Effects of herbivorous gastropod grazing on the sedimentation and succession of subtidal macroalgal assemblages

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ABSTRACT: The subtidal zone on cold temperate rocky coasts is an environment exposed to much less physical disturbance than the intertidal, and sediment deposition is continuous. Removal of this sediment by gastropod grazers is therefore presumed to affect the structure of subtidal algal communities. This concept was investigated by evaluating the grazing effects of the dominant herbivorous gastropod *Omphalius rusticus* by exclusion experiments in the field. Settlement plates of both exclusion and control treatments were placed every month from November 2014, and immersed for 1 mo. Algae colonized from May and tended to increase in biomass toward summer. No marked differences were observed in the algal composition of exclusion and control. Sediment deposition showed no apparent seasonal changes. Cumulative successional plates of both exclusion and control treatments were placed in November 2014, and immersed for 1 to 9 mo. The colonization of algae started in February and the species number peaked earlier in the exclusion and later in the control. Sediment load and algal biomass were high from February to May in the exclusion, and from April to July in the control. Seedlings of *Sargassum confusum* were found in both plots starting in July. We conclude that *O. rusticus* constantly removed sediments by its grazing activity and had a large impact on the formation of the macroalgal community by controlling sediment deposition. Its presence delayed the colonization of early-successional turf algal species, but did not affect colonization of late-successional canopy-forming algae such as *S. confusum*.

KEY WORDS: Grazing · Herbivorous snail · Macroalgal community · Subtidal rocky shore · Exclusion experiment · Sediment deposition

1. INTRODUCTION

Despite their small body size, herbivorous gastropods in high density have a great influence on macroalgal assemblages (Sala & Graham 2002, Poore et al. 2009, Sala & Dayton 2011, Piazzi et al. 2016). In contrast to the destructive grazing by sea urchins (Lawrence 1975, Ling et al. 2015), these gastropods graze selectively on microscopic stages and young sporophytes (Van Alstyne et al. 1999, Lotze & Worm 2000, Chenelot & Konar 2007), causing tissue damage which negatively affects macroalgal growth,

reproduction (O'Brien & Scheibling 2016) and tolerance to strong wave action (Duggins et al. 2001, Krumhansl & Scheibling 2011).

The effects of herbivorous gastropods on algal assemblages have been examined by various exclusion experiments (reviewed in Poore et al. 2012). When gastropods have been excluded, assemblages are dominated first by green ephemeral algae before fucoid algae become dominant (Arrontes et al. 2004, Jenkins et al. 2005), suggesting that the presence or absence of gastropods affects the construction of late-successional fucoid-dominated assemblages.

Lubchenco (1978) found that the feeding preference of the periwinkle *Littorina littorea* on ephemeral green algae *Ulva* spp. (as *Enteromorpha* spp.) resulted in an *Ulva*-dominant-assemblage in the absence of *L. littorea.* In contrast, Korpinen et al. (2007) suggested that the timing of macroalgal colonization rather than the effects of herbivore grazing has a larger effect on species richness and composition of macroalgal assemblages. In addition, Worm et al. (2001) conducted field experiments to investigate the interactions among macroalgal propagules, grazers and nutrients, and found that the presence or absence of a macro-algal propagule bank is the main factor affecting macroalgal recruitment, while grazing and nutrient-enrichment cause indirect effects. Since herbivorous gastropods can affect the microscopic stage of macro-algae, the timing of such algal colonization should be considered in exclusion experiments.

Sediments such as fine sand and silt deposited on a rocky seabed are known to affect herbivorous gastropod snails and macroalgal assemblages (Airoldi 2003). A decrease in the density of grazers with increasing sediment deposition is also widely reported (Schiel et al. 2006, Airoldi & Hawkins 2007, Kawamata et al. 2011). Therefore, moderate sediment load can cause positive effects on macroalgal assemblages by discouraging herbivores and preventing their grazing activity, and by improving the survival of red algae (D'Antonio 1986) and increasing the growth of fucoid algae (Araújo et al. 2012, Alestra et al. 2014). However, in an environment with a heavy sediment load, sediment-tolerant species and ephemeral species have been found to dominate (Littler et al. 1983, Balata et al. 2007) and recruitment of late-succession species to be inhibited (Eriksson & Johansson 2003, Irving et al. 2009, Watanabe et al. 2016, Schiel & Gunn 2019). Therefore, both sedimentation and gastropod grazing may influence the development and succession of algal assemblages. However, their interactions have been surveyed mainly in intertidal zones but rarely in subtidal assemblages (Poore et al. 2012).

Compared to the adjacent intertidal zone, subtidal rocky shores have quite different environmental characteristics (Witman & Dayton 2001). Permanent submersion greatly reduces physical disturbance and tidal effects, and sediment deposition is continuous. Recruitment of algal propagules and invertebrate larvae may have temporal variations, but not through disruption by air exposure during tidal rhythms. Habitat space has no lower depth limit and mobile animals predominate; factors tending to preclude the appearance of the key-stone predators that exert top-down control of communities. Large predominant predators in giant kelp beds, such as the sheephead wrasse, lobsters and sea otters recognized by Schiel & Foster (2015), are unknown in Japanese waters. Among these characteristics of subtidal environments, it was considered that the constant sedimentation present may have a large impact on the successional processes of the community through interactions between herbivorous grazers and macroalgae.

In the present study, the effects of *Omphalius rusticus* (Gmelin, 1791) on macroalgal succession and sediment deposition were investigated in the absence of sea urchins on a subtidal rocky shore. This herbivorous trochid gastropod snail is commonly distributed in the lower intertidal and subtidal rocky shore of Japan, southern China and the Korean Peninsula (Kulikova & Omel'yanenko 2000, Lee 2001, Williams 2012). It is a dominant benthic species in subtidal rocky shores along the Pacific coast of northeastern Japan (Ishida et al. 2002), and its biomass is sometimes equal to or greater than that of sea urchins and abalones (Omori et al. 2000). It feeds on benthic diatoms and the microscopic stages of algal gametophytes and young sporophytes (Ishida et al. 2002, Nakata et al. 2006). Its consumption rate increases with temperature, and its grazing activity may affect macroalgal assemblages (Nakata et al. 2006).

In cold temperate subtidal coastal waters, rich in nutrients and with continuous sediment deposition, the impact of falling sediment on subtidal algal communities may be significant. Our hypothesis is that gastropod grazers remove the sediments, and that this activity affects the successional processes of subtidal algal communities. To evaluate the seasonal and lasting effects of the herbivorous grazer *O. rusticus*, observations were made of the amount of sediment and macroalgal biomass, and the composition of the macroalgal assemblage established on settlement plates placed for either 1 mo (monthly effects) or for 1 to 9 mo (cumulative effects).

2. MATERIALS AND METHODS

2.1. Study site

The study was conducted in the shallow rocky subtidal area at Kitsunezaki (38° 21′ N, 141° 25′ E), on the western coast of the Oshika Peninsula, Sendai Bay, northeastern Japan. Surface seawater temperature at the study site ranged from 7°C in February to 25°C in August (Fig. 1). In this area, *Omphalius rusticus* is

distributed in high density (25.5 ind. m^{-2} in 2014; Suzuki et al. 2017). The bottom substrate of the study site is rock 30 m from the shoreline (depth < 3.0 m). Further offshore, beyond 30 m, is a sandy bottom with a seagrass bed. Therefore, the distributional range of *O. rusticus* in this site is limited to within 30 m of the coastline. Other grazers in this study area are the gastropod *Chlorostoma lischkei* (Tapparone Canefri, 1874) and sea urchins *Hemicentrotus pulcherrimus* (A. Agassiz, 1864) and *Strongylocentrotus intermedius* (A. Agassiz, 1864), but their distributional ranges are narrow and their densities are known to be very low (*C. lischkei*: 0.13 ind. m^{-2}, sea urchins: 0.18 ind. m^{-2} in 2014; Suzuki et al. 2017). The only abundant herbivorous gastropod in the experimental area is *O. rusticus*, and no other herbivorous grazers appeared during the snail exclusion experiment. The dominant perennial canopy-forming algae are the kelp *Eisenia bicyclis* and fucoids *Sargassum confusum* and *S. siliquastrum.* The dominant understory species observed were the green alga *Ulva pertusa* and the red algae *Gelidium elegans* and *Plocamium telfairiae.* To conduct exclusion experiments in a uniform environment and to reduce the influence of local distribution of macroalgae, both canopy-forming and understory algae at the study site were removed in advance. Detailed information

concerning the distribution of bottom substratum and algal flora is given by Suzuki et al. (2017).

Sixteen enclosure concrete blocks (30 × 30 cm inside dimensions, 15 cm high and 5 cm thick) were arranged in a 4 × 4 grid pattern in a Latin square design on a flat area of seabed (1.5 m in depth) with a gap of more than 50 cm separating each block (Fig. 1). Eight blocks were coated with antifouling copper paint (Sea Blue King, Dai Nippon Toryo Co.) to deter *O. rusticus* from entering; the other 8 blocks were unpainted controls. The bottom of each block was covered with plastic netting (0.7 cm mesh size) raised 5 cm above the seabed using plastic legs attached to the 4 corners. This enabled the natural exchange of sea water inside the block (Fig. 2A). Nine settlement plates (6 × 6 cm, 1.4 cm in thickness; Amakusa porcelain stone plate from LSI Amakusa) were placed on the plastic net in each block by inserting the plastic anchor screw (glued to the rear of each plate) into the mesh of the net (Fig. 2A). Once a month, macroalgae and sessile animals attached to the top and sides of the blocks were removed to prevent the possibility of *O. rusticus* using them as 'stepping stones' to invade the blocks. The numbers of *O. rusticus* individuals in both the exclusion and control blocks were counted every month from November 2014 to November 2015 by SCUBA diving to confirm the exclusion efficiency.
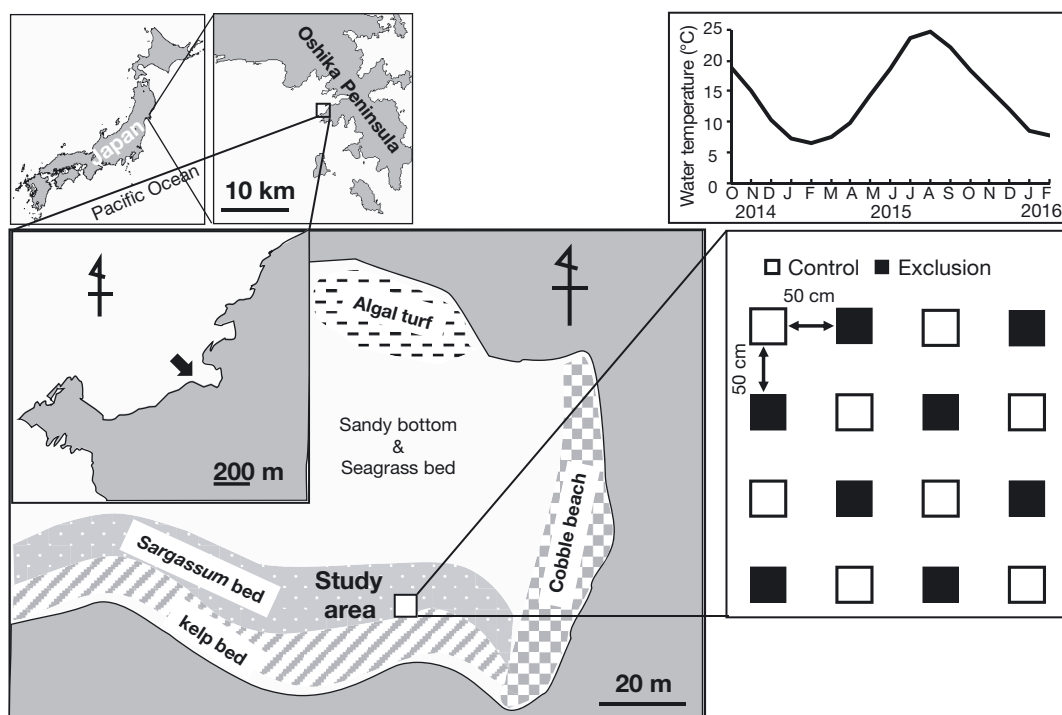

Fig. 1. Survey area on the coast of Kitsunezaki on the west coast of the Oshika Peninsula. Graph at upper right: monthly mean water temperature in the study area during the study period; diagram at right center: arrangement of control and exclusion blocks
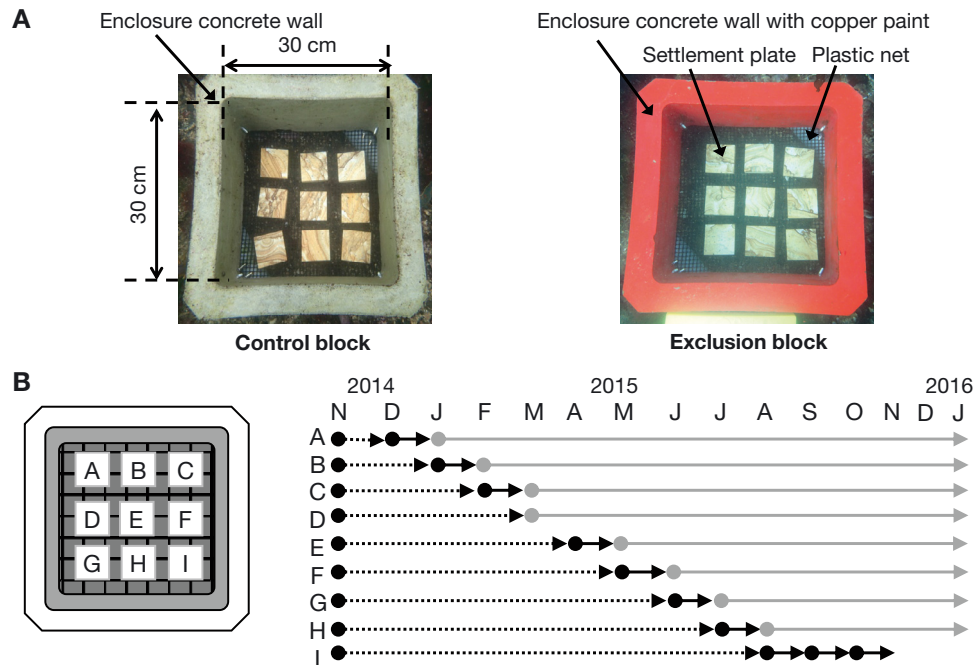
Fig. 2. Setting of concrete enclosure blocks and settlement plates. (A) Control and exclusion blocks (see Section 2.1 for details). (B) Setting and collecting schedule of settlement plates in each enclosure block. Letters indicate settlement plates. The arrangement of plates is an example: each block contains plates with a different randomized arrangement. To the right is a summary diagram of the setting and collecting schedule. For each line, circle: month of setting; triangular head: month of collection; length: plate immersion period — monthly for Expt 1 (dark solid lines); cumulative for Expt 2 (dark dotted lines). Supplementary (non-experimental) plates were introduced to avoid vacant lots for the periods indicated by gray solid lines. Note that in Expt 1, plates could not be introduced during March and April 2015 (Plate D) because of bad weather, so there is no result for that month

2.2. Data collection

To evaluate the seasonal and cumulative successional effects of *O. rusticus* on macroalgal assemblages, settlement plates were placed and collected according to the following 2 methods (Fig. 2B).

Expt 1: monthly effects. Temporal changes in the composition of the macroalgal assemblage and the amount of macroalgal biomass and sediments on settlement plates were observed after 1 mo. New settlement plates were introduced each month from November 2014 to October 2015 in each exclusion block (N = 8) and control block (N = 8) and collected 1 mo later, every month from December 2014 to November 2015 (Fig. 2B, dark solid arrows).

Expt 2: cumulative effects. Temporal changes in the amount of macroalgal assemblage and sediment deposition on settlement plates placed for 1 to 9 mo were observed. Eight settlement plates were introduced from November 2014 in each exclusion block (N = 8) and control block (N = 8). One plate from each block was collected every month from December 2014 to August 2015, thus the time of immersion of the plates ranged from 1 to 9 mo (Fig. 2B, dotted arrows).

At collection, the target settlement plate was carefully removed from the plastic net at the bottom of each block and (still under water) gently placed in a zipper bag. A new settlement plate was placed in the vacant position, so there were always 9 plates present in all blocks until November 2015 (Fig. 2B, black arrow). From November 2015 to January 2016, 8 plates were present in all blocks except position I (Fig. 2B, gray arrows). All the collected plates in their individual zipper bags were taken, on ice, to the laboratory, where macroalgae colonizing each of the collected plates were identified nondestructively. After identification, the macroalgae and accumulated sediments on the plates were scraped off and ignition-loss tests were carried out to measure the ash weight (AW; an index of inorganic matter mainly in sediments such as mud and silt) and the ash-free weight (AFW; an index of organic matter present mainly as detrital, microalgal and macroalgal biomass). Samples were dried at 80°C until constant weight. Dried samples were then calcined at 500°C for 4 h. The ignition loss (the AFW) was calculated from the difference in weight of samples before and after calcination.

2.3. Statistical analysis

The statistical differences in the mean densities of *O. rusticus* in each block and the mean value of AW, AFW, estimated biomass and sediments on each settlement plate were analyzed (N = 8). Because some data deviated from normality (Shapiro-Wilk test, p < 0.05) and homogeneous variances (Levene test, p < 0.05), the differences between treatments (exclusion vs. control) were analyzed with the Wilcoxon test, and the differences among months were analyzed with the Steel-Dwass test. All statistical analyses, including post hoc tests, were conducted using JMP 9 (SAS Institute). Statistical differences in macroalgal assemblages among settlement plates were based on Jaccard dissimilarity performed by permutational multivariate analysis of variance (PERMANOVA) using the R package 'vegan' (Oksanen et al. 2019).

3. RESULTS

3.1. Temporal changes in the density of herbivorous snails

The densities of *Omphalius rusticus* in the exclusion blocks tended to be lower than those of the control blocks throughout the study period (Fig. 3). From December 2014 to August 2015, the density of *O. rusticus* in the exclusion blocks was less than 3 individuals and significantly lower than that of the control blocks (p ≤ 0.012 for all 8 tests) except for June 2015. From September to November 2015, the density of *O. rusticus* in the exclusion blocks tended to be lower than that of the control blocks, but there were no significant differences between treatments (p ≥ 0.059 for all 3 tests). In the control blocks, the maximum density was observed in August 2015, significantly higher than in other months (p ≤ 0.036 for all 10 tests except for March). In contrast, in the exclusion blocks, there were no significant differences in density among months (p ≥ 0.096 for all 66 tests).

3.2. Expt 1: Monthly effects

Images of the settlement plates immersed for 1 mo are shown in Fig. 4. Few colonizing macroalgae and little deposited sediment were found on the plates, and there was no marked difference between the control plots and the exclusion plots throughout the year. Macroalgae colonization on the plates was found during May to October 2015 (Table 1), with 10

taxa on the control plots and 9 taxa on the exclusion plot. Eight taxa were found in both treatments, while *Ulva pertusa*, Dictyotaceae sp. and *Acrosorium* sp. were only observed on the control plots and *Lomentaria hakodatensis* was only observed on the exclusion plots. The result of PERMANOVA based on the macroalgal assemblages on each settlement plate is shown in Table 2 (Expt 1). Macroalgal assemblages were significantly different between treatments (p = 0.041) and months (p < 0.001), but there was no interaction between treatment and months (p = 0.065).

Temporal changes of AFW and AW collected from the settlement plates immersed for 1 mo are shown in Fig. 5. Comparing the treatments, AFW (index of macroalgal biomass) tended to be higher in the exclusion plots at first, gradually increased in the control plots and was finally higher in the exclusion plots (Fig. 5A). From January to May, AFW tended to be higher in the exclusion plots than that in the controls, with significant differences detected in January (p = 0.038) and February (p = 0.010). From June to October (except for August), AFW was lower in the exclusion plots, and in November it was again higher in the exclusion plots, but these trends were non-significant (p ≥ 0.093 for all 4 tests June–October, and p = 0.092 for November). Comparing between months, AFW in the control plots tended to be higher from June to October (but the differences were non-significant, p ≥ 0.204 for all 25 tests). That in September was significantly higher than that in February (p = 0.026). In the exclusion plots, although the August AFW seemed to be high (p < 0.05), variance

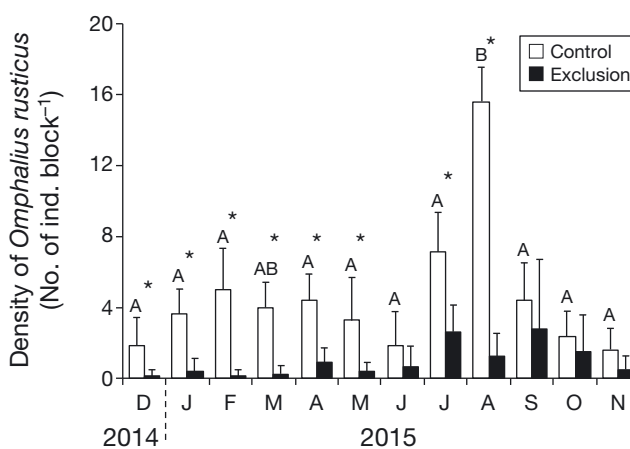Fig. 3. Mean (+SD) temporal changes in the density of *Omphalius rusticus* in the control and exclusion blocks (N = 8). Asterisks indicate a significant difference between pairs of control and exclusion treatments (Wilcoxon test, p < 0.05). Different capital letters above the bars indicate significant differences in between months in the control plots (Steel-Dwass test, p < 0.05)
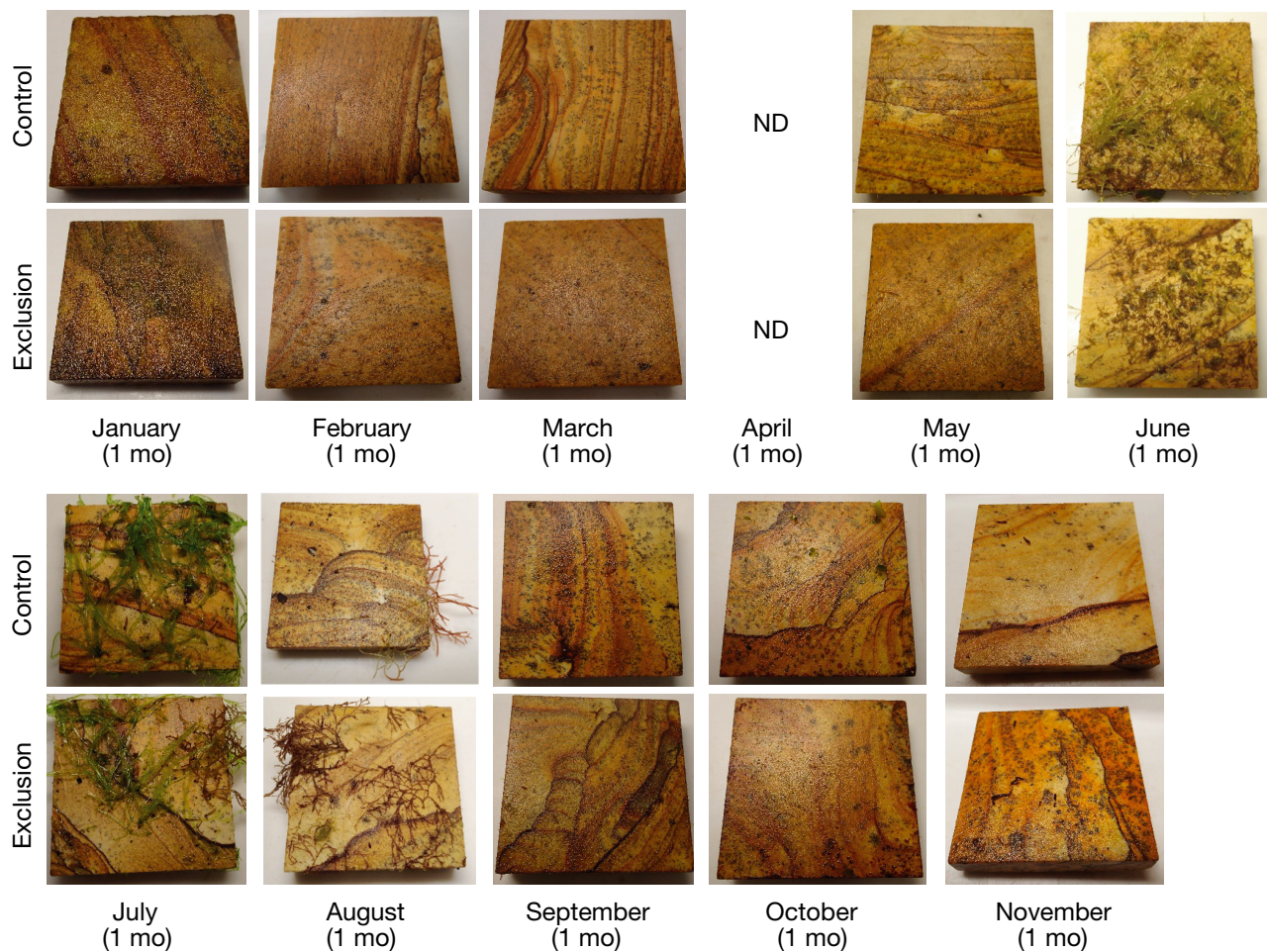
Fig. 4. Images of settlement plates placed for 1 mo (Expt 1; monthly effects) in the control and exclusion blocks. Each image is of a typical one of 9 plates collected from January to November 2015. Number of months in parentheses is the time of immersion of the plate. Note that the settlement plates are made from natural porcelain stone, each of which has a different irregular striped or mottled pattern. ND: no data

Table 1. Identification of algae colonizing the settlement plates placed for 1 mo and collected between December 2014 and November 2015 (monthly effects). The presence of a given taxon is shown for control plots (open circles) and exclusion plots (black discs). FE: filamentous ephemeral; TE: turf-forming; –: no data

Algal type	Taxa	2014 D	2015 J	F	M	A	M	J	J	A	S	O	N
FE	*Ulva pertusa*					–			?				
	Ulva sp.					–	??	??	??			??	
	Cladophora sp.					–			??	?			
	Colpomenia sinuosa					–	??						
	Filamentous red algae					–	??	?		?	?	?	
TF	Dictyotaceae sp.					–						?	
	Scytosiphon sp.					–		??	??	?		?	
	Plocamium telfairiae					–						?	
	Lomentaria catenata					–				?	??	??	
	Lomentaria hakodatensis					–			?	?			
	Acrosorium sp.					–					?	?	
	Laurencia sp.					–					?		??
No. of taxa in control		0	0	0	0	–	3	2	4	2	3	4	1
No. of taxa in exclusion		0	0	0	0	–	3	3	4	3	2	5	1

Table 2. Results of PERMANOVA testing based on the Jaccard index for macroalgal assemblages in Expts 1 and 2. The Jaccard index between assemblages with no species present was replaced with 1. **Bold** indicates p-values significant at p < 0.05

		Expt 1				Expt 2		
	df	SS	F	p	df	SS	F	p
Treatment (T)	1	0.664	1.7915	**0.041**	1	0.756	2.7047	**0.016**
Month (M)	6	9.044	4.0680	**0.001**	6	10.592	6.3120	**0.001**
T × M	6	2.748	1.2358	0.065	6	1.360	0.8105	0.781
Residual	98	36.313			98	27.409		
Total	111	48.769			111	40.117		

was high and there were no significant differences between months (p ≥ 0.094 for all 45 tests).

AW showed a similar tendency to AFW (Fig. 5B). In comparison between treatments, from January to February, AW in the exclusion plots was significantly higher than that in the control (p < 0.001 for both tests). From March to November, except for July and October, AW tended to be higher in the exclusion plots (differences were non-significant at p ≥ 0.130 for all 6 tests). Comparing between months, in the control plots, AW was significantly higher in May (p = 0.038) and September (p = 0.027) than in February. In the exclusion plots, although there was no clear seasonal tendency, AW in August was significantly higher than that in February (p = 0.038).

3.3. Expt 2: Cumulative effects

In this experiment, settlement plate immersion time ranged from 1 to 9 mo, and the number of species and the coverage of colonizing macroalgae were visibly higher than those on the 1 mo settlement plates in Expt 1 (Fig. 6). Each successive plate in Fig. 6 is the typical one of the 9 plates collected each month. Macroalgae colonizing the plates were found from February 2015 (removed after immersion for 3 mo; see Table 4 for identifications). During the experiment, 9 taxa were recorded on the control plots and 12 on the exclusion plots. The number of taxa on the latter were the same as or higher than on the control plots for each month. In both treatments, ephemeral green algae such as *Ulva* sp. and *Cladophora* sp. and the turf-forming brown alga *Scytosiphon* sp. were mainly observed until June (following immersion for 7 mo). The number of taxa increased in July (after 8 mo) and seedlings of *Sargassum confusum* were observed in July and August (Fig. 7). Macroalgal assemblages were significantly different between treatments (p = 0.016) and months (p < 0.001), but there was no interaction between treatment and month (Table 2).
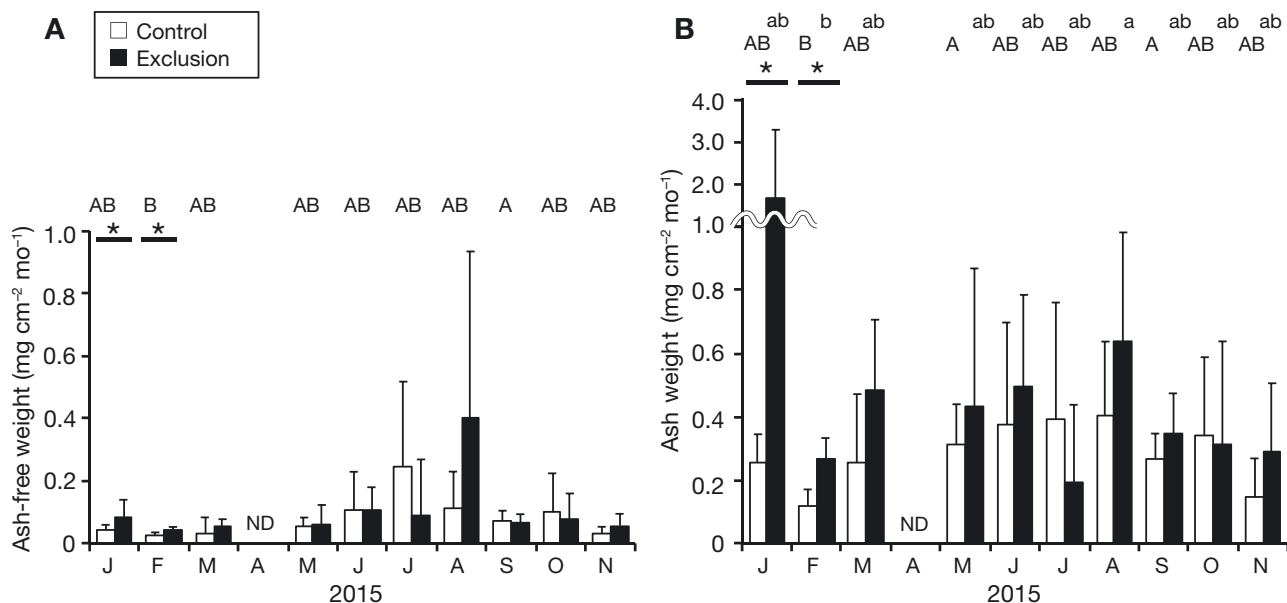

Fig. 5. Results of Expt 1: mean (+SD) temporal changes in (A) ash-free weight and (B) ash weight on settlement plates placed for 1 mo in the control and exclusion plots (N = 8). Asterisks: significant differences between treatments (Wilcoxon test, p < 0.05). Uppercase letters above the bars indicate significant differences among months in the control plots (Steel-Dwass test, p < 0.05); lowercase letters indicate significant differences among months in the exclusion plots (Steel-Dwass test, p < 0.05). ND: no data. Waving double-line in (B) indicates *y*-axis scale change. Note: the amounts of colonized algae and sediments collected in December 2014 were slight and could not be measured, so the results begin from January 2015
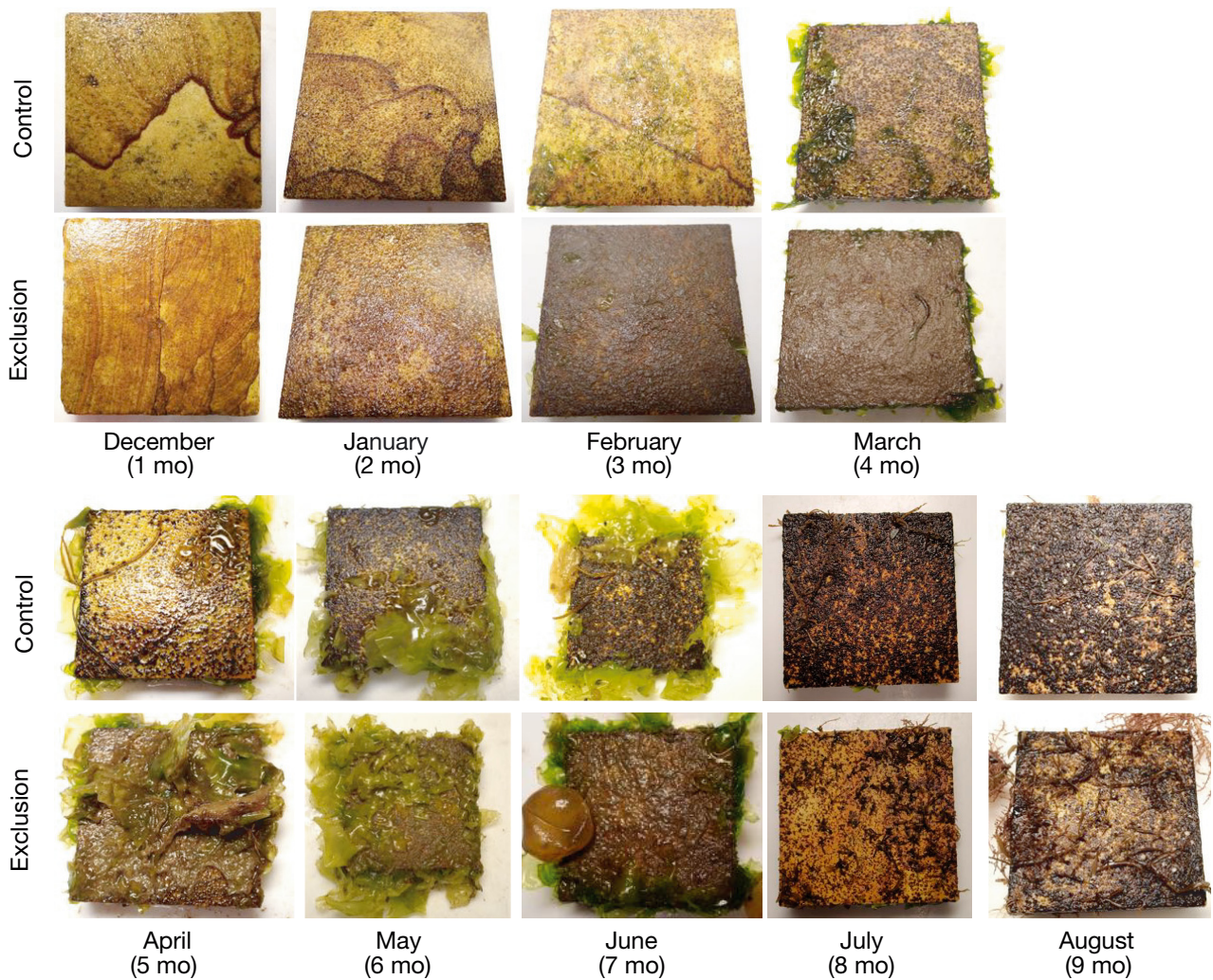
Fig. 6. Settlement plates placed for 1 to 9 mo (Expt 2; cumulative effects) collected from December 2014 to August 2015 in the control and exclusion blocks. Number of months in parentheses is the duration for which each plate was immersed

Temporal changes of AFW and AW collected from the settlement plates immersed for 1 to 9 months are shown in Fig. 8. Comparing treatments (Fig. 8A), AFW from January to April was significantly higher in the exclusion plots than that in the control plots ($p < 0.010$). From May to July, AFW tended to be lower in the exclusion plots (significantly lower in June: $p = 0.007$; no significant difference in May and July: $p = 0.505$ and 0.645 respectively) and in August became significantly higher in the exclusion plots again ($p = 0.021$). Comparing between months, AFW in the control plots tended to increase toward June; those in May and June were significantly higher than January to March ($p < 0.035$). In the exclusion plots, although there were no clear seasonal changes, AFW values in February, March, May, June and August were significantly higher than that in January ($p < 0.035$).

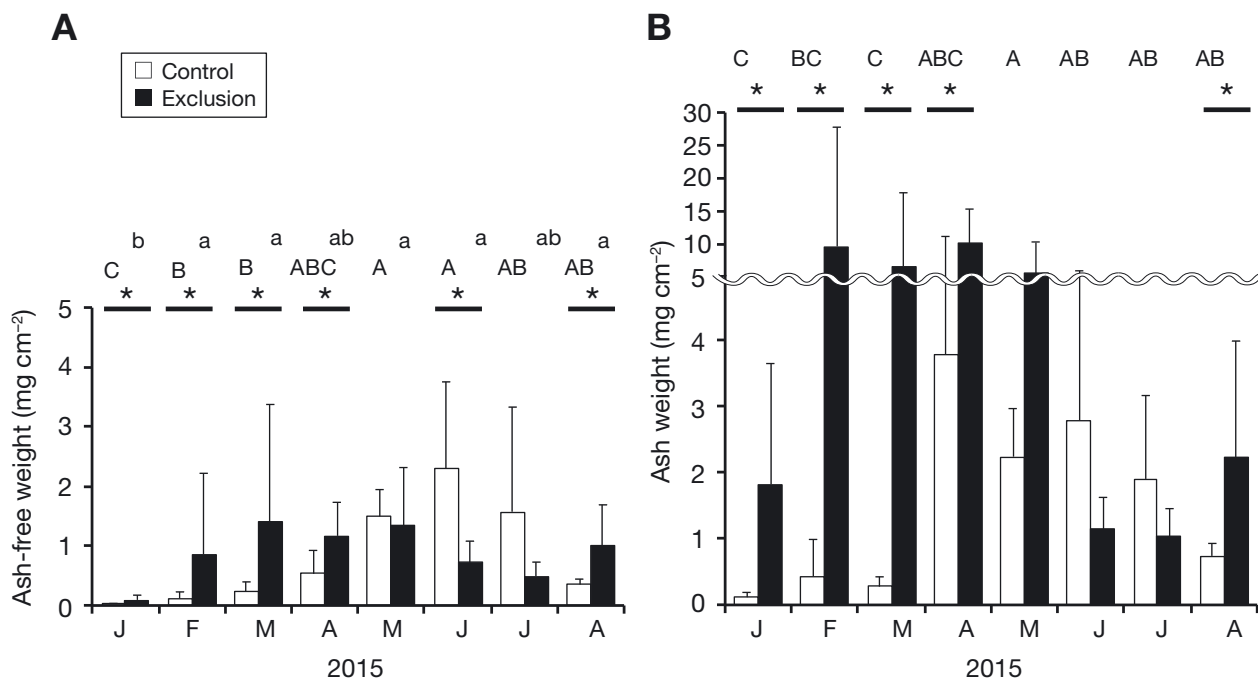Fig. 7. *Sargassum confusum* seedings colonizing the settlement plate in July

Fig. 8. Results of Expt 2: mean (+SD) temporal changes in (A) ash-free weight and (B) ash weight on settlement plates placed for 1 to 9 months in the control and exclusion plots (N = 8). For further details, see Fig. 5

Similar tendencies were seen in AW (Fig. 8B). Comparing treatments, from January to April, AW values in the exclusion plots were significantly higher than in the control plots (p < 0.036), declining during June and July and increasing again in August (p = 0.015). Comparing months, AW values in the control plots were significantly higher from May to August than those in January and March (p < 0.048); in the exclusion plots, AW tended to be higher from February to May but there were no significant differences among months (p > 0.086).

4. DISCUSSION

4.1. AW and AFW in sediment and macroalgae

Organic matter and ash are contained in both algae and sediments. In this study, it was practically impossible to separate only the organic matter of algae from total AFW. Also, it was not possible to separate only the ash of the sediment from the total AW. However, since monthly sediment deposition was relatively steady (Fig. 5), we assume that the fluctuations of AFW basically reflected those of algal biomass. Therefore, AFW was used as an index of algal biomass. In addition, judging from the high ratio of AW to AFW in the sediment amount before

seaweed recruitment (January to March in Fig. 5, January in Fig. 8), most of the sediment amount is occupied by AW. It is noted that algae also contain ash, as shown in Table 3 where the ratios of ash content in the algae were in the range of 0.2 to 0.5. However, taking into account the relatively high amount of sediment, the effect of fluctuations due to seaweed-derived ash content in the total AW is considered to be minor. Therefore, AW was used as an index of sediment amount.

4.2. Monthly effects of the herbivorous snail on the algal assemblage

A schematic summary for the monthly effect of *Omphalius rusticus* on sedimentation and algal recruitment is shown in Fig. 9. In the exclusion treatment, there was a constant appearance of AW and AFW on the monthly settlement plates through a year even in the absence of recruited algae (Fig. 5). This indicates that sediment deposition occurred continuously at the study site. It has been reported that environments with a high sedimentation load have a low species diversity in their macroalgal assemblage (Balata et al. 2015) and a low density of herbivores (Schiel et al. 2006, Airoldi & Hawkins 2007). In the present study site, however, monthly

Table 3. Estimated ash percent dry weight of recruited algae inferred from the data of the same species or species in closely related taxa. All references are from studies performed in Japan

Recruited species	Estimated ash (%)	References	Remarks
Ulva pertusa	22.6	Miyoshi et al. (2013)	Average value of *Ulva* spp.
Ulva sp.	31.9	Miyoshi et al. (2013)	Value of *Ulva prolifera*
Cladophora sp.	18.0	Ishibashi & Yamamoto (1958)	Value of *Cladophora wrightiana*
Colpomenia sinuosa	50.1	Miyoshi et al. (2013)	
Filamentous red algae	31.6	Nabata et al. (1999)	Value of *Polysiphonia morrowii*
Dictyotaceae sp.	25.9	Miyoshi et al. (2013)	Value of *Dictyota dichotoma*
Scytosiphon sp.	43.4	E. Inomata unpubl. data	Value of *Scytosiphon lomentaria*
Gelidium elegans	36.8	Miyoshi et al. (2013)	
Plocamium telfairiae	23.6	Kikuchi et al. (1967)	
Lomentaria catenata	27.8	Miyoshi et al. (2013)	
Lomentaria hakodatensis	27.8	Miyoshi et al. (2013)	Value of *Lomentaria catenata*
Acrosorium sp.	20.1	Miyoshi et al. (2013)	Value of *Acrosorium yendoi*
Laurencia sp.	42.1	Saito & Ueda (1953)	Value of *Laurencia brongniartii*
Sargassum confusum (seedlings)	35.5	Nabata et al. (1999)	Value of *Sargassum confusum* (upper part of adult thallus)

colonization by macroalgae on the settlement plates and the density of herbivorous snails in the experimental blocks increased toward summer (Table 1, Figs. 3 & 4) and showed monthly variation (Table 4). Therefore, the amount of sedimentation per month in this study site is considered insufficient to deter the colonization of macroalgae and herbivorous snails.

In general, the activity of snails, which are poikilothermic, increases with temperature, and this has been confirmed experimentally for subtidal herbivorous gastropods (Yee & Murray 2004, Nakata et al. 2006). Seasonal changes in the macroalgal flora observed near the study site have revealed that the number of mature small perennial species such as *Gelidium* spp., *Lomentaria* spp. and *Acrosorium* sp. increases toward summer (Agatsuma et al. 2000, Endo et al. 2005), and such recruitment was also observed in the present study. Recruitment and growth of early
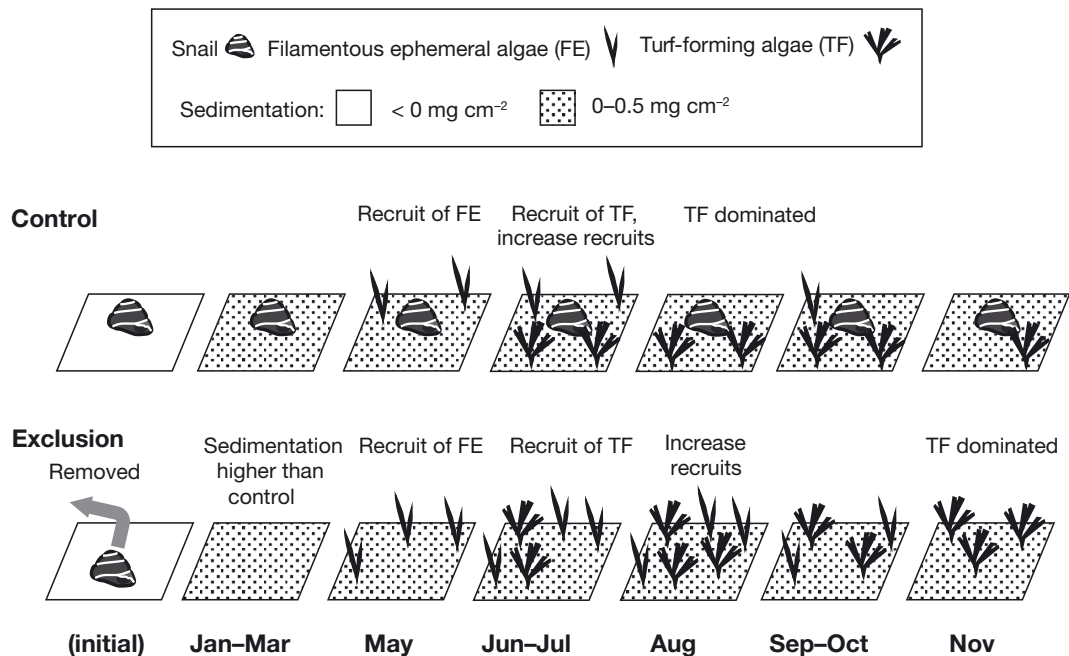

Fig. 9. Results of sedimentation and algal recruitment on the settlement plates of Expt 1 in the control (upper row) and exclusion (lower row) plots. Changes of sedimentation (density of dots), algal recruitment and growth (illustration) on settlement plates immersed for 1 mo, comparing the initial and subsequent groups. Note that higher sedimentation recorded in January is considered to be 'winter suspension', so this is not reflected in the diagram

Table 4. Identification of algae colonizing the settlement plates placed for 1 to 9 mo and collected between December 2014 and August 2015 (cumulative effects). The presence of a given taxon is shown for control plots (open circles) and exclusion plots (black discs). FE: filamentous ephemeral; TE: turf-forming; CF: canopy-forming

Algal type	Taxa	2014 D	J	F	M	A	M	J	J	A
FE	*Ulva pertusa*			?	??	??	??	??	??	
	Ulva sp.			??	??	??	?	?	??	?
	Cladophora sp.			?					?	
	Colpomenia sinuosa			?	?	??	??	??		
	Filamentous red algae			?					?	
TF	*Scytosiphon* sp.			?	?	??	?	?	??	?
	Gelidium elegans					?			??	??
	Plocamium telfairiae				?				??	
	Lomentaria hakodatensis									??
	Acrosorium sp.								?	
	Laurencia sp.								?	
CF	*Sargassum confusum* (seedlings)								??	??
	No. of species in control	0	0	1	3	4	3	3	7	4
	No. of species in exclusion	0	0	6	4	5	3	3	9	4

recruited species such as *Ulva pertusa* and *Colpomenia sinuosa* (Table 1) also contributed to the increase of algal biomass toward summer observed at our study site. Recruitment of macroalgae actually began in March, regardless of the presence of herbivorous snails (Fig. 4, Table 1), so the monthly effects of *O. rusticus* on algal assemblage recruitment are considered to be relatively small.

4.3. Cumulative effects of the herbivore snail on algal assemblage

4.3.1. Effects on early successional species

Sediments in the absence of *O. rusticus* from January to April (plots immersed for 2 to 5 mo) were significantly higher, as easily observed by visual inspection as well as by measurements (Figs. 6 & 8). In contrast, macroalgal biomass showed no significant difference between the presence or absence of *O. rusticus* from January to April (immersion for 2 to 5 mo; Fig. 8). The presence of herbivorous gastropods is known to discourage sedimentation deposit (Bertness 1984), a finding supported in the present study in which there were reduced amounts of sediments on the settlement plates in the presence of *O. rusticus*. Takada (1995) showed the presence of high inorganic content in the feces of rhipidoglossan snails such as *Monodonta labio* and

Lunella coronata, and suggested the possibility that sediments are taken up actively during their grazing activities. *O. rusticus* also has a rhipidoglossate radula (Nakata et al. 2006). Moreover, the mucus secreted as a lubricant by crawling gastropods is known to entrap benthic microalgae and macroalgal propagules (Santelices & Bobadilla 1996, Holmes 2005). Anderson & Underwood (1997) showed that removal of sediments and ephemeral algae by gastropod snails provides space for recruitment of algae and facilitates the succession of a macroalgal assemblage.

In the present study, it is suspected that *O. rusticus* removes the microscopic stages of macroalgae along with sediment and that this delays the colonization of early successional species. While the number of recruited species was lower in the presence of *O. rusticus* than in its absence, the recruitment of *Sargassum* species occurred regardless of the presence of *O. rusticus.* This shows that the grazing activity of *O. rusticus* affected the succession of turf-forming algae, but not the recruitment of the canopy-forming *Sargassum* species.

4.3.2. Effects of sediment accumulation

A schematic summary of the cumulative effects of *O. rusticus* on sedimentation and algal recruitment in the present study is shown in Fig. 10. Accumulation of sediment was found regardless of the presence of *O. rusticus*, although in its presence, sedimentation tended to be higher at first (from April to July; Fig. 8B) and then algal biomass increased (toward June; Fig. 8A). In the absence of *O. rusticus*, algal recruitment started earlier (from February; Table 4) and then higher sedimentation was found (from February to May; Fig. 8B). It is known that sediment-tolerant algae such as filamentous and turf-forming algae can trap and accumulate sediments (Airoldi & Virgilio 1998). Moreover, Bertness (1984) showed that removal of the herbivorous snail *Littorina littorea* resulted in increased accumulation of sediments and the development of green algae, but that later the algae trapped sediment and caused negative effects on subsequent development of algal succession. In the results of the present study, the accumulation of
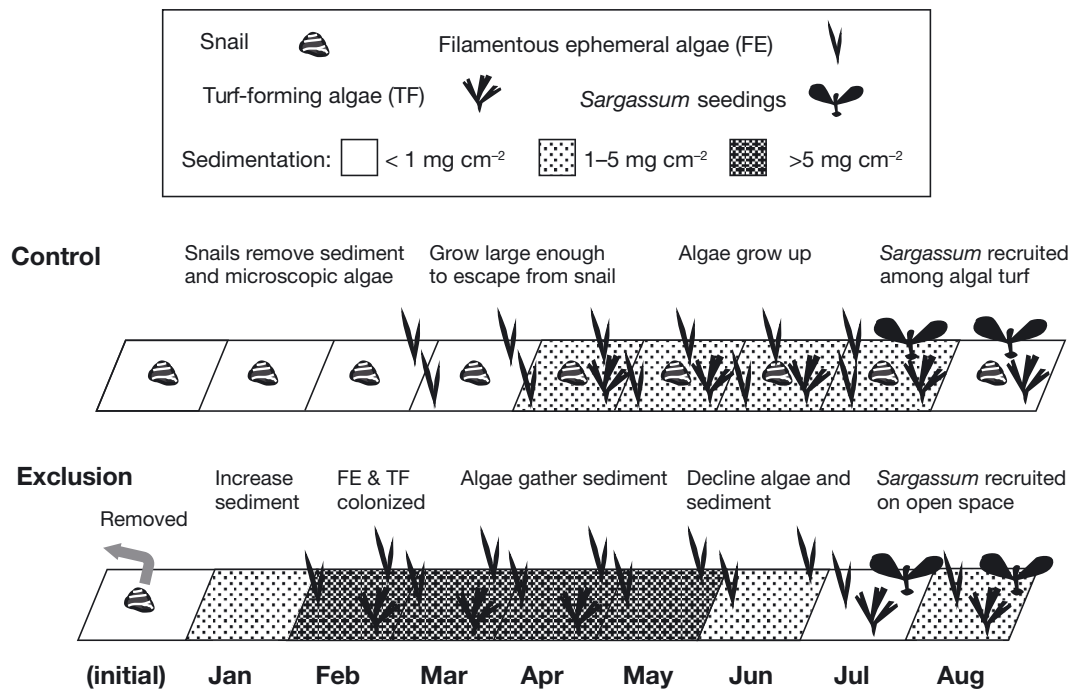
Fig. 10. Results of sedimentation and algal recruitment on the settlement plates of Expt 2 in the control (upper row) and exclusion (bottom row) plots. Changes of sedimentation (density of dots), algal recruitment and growth (illustrations) on the settlement plates introduced from November 2014 are illustrated for a representative plate for each collected monthly group of plates

sediments was found whether or not *O. rusticus* was present (Fig. 8B). However, removal of *O. rusticus* seemed to be effective at reducing sediment accumulation. Algal biomass from May to July was higher in the presence of *O. rusticus* (Fig. 8B). It is suggested that the biomass of the colonizing macroalgae decreased because of the accumulation of sediments per se, and that the amount of sediment also tended to decrease as a result of the absence of sediment-accumulating macroalgae.

4.3.3. Effects on late successional species

Seedlings of *Sargassum confusum* were found in both exclusion and control plots in July and August (Table 4, Fig. 7), despite the occurrence of some differences in the amounts of macroalgal biomass and sediments depending on the presence or absence of *O. rusticus* (Fig. 10). The dominant *Sargassum* species in this study site were *S. confusum* and *S. siliquastrum.* The former matures in early summer and releases eggs from early June to early August, with the density of newly recruited juveniles increasing in December, although young juveniles are found throughout the year (Tsuda & Akaike 2001). In the laboratory at a water temperature of 20°C, it takes

1.5 mo for fertilized eggs of *S. confusum* to develop into young thalli; at 10°C, it takes 1 yr (Kawagoe et al. 2005). In the present study site, young *Sargassum* thalli were found in July and August (summer), therefore newly recruited *Sargassum* seedlings may develop within a year from eggs released by mature adults around the study site.

Herbivores grazing on early successional ephemeral green algae have been reported to promote the colonization of late successional species. Lubchenco (1983), for example, demonstrated selective grazing by *L. littorea* on early successional species and, if not grazed, early successional species inhibited the colonization of later successional species. Moreover, Jenkins et al. (1999) showed that removal of a limpet species resulted in an increase of *Fucus serratus* recruitment; however, the removal of both the limpet and *F. serratus* resulted in an increase of ephemeral green algae and delayed the colonization of *F. serratus.* Macroalgae can escape the grazing activity of gastropod grazers by growing to a larger, 'refuge' size (Lubchenco 1983, Moore et al. 2007, Scheibling & Raymond 2009). The drastic grazing of sea urchins on canopy-forming kelp cleared space on the substrate and facilitated the development of sediment-trapping turf algae (Reeves et al. 2018). Size-limited grazing is characteristic of gastropod snails and it

may play a useful role in the succession of macro-algal assemblages. Therefore, it is suggested that grazing and removal of early successional ephemeral algae by *O. rusticus* facilitates colonization by *S. confusum*, and that rapid seasonal growth of the colonizing seedlings can result in growth to a large enough refuge size to avoid being grazed. Consequently, in the present study, colonization by *S. confusum* was found regardless of the presence or absence of *O. rusticus*. Alestra & Schiel (2014) showed that *Ulva* spp. are preferably grazed by herbivorous gastropods, but increased temperature facilitated the growth of the *Ulva* spp. and decreased the survival of canopy-forming fucoids. In the control plot in the present study, *O. rusticus* may have reduced the number of *S. confusum* recruits.

Generally, sedimentation inhibits the recruitment of late successional species (Airoldi 2003, Irving et al. 2009). If so, how could *Sargassum* sp. have colonized the exclusion plots in this study? Although Geange et al. (2014) showed (in laboratory experiments) that not only sediment load but also the timing of sedimentation affects spore establishment (of the laminarian kelps *Macrocystis pryifera* and *Undaria pinnatifida*), they also showed that even a thin layer of sedimentation can affect spore establishment during the settlement period. In the results of the present study, the timing of *Sargassum* spore establishment seemed to coincide with months where sedimentation was lower on the exclusion plots (May to July; Fig. 10), because the early colonizing macroalgae and accumulated sediments disappeared together. The subsequent growth of *Sargassum* spores might be enhanced by the higher water temperature in summer (Kawagoe et al. 2005). If the present study were to be conducted during a different season, the timing of spore recruitment and the progress of the succession of macroalgal assemblages might well be different. Further studies are therefore required in different seasons to consider the effects of the timing of *Sargassum* species recruitment.

4.4. The role of *O. rusticus* in the subtidal algal community

In our study area, there are no keystone predators which eat grazing snails and thereby adversely affect the entire community structure. Moreover, there are no apparent effects of sea urchins, herbivorous fishes or mesograzers such as dominating amphipods or isopods. *O. rusticus* is the dominant herbivorous gastropod snail (with no other gastropod species de-

tected in the study area) and is distributed fairly evenly on this subtidal rocky bottom in high density (Suzuki et al. 2017). Therefore, this study area is ideal for evaluating the effects of a single species of grazing snail on the succession of the local algal community by field exclusion experiments.

O. rusticus constantly removed sediment deposition and recruiting settlers in the rocky subtidal community by its nocturnal grazing activity every night throughout the year, though the activity slowed down in low-temperature seawater in winter (Nakata et al. 2006). In the study area, succession of the algal community seemed to be controlled by a combination of the rate of sediment deposition, the strength of grazing pressure and the timing and density of recruiting settlers (Korpinen et al. 2007). The functioning of this combination may be affected by environmental factors such as temperature, irradiation and nutrient availability. In other words, the very high density of *O. rusticus* in our study site may reflect the richness of nutrient supply occurring through sediment deposition.

In studies of rocky subtidal communities, the direct effects of large dominant grazers such as sea urchins have been investigated in relation to their predators, such as fish, lobsters and sea otters. In general, the direct effects of grazing gastropod snails on algae have been considered to be small (e.g. Schiel & Foster 2015). Although the direct effects of sedimentation on algae have often been examined (e.g. Foster & Schiel 2010), the grazing effect of gastropod snails on the algal community through the removal of sediment deposition has not been considered. In tropical waters with high transparency and low nutrient content, no constant sediment deposition is observed. In contrast, in cold waters rich in nutrients and with continuous sediment deposition, the impact of falling sediment on the subtidal algal communities may be substantial. Therefore, the grazing activities of herbivorous gastropod snails (which constantly remove sediments) may well have larger impacts on the subtidal algal communities than expected. The interrelationships between sedimentation and the grazing activity of gastropod snails warrant further investigation in a variety of subtidal algal communities with different rates of sediment deposition.

5. CONCLUSIONS

The study reported here investigated the effects of a subtidal herbivorous snail, *Omphalius rusticus*, on algal assemblage and sediment deposition. It is concluded that (1) *O. rusticus* removed microscopic

stages of macroalgae, together with sediment; (2) the surviving ephemeral or turf-forming algal species grew large enough to escape from *O. rusticus* grazing; (3) sediment was gathered and deposited by established turf algae; and (4) *Sargassum confusum* colonization began among sediment and turf algae. In contrast, in the absence of *O. rusticus*, (1) sediment increased and sand-tolerant ephemeral algal turf species colonized the plot; (2) the colonizing algae grew and gathered sediment; (3) dense sediment deposition inhibited the later recruitment of turf algae; and (4) *S. confusum* colonization coincided with the timing of decreased turf algae and sediment deposition. Overall, the results suggest that the snails constantly remove sediments from the surface of the sea bottom. Along with sediment removal, the herbivorous snails affect the colonization of early successional turf algal species. However, due to sediment accumulation by colonizing turf algae and its inhibitory effect on later recruit of algal turf species, the presence of herbivorous snails did not affect the colonization of late-successional canopy-forming species such as *Sargassum* species.

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