



Seasonal dispersal of gammaridean amphipods away from *Sargassum* beds in relation to macroalgal host defoliation

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ABSTRACT: Epibenthic invertebrate assemblages in macroalgal beds generally show remarkable seasonal fluctuations in abundance and species composition, reflecting macroalgal host growth and defoliation. Notably, they often drastically decrease during macroalgal host defoliation. Though this reduction has been explained in terms of dispersal away from the macroalgal bed in relation to macroalgal host defoliation, this hypothesis has not previously been experimentally detailed. We conducted a field experiment using an imitation of *Sargassum* that was set 1 m away from a *Sargassum yezoense* bed to examine whether the epibenthic gammarids disperse away from the *Sargassum* bed as a result of *Sargassum* defoliation. The imitations were replaced monthly throughout the *Sargassum* defoliation season; subsequently, gammarids associated with the imitation (assumed as migrants from the *Sargassum* beds) as well as the gammarids that occurred in the *Sargassum* bed were investigated. Seasonal patterns of gammarid abundance in the *Sargassum* bed and their dispersal to the imitations were found to be quite different among gammarid species. In particular, 2 dominant gammarids, the suspension-feeding *Jassa morinoidi* and *Podocerus* sp., drastically decreased in the *Sargassum* bed and coincidentally increased in the imitations during the *Sargassum* defoliation season, indicating their defoliation-associated dispersal from the *Sargassum* bed. This is the first field experimental study demonstrating the defoliation-associated dispersal of epibenthic invertebrates in macroalgal beds. The dispersal is likely caused by a reduction of habitat space and quality due to thalli defoliation. Since many macroalgae show seasonal growth and defoliation, the concept of defoliation-associated dispersal is potentially applicable to various macroalgal species.

KEY WORDS: *Sargassum* beds · Algal phenology · Defoliation · Gammarid · Dispersal · Algal imitation

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1. INTRODUCTION

Macroalgal bed ecosystems are one of the most important ecosystems in coastal areas, supporting various ecological functions and/or ecosystem services (Costanza et al. 1997) such as providing extensive amounts of primary production, protection from waves, and complex habitats for a diverse array of marine organisms including many commercial species (Steneck et al. 2002, Graham et al. 2007, de Juan

et al. 2015). Furthermore, canopy-forming macroalgae host a diverse and abundant fauna of epibenthic invertebrates by providing shelter and forage (Wikström & Kautsky 2007, Tait & Schiel 2011, Filbee-Dexter et al. 2016, Olafsson 2016). These epibenthic invertebrates are known to have strong positive effects on macroalgal productivity by removing competitive epiphytes as well as negative effects through consumption of the host algae (Duffy 1990, Mancinelli & Rossi 2001, Kamermans et al. 2002).

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They also play a major role in transferring energy in food webs as primary consumers and act as prey for higher consumers (Pinnegar et al. 2000, Stål et al. 2007, Aumack et al. 2017). Epibenthic invertebrates are, therefore, an essential component for understanding macroalgal bed ecosystems.

Temperate macroalgal beds generally show clear seasonal growth and defoliation, leading to seasonal changes in biomass and morphology (e.g. Sideman & Mathieson 1983, Pickering et al. 1990, Gillespie & Critchley 1999). Reflecting this algal phenology, the abundance and species composition of the epibenthic assemblage also show a remarkable seasonal fluctuation (Edgar 1983, Takeuchi et al. 1987, 1990, Russo 1989, Taylor 1998a, Garcia et al. 2019). Notably, epibenthic invertebrates have been reported to drastically decrease during macroalgal host defoliation (e.g. Mukai 1971, Kodama et al. 2020, Leite et al. 2021).

The seasonal decrease of epibenthic invertebrates in macroalgal beds has been discussed in several studies and explained by the following 2 possibilities: (1) they die and get mainly eaten by predators, and/or (2) they migrate from the macroalgal bed (Choat & Kingett 1982, Aoki 1988, Takeuchi et al. 1990, Edgar & Aoki 1993, Taylor 1998a, Kodama et al. 2020). Of these 2 possibilities, the effects of predation on epibenthic assemblages have been tested in some previous studies using caging experiments (predator exclusion experiments) (Choat & Kingett 1982, Aoki 1988, Kennelly 1991, Edgar & Aoki 1993). On the other hand, dispersal of epibenthic invertebrates has been inferred from indirect circumstantial evidence but has not been experimentally detailed. The relationship between the seasonal decrease of epibenthic invertebrates in macroalgal beds and their dispersal remains poorly understood.

The purpose of this study was to confirm that epibenthic invertebrates disperse away from macroalgal beds as a result of macroalgal defoliation. To this purpose, we examined the gammaridean amphipods associated with a macroalgal bed of *Sargassum yezoense* in Otsuchi Bay, Japan. Epibenthic invertebrates in macroalgal beds are commonly dominated by gammaridean amphipods in both abundance and richness (Tararam & Wakabara 1981, Taylor & Cole 1994, Taylor 1998a,b, Tanaka & Leite 2003, Jacobucci et al. 2009), and members of the genus *Sargassum* are one of the dominant macroalgae forming algal beds in shallow tropical to temperate waters (Hanisak & Samuel 1987, Mattio et al. 2008, Mattio & Payri 2011). As we previously found that the gam-

marid assemblage associated with the *S. yezoense* bed in Otsuchi Bay showed a clear and rapid decrease during the algal defoliation season (Kodama et al. 2020), the *S. yezoense* beds and associated gammarids were considered a good model system to study the seasonal dispersal of epibenthic invertebrates during macroalgal host defoliation.

S. yezoense has a characteristic defoliation pattern from July to October (Fig. 1). The following describes the typical defoliation pattern of *S. yezoense* in Otsuchi Bay. (1) In July, defoliation starts with the loss of some leaves from the branches. (2) In August to September, all the leaves and branches are lost, and only the main axis remains attached to the holdfast; at the same time, newly developing thalli also occur. (3) In October, old defoliating thalli are completely lost, and new thalli appear (Kodama et al. 2020). During this defoliation, some dominant gammarid species in the *Sargassum* bed show a strong reduction in abundance, leading to a rapid and drastic change in the gammarid assemblage structure (Kodama et al. 2020). It is very likely that these gammarids migrate away from the *Sargassum* bed in this period. Gammarids as well as many other peracarids, do not have a diapause or larval phase and thus always require suitable habitat to be available. Therefore, it is important to understand how they adapt to the almost disappearance of their habitat during *Sargassum* defoliation.

Experiments using macroalgal imitations have often been used for evaluating the importance of various aspects of habitat quality, such as depth, height, size, complexity, structure, or food value (e.g. Norderhaug et al. 2002, Hauser et al. 2006, Rule & Smith 2007, Cacabelos et al. 2010, Hansen et al. 2011, Bueno et al. 2020). The imitation method is also effective for evaluating some aspects of the mobility of epibenthic invertebrates including dispersal (Virnstein & Curran 1986, Edgar 1991, Norderhaug et al. 2002). In the present study, we conducted a field experiment using an imitation of *Sargassum* to detect seasonal gammarid dispersal from a *Sargassum* bed as well as to examine the synchronization of gammarid decrease in the *Sargassum* bed and their dispersal during the defoliation season.

2. MATERIALS AND METHODS

2.1. Field sampling

This study was conducted at a subtidal rocky reef at Akahama in Otsuchi Bay, Iwate, northeastern

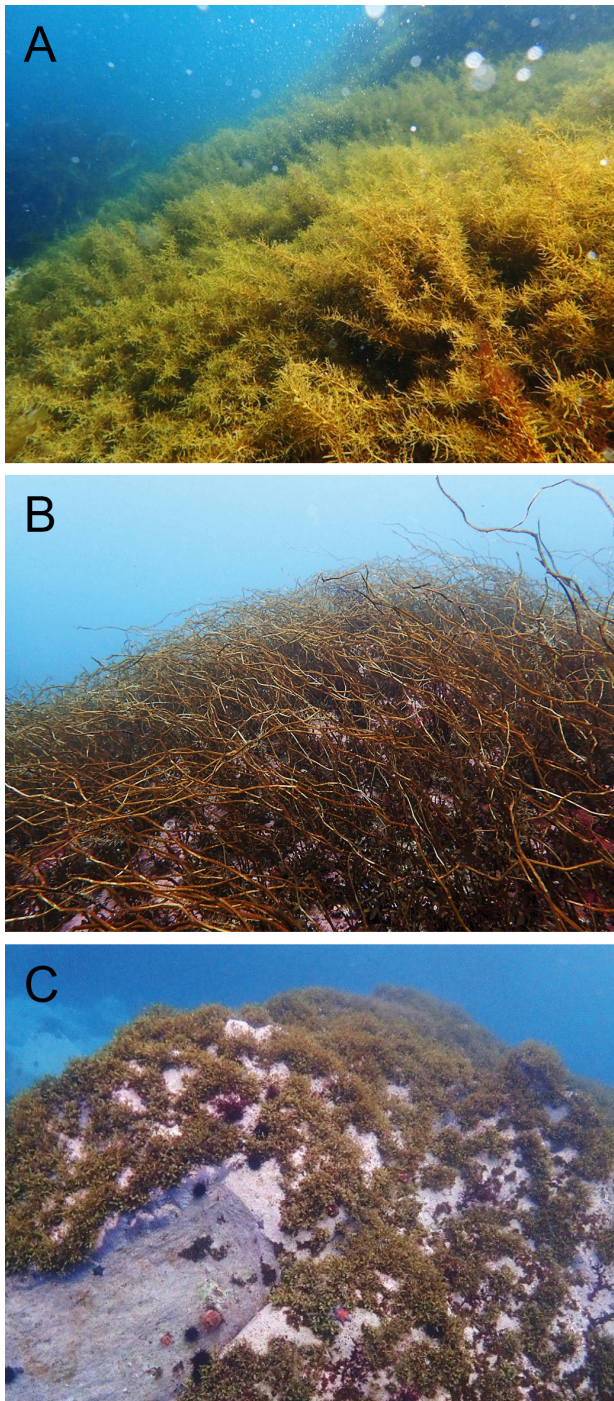


Fig. 1. Seasonal change in a *Sargassum yezoense* bed in Otsuchi Bay, Japan. (A) Early July, the season with most abundant foliage (photo: Kenta Nakamoto): thalli are long with many leaves. (B) September, defoliation season (photo: Masafumi Kodama): all leaves and branches are lost, and only the main axis remains attached to the holdfast. (C) December, post-defoliation season (photo: Takayuki Kanki): all old thalli are lost and replaced by newly occurred short thalli

Japan (Fig. 2A; 39° 21' 00" N, 141° 56' 10" E) from June to October 2020, during the defoliation season of *S. yezoense*, July to September (Kodama et al. 2020). Field samplings were conducted monthly using SCUBA from June to October 2020. Six quadrats (10 × 10 cm) were haphazardly set in a macroalgal bed of *S. yezoense* that formed on the subtidal rocky reef (<4 m deep). In each quadrat, individual thalli of *S. yezoense* were cut with scissors at just above the holdfast and put into a 0.6 mm meshed net bag.

2.2. Field experiments using algal imitation

The field experiment was carried out at the edge of the *Sargassum* bed (Fig. 2B) using imitation macrophyte aquarium ornaments made of polypropylene with a height of about 20 cm (JAN 4972547028464, GEX) as algal imitations of *Sargassum* and attached to concrete blocks (Fig. 2C). Six algal imitations were placed about 1.0 m away from the edge of the *Sargassum* bed in June 2020 and attached to concrete blocks (Fig. 2D). Since the thalli length of *S. yezoense* is always shorter than 1.0 m year-round (Kodama et al. 2020), gammarids on the *Sargassum* bed cannot directly move by crawling from the *Sargassum* bed to the algal imitation, meaning that they cannot reach the imitations unless they leave the *Sargassum* bed (either by swimming or crawling across the sea bed). If the gammarids that decreased in the *Sargassum* bed were to disperse to outside of the *Sargassum* bed, then they could settle on the neighboring algal imitation. Furthermore, viewed from the imitations, there was only a *Sargassum* bed on the shoreward side and only sandy bottom substrate without any algal beds on the offshore side (Fig. 2D). Therefore, the majority of gammarids that occurred on the imitations were assumed to be migrants from the adjacent *Sargassum* bed.

All the imitations were replaced monthly from July to October 2020. Each imitation was gently detached from the concrete block and immediately put into a 0.6 mm meshed net bag, and a new imitation was attached to the concrete block. In this article, these imitation samples are referred as the 'setting month–collecting month' sample. For example, Jun–Jul sample means that the imitation sample was set in June and collected in July. Two imitations were lost in September, probably due to strong water movements associated with waves. Thus, the Aug–Sep sample includes only 4 replicates.

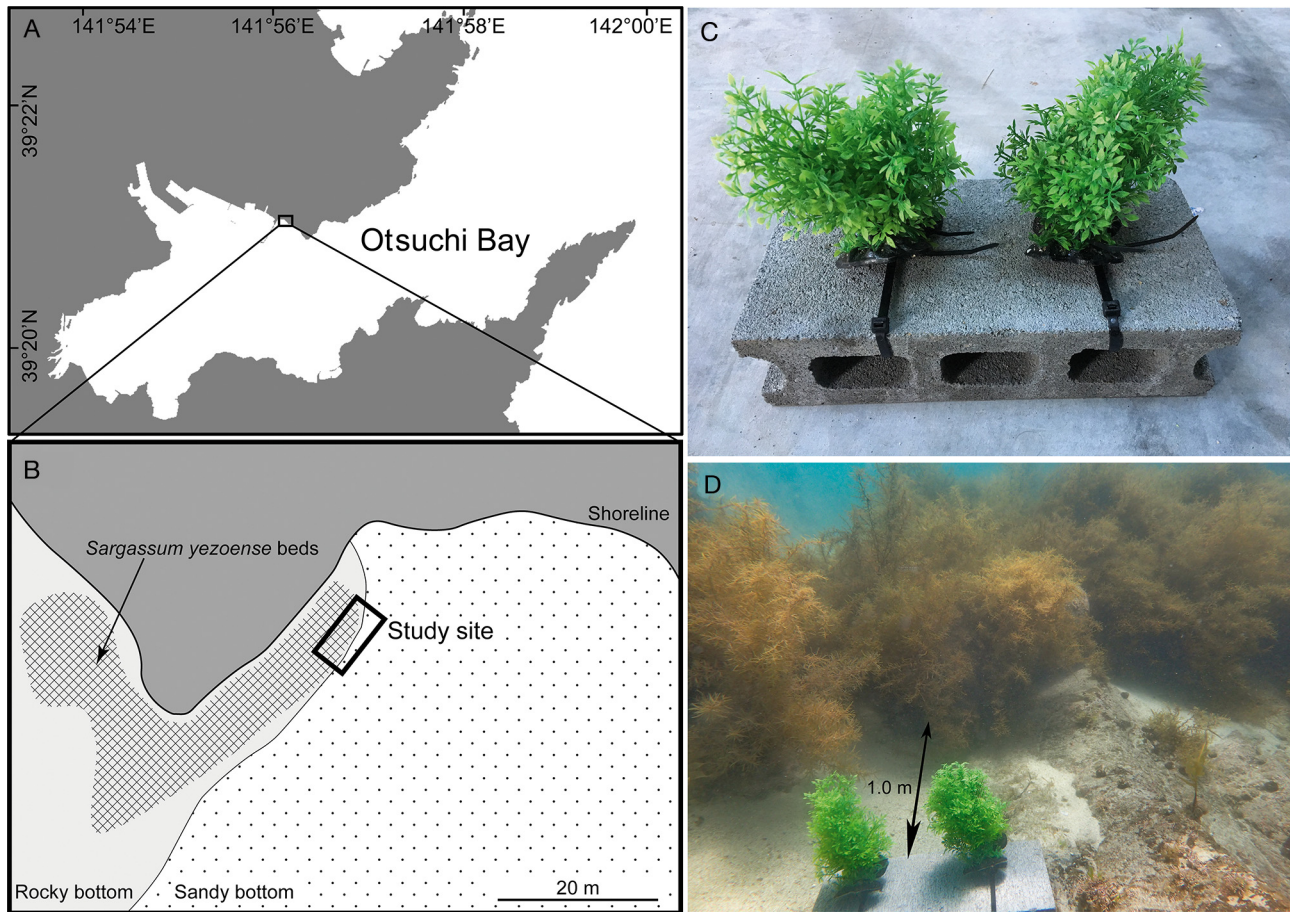


Fig. 2. (A) Study area in Otsuchi Bay, Iwate, Japan. (B) Study site for field experiment: dark gray with black line indicates land and shoreline; light gray indicates rocky bottom; white with dots indicates sandy bottom; shaded area indicates *Sargassum yezoense* bed; study site indicates the edge area of the *S. yezoense* bed where the algal imitations were set. (C) Algal imitations and concrete block used in the field experiment. (D) Algal imitations set about 1.0 m from the edge of the *S. yezoense* bed

2.3. Processing of samples and statistical analysis

In gammarids, egg hatching, as well as early growth of juveniles, takes place in the brood pouch of females (Lincoln 1979, Borowsky 1980, Dick et al. 1998, 2002, Bellan-Santini 2015). Accordingly, newly hatched small juveniles found on the imitations were thought to have hatched after their parents had settled on the imitations. Hence, newly hatched small juveniles on the imitations would not fully represent emigrants from the *Sargassum* bed. Therefore, small gammarid individuals were excluded from the statistical analyses, and we targeted relatively large individuals. All the samples were sieved through a 1.0 mm mesh to remove newly hatched small juveniles; gammarids left on the mesh were identified to the lowest possible taxon. Although the systematics of the order Amphipoda

have been recently revised, in the present study we use the term 'gammarids' to mean members of the historical suborder Gammaroidea (see Kodama et al. 2020).

In each sample of the *Sargassum* bed, all the *S. yezoense* left on the mesh were collected, from which 10 thalli were haphazardly selected and their lengths measured. Since 6 samples of the *Sargassum* bed were obtained for each month, 60 thalli were measured for each month except for September. Because *Sargassum* samples consisted of old defoliating thalli and newly developed thalli in September, both 10 old defoliating thalli and 10 newly developed thalli were haphazardly selected and their lengths measured in September; thus, 120 thalli (60 old and 60 new thalli) were measured in September. Because it was not possible to dry all the algal samples due to the capacity limitation of our drying room, *S. yezoense* biomass

was calculated for each sample by the following procedure. The total wet weight of *S. yezoense* was measured with an accuracy of 0.001 g for each monthly sample. After that, the wet weight of a partial algal sample (about 1/4 of total algal sample) was measured with an accuracy of 0.001 g, and the partial algal sample was dried at 60°C for at least 48 h. The dry weight (DW) of a partial algal sample was measured with an accuracy of 0.001 g. The biomass of *S. yezoense* (g DW 100 cm⁻²) was calculated from the total wet weight and the ratio of DW to wet weight of the partial algal sample.

Gammarid abundances per quadrat ($Abund_{area}$: ind. 100 cm⁻²) and per *Sargassum* biomass ($Abund_{DW}$: ind. g⁻¹ DW) in the *Sargassum* bed as well as those per algal imitation ($Abund_{imit}$: ind. imitation⁻¹) were calculated for all the gammarid taxa. To analyze fluctuations of gammarid $Abund_{area}$, $Abund_{DW}$, and $Abund_{imit}$ in the 4 most dominant species, the effect of the sampling month was assessed by a generalized additive model (GAM) using the 'mgcv' package (Wood 2017) in R version 3.5.1. Negative binomial distributions with log link functions were used in the GAM for $Abund_{area}$ and $Abund_{imit}$. Gaussian distributions with identity link functions were used in the GAM for $Abund_{DW}$. In all the GAMs, sampling month data were transformed as the number of elapsed months from the first sampling and thus treated as a discrete data set (not categorical data). In addition, the effect of *Sargassum* biomass on gammarid $Abund_{area}$ was assessed by a generalized linear model (GLM) using the MASS package (Venables & Ripley 2002). The data for all months were pooled, and negative binomial distributions with log link functions were used in this GLM.

3. RESULTS

Sargassum yezoense biomass increased from June to July and decreased from July to September (Fig. 3A). Similarly, thalli length increased from June to July and decreased from July to September (Fig. 3B). Algal bodies of *S. yezoense* defoliated from July to September. Newly developed thalli were found in September and October.

A total of 3406 and 6550 individuals of gammarids were collected from the *Sargassum* bed samples and imitation samples, respectively. The most dominant species in the *Sargassum* bed was *Jassa morinoid*, which comprised 34.9% of total gammarid individuals, followed by *Ericthonius pugnax* (20.6%), *Sunamphitoe* spp. (15.7%), and *Podocerus* sp. (12.1%). These species, except for *Sunamphitoe* spp., were

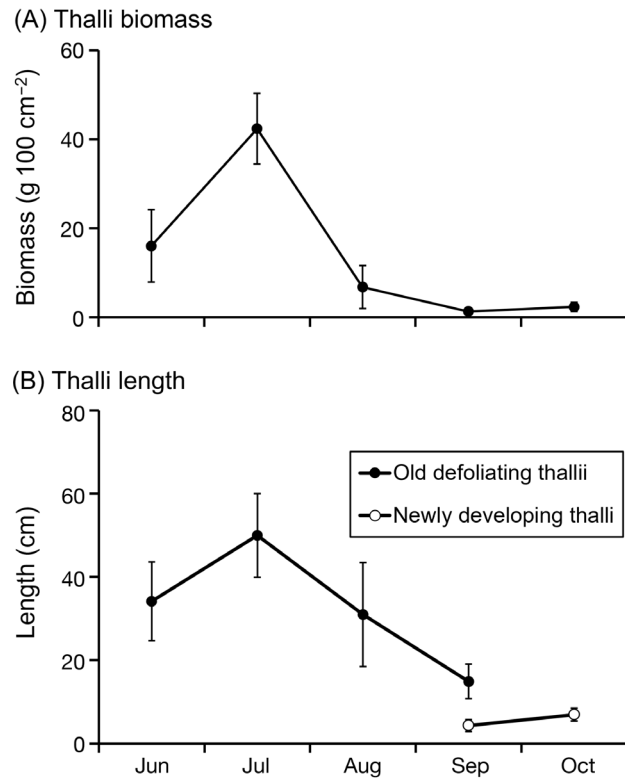


Fig. 3. Changes in (A) biomass and (B) length of *Sargassum yezoense* thalli. Error bars show SD

also abundant in the imitation samples; *J. morinoid* 9.7%; *E. pugnax*, 37.3%; *Sunamphitoe* spp., 0.3%; and *Podocerus* sp., 18.2%. In addition, *Gammaropsis japonica* were also abundant (14.2%) in the imitation samples. Seasonal patterns of $Abund_{area}$, $Abund_{DW}$, and $Abund_{imit}$ for the total gammarids collected in this study are summarized in Fig. 4. $Abund_{area}$ peaked in July but decreased during the *Sargassum* defoliation season, whereas $Abund_{DW}$ increased during the defoliation season due to the reduction of *Sargassum* biomass. The most dominant species in the *Sargassum* bed was *J. morinoid* in June and July but was subsequently replaced by *E. pugnax* during and after *Sargassum* defoliation. $Abund_{imit}$ was highest in the defoliation season rather than the non-defoliation season.

Seasonal changes of $Abund_{area}$, $Abund_{DW}$, and $Abund_{imit}$ of the 4 dominant gammarid taxa, *J. morinoid*, *Podocerus* sp., *Sunamphitoe* spp., and *E. pugnax*, as well as their GAM fitted lines show quite different patterns among species (Fig. 5). Among them, *J. morinoid* and *Podocerus* sp. showed a relatively similar pattern (Fig. 5A,B). Their $Abund_{area}$ in the *Sargassum* bed increased from June to July and decreased from July to August or September, clearly corresponding with the increase and decrease in *Sargassum* biomass

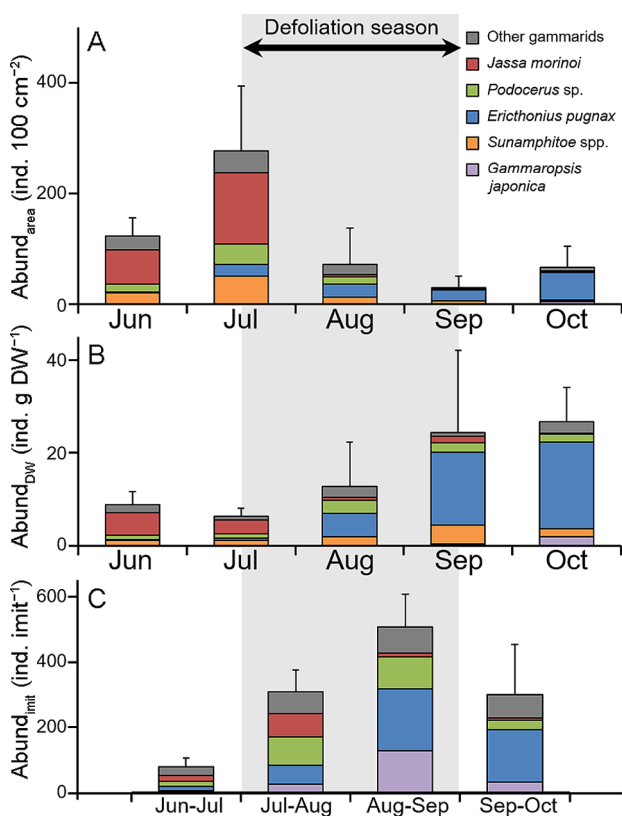


Fig. 4. Changes in total abundances and species composition of gammarids. (A) Gammarids per area in *Sargassum* beds; (B) gammarids per *Sargassum* dry weight in *Sargassum* beds; (C) dispersed gammarids found on *Sargassum* imitations. Error bars show SD

and thalli length. The correlation between $Abund_{area}$ and *Sargassum* biomass was also supported by the GLM (Fig. 6A,B). However, seasonal patterns of abundance per algal biomass ($Abund_{DW}$) differed between *J. morinoi* and *Podocerus* sp. Gammarids found on algal imitations ($Abund_{imit}$) in the *Sargassum* defoliation season, i.e. Jul–Aug and/or Aug–Sep samples, were abundant compared to those found in the non-defoliation season, i.e. Jun–Jul or Sep–Oct samples.

$Abund_{area}$ and $Abund_{DW}$ of *Sunamphitoe* spp. (Fig. 5C) also showed similar patterns to those of *Podocerus* sp. Their $Abund_{area}$ increased from June to July and decreased from July to September, coinciding with the increase and decrease in *Sargassum* biomass and thalli length. The correlation between $Abund_{area}$ and *Sargassum* biomass was also supported by the GLM (Fig. 6C). In the imitation samples ($Abund_{imit}$), however, they were rarely found throughout the study period.

E. pugnax showed fluctuation and dispersal patterns different from the other 3 species (Fig. 5D). In

the *Sargassum* bed, $Abund_{area}$ of *E. pugnax* increased from June to July but did not decrease or even increased during the algal defoliation season. The correlation was also not supported between $Abund_{area}$ of *E. pugnax* and *Sargassum* biomass by the GLM (Fig. 6D). Moreover, their $Abund_{DW}$ increased during the defoliation season due to the reduction of *Sargassum* biomass in this season. On the algal imitation, they increased from the Jun–Jul to Aug–Sep samples and had high abundances even in the post-defoliation season.

4. DISCUSSION

Jassa morinoi and *Podocerus* sp. showed drastic decreases in $Abund_{area}$ in the *Sargassum* bed with algal defoliation; at the same time individuals that occurred on the neighboring algal imitations, which were assumed to be an indicator of gammarid dispersal from the *Sargassum* bed, significantly increased. This result strongly suggests that the gammarids that decreased in the algal bed dispersed away from the bed. This is the first experimental field study demonstrating a dispersal of epibenthic invertebrates with macroalgal host defoliation.

Another dominant taxon, *Sunamphitoe* spp., also decreased $Abund_{area}$ in the *Sargassum* bed with algal defoliation but was not found in the imitations. This can be explained by 2 possible processes: (1) they died in the *Sargassum* bed during its defoliation season and did not disperse from the algal bed, and/or (2) they dispersed from the *Sargassum* bed but did not settle on the algal imitations. Since *Sunamphitoe* are known to be herbivorous (Poore et al. 2008) and also known to build their nests by rolling up algal leaves (Cerdeira et al. 2010), the algal imitations made of polypropylene were probably an unsuitable habitat for them. Therefore, the latter hypothesis is thought to be more likely, though further experiments are needed to verify this.

Ericthonius pugnax kept both its abundance and dispersal at high levels throughout the study period. $Abund_{area}$ was found to be at a high level even during algal host defoliation and also was not correlated with *Sargassum* biomass. $Abund_{DW}$ showed a clear increase according to the reduction of *Sargassum* biomass. These results suggest that *Sargassum* biomass as well as defoliation had only a limited effect on the abundance of *E. pugnax*, probably explained by its colony-dwelling life form. It is known to build large colonies that are made of congregations of nests of many individuals (Ariyama 2009). The

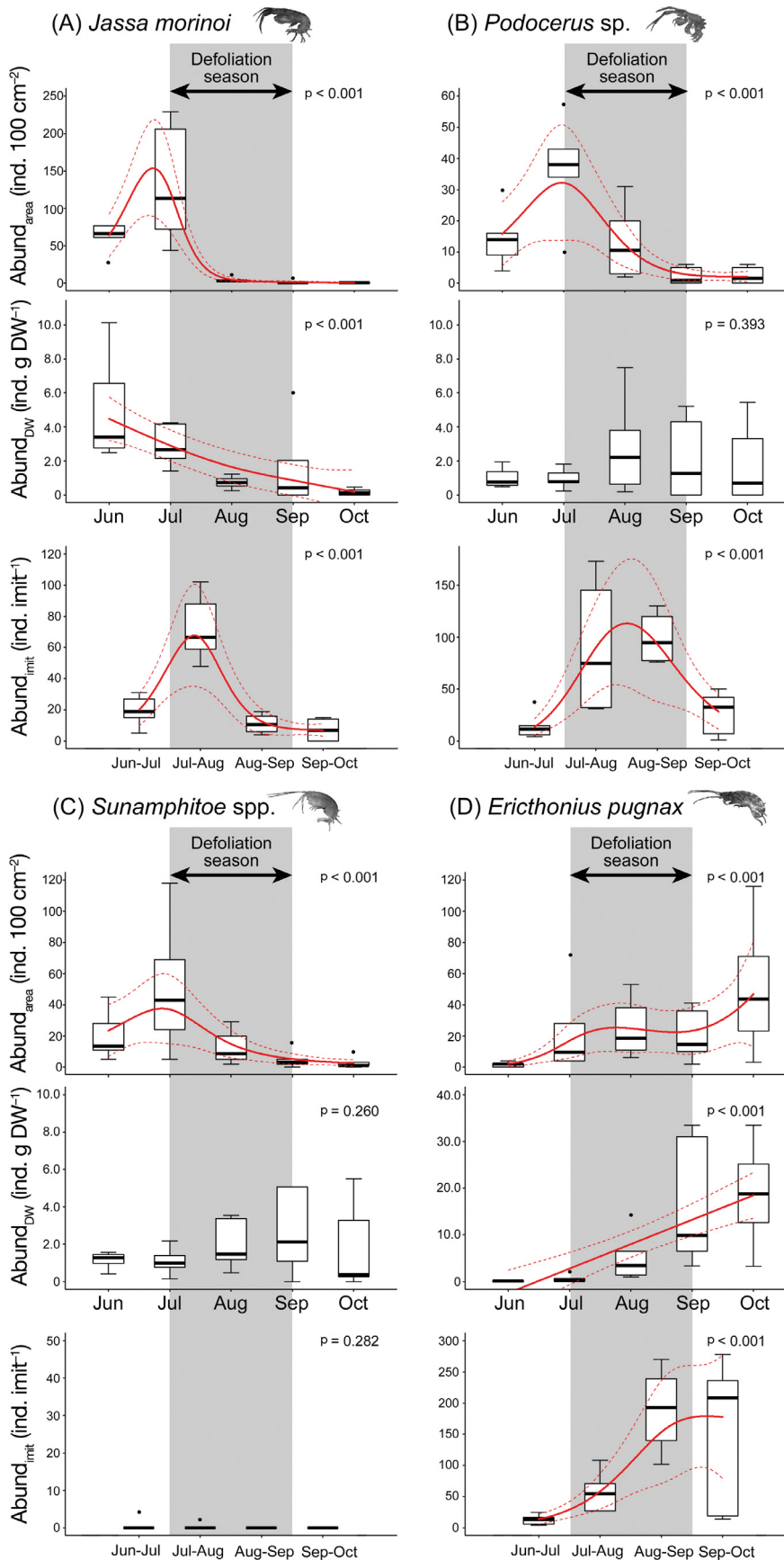


Fig. 5. Change in abundance of the 4 dominant gammarid species in *Sargassum* beds and *Sargassum* imitations. Upper panels: abundance per area in *Sargassum* beds; middle panels: abundance per *Sargassum* dry weight in *Sargassum* beds; lower panels: abundance of gammarids associated with *Sargassum* imitations. (A) *Jassa morinoi*; (B) *Podocerus* sp.; (C) *Sunamphitoe* spp.; (D) *Erichthonius pugnax*. Boxes represent the lower and upper quartiles. Black bold line in each box indicates the median. Whiskers indicate minimum and maximum values excluding outliers, while black dots represent outliers. Values outside 1.5 times the interquartile range above the upper quartile and below the lower quartile are shown as outliers. Red solid and broken lines indicate the generalized additive model (GAM) fitted line and 95% confidence (± 2 SE). The lines were drawn when the effect of sampling month was found to be significant in the GAM ($p < 0.05$)

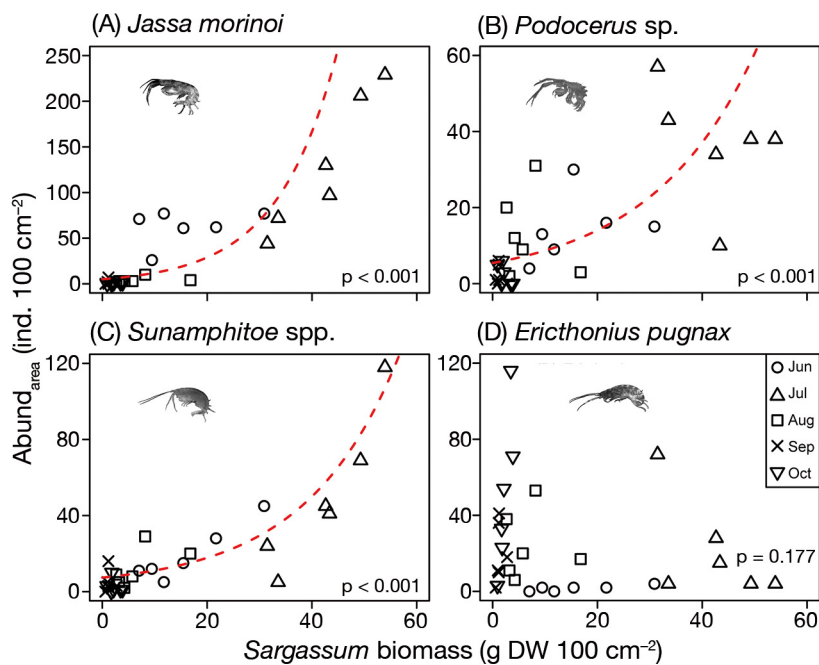


Fig. 6. Abundance per area of 4 dominant gammarid species in *Sargassum* beds, in relation to *Sargassum* biomass. (A) *Jassa morinoi*; (B) *Podocerus* sp.; (C) *Sunamphitoe* spp.; (D) *Erichthonius pugnax*. Symbols indicate sampling months. Red broken line indicates generalized linear model (GLM) fitted line. The lines were drawn when the effect of *Sargassum* biomass on gammarid abundance per area was found to be significant in the GLM ($p < 0.05$)

colonies of *E. pugnax* were found around relatively low positions on *Sargassum* thalli near the holdfast; moreover, they were found to remain even after defoliation of the *Sargassum* thallus at the present study site (Fig. 7), which would maintain the high abundance and high dispersal of *E. pugnax* during (and even after) the *Sargassum* defoliation season.

Gammaropsis japonica was rarely found in the *Sargassum* bed; however, it was unexpectedly found in high abundance in the Aug–Sep imitation sample (Fig. 4). Kodama et al. (2020) reported that *G. japonica* was one of the most dominant gammarid species in the understory strata (among holdfasts) of the *Sargassum* bed but rarely found in the canopy strata (among algal thalli) at Akahama in Otsuchi Bay, the same location as the study site of this study. Thus, in the present study, *G. japonica* that occurred in the algal imitation was thought to have migrated from the understory strata of the neighboring *Sargassum* bed, though the understory was not investigated in the present study.

The defoliation-related dispersal observed in this study is thought to have been caused by a reduction of habitable space as well as a decrease in habitat quality. Macroalgal defoliation generally reduces the

habitable space for epibenthic invertebrates by reducing their biomass and surface area and therefore can promote the dispersal of epibenthic invertebrates. In the present study, $Abund_{area}$ of *Podocerus* sp. and *Sunamphitoe* spp. in the *Sargassum* defoliation season decreased; however, $Abund_{DW}$ remained at high levels or even increased in the defoliation season. These results may indicate a process of their accumulation (sensu Jacobucci et al. 2009), with more individuals occupying less available space in the defoliating thalli. This accumulation probably facilitated competition for habitable space among gammarids, and thus smaller and/or weaker individuals were forced to disperse (e.g. density-dependent dispersal; Franz 1989, Franz & Mohamed 1989, Wilson 1989, Tanaka & Leite 2004, Kumagai 2006). Accordingly, these results suggest that the reduction of *Podocerus* sp. and *Sunamphitoe* spp. per area as well as the increase of dispersal in *Podocerus* sp. were caused by the limitation of their

habitable space. In contrast, both $Abund_{area}$ and $Abund_{DW}$ of *J. morinoi* greatly decreased from July to August, indicating that the reduction in $Abund_{area}$ was not explained only by the limitation of habitable space. One possibility leading to the reduction of *J. morinoi* $Abund_{area}$ and $Abund_{DW}$ is the reduction in habitat quality in this season. The defoliation of *Sargassum yezoense* reduced not only the habitable space but also the habitat complexity for the epibenthic invertebrates by loss of leaves from the thalli (Kodama et al. 2020). Since the complexity of the algal body has various positive effects on epibenthic inhabitants, such as providing shelter, trapping more detritus, and providing larger surface area per biomass (Coull & Wells 1983, Hicks 1985, Gibbons 1988, Hixon & Menge 1991, Diehl 1992, Carvalho et al. 2018), defoliation is considered to reduce the habitat quality of *Sargassum* thalli and can therefore promote the dispersal of epibenthic invertebrates. The different patterns of $Abund_{DW}$ among gammarid species suggests different responses to the change of habitat quality including the loss of microhabitats such as algal leaves. This would be explained by differences in their habitat quality requirements and/or requirement for specific microhabitats among the

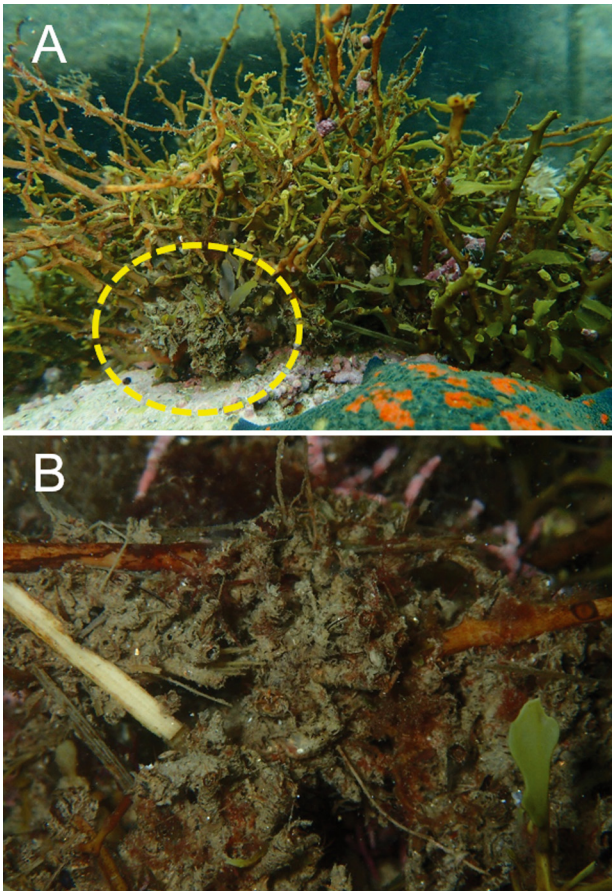


Fig. 7. Colony of *Erichthonius pugnax* in September, after the defoliation season (A) built near the holdfast of *Sargassum* beds; (B) magnified

different gammarid species (e.g. Hacker & Steneck 1990, Beermann & Franke 2012). Hence, this result also suggests that the change of habitat quality in algal beds affects the dispersal of various epibenthic species in different ways.

In the present study and in Kodama et al. (2020), the abundance of the dominant species *J. morinoi*, *Sunamphitoe* spp. and *Podocerus* sp., was strongly reduced in *Sargassum* beds during the *Sargassum* defoliation season. Notably, however, their abundance did not reach a level of zero; they continued to occur year-round in the *Sargassum* beds though their abundance was quite low in some seasons, especially the defoliation season and post-defoliation season in the *Sargassum* bed (Kodama et al. 2020). This suggests that when the *Sargassum* defoliates, the habitable space indeed strongly reduces but does not become a completely unsuitable habitat for the gammarids. The small number of survived gammarids breed and contribute to an increase in the population size in correlation with *Sargassum* growth by the next summer.

Microcosm experiments conducted in a seagrass bed of the genus *Amphibolis* showed that abundances of epibenthic invertebrates drastically decreased in response to the declines of epiphytic algal production, and the reductions of their abundance were suggested to be due to emigration rather than death by predation or starvation (Edgar 1990). In the present study, defoliation-related dispersal was at least detected in some species; however, the effects of predation or starvation on gammarid reduction in the *Sargassum* bed were not evaluated.

Another important question that arises from our results is where the gammarids moved to and settled after they dispersed from the macroalgal bed. Some species of gammarids have been suggested to have the ability for long-distance dispersal (discussed below) and show selective settlement onto their preferred habitat(s) (Poore & Steinberg 1999, Poore 2004, Bueno et al. 2020). The algal imitation used in the present study could be an adequate habitat for some gammarid species to settle but may not be a suitable habitat for the herbivorous *Sunamphitoe* spp. Since each gammarid species would settle onto its own preferred habitat(s), the places where each gammarid species settled after they dispersed from the macroalgal bed are probably strongly dependent on how far they could disperse and what kind of habitats occur in the area to which they moved.

Some gammarid species were unexpectedly found among the algal imitation samples although very few were collected from the neighboring *Sargassum* bed at the time. For example, *J. morinoi* almost disappeared from the *Sargassum* bed by August; nevertheless, they still occurred in Aug–Sep and Sep–Oct samples of the algal imitation. These results suggest that these gammarids on the imitation may have come from habitats other than the neighboring *Sargassum* bed. Some gammarids have been suggested to have a long-distance dispersal ability by using currents, rafting, or even a typhoon event (e.g. Thiel & Gutow 2005, Kumagai 2006, Havermans et al. 2007, Navarro-Barranco et al. 2020). Havermans et al. (2007) suggested from laboratory experiments that adult *J. herdmani* can exhibit long-distance dispersal by using tidal or surface currents and tolerance for a long period of starvation. In our field experiment, the gammarids unexpectedly found on the algal imitations may have originated from sources 100s of m or even several km away. The results of the present study, however, still indicate that some species of gammarids dispersed from the *Sargassum* bed and moved to different habitats in the algal defoliation season, since our experimental design successfully

detected the gammarid decrease in the *Sargassum* bed and the coincident increase in the imitation.

In conclusion, the present study highlights the defoliation-associated dispersal of epibenthic gammarids from a macroalgal bed. Defoliation-associated dispersal could be caused by the reduction of habitable space and habitat quality due to thalli defoliation, though the patterns of reductions and dispersal were found to depend largely on the epibenthic species, probably due to differences of their feeding behavior and microhabitat use. Since many kinds of macroalgae generally show seasonal growth and defoliation, the concept of defoliation-associated dispersal of inhabitants is expected to be applicable to a wide range of macroalgal species. The dispersal has important consequences not only for the population dynamics of certain species but also for epibenthic assemblage dynamics, habitat connectivities, and even ecosystem functions in aquatic environments (Edgar 1990, Hansson 1991, Ronce 2007, Little et al. 2019, White et al. 2019). For further understanding, the concept of defoliation-associated dispersal should also be examined in other types of macroalgal beds.

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LITERATURE CITED

- ✦ Aoki M (1988) Factors affecting population fluctuations of caprellid amphipods inhabiting *Sargassum patens* bed (preliminary report). *Benthos Res* 32:42–49
- Ariyama H (2009) Species of the genus *Ericthonius* (Crustacea: Amphipoda: Ischyroceridae) from western Japan with description of a new species. *Bull Natl Mus Nat Sci Ser A (Suppl 3)*:15–36
- ✦ Aumack CF, Lowe AT, Amsler CD, Amsler MO, McClintock JB, Baker BJ (2017) Gut content, fatty acid, and stable isotope analyses reveal dietary sources of macroalgal-associated amphipods along the western Antarctic Peninsula. *Polar Biol* 40:1371–1384
- ✦ Beermann J, Franke HD (2012) Differences in resource utilization and behaviour between coexisting *Jassa* species (Crustacea, Amphipoda). *Mar Biol* 159:951–957
- Bellan-Santini D (2015) Order Amphipoda Latreille, 1816. In: Von Vaupel Klein JC, Charmantier-Daures M, Schram FR (eds) *Treatise on zoology — anatomy, taxonomy, biology. The Crustacea, Vol 5*. Brill, Leiden, p 93–248
- ✦ Borowsky B (1980) Reproductive patterns of three intertidal salt-marsh gammaridean amphipods. *Mar Biol* 55:327–334
- ✦ Bueno M, Machado GBO, Leite FPP (2020) Colonization of novel algal habitats by juveniles of a marine tube-dwelling amphipod. *PeerJ* 8:e10188
- ✦ Cacabelos E, Olabarria C, Incera M, Troncoso JS (2010) Effects of habitat structure and tidal height on epifaunal assemblages associated with macroalgae. *Estuar Coast Shelf Sci* 89:43–52
- ✦ Carvalho NF, Grande H, Filho JSR, Jacobucci GB (2018) The structure of gammarid amphipod (Crustacea, Peracarida) assemblages associated with *Sargassum* (Phaeophyta, Fucales) and their link with the structural complexity of algae. *Hydrobiologia* 820:245–254
- ✦ Cerda O, Hinojosa AA, Thiel M (2010) Nest-building behavior by the amphipod *Peramphithoe femorata* (Krøyer) on the kelp *Macrocystis pyrifera* (Linnaeus) C. Agardh from northern-central Chile. *Biol Bull* 218:248–258
- ✦ Choat JH, Kingett PD (1982) The influence of fish predation on the abundance cycles of an algal turf invertebrate fauna. *Oecologia* 54:88–95
- ✦ Costanza R, d'Arge R, de Groot R, Farber S and others (1997) The value of the world's ecosystem services and natural capital. *Nature* 387:253–260
- ✦ Coull BC, Wells JBJ (1983) Refuges from fish predation: experiments with phytal meiofauna from the New Zealand rocky intertidal. *Ecology* 64:1599–1609
- ✦ de Juan S, Gelcich S, Ospina-Alvarez A, Perez-Matus A, Fernandez M (2015) Applying an ecosystem service approach to unravel links between ecosystems and society in the coast of central Chile. *Sci Total Environ* 533:122–132
- ✦ Dick JTA, Faloon SE, Elwood RW (1998) Active broodcare in an amphipod: influences of embryonic development, temperature and oxygen. *Anim Behav* 56:663–672
- ✦ Dick JTA, Bailey RJE, Elwood RW (2002) Maternal care in the rockpool amphipod *Apherusa jurinei*: developmental and environmental cues. *Anim Behav* 63:707–713
- ✦ Diehl S (1992) Fish predation and benthic community structure: the role of omnivory and habitat complexity. *Ecology* 73:1646–1661
- ✦ Duffy JE (1990) Amphipods on seaweeds: partners or pests? *Oecologia* 83:267–276
- ✦ Edgar GJ (1983) The ecology of south-east Tasmanian phytal animal communities. II. Seasonal change in plant and animal populations. *J Exp Mar Biol Ecol* 70:159–179
- ✦ Edgar GJ (1990) Population regulation, population dynamics and competition amongst mobile epifauna associated with seagrass. *J Exp Mar Biol Ecol* 144:205–234
- ✦ Edgar GJ (1991) Artificial algae as habitats for mobile epifauna: factors affecting colonization in a Japanese *Sargassum* bed. *Hydrobiologia* 226:111–118
- ✦ Edgar GJ, Aoki M (1993) Resource limitation and fish predation: their importance to mobile epifauna associated with Japanese *Sargassum*. *Oecologia* 95:122–133
- ✦ Filbee-Dexter K, Feehan CJ, Scheibling RE (2016) Large-scale degradation of a kelp ecosystem in an ocean warming hotspot. *Mar Ecol Prog Ser* 543:141–152
- ✦ Franz DR (1989) Population density and demography of a fouling community amphipod. *J Exp Mar Biol Ecol* 125:117–136
- ✦ Franz DR, Mohamed Y (1989) Short-distance dispersal in a fouling community amphipod crustacean, *Jassa marmorata* Holmes. *J Exp Mar Biol Ecol* 133:1–13
- ✦ Garcia ICP, Cunha KVS, Jacobucci GB (2019) Population and reproductive biology of two caprellid species (Crustacea: Amphipoda) associated to *Sargassum cymosum*

- (Phaeophyta: Fucales) on the southeast coast of Brazil. *Nauplius* 27:e2019002
- ✦ Gibbons MJ (1988) The impact of wave exposure on meiofauna of *Gelidium pristoides* (Turner) Kuetzing (Gelidiales: Rhodophyta). *Estuar Coast Shelf Sci* 27:581–593
- ✦ Gillespie RD, Critchley AT (1999) Phenology of *Sargassum* spp. (Sargassaceae, Phaeophyta) from Reunion Rocks, KwaZulu-Natal, South Africa. *Hydrobiologia* 398–399: 201–210
- Graham MH, Vasquez JA, Buschmann AH (2007) Global ecology of the giant kelp *Macrocystis*: from ecotypes to ecosystems. *Oceanogr Mar Biol Annu Rev* 45:39–88
- ✦ Hacker SD, Steneck RS (1990) Habitat architecture and the abundance and body-size-dependent habitat selection of a phytal amphipod. *Ecology* 71:2269–2285
- Hanisak MD, Samuel MA (1987) Growth rates in culture of several species of *Sargassum* from Florida, USA. *Hydrobiologia* 151–152:399–404
- ✦ Hansen JP, Wikström SA, Axemar H, Kautsky L (2011) Distribution differences and active habitat choices of invertebrates between macrophytes of different morphological complexity. *Aquat Ecol* 45:11–22
- ✦ Hansson L (1991) Dispersal and connectivity in metapopulations. *Biol J Linn Soc* 42:89–103
- ✦ Hauser A, Attrill MJ, Cotton PA (2006) Effects of habitat complexity on the diversity and abundance of macrofauna colonising artificial kelp holdfasts. *Mar Ecol Prog Ser* 325:93–100
- ✦ Havermans C, De Broyer C, Mallefet J, Zintzen V (2007) Dispersal mechanisms in amphipods: a case study of *Jassa herdmani* (Crustacea, Amphipoda) in the North Sea. *Mar Biol* 153:83–89
- Hicks GRF (1985) Meiofauna associated with rocky shore algae. In: Moore PG, Seed R (eds) *The ecology of rocky coasts*. Hodder & Stoughton, London, p 36–56
- ✦ Hixon MA, Menge BA (1991) Species diversity: prey refuges modify the interaction effects of predation and competition. *Theor Popul Biol* 39:178–200
- ✦ Jacobucci GB, Tanaka MO, Leite FPP (2009) Temporal variation of amphipod assemblages associated with *Sargassum filipendula* (Phaeophyta) and its epiphytes in a subtropical shore. *Aquat Ecol* 43:1031–1040
- ✦ Kamermans P, Malta EJ, Verschuure JM, Schrijvers L, Lentz LF, Lien ATA (2002) Effect of grazing by isopods and amphipods on growth of *Ulva* spp. (Chlorophyta). *Aquat Ecol* 36:425–433
- ✦ Kennelly SJ (1991) Caging experiments to examine the effects of fishes on understory species in a sublittoral kelp community. *J Exp Mar Biol Ecol* 147:207–230
- ✦ Kodama M, Kawamura T, Nakamoto K, Ohtsuchi N and others (2020) Effect of algal phenology on seasonal dynamics of gammarid assemblages: differences between canopy and understory strata in a *Sargassum yezoense* bed. *Mar Ecol Prog Ser* 634:63–76
- ✦ Kumagai NH (2006) Distance effects on patterns and processes of dispersal in an octocoral-associated amphipod. *Mar Ecol Prog Ser* 321:203–214
- ✦ Leite FPP, Bottcher C, Lewinsohn IDA, Siqueira SGL, Mansur KFR, Longo PAS, Vieira EA (2021) Asymmetric effects of changes in the habitat-forming algae *Sargassum* on different associated mobile faunas along São Paulo coast, Brazil. *Mar Ecol* 42:e12649
- Lincoln RJ (1979) *British marine Amphipoda: Gammaridea*. British Museum (Natural History), London
- ✦ Little CJ, Fronhofer EA, Altermatt F (2019) Dispersal syndromes can impact ecosystem functioning in spatially structured freshwater populations. *Biol Lett* 15:20180865
- ✦ Mancinelli G, Rossi L (2001) Indirect, size-dependent effects of crustacean mesograzers on the Rhodophyta *Gracilaria verrucosa* (Hudson) Papenfuss: evidence from a short-term study in the Lesina Lagoon (Italy). *Mar Biol* 138: 1163–1173
- ✦ Mattio L, Payri CE (2011) 190 years of *Sargassum* taxonomy, facing the advent of DNA phylogenies. *Bot Rev* 77:31–70
- ✦ Mattio L, Dirberg G, Payri C, Andréfouët S (2008) Diversity, biomass and distribution pattern of *Sargassum* beds in the south west lagoon of New Caledonia (South Pacific). *J Appl Phycol* 20:811–823
- ✦ Mukai H (1971) The phytal animals on the thalli of *Sargassum serratifolium* in the *Sargassum* region, with reference to their seasonal fluctuations. *Mar Biol* 8:170–182
- ✦ Navarro-Barranco C, Irazabal A, Moreira J (2020) Demersal amphipod migrations: spatial patterns in marine shallow waters. *J Mar Biol Assoc UK* 100:239–249
- ✦ Norderhaug KM, Christie H, Rinde E (2002) Colonisation of kelp imitations by epiphyte and holdfast fauna; a study of mobility patterns. *Mar Biol* 141:965–973
- Olafsson E (2016) *Marine macrophytes as foundation species*. CRC Press, Boca Raton, FL
- ✦ Pickering TD, Gordon ME, Tong LJ (1990) Seasonal growth, density, reproductive phenology and agar quality of *Gracilaria sordida* (Gracilariales, Rhodophyta) at Mokomoko Inlet, New Zealand. *Hydrobiologia* 204–205: 253–262
- ✦ Pinnegar JK, Polunin NVC, Francour P, Badalamenti F and others (2000) Trophic cascades in benthic marine ecosystems: lessons from fisheries and protected-area management. *Environ Conserv* 27:179–200
- ✦ Poore AGB (2004) Spatial associations among algae affect host use in a herbivorous marine amphipod. *Oecologia* 140:104–112
- Poore AGB, Steinberg PD (1999) Preference–performance relationships and effects of host plant choice in a herbivorous marine amphipod. *Ecol Monogr* 69:443–464
- ✦ Poore AGB, Hill NA, Sotka EE (2008) Phylogenetic and geographic variation in host breadth and composition by herbivorous amphipods in the family Ampithoidae. *Evolution* 62:21–38
- ✦ Ronce O (2007) How does it feel to be like a rolling stone? Ten questions about dispersal evolution. *Annu Rev Ecol Syst* 38:231–253
- ✦ Rule MJ, Smith SDA (2007) Depth-associated patterns in the development of benthic assemblages on artificial substrata deployed on shallow, subtropical reefs. *J Exp Mar Biol Ecol* 345:38–51
- ✦ Russo AR (1989) Fluctuations of epiphytal gammaridean amphipods and their seaweed hosts on an Hawaiian algal reef. *Crustaceana* 57:25–37
- ✦ Sideman EJ, Mathieson AC (1983) The growth, reproductive phenology, and longevity of non-tide-pool *Fucus distichus* (L.) Powell in New England. *J Exp Mar Biol Ecol* 68:111–127
- ✦ Stål J, Pihl L, Wennhage H (2007) Food utilisation by coastal fish assemblages in rocky and soft bottoms on the Swedish west coast: inference for identification of essential fish habitats. *Estuar Coast Shelf Sci* 71:593–607
- ✦ Steneck RS, Graham MH, Bourque BJ, Corbett D, Erlandson JM, Estes JA, Tegner MJ (2002) Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environ Conserv* 29:436–459

- ✦ Tait LW, Schiel DR (2011) Legacy effects of canopy disturbance on ecosystem functioning in macroalgal assemblages. *PLOS ONE* 6:e26986
- Takeuchi I, Kuwabara R, Hirano R, Yamakawa H (1987) Species composition of the Caprellidea (Crustacea: Amphipoda) of the *Sargassum* zone on the Pacific coast of Japan. *Bull Mar Sci* 41:253–267
- Takeuchi I, Yamakawa H, Fujiwara M (1990) Density fluctuation of caprellid amphipods (Crustacea) inhabiting the red alga *Gelidium amansii* (Lamouroux) Lamouroux, with emphasis on *Caprella okadai* Arimoto. *Mer (Paris)* 28:30–36
- ✦ Tanaka MO, Leite FPP (2003) Spatial scaling in the distribution of macrofauna associated with *Sargassum stenophyllum* (Mertens) Mertens: analysis of faunal group, gammarid life habit, and assemblage structure. *J Exp Mar Biol Ecol* 293:1–22
- ✦ Tanaka MO, Leite FPP (2004) Distance effects on short-term recolonization of *Sargassum stenophyllum* by mobile epifauna, with an analysis of gammarid life habits. *J Mar Biol Assoc UK* 84:901–910
- ✦ Tararam AS, Wakabara Y (1981) The mobile fauna—especially Gammaridea—of *Sargassum cymosum*. *Mar Ecol Prog Ser* 5:157–163
- ✦ Taylor RB (1998a) Seasonal variation in assemblages of mobile epifauna inhabiting three subtidal brown seaweeds in northeastern New Zealand. *Hydrobiologia* 361:25–35
- Taylor RB (1998b) Short-term dynamics of a seaweed epifaunal assemblage. *J Exp Mar Biol Ecol* 227:67–82
- ✦ Taylor RB, Cole RG (1994) Mobile epifauna on subtidal brown seaweeds in northeastern New Zealand. *Mar Ecol Prog Ser* 115:271–282
- Thiel M, Gutow L (2005) The ecology of rafting in the marine environment. II. The rafting organisms and community. *Oceanogr Mar Biol Annu Rev* 43:279–418
- Venables WN, Ripley BD (2002) *Modern applied statistics with S*, 4th edn. Springer, New York, NY
- ✦ Virnstein RW, Curran MC (1986) Colonization of artificial seagrass versus time and distance from source. *Mar Ecol Prog Ser* 29:279–288
- ✦ White JW, Carr MH, Caselle JE, Washburn L and others (2019) Connectivity, dispersal, and recruitment: connecting benthic communities and the coastal ocean. *Oceanography (Wash DC)* 32:50–59
- ✦ Wikström SA, Kautsky L (2007) Structure and diversity of invertebrate communities in the presence and absence of canopy-forming *Fucus vesiculosus* in the Baltic Sea. *Estuar Coast Shelf Sci* 72:168–176
- ✦ Wilson WHJ (1989) Predation and the mediation of intraspecific competition in an infaunal community in the Bay of Fundy. *J Exp Mar Biol Ecol* 132:221–245
- Wood SN (2017) *Generalized additive models: an introduction with R*, 2nd edn. CRC Press, Boca Raton, FL

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