Vertical distribution of epifauna on Sargassum horneri, with special reference to the occurrence of bivalve spat

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Abstract: The annual macroalga Sargassum horneri often forms a dense canopy at the sea surface. To evaluate the effects of the vertical structure and presence of the sea-surface canopy of S. horneri on the distribution of its epifauna, we collected epifauna from four different vertical portions of S. horneri at Kitsunezaki, west coast of Oshika Peninsula, Miyagi, Japan. The vertical portions of the thalli were defined as follows: sea surface (S), the portion that was always lying on the sea surface; intermediate (I), which was periodically lying on the sea surface with tidal changes; underwater (U), which was always submerged; and bottom (B), the portion around the holdfast. The mean total density of epifauna in the sea-surface portions (S and I) was significantly higher than that in the underwater portions (U and B). Harpacticoid copepods and bivalve spat accounted for more than 90% of the epifauna in all portions. It seems that the canopy of S. horneri collects bivalve larvae and other epifauna from the water column by sweeping the sea surface with the changing of the tide. We proposed the Seasonal Coincidence Hypothesis to explain the dense occurrence of bivalve spat on S. horneri in this study.

Key words: bivalve spat, harpacticoid copepod, Mytilus galloprovincialis, Sargassum horneri, vertical distribution

Introduction

Sargassum seaweeds (Fucales, Sargassaceae) have highly differentiated fronds bearing air bladders that keep them afloat. They form large and structurally complex habitats for various marine macroorganisms, such as fishes, decapod crustaceans, mollusks, and echinoderms. Epifaunal assemblages consisting mainly of small crustaceans and gastropods occur on the thalli of Sargassum seaweeds (Norton & Benson 1983; Taylor & Cole 1994; Gestoso et al. 2012). Norton and Benson (1983) found that the epifauna living on Sargassum muticum comprised members of more than 10 phyla. The number of epifaunal organisms occurring on Sargassum is also often very large. Mukai (1971) reported that the abundance of epifaunal organisms occurring on Sargassum serratifolium reached up to 266,000 individuals per plant in early spring. It has also been reported that positive relationships occur between the vertical distribution of the abundance of Sargassum epifauna and the biomass of their substratum. Imada et al. (1981) reported that six species of amphipods occurred in high densities on the upper parts of Sargassum seaweeds. They found strongly positive correlations between amphipod density and the changes in biomass of Sargassum seaweeds with depth. Fujita et al. (2003) also demonstrated the occurrence of high densities of epifauna at depths with high Sargassum seaweed biomass. They related the vertical patterns in the occurrence of epifauna to the structural complexity of the substratum. Kodama et al. (2017) found a higher abundance and higher diversity of amphipod assemblages in the understory algae than in the Sargassum canopy.

In temperate coastal areas, the abundance of epifauna on Sargassum seaweeds generally shows drastic seasonal fluctuations concurrent with changes in host plant biomass (Mukai 1971; Edgar 1983; Imada & Kikuchi 1984; Aoki 1988; Duffy 1990; Edgar & Aoki 1993). The epifauna-
nal abundance increases rapidly from late winter to early spring, and then suddenly decreases when there is a major loss of habitat (seaweed biomass) in early summer. While perennial Sargassum species start to regrow from their holdfast or from their oversummered thallus in autumn, annual Sargassum species need to settle in a new habitat every spring. This means that the epifaunal assemblages on annual Sargassum species, such as Sargassum horneri, are renewed every year.

Sargassum horneri is an annual species with a wide distribution along the rocky subtidal shores of Japan that shows drastic seasonal changes in its biomass. It grows rapidly from autumn to winter, with 1–2 cm of growth per day in the main branch (Umezaki 1984), and often reaches more than 5 m in total length. After reproduction, the whole thallus of S. horneri detaches from the substratum along with its holdfast and becomes a floating seaweed, either at the sea surface or as a benthic-drifting seaweed. When the thallus grows longer than the water depth, it starts to lie on the sea surface and forms a large macroalgal canopy. The floating macroalgal canopy is subjected to water flow and rotates in the horizontal direction as a smaller canopy at high tide and as a larger canopy at low tide. At low water during spring tides, the coastal sea surface above S. horneri beds is covered by densely distributed patches of the S. horneri canopy.

There seems to be much available space for epifauna on the highly branched and structurally complex thalli of S. horneri, as noted by Imada et al. (1981) and Fujita et al. (2003). However, the environmental conditions in the portion of the S. horneri canopy lying on the sea surface, such as light intensity, water temperature, salinity, and wave action, may fluctuate substantially, and thus these conditions may be harsh for epifauna. Therefore, the epifaunal composition and density in the floating canopy could differ from those on the submerged thallus, and this could cause vertical differences in epifaunal distributions with depth. From another point of view, the conditions in Sargassum canopies are similar to those of floating seaweeds. Several studies have examined the epifauna on drifting S. horneri (Sano et al. 2003; Abe et al. 2013), but little is known about the changes in the composition of epifauna during the transition from nearshore beds to offshore environments. The canopy of S. horneri can be considered a transitional stage between benthic and floating environments. The study of epifauna on the S. horneri canopy should thus provide some insight into the formation of floating seaweed communities.

In this study, we examined the vertical differences in the community composition of epifauna on S. horneri to identify the factors affecting the vertical distribution of epifauna. As a result, we found a very high number of bivalve spat on S. horneri at the sea surface. There have been few reports of the occurrence of bivalve spat on Sargassum seaweeds. To explain their occurrence in the Sargassum epifauna, we proposed a hypothesis regarding the timing of bivalve recruitment and discussed its applicability.

Materials and Methods

Study site

Field work was conducted in an embayment at Kitsunezaki (38°21′N, 141°25′E; Fig. 1), on the west coast of Oshika Peninsula, Miyagi, Japan. The embayment has a circumference of approximately 300 m, open to the north-west, and surrounded by an artificial sea wall to the south, a cobbly shore to the east, and a natural rocky shore to the north. Eisenia bicyclis and Sargassum seaweeds dominate on rocky bottoms here (0–30 m offshore, 1–4 m depth), while Zostera caespitosa dominates on sandy bottoms (30–70 m offshore, 4–6 m depth). Every spring, Sargassum beds composed of S. horneri, S. muticum, S. siliquastrum, S. confusum, and Myagropsis myagroides are formed. During this season, S. horneri is observed to form floating canopies at the sea surface, even during the extremely high flood cycle of the spring tide (Fig 2).

Sampling of Sargassum horneri epifauna

To examine the vertical distribution of the epifauna on the thalli of S. horneri, a depth-dependent vertical sampling survey was conducted at two sites with different depth profiles on June 2, 2015. The water depth was 1.1 m at the shallower site (Site-1), and 2.2 m at the deeper site (Site-2) (Fig. 3). The depth was measured from the lowest low-water level. Four different plants of S. horneri that were at least 1 m apart were selected for sampling at the same depth at each site. The distal end of each thallus was lying on the sea surface at all times, even at high water during spring tides.

At the shallower site (Site-1), four vertical portions on the thalli of S. horneri were defined according to their submergence pattern as follows: sea surface (S), the portion that was always lying on the sea surface; interme-
diate (I), which periodically appeared on the sea surface with tidal movements; underwater (U), which always remained underwater; and bottom (B), which was just above the holdfast on the sea bottom. At the deeper site (Site-2), in addition to portions S, I, and B, portion U was divided into U₁ and U₂. The depths of U₁ and U₂ at Site-2 were located at the same depths as the U and B portions at Site-1, respectively (Fig. 3). From each vertical portion, a 20 cm-long sample of thallus from along the main branch, as well as its associated epifauna, was carefully removed using scissors. The samples were gently placed in separate plastic bags (Ziploc Freezer Bag L, Asahi Kasei Home Products Corp., Japan). To remove excess seawater from the bags, approximately 2000–3000 pores with a diameter of 0.1 mm were made in the lower sides of the bags using a needle-point holder used for flower arrangement. All sampling procedures were conducted underwater via SCUBA diving. All samples were transported on ice to our laboratory at Tohoku University, Miyagi, and kept in a freezer at −25°C.

**Sample treatments**

In the laboratory, the epifaunal assemblages were removed from the thalli of *S. horneri* by washing them in freshwater, and the epifaunal samples were then sieved through a 0.1 mm mesh. The epifauna remaining on the mesh were classified into 10 taxonomic groups as follows: Bivalvia, Caprellidea, Foraminifera, Gammaridea, Gastropoda, Harpacticoidea, Isopoda, Nematoda, Ostracoda, and Polychaeta. Classification was based on the survey report of the epifauna on Sargassaceae seaweeds conducted by the Ministry of Environment (2008). The number of individual animals in each taxon was counted. In cases when
the number of epifauna was too high to count accurately, the following method to extract subsamples was employed. The epifauna in the sample were evenly placed on a 36-cell grid (6×6 cells) in a Petri dish. The numbers of epifauna in six squares that were selected using a random number table were then counted. Finally, the sum of the counts from the six subsamples multiplied by six was used as the estimated density of the whole sample. The thallus substrate of \(S. \) horneri was dried at 80 °C for more than 48 h to obtain the dry weight. The epifaunal abundance and substrate dry weight were then used to determine the epifaunal density (number per 1 g of algal dry weight). The Shannon-Wiener diversity index (\(H'\)) for each vertical portion was also calculated. Only the bivalves were preserved in 99% ethanol for species identification using DNA analysis, while the other taxa were fixed and stored in hexamine-buffered 5% formalin in seawater.

**Data analyses**

To test for statistically significant differences in the total density and the Shannon-Wiener diversity index (\(H'\)) of the epifaunal assemblages among the vertical portions, one-way analysis of variance (ANOVA) followed by Tukey-Kramer post-hoc test was employed. Before performing the ANOVA, the density data were \(\log_{10}(x+1)\)-transformed when necessary to meet the assumptions of ANOVA (normality and homoscedasticity). To group the data and graphically visualize them, cluster analysis and nonmetric multidimensional scaling (nMDS) ordination were performed. Bray-Curtis dissimilarities were calculated using the \(\log_{10}(x+1)\)-transformed density data, and a dendrogram was produced using group-averaged clustering. A one-way analysis of similarities (ANOSIM) (Clarke 1993) was used to examine the similarity in the epifaunal assemblages among vertical portions, and similarity percentage analysis (SIMPER) (Clarke & Gorley 2006) was used to identify the taxa that contributed the most to the dissimilarities among clusters. The significance level of the contributions of taxa included in the SIMPER was set at greater than 3% (Benedetti-Ceccchi & Chato Osio 2007; Gestoso et al. 2012). All statistical analyses were performed using the PRIMER software (Clarke & Gorley 2006).

**Results**

**Vertical distribution of Sargassum horneri biomass and epifaunal density**

The algal biomass of \(S. \) horneri per 20 cm length along the main branch was the smallest in the vertical portion S at both Site-1 and Site-2. The biomass of the other portions decreased with depth at Site-1. However, at Site-2, the differences in biomass among the vertical portions I, U1, U2, and B did not show this trend (Fig. 4A).

At both sites, the epifaunal abundance significantly differed among vertical portions (one-way ANOVA, \(p < 0.01\); Fig. 4B). The mean total density of epifauna in the portions exposed to the sea surface (S and I) was significantly higher than that in the underwater portions (U, U1, U2, and B) (Tukey-Kramer test, \(p < 0.05\); Fig. 4B). Bivalves and harpacticoids accounted for over 90% of the density of all groups near the sea surface (S and I).

![Fig. 4.](image-url) Vertical distributions of Sargassum horneri biomass and epifauna. (a) Dry weight (g) of Sargassum horneri per 20 cm along the main branch at the sampling portions S, I, U, and B at Site-1 and S, I, U1, U2, and B at Site-2. (b) The epifaunal density of each faunal group on Sargassum horneri at both Site-1 and Site-2. The horizontal axis shows the mean density (n=4), and the vertical axis shows each sampling portion of \(S. \) horneri. The F-values (df=3, 12 at Site-1; 4, 15 at Site-2) for one-way ANOVA are shown along with their significance (**\(p < 0.01\); ***\(p < 0.001\); n.s., not significant). Different letters indicate significant differences among groups (Tukey-Kramer test, \(p < 0.05\)).
Bivalves in particular contributed to the high faunal density observed (Fig. 4B). At the sea surface (S) at both sites, bivalves (Site-1: 49.6%; Site-2: 61.0%) and harpacticoids (Site-1: 43.1%; Site-2: 28.1%) dominated. At the bottom (B), harpacticoids (59.6%) and gastropods (21.6%) dominated at Site-1, and harpacticoids (78.8%) dominated at Site-2. However, at both sites, there were no significant differences in the number of faunal groups (S) and the Shannon-Wiener diversity index ($H'$) among the vertical portions (one-way ANOVA, $p>0.1$; Fig. 5).

Cluster analysis and nMDS

In the results of the cluster analysis of the vertical distribution of the epifauna, five clusters were identified at 80% similarity (Fig. 6). Cluster I consisted mainly of U and B at Site-1; cluster II contained S and I at both Site-1 and Site-2; cluster III mainly consisted of S, I, and U at both Site-1 and Site-2; cluster IV included U₁, U₂, and B at Site-2; and cluster V contained B at Site-2. In general, the epifaunal assemblages near the sea surface were placed in clusters II and III, and those near the bottom were placed in clusters I, IV, and V. In the ANOSIM results, the epifaunal compositions of these clusters were confirmed to be significantly different overall (Global $R=0.818, p<0.05$; Table 1).

The results of the nMDS ordination of the epifaunal assemblages based on their vertical distributions are shown in Fig. 7. The stress value was 0.09, indicating that the nMDS provided a usable description of the data. All sample data for distinct vertical portions (S, I, U, and B) were plotted, and separated based on the site number (1 or 2). Data for portions U₁ and U₂ from Site-2 were combined into one group (U) for the nMDS. Groups of the data divided at the 80% similarity level are shown by enclosure lines in the figure. The compositions of the epifaunal assemblages near the sea surface, such as those in portions S and I, were similar to each other and differed from those near the bottom, such as those in portions U and B, regardless of the site. We got the same results when the two sites were not pooled, and thus all four replicate samples of each algal portion were pooled in both the main cluster analysis...
SIMPER results

SIMPER was employed to identify the taxonomic groups that significantly contributed to the separation of clusters I–V at an 80% similarity level (Table 2). The epifaunal assemblages were classified into sea-surface groups (clusters II and III) and near-bottom groups (clusters I, IV, and V). High average dissimilarity values of more than 40% were found between clusters II–V, III–IV, and III–V. The taxa that significantly contributed to the differences in epifaunal composition with a high percentage contribution were bivalves (I–II, I–III, I–V, II–IV, II–V, III–IV, and III–V), gastropods (I–IV and II–III), and harpacticoids (IV–V). Bivalves contributed greatly to the differences in epifaunal composition between S and both U and B.

Discussion

Vertical distribution of epifaunal assemblages on Sargassum horneri

A nationwide survey of the epifauna of Sargassaceae seaweeds in Japan was conducted by the Ministry of the Environment for five years starting in 2002 (Ministry of the Environment 2008). In this survey, eleven taxonomic groups (Acaridi, Caprellidea, Copepoda, Cumacea, Gammaridea, Gastropoda, Isopoda, Nematoda, Ostracoda, Polychaete, and Tanaidacea) were used for the identification of epifauna. According to that report, crustaceans and gastropods comprised more than 90% of the Sargassum epifauna. We used the same sorting method as that used in this nationwide survey for the Sargassum horneri epifauna. In our study, bivalves and harpacticoids accounted for over 90% of the epifauna in all of the vertical portions of the alga (Fig. 4). The number of faunal groups and the proportional distribution of fauna among different groups were not significantly different among the algal portions (Fig. 5). The epifaunal composition was, however, clearly divided among the algal portions in the cluster analysis (Fig. 6). This meant that the faunal groups, except for bivalves and harpacticoids, were different among the algal portions. For example, gastropods were abundant in the bottom portions U and B, whereas in the canopy portions S and I they were not.

Generally, with the exception of S at Site-1, the faunal abundance was higher as one moved closer to the sea surface, and it was the lowest at the bottom. There are two possible explanations for the water surface-oriented dis-

![Fig. 7. nMDS (nonmetric multidimensional scaling) of the epifaunal assemblages on Sargassum horneri. All sample data plotted are distinguished by their sampling portions (S, I, U, and B) and site number (1 or 2). The lines surrounding the groups of symbols indicate those samples grouped at 80% similarity.](image-url)
Table 2. Results of similarity percentage analysis (SIMPER) showing which epifaunal groups made the greatest contributions to the dissimilarity observed among the five clusters (I–V) found in the cluster analysis.

| Epifaunal group | Average abundance | Average dissimilarity | Average dissimilarity/SD | Contribution (%) |
|-----------------|-------------------|------------------------|--------------------------|------------------|
|                 | Cluster I | Cluster II | 23.85 |                      |                  |
| Bivalvia        | 6.12      | 3.00        | 7.28  | 2.52               | 30.54            |
|                 | Total     |                          |                      |                  | 30.54            |
|                 | Cluster I | Cluster III | 24.93 |                      |                  |
| Bivalvia        | 6.04      | 3.00        | 5.92  | 1.92               | 23.72            |
| Nematoda        | 3.02      | 0.90        | 4.12  | 1.84               | 16.52            |
|                 | Total     |                          |                      |                  | 40.24            |
|                 | Cluster I | Cluster IV | 25.00 |                      |                  |
| Gastropoda      | 3.27      | 1.95        | 4.23  | 1.65               | 16.91            |
| Bivalvia        | 3.00      | 1.85        | 3.80  | 1.34               | 15.21            |
|                 | Total     |                          |                      |                  | 57.46            |
|                 | Cluster I | Cluster V | 34.61 |                      |                  |
|                 | Bivalvia  | 3.00        | 0.97  | 6.31               | 18.23            |
| Harpacticoida   | 5.20      | 3.52        | 8.72  | 3.35               | 15.19            |
| Ostracoda       | 2.67      | 1.00        | 3.67  | 1.91               | 14.96            |
| Gammaridea      | 2.56      | 1.58        | 4.14  | 2.76               | 9.08             |
|                 | Total     |                          |                      |                  | 57.46            |
|                 | Cluster II| Cluster IV| 30.51 |                      |                  |
| Bivalvia        | 6.12      | 1.85        | 11.89 | 4.45               | 38.98            |
| Nematoda        | 1.88      | 0.16        | 4.80  | 2.03               | 15.73            |
| Harpacticoida   | 5.90      | 4.72        | 3.27  | 1.97               | 10.72            |
|                 | Total     |                          |                      |                  | 65.43            |
|                 | Cluster II| Cluster V | 40.89 |                      |                  |
| Bivalvia        | 6.12      | 0.97        | 15.20 | 4.76               | 37.17            |
| Harpacticoida   | 5.90      | 2.52        | 6.93  | 3.70               | 16.94            |
| Nematoda        | 1.88      | 0.00        | 5.51  | 2.17               | 13.47            |
|                 | Total     |                          |                      |                  | 67.58            |
|                 | Cluster III| Cluster IV| 40.89 |                      |                  |
| Bivalvia        | 6.04      | 1.85        | 9.24  | 2.74               | 22.61            |
| Nematoda        | 3.02      | 0.16        | 6.36  | 3.11               | 15.54            |
| Gammaridea      | 3.88      | 1.63        | 5.10  | 3.76               | 12.48            |
| Caprellidea     | 2.42      | 0.58        | 3.96  | 1.75               | 9.69             |
| Polychaeta      | 1.92      | 0.30        | 3.58  | 2.34               | 8.76             |
| Gastropoda      | 3.28      | 1.95        | 3.07  | 1.61               | 7.52             |
|                 | Total     |                          |                      |                  | 76.60            |
|                 | Cluster III| Cluster V | 49.22 |                      |                  |
| Bivalvia        | 6.04      | 0.97        | 11.77 | 3.33               | 23.91            |
| Nematoda        | 3.02      | 0.00        | 7.01  | 3.36               | 14.24            |
| Harpacticoida   | 5.98      | 3.52        | 5.74  | 4.02               | 11.65            |
| Gammaridea      | 3.88      | 1.58        | 5.42  | 4.85               | 11.01            |
| Ostracoda       | 2.94      | 1.00        | 4.55  | 3.74               | 9.25             |
| Caprellidea     | 2.42      | 0.40        | 4.53  | 1.96               | 9.20             |
| Polychaeta      | 1.92      | 0.52        | 3.31  | 1.67               | 6.73             |
|                 | Total     |                          |                      |                  | 85.99            |
|                 | Cluster IV| Cluster V | 24.72 |                      |                  |
| Harpacticoida   | 4.72      | 3.52        | 4.97  | 2.38               | 20.10            |
| Bivalvia        | 1.85      | 0.97        | 4.34  | 1.42               | 17.56            |
| Isopoda         | 0.05      | 0.83        | 3.06  | 1.80               | 12.38            |
| Gastropoda      | 1.95      | 2.55        | 3.05  | 1.45               | 12.33            |
|                 | Total     |                          |                      |                  | 62.37            |
tribution of epifauna in our study. One is that the epifauna, such as mobile harpacticoids, actively migrated to the canopy portion of *S. horneri*. In the results of the cluster analysis, the epifaunal assemblages of the same morphological portions were similar between sites, such as those of B at Site-1 and B at Site-2, but not between the portions at the same depth, such as B at Site-1 and U at Site-2. It has been suggested that the morphological characteristics of *S. horneri* affect the vertical distribution of its epifauna. The canopy portions S and I, which have particularly complex structures, may be important as stable habitats and as shelter from predators for harpacticoids. The high-density occurrence of harpacticoid copepods in *Sargassum* beds has been reported in some past studies. Mukai (1971) examined the seasonal changes in the biomass of *Sargassum serratifolium* and the composition of the epifaunal assemblages associated with it and reported that harpacticoids were the most abundant in all months except from spring to early summer. Mukai showed that the proportion of the epifauna composed of harpacticoids was the highest (82.8%) in October, when epifauna started to recruit to *Sargassum* fronds, and was the second highest (35–40%), next to that of nematodes, from spring to early summer, when epifauna were the most abundant overall. Kito (1975, 1977) also reported a high proportion of harpacticoids (42.1%) in the epifaunal assemblages on *Sargassum confusum* in Oshoro Bay in Hokkaido, Japan. Since harpacticoids usually have high reproductive potential (Hicks 1980), they may be able to quickly recruit to host substrata and dominate epifaunal assemblages by responding to the rapid growth of *Sargassum* seaweeds.

The other potential explanation is that planktonic or neustonic animals, such as drifting bivalve larvae, were passively caught by the canopy of *S. horneri*. Highsmith (1985) suggested that amphipods and tanaids can be transported by attachment to the sea surface because of the surface tension of the water, and then settle on encountered objects. Therefore, there may be a certain number of animals passively drifting on the sea surface, which may be caught by the surface-sweeping canopy of *S. horneri*. In the results of our nMDS, the epifaunal composition was more similar near the sea surface, but less so near the sea bottom, between the two sites. Although little is known about the recruitment processes of epifauna in *Sargassum* beds, this seems to support the possibility that the canopy of *S. horneri* swept the water near the sea surface and caught drifting animals and larvae.

**Bivalve spat found in the canopies of *Sargassum horneri***

In this study, we found three bivalve species in the bivalve spat that occurred on the canopy of *S. horneri*: *Mytilus galloprovincialis* (Fig. 8a), which was the most dominant,
Clinocardium californiense (Fig. 8b), and Hiatella arctica (Fig. 8c) (Ito et al. unpublished data). There have been few records of the occurrence of bivalve spat in Sargassum beds. Kikuchi (1964) reported that Musculista senhousia, which lives on the bottom sediment, occurred on the thallus of Sargassum hemiphyllum in Lake Nakaumi, Shimane. Mukai (1976) reported the occurrence of Hiatella orientalis and Monia umbonata, which inhabit rock surfaces and bottom sediments, on the thallus of Sargassum serratifolium, suggested that the settlement of these two species coincided with the period of peak biomass of S. serratifolium.

The maturation of Sargassum horneri occurs during June–August in Oshoro Bay, Hokkaido (Marui et al. 1981), May–July in Matsushima Bay, Miyagi (Taniguchi & Yamada 1988), March–May in Obama Bay, Fukui (Umeza-ki 1984), and December–April in Odawa Bay, Kanagawa (Terawaki 1986), indicating that there are different periods of Sargassum maturation among marine habitats in Japan. On the other hand, the settlement peak of M. galloprovincialis occurs in May–July in Japan (Hosomi 1966; Kajihara et al. 1978). Thus, the occurrence of spat of M. galloprovincialis may coincide with the timing of the seasonal maximum biomass of S. horneri in Miyagi. In this study, we propose the ‘Seasonal Coincidence Hypothesis’ to explain the occurrence of bivalve spat on Sargassum seaweeds. This hypothesis predicts that the Sargassum canopy serves as a temporary settlement substratum for bivalve spat when the timing of the reproductive peak of bivalves coincides with that of the peak biomass of Sargassum. Considering the earlier maturation of S. horneri in the central parts of Japan than elsewhere, it may detach from the rocky substratum there before the settlement of M. galloprovincialis can occur.

In this study, the spat of Clinocardium californiense, which has been recently cultured in Hirota Bay, Iwate Prefecture, occurred in the epifaunal assemblages examined (Ito et al. unpublished data). The domestic production of fishery-targeted bivalve species, such as C. californiense and Patinopecten yessoensis, depends on natural seed. Therefore, it is important to secure a stable supply of natural seeds. These species may settle on Sargassum seaweeds under certain circumstances, as observed for M. galloprovincialis in this study. To test our ‘Seasonal Coincidence Hypothesis,’ broad sampling surveys must be conducted to examine the timing of bivalve spat occurrence in Sargassum beds in different marine habitats in Japan.

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