*). The average wet weight of each seaweed (Fig. 2) exceeded
- 108 300 g for *M. myagroides*, *S. horneri*, *S. microceratium*, and *S. piluliferum*, while *S. macrocarpum*, *S.*

109 patens, and S. siliquastrum averaged around 200 g. Sargassum autumnale, S. confusum, S. thunbergii,

110 *E. cava*, and *U. pinnatifida* had average weights of approximately 100 g, with *G. textorii* being the 111 lightest at about 20 g.

Epifaunal abundance (Fig. 2) was highest in *S. siliquastrum* (403 individuals), approximately 1.5
times higher than in *S. patens* (241 individuals). *Sargassum autumnale* and *S. macrocarpum* had 141
individuals each. Other species, including *M. myagroides*, *S. confusum*, *S. microceratium*, and *S. piluliferum*, harbored around 100 individuals, while *S. horneri*, *S. thunbergii*, *E. cava*, *U. pinnatifida*,
and *G. textorii* supported fewer than 50 individuals.
Cluster analysis (Fig. 3) revealed five distinct clusters: (1) *S. thunbergii*, *E. cava*, *U. pinnatifida*,

118 and G. textorii; (2) S. horneri, S. macrocarpum, S. thunbergii, E. cava, and U. pinnatifida; (3) S. 119 macrocarpum, S. patens, and S. siliquastrum; (4) S. autumnale, S. macrocarpum, and S. patens; (5) M. 120 myagroides, S. autumnale, S. confusum, S. horneri, S. microceratium, S. patens, S. piluliferum, S. 121 thunbergii, and G. textorii. Cluster 1 and 2 formed a sister group, as did clusters 4 and 5. Clusters 3, 122 4, and 5 formed a higher-level sister group. Additionally, samples clustered partly by collection site. 123 Half of cluster 2 consisted of Laminariales species from HP and OP, cluster 3 composed mostly Fucales 124 in HP, and half of cluster 5 included seaweeds from NMC. Community structure significantly differed 125 among host seaweed species and collections (PERMANOVA, p = 0.001 for both), with interactions 126 between these factors (p = 0.006).

127 The nMDS plots (Fig. 4) exhibited an acceptable stress value (0.121), supporting adequate 128 ordination of samples. Environmental factors contributing to sample similarity (10% significance 129 level) included flow velocity, salinity, and water depth, while water temperature, air temperature, and 130 illumination were not significant. Significant taxa contributing to community differences (5% 131 significance level) were Annelida, Caprellidea, Caridea, Gammaridea, Gastropoda, and Isopoda. 132 Renyi's diversity profiles (Fig. 5A) indicated that the 10 Fucales species showed a marked decline 133 from q = 0 to q = 2, whereas E. cava, U. pinnatifida, and G. textorii exhibited little variation. The top 134 three species in epifaunal richness (q = 0) were *M. myagroides*, *S. siliquastrum*, and *S. patens*, while 135 the lowest were U. pinnatifida, G. textorii, and E. cava. Shannon's diversity index (q = 1) ranked S. 136 confusum, M. myagroides, and S. siliquastrum highest, with U. pinnatifida, S. microceratium, and G. 137 *textorii* lowest. The inverse of Simpson's diversity index (q = 2) ranked S. confusum, M. myagroides, 138 and E. cava highest, while U. pinnatifida, S. microceratium, and S. piluliferum were lowest. Similarity, 139 E. cava, S. confusum, and M. myagroides exhibited the highest inverse dominance values (q = Inf), 140 whereas U. pinnatifida, S. microceratium, and S. piluliferum had the lowest. Undaria pinnatifida 141 showed the lowest diversity across all q values. Community prosperity (Fig. 5B) was highest for S. 142 siliquastrum across all q values, followed by S. patens and S. macrocarpum. Conversely, U. pinnatifida 143 consistently showed the lowest values, followed by E. cava and G. textorii. In terms of epifaunal

144 composition (Fig. 6), Gastropoda accounted for over 50% of the abundance in S. autumnale, S.

145 microceratium, S. piluliferum, S. thunbergii, and G. textorii, while Gammaridea dominated in S.

146 *horneri*, *S. patens*, and *S. siliquastrum*. Caprellidea made up 50% of the epifauna in *Ecklonia cava* and

147 U. pinnatifida. In al seaweed species except S. confusum, Caprellidea, Gammaridea, and Gastropoda

148 collectively represented over 85% of total epifauna. In S. confusum, these groups accounted for about

- 149 60%, with Isopoda contributing around 35%. Other taxa, such as Annelida in S. thunbergii and E. cava,
- 150 comprised about 10%, while all remaining taxa were under 5%.
- 151

## 152 Discussion

153 This study examined how epifaunal communities varied by location and host seaweed species. Wet 154 weights of S. autumnale, S. confusum, S. thunbergii, E. cava, and U. pinnatifida were similar. However, 155 epifaunal abundance varied, with S. autumnale and S. confusum supporting 140 and 100 individuals, 156 respectively, whereas S. thunbergii, E. cava, and U. pinnatifida had fewer than 50 individuals. These 157 differences may be attributed to seaweed morphology and ecology. Sargassum thunbergii has smaller 158 leaves and pneumatocytes than other Sargassum species (Yoshida, 1983), providing fewer food 159 resources and hiding places. It also inhabits shallower water (Yatsuya et al., 2006), making it more 160 susceptible to environmental fluctuations (Inoue, 1977; Ito et al., 2019). Ecklonia cava and U. pinnatifida, both Laminariales, have simpler morphologies than Fucales, potentially explain their 161 162 lower epifaunal abundance. Dotsu et al. (2010) found that epifaunal abundance correlates with 163 seaweed complexity, a trend supported by this study. The nMDS plot also suggested that S. thunbergii, 164 E. cava, and U. pinnatifida were associated with fewer key epifaunal taxa, including Annelida, 165 Caprellidea, Caridea, Gammaridea, Gastropoda, and Isopoda. Gracilaria textorii had low epifaunal 166 abundance and occupied an nMDS position opposite the depth vector, suggesting its simple 167 morphology and shallow habitat contribute to low epifaunal density. Sargassum horneri, despite its 168 large wet weight, had the lowest epifaunal abundance among Fucales. Ito et al. (2019) reported that 169 its epifaunal assemblage primarily consists small bivalve spats and harpacticoid copepods, which may 170 have been underrepresented in this study due to the use of a 1 mm sieve instead of a 100 µm sieve.

171 Cluster analysis categorized the samples into two primary groups: Laminariales-dominated clusters

(clusters 1 and 2) and Fucales-dominated clusters (clusters 3, 4, and 5). Renyi's diversity profile also distinguished these groups, with Fucales exhibiting greater species richness and diversity. Fucales hosted more rare species and had higher community prosperity values, likely due to their complex structures providing abundant niches. *Myagropsis* and *Sargassum*, both in the family Sargassaceae, did not form distinct epifaunal communities, suggesting structural complexity rather than taxonomy is the primary determinant of epifaunal diversity. *Gracilaria textorii* appeared in clusters 1 and 5, indicating inconsistent similarity. As the only red alga in this study, its epifaunal community remains

179 insufficiently understood, necessitating further research.

180 Community structure also varied significantly by site, likely due to differences in environmental

conditions such as flow velocity and salinity. Site facing the open ocean (NIYH, NMC, S) exhibited
high flow velocity and suspended sediments, while inner bay sites (HP, OP, HN) had slower currents
and higher sediment deposition (Tamaki, 1981). These conditions affect seaweeds function as habitat

and food source, shaping distinct community structures at each location.

Across all seaweed species, Caprellidea, Gammaridea, and Gastropoda dominated the epifaunal communities, consistent with previous studies (Yamamoto *et al.*, 1999; Yatsuya *et al.*, 2008; Dotsu *et al.*, 2010; Shinohara & Shimooka, 2024). Caprellids were abundant only on two Laminariales species, possibly due to their ability to mimic seaweed and evade predation (Goto, published online 2023).

189 The Noto Peninsula Earthquake on January 1, 2024, severely impacted the Tsukumo Bay area, 190 leading tsunamis, sediment deposition, and seafloor alterations. Among the surveyed sites, Shiromaru 191 (S) was particularly affected by the tsunami, which caused severe coastal disturbances. This 192 disturbance likely affected not only Sargassum species but the entire seaweed assemblage, potentially 193 leading to shifts in species composition and structural complexity. Given the role of diverse seaweeds in maintaining epifaunal biodiversity, future surveys should assess long-term ecological impacts and 194 195 recovery processes. Similar effects were observed following the 2011 Tohoku Earthquake, which 196 significantly altered benthic habitats and community structures in coastal Japan (e.g. Kanaya et al., 197 2012; Abe et al., 2015; Noda & Iwasaki, 2017; Sugiura et al., 2024). The ecological data from this 198 study will serve as a critical baseline for evaluating post-earthquake changes in small invertebrate 199 communities in the Noto Peninsula coastal region. Long-term monitoring will be crucial for assessing 200 ecosystem resilience and recovery following seismic disturbances.

This study revealed variations in epifaunal abundance and composition across 13 seaweed species.
 Future research should monitor seasonal changes to better understand epifaunal life cycles in relation
 to seaweed phenology.

204

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210

#### 211 Author contributions

Keito Tsunoda: conceptualization, investigation, analysis, writing of first draft; Yukimasa
Higashide: species identification of seaweed; Kenji Toyota: conceptualization, investigation, writing.

214

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219	
220	Competing interest
221	The authors declare none.
222	
223	Data availability
224	All research data are available upon request to Kenji Toyota (toyotak@hiroshima-u.ac.jp).
225	
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Fig. 1. Sampling site of this study around Tsukumo Bay, Noto Peninsula, Japan. Abbreviation is the
name of seaweed collection sites. HN: Hotel Notokinpura, HP: Hime port, NIYH: Noto Isaribi
Youth Hostel, NMC: Noto Marine Center, OP: Ogi port, S: Shiromaru.



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Fig. 2. Wet weight of seaweed species and epifaunal abundance. The bars represent seaweed wet
 weight, and the plots represent epifaunal abundance. Error bars are expressed as mean + standard
 deviation. The number after the scientific name indicates the number of samples.



Fig. 3. Cluster analysis of epifauna in each seaweed sample. Sample names were represented by "the
 scientific name\_collection location\_ seaweed replication number". The red dashed line represents
 the position of the 50% similarity, and each color corresponds to each cluster.







Fig. 4. Non-metric multidimensional scaling grouped by seaweed species. nMDS plot with
environmental information selected at the 10% significance level (A), and with the taxon selected
at the 5% significance level (B). The number after the scientific name indicates the number of
samples.



Fig. 5. Renyi's diversity profiles by seaweed species (A) and community prosperity by seaweed
species (B). The vertical axis is expressed on a log scale (B). The number after the scientific name
indicates the number of samples.



356 Fig. 6. Percentage of epifauna by seaweed species. The number after the scientific name indicates the

number of samples.

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364	Table	1.	Collected	seaweed.

Order	Species	Number of samples	Site
	M. myagroides	2	NIYH
	S. autumnale	4	NMC, S
	S. confusum	1	S
	S. horneri	2	HP
Fuenles	S. macrocarpum	5	HP, OP, S
Fucales	S. microceratium	3	NMC
	S. patens	5	HP, HN
	S. piluliferum	1	NMC
	S. siliquastrum	2	HP
	S. thunbergii	4	NMC, S
Laminariales	E. cava	2	HP
	U. pinnatifida	6	HP, NIYH, OF
Gracilariales	G. textorii	2	NMC

365 HN: Hotel Notokinpura, HP: Hime port, NIYH: Noto Isaribi Youth Hostel, NMC: Noto Marine Center,

366 OP: Ogi port, S: Shiromaru.