# Seasonal dynamics of epifaunal communities on the *Sargassum* beds of the coast of Noto Peninsula, Japan

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## ABSTRACT

Epifaunal communities inhabiting seaweeds are key components of temperate rocky reef ecosystems, playing vital roles in nutrient cycling and biodiversity maintenance. However, limited research has addressed their seasonal dynamics in the semi-enclosed Sea of Japan. This study examined the seasonal changes in epifaunal communities associated with two dominant brown algae, *Sargassum macrocarpum* and *S. patens*, in Tsukumo Bay, Noto Peninsula. Over the course of one year, we recorded fluctuations in seaweed biomass and associated epifaunal abundance and composition. The wet weight of both host seaweed species peaked in spring and winter and declined during summer and autumn, reflecting their life history traits. Seasonal changes in epifaunal communities were more pronounced than differences between host species. Caprellid and gammarid amphipods exhibited synchronized abundance peaks with seaweed growth in spring and winter, while gastropods remained relatively stable year-round, likely favoring understory habitats. Bivalves increased in summer on *S. macrocarpum*, potentially due to structural differences facilitating larval settlement. Multivariate analyses (PERMANOVA and nMDS) revealed clear seasonal shifts in community composition, with caprellids, gammarids, and gastropods contributing most to these patterns. Our findings highlight the strong coupling between macroalgal phenology and epifaunal dynamics, suggesting that algal bed seasonality significantly shapes coastal community structure. This study provides a baseline for understanding the ecological functioning of *Sargassum* beds in the Sea of Japan and informs conservation and management strategies under changing environmental conditions.

**Key words:** *Sargassum*, epifauna, caprellids, gammarids, gastropods, Sea of Japan

## BACKGROUND

Temperate rocky reef ecosystems provide essential habitats for various small animals, including crustaceans and gastropods. These epifaunal organisms play a crucial role in material cycling and influence algal bed ecosystems by grazing on epiphytic algae (Taylor 1998; Aumack et al. 2017; Chen et al. 2021). This grazing activity promotes the growth and productivity of host seaweeds (Duffy 1990; Kamermans et al. 2002; Lavaut et al. 2022; Verhoeven et al. 2012). However, excessive feeding can negatively impact host seaweeds (Duffy 1990; Poore et al. 2014), making epifaunal dynamics a critical factor in the regulation of these ecosystems. While numerous studies have examined epifaunal communities along Japan's Pacific coast and the Seto Inland Sea (e.g., Mukai 1971; Imada et al. 1981; Ito et al. 2019; Kodama et al. 2022), research on the Sea of Japan remains limited (Fujita et al. 2003; Yatsuya et al. 2008; Kawai 2023; Tsunoda et al. 2025). The Sea of Japan is a semi-enclosed body of water with unique environmental characteristics, such as a small tidal range and seasonal sea level changes influenced by the Tsushima Current (Inoue, 1977; Naganuma, 2000). Understanding the structure of epifaunal communities in this region is essential for discussing algal bed ecosystems along the Japanese coast.

Tsunoda et al. (2025) clarified the differences in epifaunal assemblages associated with different seaweed species in the Noto Peninsula, central Sea of Japan. However, their study provided only a snapshot, leaving seasonal dynamics unexplored. This study focuses on the dominant seaweed species *Sargassum macrocarpum* and *S. patens* in Tsukumo Bay of the Noto Peninsula, aiming to (1) elucidate the seasonal growth and decline of host seaweeds, (2) compare species composition and diversity of epfaunal communities across seasons, and (3) identify seasonal patterns in population density and structural changes. This research provides fundamental ecological insights into the coastal region of the Sea of Japan, serving as a baseline for evaluating the potential impacts of environmental changes and anthropogenic disturbances on algal bed ecosystems. By deepening our understanding of *Sargassum* beds and their associated epifaunal communities under the unique environmental conditions of the Sea of Japan, this study contributes to scientific knowledge for ecosystem management and conservation planning.

## MATERIALS AND METHODS

### Sampling and Sorting

In 2023, *Sargassum macrocarpum* and *S. patens* were collected around Tsukumo Bay, Ishikawa Prefecture (37°18'27.8"N, 137°13'57.5"E). The collection periods were categorized as winter (January–March), spring (April–June), summer (July–September), and autumn (October–December). Seaweeds growing in shallow areas were collected using waders, while those growing at depths of up to 10 meters were sampled via SCUBA diving. Harvested seaweeds were cut from their holdfasts, placed in mesh bags (<1.0 mm mesh size), transported, and stored in -20°C until use.

The collected seaweeds were washed three times in a bucket following the method of Kondo et al. (2019). Dislodged animals were recovered using a 1.0 mm mesh sieve and classified into 11 taxonomic groups based on Ministry of Environment (2008) and Tsunoda et al. (2025): Nematoda, Gastropoda, Bivalvia, Annelida, Gammaridea, Caprellidea, Isopoda, Tanaidacea, Caridea, Anomura, and Brachyura. The taxa Foraminifera, Acarina, Ostracoda, Cumacea, and Harpacticoida, which were investigated in the Ministry of Environment (2008), were not found in this study and were therefore excluded from the analysis. In this survey, moss animals were observed year-round, and the swimming anemone *Boloceroides mcmurrichi* was observed during the summer and autumn. However, these taxa were excluded from the analysis due to the difficulty in accurately counting their individuals. The wet weight of seaweeds was measured using an electronic balance (precision: 0.1 g).

### Data analysis

A Kruskal-Wallis test was performed to examine seasonal differences in the wet weight of *S. macrocarpum* and *S. patens*. When significant differences were detected, a Dunn-Bonferroni post hoc test was conducted.

Epifaunal abundance was standardized to the number of individuals per 100 g of host seaweed. The effects of host seaweed species and seasons on community structure were evaluated using Permutational multivariate analysis of variance (PERMANOVA). Community similarity was visualized for each seaweed species using non-metric multidimensional scaling (nMDS) based on Bray-Curtis dissimilarity. Species significantly influencing community structure were identified at a 1% significance level. Pairwise PERMANOVA was conducted to assess seasonal differences, and similarity percentage analysis (SIMPER) was used to identify taxonomic groups contributing to seasonal dissimilarities. All analyses were performed using R (version 4.3.2), with a fixed random seed (set.seed(123)).

## RESULTS

A total of 51 individuals of *Sargassum macrocarpum* and 34 individuals of *S. patens* were collected over the course of one year. The wet weight of *S. macrocarpum* varied significantly across seasons (Kruskal-Wallis test, $p < 0.05$), with the highest weight recorded in spring and lowest in autumn (Dunn-Bonferroni post hoc test, $p < 0.05$) (Fig. 1A). The median wet weights (first quartile–third quartile) for spring, summer, autumn, and winter were 276.1 (168.6–458.5), 122.3 (72.0–157.0), 44.0 (21.5–123.2), and 130.5 (92.1–264.2), respectively. Similarly, *S. patens* exhibited significant seasonal variation in wet weight (Kruskal-Wallis test, $p < 0.05$), peaking in spring and reaching its lowest weight in summer (Dunn-Bonferroni post hoc test, $p < 0.05$) (Fig. 1B). The wet weight varied seasonally, with median values (first quartile–third quartile) of 244.8 (177.7–310.5) in spring, 25.7 (23.3–29.0) in summer, 80.6 (30.6–155.5) in autumn, and 96.3 (83.4–214.5) in winter.

Epifaunal communities were more strongly influenced by seasonal variations than by host seaweed species (PERMANOVA, season: $p < 0.001$; seaweed species: $p = 0.42$). The nMDS plots of epifaunal communities associated with *S. macrocarpum* and *S. patens* are shown in Fig. 2, with stress values of 0.124 and 0.095, respectively, indicating that the nMDS effectively captured the community structure. Distinct seasonal clusters were observed, particularly for *S. patens*. At the 1% significance level, four taxonomic groups—Annelida, Caprellidea, Gammaridea, and Gastropoda—were identified as key contributors to community structure in *S. macrocarpum*, while *S. patens* exhibited an additional significant taxon, Bivalvia. The vectors representing these taxa primarily pointed in the opposite direction of the autumn community plots, indicating seasonal shifts. Seasonal variations in epifaunal communities are presented in Fig. 3. For *S. macrocarpum*, abundance was highest in spring and winter and lowest in summer and autumn. The total abundance in each season was 269.7 ± 435.5 in spring, 50.9 ± 38.7 in summer, 17.8 ± 16.5 in autumn, and 122.1 ± 114.3 in winter. In contrast, *S. patens* exhibited peak abundance in winter and the lowest abundance in autumn. The total abundance in each season was 203.5 ± 283.7 in spring, 193.4 ± 241.9 in summer, 62.2 ± 64.1 in autumn, and 855.7 ± 1117.1 in winter. Overall, epifaunal abundance was higher in *S. patens* than in *S. macrocarpum*. Clear seasonal patterns were observed for caprellids and gammarids, which increased in spring and winter but declined in summer and autumn. Gastropods displayed a different seasonal pattern, reaching their highest abundant in winter, followed by summer, autumn, and spring. In *S. macrocarpum*, bivalves showed a notable increase in summer, while isopods peaked in winter. In all seasons except summer for *S. macrocarpum*, caprellids, gammarids, and gastropods collectively accounted for over 90% of the total community composition for both seaweed species. During summer in *S. macrocarpum*, these three taxa constituted apporoximately 80% of the community, but when bivalves were included, the proportion increased to 97%. Other taxonomic groups consistently represented minor fractions of the community across both seaweed species and seasons. The community structure of *S. macrocarpum* exhibited significant seasonal differences between spring and summer, spring and autumn, and summer and autumn (pairwise PERMANOVA, $p < 0.05$ for each). Similarly, for *S. patens*, significant differences were observed between spring and summer, spring and autumn, and autumn and winter (pairwise PERMANOVA, $p < 0.05$ for each). SIMPER analysis revealed that seasonal dissimilarities were primarily explained by caprellids, gammarids, and gastropods (Table 1, 2). For all comparisons except summer vs. autumn for *S. macrocarpum*, the cumulative contribution of these three taxa exceeded 90%. In *S. macrocarpum*, bivalves ranked as the third-highest contributor to dissimilarity in spring vs. summer (contribution = 0.077) and summer vs. autumn (contribution = 0.186). For *S. patens*, caridean shrimps ranked third in summer vs. autumn (contribution = 0.022).

## DISCUSSION

This study exmined the seasonal dynamics of epifaunal communities associated with *S. macrocarpum* and *S. patens*. The observed changes in epifaunal abundance were primarily driven by seasonal fluctuations rather than differences between host seaweed species. Tsunoda et al. (2025) compared epifaunal community structures across multiple seaweed species and collection sites in Tsukumo Bay, the study area of this research. Their findings indicated that communities associated with *S. macrocarpum* and *S. patens* clustered together when collected from the same location. This suggests that the seasonal variation in epifaunal community structures in Tsukumo Bay is largely independent of host seaweed species. Fujita et al. (2003) investigated epifauna on *S. macrocarpum* and *S. patens* at Abugashima Island, approximately 45 km south of the present study site. They identified 24 species across 8 taxonomic groups on *S. macrocarpum* and 18 species across 9 taxonomic groups on *S. patens*, with only 10 species from 3 taxonomic groups shared between the two host seaweeds. These findings suggest that the similarity of epifaunal communities among co-occurring *Sargassum* species may vary depending on location. The higher abundance of epifauna on *S. patens* compared to *S. macrocarpum* in this study is consistent with the findings of Yatsuya et al. (2008). However, the direct cause of this difference remains unclear. Further detailed comparisons, including an assessment of which parts of the seaweeds harbor more individuals, are needed in future studies.

*Sargassum macrocarpum* is a perennial seaweed that grows from autumn to spring and undergoes frond loss from summer to autumn (Murase 2001). A study conducted in Iida Bay, near this present study site, divided the growth cycle of *S. macrocarpum* [previously reported as *S. serratifolium* at Taniguchi & Yamada (1978)] into four stages: the emergence period (May–July), the growth period (August–January), the thickening period (February–April), and the maturation and defoliation period (May–July) (Taniguchi & Yamada 1978). In this study, the wet weight of *S. macrocarpum* was lower in autumn than in summer, despite autumn being expected to be its growth period. This discrepancy is likely due to the simultaneous presence of newly emerged fronds and post-maturation defoliated remnants. Similarly, *S. patens*, another perennial seaweed, exhibits growth from autumn to spring, with growth stagnation typically observed in winter (Tsuchiya et al. 2011). A study in Iida Bay identified five growth phases for *S. patens*: emergence period (May–July), growth (August–January), growth stagnation (February–March), thickening (April–May), and maturation and defoliation (June–July) (Taniguchi & Yamada 1978). The seasonal wet weight pattern observed in this study was consistent with these growth stages, with biomass increasing from summer to spring. Both seaweed species exhibited similar seasonal size changes, with smaller sizes in summer and autumn and larger sizes in winter and spring. Yatsuya et al. (2008), Carvalho et al. (2018), and Tsunoda et al. (2025) suggested that epifaunal communities tend to differ among *Sargassum* species. However, in this study, no clear differences were detected between *S. macrocarpum* and *S. patens*. Yatsuya et al. (2008) reported that these two seaweed species reached their smallest size in September along the Sea of Japan coast, which aligns with the present findings of reduced sizes during summer and autumn. These similar phenological patterns may explain the resemblance in epifaunal community structures between the two seaweed species.

This study revealed distinct seasonal changes in epifaunal communities, particularly in gammarids and caprellids. According to the latest taxonomic classification, Caprellidea is now considered a subgroup within the former Gammaridea (Lowry and Myers 2013). This explains the similar seasonal dynamics exhibited by these two taxa, both of which increased in abundance during spring and winter. Gammarids are known to dominate algal beds, and previous studies focusing on amphipods in such habitats have shown that their population density increases during seaweed growth periods and declines during degradation phases (Kodama et al. 2020). This present study demonstrated similar trends. The decline in amphipods abundance may be attributed to reduction in host seaweed biomass, leading to increased predation by higher trophic levels (Choat and Kingett 1982; Aoki 1988; Kennelly 1991) or dispersal to alternative habitats (Kodama et al. 2022; Kawai, 2023). These factors likely contributed to the observed population decline. During the period of amphipods decline, gastropods became dominant. Although gastropod abundance exhibited seasonal fluctuations, it remained relatively stable overall (except for a notable decrease in spring for *S. patens*). Ito et al. (2019) exmined the vertical distribution of epifauna and found that gastropods were more abundance in the understory than in the canopy of algal beds. Similarly, Kuramochi (2000) observed that gastropods were densely concentrated at the base of *Eisenia bicyclis*, while Fujita et al. (2008) reported high densities of *Petalifera punctulata* at the base of *S. macrocarpum*. These findings suggest that the dominance of gastropods in summer and autumn in this study may be related to the detachment of *Sargassum* canopy, leaving only the understory habitat available. Unlike gammarids, gastropods appear to prefer more stable substrates such as understory habitats or rocky surfaces within algal beds. In summer, bivalves were notably abundant only on *S. macrocarpum*. Ito et al. (2019) observed large numbers of bivalves in algal beds and suggested that seaweed canopies may trap bivalve larvae. In this study, the wet weight of *S. macrocarpum* tended to be higher than that of *S. patens* during summer. This suggests that *S. patens* may have shortened during this summer, while the remaining *S. macrocarpum* continued to grow longer, possibly making it more effective at capturing bivalves. Additionally, the distinct serrated leaves of *S. macrocarpum* may have facilitated greater larval retention.

## CONCLUSIONS

This study investigated the seasonal dynamics of epifaunal communities associated with *S. macrocarpum* and *S. patens* in Tsukumo Bay, Noto Peninsula. Epifaunal population fluctuations closely followed the seasonal growth cycles of their host seaweeds, with major changes driven by variations in gammarids and caprellids abundance. In contrast, gastropod abundance remained relatively stable throughout the year, indicating minimal influence from seaweed seasonality. These findings provide valuable insights into the faunal communities of algal beds in the central Sea of Japan, particularly around the Noto Peninsula.

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## Authors' contributions:

Keito Tsunoda: conceptualization, investigation, analysis, writing of first draft; Yukimasa Higashide: investigation; Shouzo Ogiso: investigation; Nobuo Suzuki: investigation; Kenji Toyota: conceptualization, investigation, writing.

## Competing interests:

The authors declare that they have no competing interests.

## Availability of data and materials:

The datasets generated and/or analyzed during the current study are available from the corresponding author upon request.

## Consent for publication:

All the authors consent to the publication of this manuscript.

## Ethics approval consent to participate:

Not applicable.

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## Preparing Tables

Table 1. Seasonal dissimilarities of *Sargassum macrocarpum* based on similarity percentage analysis. Bold text indicates the top three taxonomic groups for each season.

| | Spring vs Summer | Summer vs Autumn | Autumn vs Winter | Winter vs Spring |
|---|---|---|---|---|
| Bivalvia | **0.077** | **0.186** | 0.043 | 0.019 |
| Caprellidea | 0.056 | 0.011 | **0.207** | **0.127** |
| Gammaridea | **0.619** | **0.273** | **0.320** | **0.599** |
| Gastropoda | **0.227** | **0.497** | **0.376** | **0.210** |

Table 2. Seasonal dissimilarities of *Sargassum patens* based on similarity percentage analysis. Bold text indicates the top three taxonomic groups for each season.

| | Spring vs Summer | Summer vs Autumn | Autumn vs Winter | Winter vs Spring |
|---|---|---|---|---|
| Caprellidea | **0.035** | **0.076** | **0.047** | **0.045** |
| Caridea | 0.006 | **0.022** | 0.007 | 0.004 |
| Gammaridea | **0.434** | 0.016 | **0.582** | **0.628** |
| Gastropoda | **0.490** | **0.838** | **0.331** | **0.287** |

## Figure Legends

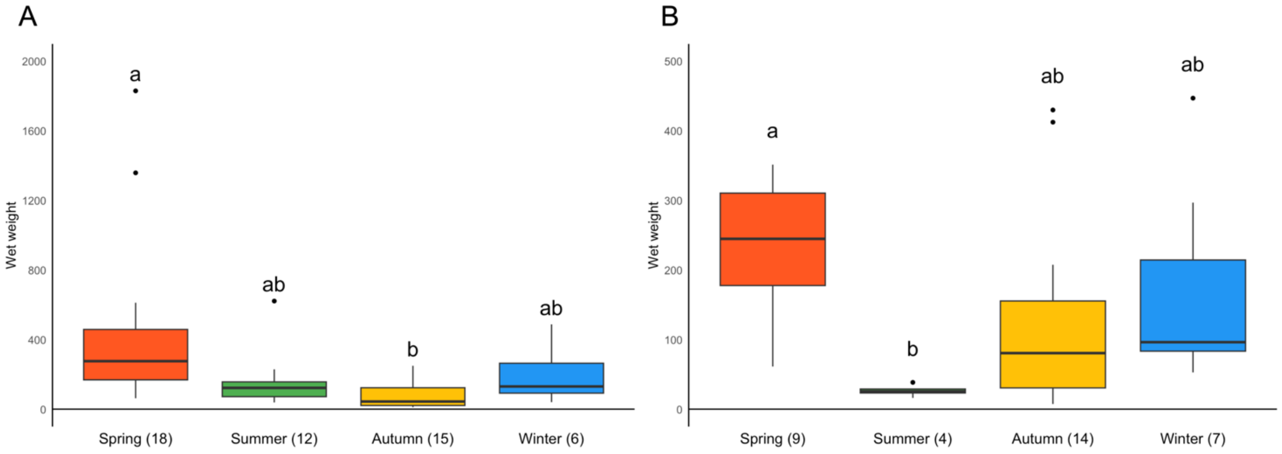

Figure 1. Seasonal changes in the wet weight of *Sargassum macrocarpum* (A) and *S. patens* (B). Different letters indicate significant differences (Dunn-Bonferroni post hoc test, $p < 0.05$). The numbers in parentheses following each season indicate the sample size.

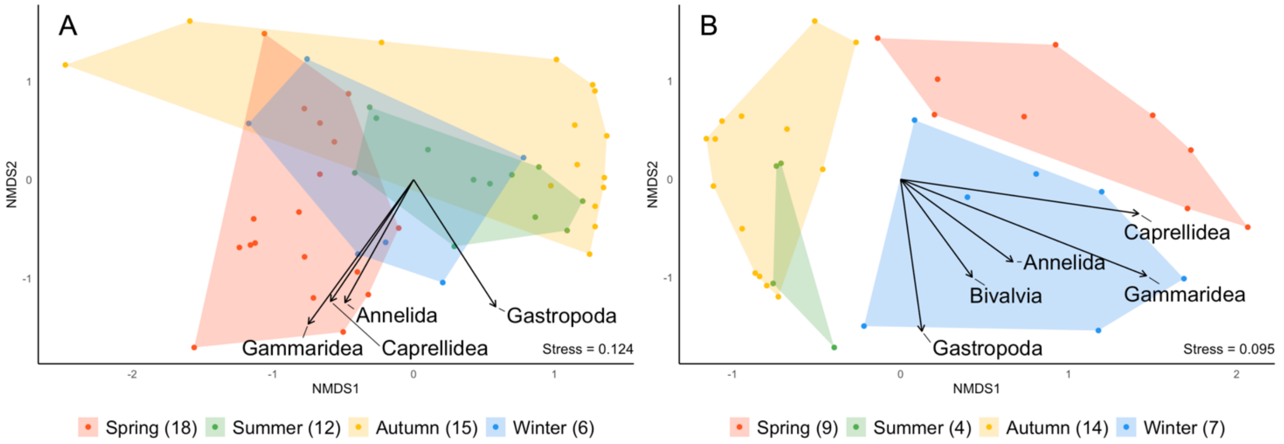

Figure 2. The nMDS of *Sargassum macrocarpum* (A) and *S. patens* (B) with taxa selected at the 1% significance level. The numbers in parentheses following each season indicate the sample size.

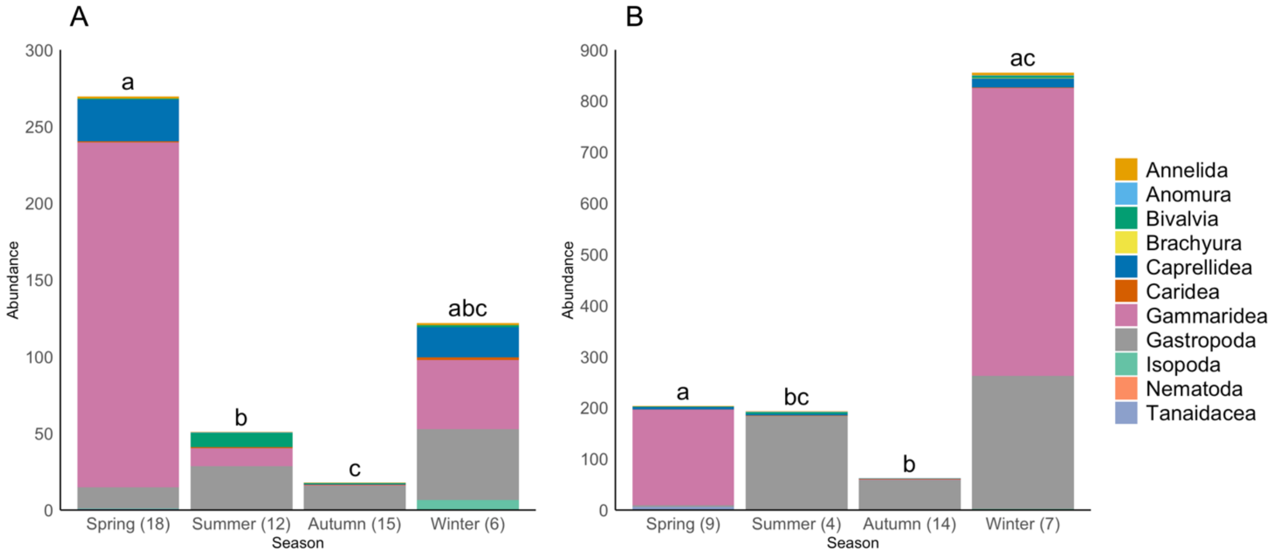

Figure 3. The abundance and proportion of epifauna on *Sargassum macrocarpum* (A) and *S. patens* (B). Different letters indicate significant differences (pairwise PERMANOVA, $p < 0.05$). The numbers in parentheses following each season indicate the sample size.