

NOTE

Effects of mussels on competitively inferior species: competitive exclusion to facilitation

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ABSTRACT: Intertidal mussel species often provide a secondary substrate for competitively inferior species, while excluding them from the primary substrate. To evaluate the net effect, we conducted field experiments that specifically focused on interactions between mussels *Septifer virgatus* (Mieggmann) and algae species. Mussels affected the abundance of 7 algal species differentially, with effects being positive, neutral, or negative. The red alga *Porphyra yezoensis* grew more abundantly on mussel shells than on rock surfaces. Mussels facilitated recruitment intensity of this species, resulting in increased adult cover on the shells. In contrast, the green alga *Monostroma angicava* grew less abundantly on mussel shells than on rock surfaces. Mussel shells did not modify recruitment intensity of this alga, but did inhibit its frond growth, and would thus seem to reduce adult cover. Modifications of grazer density by the mussels did not affect either of these algae species. The results indicate that the net effect of mussels on competitively inferior species is not grazer-mediated, and varies from species to species.

KEY WORDS: Competitively dominant species · Net mussel effect · Competitive exclusion · Facilitation · Ecosystem engineer · Mussel · Algae

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INTRODUCTION

Dominant species such as mussels strongly affect the benthic community structure in intertidal habitats. In the history of intertidal ecology, a well-known role of dominant species in structuring the community is 'competitive exclusion' (e.g. Paine 1966, Dayton 1971, Menge 1976, Lubchenco 1983). However, recent studies have indicated that dominant species do not always competitively exclude inferior species, since they often comprise a secondary substrate (i.e. their shell surface) for competitively inferior species while monopolizing the rock surface (e.g. Suchanek 1986, Lee & Ambrose 1989, Lohse 1993a,b, Seed 2000). This seems to be a world-wide phenomenon; in fact, competitively inferior species such as barnacles, algae, anthozoans and sessile polychaete worms have been observed to sur-

vive on dominant species including mussels, macroalgae and ascidians on the shores of North America (Paine 1974, Sousa 1984, Witman & Suchanek 1984, Dittman & Robles 1991, Connolly & Roughgarden 1998), South America (Tokeshi & Romero 1995), Asia (Tsuchiya & Nishihira 1985, Ong Che & Morton 1992, Miyamoto 2000, Noda et al. 2003), Oceania (Peake & Quinn 1993, Monteiro et al. 2002), and Europe (Laiho-nen & Furman 1986, Lintas & Seed 1994, Benedetti-Cecchi et al. 1996, Seed 1996). Thus, in order to understand the role of dominant species in a rocky intertidal habitat, we need to evaluate their net effect on primary and secondary substrates.

Previous studies have attempted to define the net effect of mussels on other sessile species (e.g. Lee & Ambrose 1989, Lohse 1993a,b). These studies reported that the secondary substrate could comprise an alternative

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habitat for competitively inferior species, and termed this net mussel effect 'substrate displacement' (Lee & Ambrose 1989). However, it is not obvious whether a secondary substrate constitutes an alternative habitat or a completely separate habitat for competitively inferior species, since mussels play the role of 'ecosystem engineer' (see Seed 2000, Gutiérrez et al. 2003). Some factors such as surface temperature, surface texture and hardness of the substrate often differ between primary and secondary substrates (e.g. Lohse 1993a,b, Miyamoto 2000, Gutiérrez et al. 2003), and these differences may modify the population dynamics of competitively inferior species settling on secondary substrates. Some aspects of the population dynamics of competitively inferior species, such as recruitment and survivorship, are known to be enhanced by settlement on mussel shells (Laihonen & Furman 1986, Stephens & Bertness 1991, Lohse 1993b). Lee & Ambrose (1989) reported both decreased and increased barnacle abundance on mussel shells compared to rock surfaces, and Tokeshi & Romero (1995) showed that mussels completely excluded sessile polychaete worms, but compensated the barnacle population for the loss of bare rock substrate by providing them with a secondary substrate. These studies suggested that the net effect of mussels on competitively inferior species can vary, sometimes being negative, sometimes positive or neutral. However, the net effect of mussels on other species within intertidal mussel-bed systems has not been clarified.

This study focused on an intertidal mussel-bed community in northern Japan. Field experiments were conducted to determine the net mussel effect on competitively inferior species. We tested the following hypotheses: (1) that the net effect on the abundance of competitively inferior algae species can be negative, positive or neutral; (2) that the secondary substrate modifies the abiotic (surface temperature) and biotic (recruitment intensity of the algae and grazer density) environment; (3) that the effects of the secondary substrate on algae are not grazer-mediated.

MATERIALS AND METHODS

Study site and organisms. This study was undertaken on an exposed rocky shore at Hiura (41°44'N, 141°04'E) on southern Hokkaido Island, northern Japan, between December 1996 and June 1998. In the mid-intertidal area of the site, a dense mussel zone is comprised mostly of *Septifer virgatus* (Miegmann). In the mussel zone are scattered bare-rock patches created by wave scour. Bare rock cover is highest in spring, because of the frequent storms in this season (Miyamoto 2000). Different algae species dominate the rock surfaces and mussel shells: a green alga (*Mono-*

stroma angicava)-dominated assemblage occupies the bare rock and a red alga (*Porphyra yezoensis* and *Bangia atropurpurea*)-dominated assemblage the mussel shells (Miyamoto 2000, Noda et al. 2003). The occurrence of the algae is strictly seasonal; they grow in great abundance on each substrate in spring (mainly from March to May), but not during the other seasons (Miyamoto 2000, Noda et al. 2003). The 2 substrates have a different abiotic and biotic environment; e.g. the density of grazers, including limpets (*Lottia kogamogai* and *L. tenuisculpta*) and littorinids (*Littorina brevicula* and *Neritrema sitkana*) is higher on the mussel shells than on the rock (Miyamoto 2000), and the surface temperature of the mussel shells is higher than that of the rock surface (Miyamoto 2000).

Mussel removal experiments. To test whether the abundance of algae differed between the substrates, we conducted 2 mussel-removal experiments. Since December and July are both months in which most algae disappear from the intertidal habitat, we removed five 50 × 50 cm areas of mussel clumps from the mussel beds in December 1996 and July 1997 (hereafter called 'the treatment areas'). Then, 3 times during the algae growth season (March, April and May) in 1997 and 1998, we compared the cover of all algae species in a 30 × 30 cm area (the center of the 50 × 50 cm treatment area) without mussels with that in adjacent areas with mussels present.

Mussel-, grazer-, and algae-removal experiments. To test (1) whether mussels modify their abiotic (i.e. surface temperature) and biotic (i.e. recruitment intensity of algae and grazer density) environment, and (2) whether any effect of the mussels on the algae is grazer-mediated, we conducted mussel-, grazer- and algae-removal experiments during the spring of 1998. We selected 5 experimental blocks (ca. 2 × 2 m) within the mussel zone in early February. Each block contained a mussel bed and an artificial bare-rock patch, created by removing all mussels from a 70 × 100 cm area. On each substrate, the presence/absence of all herbivorous gastropods (limpets and littorinids) and algae were manipulated in 25 × 25 cm experimental plots. Finally, we set up 6 treatments in each experimental block: (1) mussels, grazers, and algae undisturbed; (2) mussels and algae undisturbed; grazers removed; (3) mussels removed and grazers and algae undisturbed; (4) mussels and grazers removed, algae undisturbed; (5) mussels undisturbed and both grazers and algae removed; (6) mussels, grazers, and algae removed. Treatments 1 to 4 were designed to test the effects of the mussels on adult algae abundance in the presence/absence of grazers, and Treatments 5 and 6 were designed to evaluate the effect of the mussels on algae recruitment. These 6 treatments were not replicated within each block. In these treatments, mussel

removal always resulted in removal of grazers; however, we did not compensate for these losses on the artificial bare patches, since we wanted to mimic natural grazer conditions, whereby bare patches are colonized by invasion of grazers from adjacent mussel beds after a disturbance. In all these treatments, algae and grazers were manually removed with forceps every 2 wk (i.e. at every tidal phase), throughout the investigation. The manual removal of mobile grazers effectively excluded them from winter to early spring (Noda et al. 2003).

The percentage cover of each algal species over a 15×15 cm quadrat centered in each experimental plot was measured monthly from March to June 1998. At the same time, we measured surface temperature and grazer density as indices of the abiotic and biotic environments, respectively.

Statistical analyses. Since the data in most of the comparisons (13 of 14) did not meet the assumption of homogeneity of variance, a Wilcoxon signed-ranks test was used to examine the effect of the mussels on the abundance of 7 algal species. To determine the effects on the abiotic (i.e. surface temperature) and biotic (i.e. grazer density and recruitment intensity of algae) environments, we conducted paired *t*-tests or Wilcoxon signed-ranks tests. The assumption of homoscedasticity was checked by an *F*-test. In addition, to determine the effects of the mussels and grazers on the cover of 2 representative algae species (*Porphyra yezoensis* and *Monostroma angicava*), we conducted 3-way ANOVAs using the mussels and grazers as fixed factors, and the experimental block as random factor. To test the validity of mussel and grazer effects, the assumption of a no significant mussel \times grazer \times block interaction is necessary; however, we could not test this because of the lack of replicate units within blocks. In these analyses, only the data for 2 mo (April and May), the months in which the algae were most abundant, have been used, to reduce the number of Type I errors arising from multiple testing. A Bonferroni method was used to adjust values of the Type I errors (Sokal & Rohlf 1995). The grazer density data were $\log(x + 1)$ -transformed and the percentage algae cover was arcsine-transformed to remove heterogeneity of variance for all analyses. Cochran's *C*-tests were used prior to the ANOVAs to test the assumption of homoscedasticity.

RESULTS

Effect of mussels on algae abundance

Mussels modified algae abundance, but the effect differed among algae species (Fig. 1). The red algae

Porphyra yezoensis and *Bangia atropurpurea* were more abundant on the mussel shells in both the 1997 and 1998 experiments (Fig. 1). In contrast, the green alga *Monostroma angicava* and the brown alga *Scytosiphon lomentaria* were always more abundant on the primary substrate (Fig. 1). The effects on the cover of the less abundant species *Urospora pencilliformis* (green alga), *Analipus japonicus* (brown alga), and diatoms differed between the 2 years, and were not always significant (Fig. 1).

Effect of mussels on abiotic and biotic environments

Surface temperature on mussel shells did not differ from bare rock (Fig. 2a; paired *t*-test: $t_{APR} = -2.064$, $p = 0.054$; $t_{MAY} = -2.449$, $p = 0.036$) (note: significance levels were adjusted for multiple testing). However, the mussel shells supported a higher grazer density—more than 20-fold that on bare rock (Fig. 2b), which was sta-

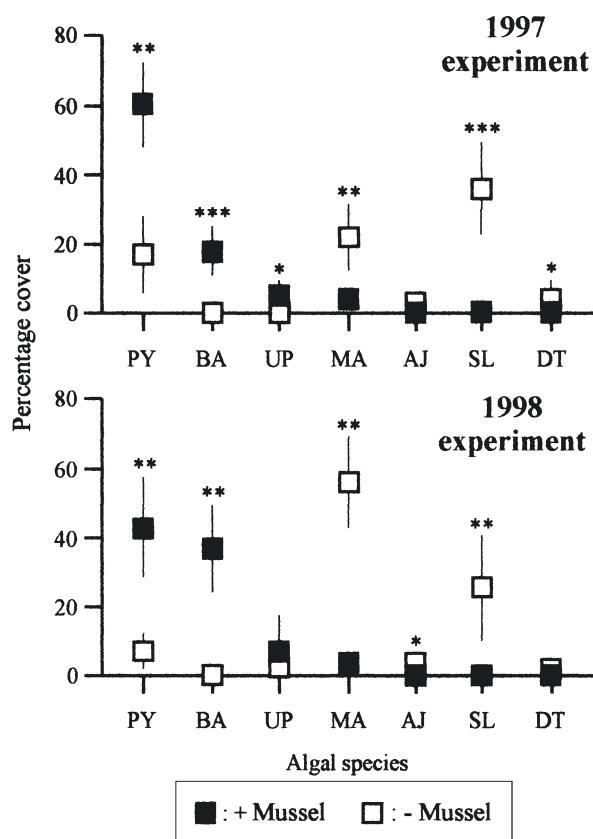


Fig. 1. Percentage cover (mean \pm 95% CI) of major algal species on mussel *Septifer virgatus* shells (■) and rock surface (□) (Wilcoxon signed-ranks tests) * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. PY: *Porphyra yezoensis*; BA: *Bangia atropurpurea*; UP: *Urospora pencilliformis*; MA: *Monostroma angicava*; AJ: *Analipus japonicus*; SL: *Scytosiphon lomentaria*; DT: diatoms

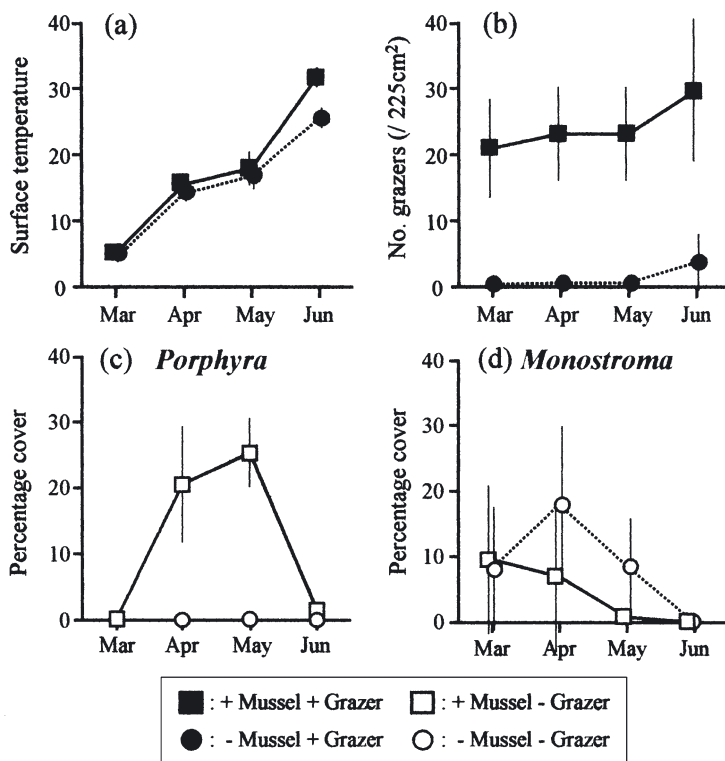


Fig. 2. (a) Surface temperature; (b) density of herbivorous snails; (c,d) recruitment intensity of (c) *Porphyra yezoensis* and (d) *Monostroma angicava* (mean recruits cover \pm 95% CI) on surfaces of mussel *Septifer virgatus* shells (■, □) and on bare rock (●, ○) with (+) and without (-) grazers

tistically significant (Wilcoxon signed-ranks test: $W_{APR} = -2.032$, $p = 0.021$; $W_{MAY} = -2.023$, $p = 0.022$). The mussels modified algae recruitment intensity, but their effects on recruitment intensity differed between algae species (Fig. 2c,d); they significantly increased *Porphyra yezoensis* recruitment ($W_{APR} = -2.032$, $p = 0.021$; $W_{MAY} = -2.023$, $p = 0.022$), but did not affect *Monostroma angicava* recruitment ($W_{APR} = -1.214$, $p = 0.113$; $W_{MAY} = -1.490$, $p = 0.068$).

Effects of mussel and grazer removal

Mussel substrate increased the cover of *Porphyra yezoensis*, but grazers had no effect (Fig. 3, Table 1); the effect of the mussels on this alga did not differ significantly whether grazers were present or not (Table 1). In contrast, the mussels reduced the cover of *Monostroma angicava*, but again grazers had no effect (Fig. 3, Table 1); the effect of the mussels on this species was not significantly modified by the presence of grazers (Table 1). These effects were constant in both April and May (Table 1).

DISCUSSION

Mussels modified the relative abundance of algae species in comparison to their abundance on bare rock. Some algae species (*Porphyra yezoensis* and *Bangia atropurpurea*) grew more abundantly on mussel shells than on bare rock, while some (*Monostroma angicava* and *Scytosiphon lomentaria*) grew less abundantly on mussel shells. In the latter case, *S. lomentaria* was completely excluded when mussels monopolized the primary space. For other species (*Urospora pencilliformis*, *Analipus japonicus* and diatoms), no significant difference in the abundance of algae species between the substrates was observed. These results illustrate that space monopolization by mussels can result in facilitation and inhibition, or have no effect on the abundance of algae species, and that true competitive exclusion (total exclusion) rarely occurs in this system.

Mussel substrate increased the abundance of *Porphyra yezoensis* (Fig. 1). The experiment clearly revealed that mussels facilitated recruitment of this alga (Fig. 2c), and also greatly increased its cover at the post-recruitment stage (Fig. 3, Table 1). These results indicate that recruitment facilitation by mussels resulted in increased *P. yezoensis* abundance on the shells. In contrast, grazer-density modification seemed unimportant in increasing *P. yezoensis* abundance on mussel shells, since grazers had no significant effect on *P. yezoensis* cover during the study period (Fig. 3, Table 1). These results indicate that recruitment facilitation by mussels is responsible for greater abundance of *P. yezoensis* on mussel shells, but that increased grazer density on the shells is not.

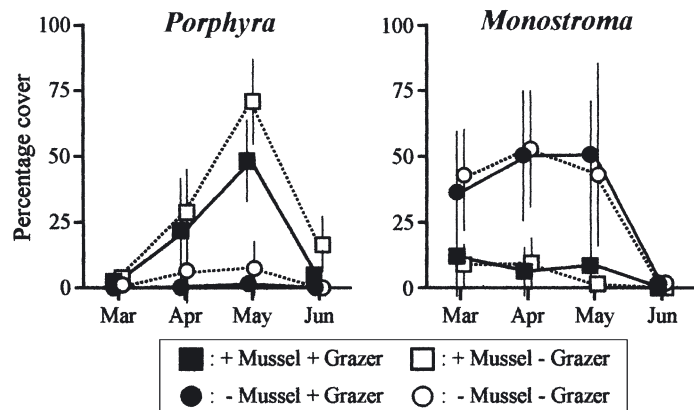


Fig. 3. *Porphyra yezoensis* and *Monostroma angicava*. Mussel and grazer effects on abundance (mean algae cover \pm 95% CI)

Table 1. Results of ANOVA examining effects of mussels *Septifer virgatus* and grazers on algae cover in April and May 1998. Significant results are given in **bold** (significance levels adjusted using Bonferroni method). All algae cover data were arcsine-transformed

Source of variation	df	Apr			May		
		MS	F	p	MS	F	p
<i>Porphyra yezoensis</i>							
Mussel = M	1	2629.6	20.34	0.011	9134.3	46.76	0.002
Grazer = G	1	159.81	2.06	0.225	620.03	8.01	0.047
Block (M × G) = B	4	437.34			80.16		
M × G	1	2.91	0.02	0.900	41.14	0.52	0.512
M × B	4	129.30			195.35		
G × B	4	77.57			77.46		
M × G × B	4	162.01			79.55		
Cochran's C-test			0.433	p > 0.05		0.333	p > 0.05
<i>Monostroma angicava</i>							
Mussel = M	1	5745.6	18.69	0.012	6201.3	18.46	0.013
Grazer = G	1	31.96	0.28	0.626	318.70	1.20	0.230
Block (M × G) = B	4	372.28			1048.5		
M × G	1	1.95	0.02	0.895	0.09	0.002	0.971
M × B	4	307.37			335.92		
G × B	4	115.24			159.47		
M × G × B	4	98.97			61.03		
Cochran's C-test			0.352	p > 0.05		0.452	p > 0.05

In contrast to their effect on *Porphyra yezoensis*, mussels reduced the abundance of *Monostroma angicava* (Fig. 1), although they did not significantly affect recruitment intensity of this alga (Fig. 2d). Since grazer density was much higher on the mussel shells than on the rock substrate, this could have been the reason for the reduced abundance of *M. angicava* on the shells. However, the removal of grazers from the mussels did not result in increased abundance of this species (Fig. 3, Table 1). This suggests that modification of algae recruitment and grazing pressure were not major factors in reducing the abundance of *M. angicava* on mussel shells. Therefore, some other post-recruitment factor is probably responsible for this decrease. A plausible explanation would be that the mussels reduce the growth rate of this alga. The rate of frond growth was significantly lower on mussel shells than on the rock substrate (t -test: $t = 3.02$, $p < 0.05$), with frond-length increments (mm mo^{-1}) on the primary and secondary substrates of 33.9 ± 7.84 ($n = 7$) and 18.0 ± 6.74 ($n = 6$), respectively. Thus, a major causative factor for decreased abundance of *M. angicava* on mussels shells may be a reduction in algae growth. Inhibition of algae recruitment and increased grazer density were minor factors.

These results suggest that the mussels altered some aspects of algae population dynamics, such as recruitment and growth rate through ecosystem engineering effects (*sensu* Jones et al. 1994, 1997). In this study, mussels facilitated recruitment of *Porphyra yezoensis*. Some species of the genus *Porphyra* are known to utilize calcic substrates, including mussel shells, at a specific life stage

called the 'conchocelis phase' (Bird et al. 1972, Bird 1973, Lubchenco & Cubit 1980). Mussel beds are rich in calcic substrate, suggesting suitable substrate provision by mussels as a plausible mechanism facilitating the recruitment of *P. yezoensis*. However, mussels inhibited the growth of *Monostroma angicava* (Fig. 3). Compared with red ephemeral algae such as *P. yezoensis*, the green alga *M. angicava* tends to grow at a lower tide level (where desiccation stress is low at our study site) and during an earlier season (when desiccation stress is also low at our site) (Miyamoto 2000, Noda et al. 2003). As mussel shells comprise a drier environment than rock (Y. Miyamoto & T. Noda unpubl. data), growth of this alga could be depressed on mussel shells because the environment they provide is harsher. The effect of mussels in increasing grazer density did not affect either of these algae species, perhaps because of the low activity of grazers in early spring. In fact, the impact of grazing on algae abundance on mussel shells does increase later in the season at this site (Noda et al. 2003). A decrease in grazer activity (Castenholz 1961, Lubchenco & Cubit 1980) and thus in their grazing impact on algae (Cubit 1984, Lubchenco 1986) during low-temperature periods has also been reported for other systems.

In conclusion, we have shown that in the rocky intertidal habitat studied, mussels affected the abundance of 7 competitively inferior species in different ways. The net effect on the red alga *Porphyra yezoensis* was positive, because of recruitment facilitation by the mussels. In contrast, the net effect on the green alga *Monostroma angicava* was negative due to growth

inhibition by the mussels. These results indicate that the net effect of mussels on competitively inferior species varies from species to species, and is a result of the combined effect of competitive exclusion and ecosystem engineering. We therefore conclude that the net effect of mussels on algae varies, and can be negative, positive or neutral; and that 'competitive exclusion' (e.g. Paine 1966, Dayton 1971, Menge 1976) and 'substrate displacement' (Lee & Ambrose 1989) could both occur at some point(s) along this continuum.

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