

Variable modes of facilitation in the upper intertidal: goose barnacles and mussels

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ABSTRACT: Two sessile filter-feeders of similar body sizes, the goose barnacle *Capitulum mitella* and mussel *Septifer virgatus*, occur in patches on a moderately wave-exposed rocky shore of south Japan in the western Pacific. Their pattern of coexistence was investigated through field observations and experimental manipulation, focusing in particular on seasonally variable modes of facilitation under harsh environmental conditions found in the upper intertidal. Field observations and reciprocal-removal experiments showed a high survivorship of *C. mitella* in both mixed patches (containing *C. mitella* and *S. virgatus*) and *Capitulum*-only patches. In contrast, *S. virgatus* exhibited a substantially higher survivorship in the mixed than in single situations, indicating that *S. virgatus* was positively affected by the presence of *C. mitella*, while the latter was not influenced by the presence of the former in the upper intertidal. An artificial patch transplant experiment demonstrated that *C. mitella* enhanced *S. virgatus* survivorship and growth both in summer when thermal stress was severe and in winter when physical disturbance caused by wave action was strong. In contrast, the artificial shade treatment enhanced *S. virgatus* survivorship only in summer. In summer, thermal conditions (temperature and interstitial humidity within patches) were harsher in the unshaded (*S. virgatus*-only) than in the mixed (*C. mitella* + *S. virgatus*) and shaded treatments (*S. virgatus* with artificial shade). In contrast, the effect of severe physical condition as evidenced by the extent of shell wear in mussels was more pronounced in the shaded and unshaded treatments than in the mixed treatment in winter. These results suggest that *C. mitella* had 2 different habitat-modifying functions: (1) amelioration of thermal stress and (2) amelioration of physical stress; the artificial shade performed only the first of these.

KEY WORDS: Facilitation · Temporal variability · Habitat amelioration · Thermal stress · Physical disturbance · Goose barnacles · Mussels

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INTRODUCTION

Clarifying mechanisms of species coexistence is one of the main themes of community ecology (Tokeshi 1999). Niche differentiation (Schoener 1974, Tilman 1982) and predator- or disturbance-mediation (Paine 1966, Connell 1978) including, in particular, indirect interactions (Strauss 1991, Miller 1994, Schoener 1994, Wootton 1994a,b, Menge 1995, Abrams et al. 1996) have been studied intensively. All these processes concern the mediation of negative elements of species interaction. At the same time, the commonness and importance of positive interactions in species coexis-

tence have been increasingly recognised with critical evaluation in a wide range of natural communities in both marine and terrestrial habitats (Bertness & Callaway 1994, Callaway 1995, Bruno et al. 2003). In marine systems, mussels (Suchanek 1985, Witman 1987, Tokeshi & Romero 1995), seaweeds (Dayton 1975, Menge 1978a,b, Thompson et al. 1996, Bertness et al. 1999) and seagrasses (Heck & Orth 1980, Stoner & Lewis 1985, Irlandi & Peterson 1991) have been frequently identified as habitat-modifying organisms that can influence the success of associated organisms by modifying physically and/or biologically stressful conditions (e.g. thermal stress: Dayton 1975, Hawkins

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1981, Bertness et al. 1999, Leonard 1999; low nutrient levels: Williams 1990; disturbance: Bertness & Groscholz 1985; predation: Heck & Orth 1980, Witman 1987). In terrestrial habitats, many plants can facilitate other plants by ameliorating physical stresses (Nobel 1984, Callaway 1992), altering substrate characteristics (Callaway et al. 1991), increasing resource availability (Walker & Vitousek 1991, Chapin et al. 1994), or providing protection from herbivores (Hjältén et al. 1993).

In these cases of positive interaction, the size scales of interacting species are generally very different: the facilitator is often substantially larger than the facilitated. In fact, few studies have demonstrated positive interactions between similar-sized species (e.g. Navarrete & Castilla 1990, Bertness & Yeh 1994). Furthermore, even in those rare cases, coexistence is generally transient and cannot persist as succession proceeds (cf. the facilitation model: Connell & Slatyer 1977). Therefore, a fundamental question arises as to whether there are cases in which the coexistence of potentially competing, similar-sized species is facilitated by the positive effect of one species on another in a non-transient manner.

Generally, environmental stress factors and their magnitudes show spatial and temporal variation. It has been suggested that the nature of interactions may shift from positive, under environmentally stressful conditions, to neutral, and eventually become negative with decreasing stresses (Bertness & Callaway 1994, Callaway & Walker 1997, Brooker & Callaghan 1998). Indeed, some previous studies have indicated such shifts on different spatial scales (e.g. intertidal assemblages: Bertness et al. 1999; alpine plants: Callaway et al. 2002). On the other hand, few studies have assessed temporal variability in stress factors and the nature of interactions at the same site.

The organisms chosen for the present study, the goose barnacle *Capitulum mitella* and the mussel *Septifer virgatus*, occur in the mid- to upper intertidal on temperate to subtropical rocky shores of the western Pacific. The 2 species have broadly overlapping geographical ranges (Mori et al. 1985a,b, Tanaka et al. 1985, Nakamura & Tanaka 1989), and similar modes of life (sessile, filter feeding) and body sizes. On moderately wave-exposed rocky shores of Amakusa, southern Japan, *C. mitella* individuals usually form patches of various sizes on rock surfaces and *S. virgatus* individuals often occur within *C. mitella* patches, thus forming mixed patches (Nakamura & Tanaka 1995). Our work was stimulated by an observation that *S. virgatus* occurred only within *C. mitella* patches on flat rock surfaces in the upper intertidal in Amakusa. This suggested that the goose barnacle *C. mitella* might positively influence the survivorship and growth of *S. virgatus* through mitigation of certain factors in the upper intertidal.

The present study aimed to evaluate the pattern of coexistence in *Capitulum mitella* and *Septifer virgatus*, with special reference to variable modes of facilitation under seasonally different environmental conditions. In particular, a hypothesis that *C. mitella* can have significant positive effects on the demography of *S. virgatus* through amelioration of seasonally varying thermal stress and physical disturbance was tested by field observations and experimental manipulation.

MATERIALS AND METHODS

Study site. The study was carried out on a moderately wave-exposed rocky shore of the Shikizaki promontory (32° 31' N, 130° 02' E) on the Amakusa Shimoshima Island, western Kyushu, in southern Japan. This region has a subtropical climate, with the surface water temperature ranging from 13 to 29°C. The study site was on the open coast, where strong waves caused by wind were often observed in winter. The mean tidal difference was 3.3 m at spring tide, with a mean tide level of 1.9 m above sea level. The goose barnacle *Capitulum mitella* generally occurs on both horizontal and vertical rock surfaces from the mid to upper intertidal. *C. mitella* usually aggregates around crevices and depressions, forming patches of various sizes (1 to 350 cm²) often mixed with the mussel *Septifer virgatus*. The small acorn barnacle *Chthamalus challengerii* also occurs on horizontal and vertical rock surfaces, while the large acorn barnacle *Tetraclita japonica* occurs mainly on vertical rock surfaces. Mobile organisms in this community include the herbivorous snail *Nodilitorina radiata*, the chiton *Acanthopleura japonica*, the limpet *Siphonaria japonica* and the predatory snails *Morula musiva* and *Thais clavigera*. Field observations and experiments were carried out in the upper intertidal zone (2.0 to 2.5 m above sea level) between August 2000 and February 2002.

Field observations. Patches of *Capitulum mitella* and *Septifer virgatus* were categorised into the following 2 types: (1) mixed patches composed of both *C. mitella* and *S. virgatus*, and (2) *Capitulum*-only patches. *Septifer*-only patches were not observed in our study site at any time during the year. To examine the effects of patch types on *C. mitella* and *S. virgatus* survivorship under natural conditions, photographic surveys were conducted in subtropical 'summer' (August 2001 to October 2001) and 'winter' (December 2001 to February 2002). From 15 to 42 natural patches of each type were chosen in the upper intertidal zone and all individuals of the 2 species within each patch were identified. Survivorship was defined as the proportion of the identified individuals that persisted until the end of a 3 mo monitoring period.

Removal experiment. A removal experiment was conducted to examine interspecific interactions between the goose barnacle *Capitulum mitella* and mussel *Septifer virgatus* within the naturally occurring mixed patches between August and December 2000. In August 2000, 36 middle-sized mixed patches (mean area = 44.5 cm²) were chosen in the upper intertidal zone and randomly assigned to each of the 3 treatments (12 replicates each): (1) *Septifer*-removal, (2) *Capitulum*-removal, and (3) control. Patch sizes did not differ significantly among the treatments (ANOVA: $F_{2,33} = 3.13$, $p > 0.05$). At the beginning of this experiment, all individuals of *S. virgatus* (Treatment 1) and *C. mitella* (Treatment 2) were carefully removed from rock surfaces with a knife. Both goose barnacles and mussels within patches of the control treatment were left untouched. Immediately after removal, these patches were photographed for identification of individuals. After 15, 25, 60 and 100 d from the start of experimental treatment, these patches were monitored for survivorship of each species. Survivorship was defined as the proportion of the identified individuals that persisted until the following monitoring date.

Transplant experiment. In order to test the hypothesis that the positive effect of *Capitulum mitella* on *Septifer virgatus* involves amelioration of seasonally varying thermal stress and physical disturbance, an artificial patch transplant experiment was run twice (August to November 2001 and December 2001 to February 2002). A total of 24 artificial patches were prepared and assigned to 3 treatments (8 replicates each): (1) mixed, (2) *Septifer*-only without shade, and (3) *Septifer*-only with shade. Middle-sized *C. mitella* (10 to 20 mm in R-T length, see below) and *S. virgatus* (25 to 40 mm in shell length, see below) were collected from the upper intertidal habitats near the transplant site. Size of each species was defined as the length between the rostrum and the tip of the tergum ('R-T length') in *C. mitella* and shell length (the maximum anterior-posterior axis) in *S. virgatus*. Individuals were measured with digital callipers to the nearest 0.01 mm and marked with small numbered tags.

For the mixed patches, 16 *Capitulum mitella* were glued in a circle onto a 10 × 10 × 1 cm ceramic tile using water-resistant epoxy resin, and 10 *Septifer virgatus* were placed within the *Capitulum*-circle and allowed to adjust their positions and attach to the tile and to one another by byssal threads. These tiles were kept in a laboratory running-seawater aquarium for 1 wk to allow firm attachment and acclimatisation. The size of artificial mixed patches (50 to 60 cm²) corresponded to natural patches and the proportion of *S. virgatus* within the artificial patch (~40%) was adjusted to a relatively high level observed in the upper intertidal zone. For the unshaded and the shaded treatments,

10 *S. virgatus* were placed in the centre of a ceramic tile and allowed to attach to the tile in the aquarium for 1 wk. After all the mussels had attached firmly, the tiles were taken to the field and randomly placed on rock surfaces using stainless steel screws on a slightly sloping flat rock in the upper intertidal. Each artificial patch was covered with a predator exclusion cage (10 × 10 × 5 cm) constructed of 5 × 5 mm stainless mesh. This excluded predatory snails *Morula musiva* and *Thais clavigera*; in the field, the actual density of these predatory snails was very low in summer and virtually nil in winter in the experimental area. The shaded treatment involved coverage by a 10 × 10 cm double-layered canopy of white plastic screen (0.5 × 0.5 mm mesh) attached to the top of the cage to reduce solar radiation. All marked individuals of the 2 species were monitored for survivorship throughout the experiment and measured for growth during the first 6 wk of the experimental period. Growth rate was calculated as relative size increase per day for each individual, using the following formula:

$$r = \frac{L_{t_2} - L_{t_1}}{L_{t_1}(t_2 - t_1)} \times 100$$

where r is the growth rate, L_{t_1} and L_{t_2} are the shell length at time t_1 and t_2 , respectively, and t is time in days. At the end of the experiment, shell length of dead mussels was measured and the magnitude of shell wear was estimated by calculating the proportional decrease in shell length of dead mussels from the initial length.

Mussel shell surface temperature, interstitial temperature, humidity within the artificial patches and the amount of water retained on the bottom of a patch were quantified to characterise thermal conditions in the treatments. Shell surface temperature of a living mussel was taken with a radiant thermometer (IT-330, Horiba) placed centrally in each artificial patch. Interstitial temperature and humidity were measured with a thermo-hygrometer (SU-610, Testo) inserted into interstices of mussels. Measurements (5 to 8) of shell surface temperature, interstitial temperature and humidity were taken 1 and 3 h after all experimental patches were exposed by the receding tide at midday on windless, fine days in September 2001 and January 2002. The amount of water retained in a patch was estimated with 20 g completely dried silica gel scattered into interstices for 10 min. Water gain was calculated as the difference between the initial and final weight of the silica gel. Five to 8 replicate measurements were taken after 30 min and 3 h of low-tide exposure.

Data analysis. A 2-tailed Fisher's exact test was used to assess the survivorship of each species within natural patches. Temporal pattern in the survivorship of the 2 species was evaluated using repeated-measures

ANOVA. Most other data were analysed with 1-factor ANOVA with experimental treatment as a fixed factor, or 2-factor ANOVA with experimental treatment and season as fixed factors. Where appropriate, Scheffé's test was used for *a posteriori* multiple comparison of means ($\alpha = 0.05$; where the homoscedasticity assumption was violated, the significance level α was set at 0.01). Bartlett's test was used to check the assumption of homogeneity of variances and, where necessary, proportional data were arcsine transformed (Zar 1996) (note, however, that untransformed means were used for graphic presentation).

RESULTS

Survivorship

Field observations

In the upper intertidal, mixed and *Capitulum*-only patches occurred throughout the year, while no *Septifer*-only patch occurred. The survivorship of *C. mitella* was very high (over 88%) and not significantly

different between the mixed and the *Capitulum*-only patches in either summer or winter (2-tailed Fisher's exact test: summer, $p = 0.87$; winter, $p = 0.16$; Fig. 1). Mussel survivorship was also high (over 85%) in the mixed patches and did not show seasonal variation (2-tailed Fisher's exact test: $p = 0.13$; Fig. 1).

Removal experiment

The survivorship of *Septifer virgatus* was positively affected by the presence of *Capitulum mitella*, while that of *C. mitella* was not influenced by *S. virgatus* in the upper intertidal (Fig. 2). There was no difference in *C. mitella* survivorship between the control and the *Septifer*-removal treatments (Fig. 2a, Table 1a). *C. mitella* survivorship was uniformly high (over 90%) throughout the experimental period in both treatments. In contrast, the survivorship of *S. virgatus* varied with treatment \times time interaction (Fig. 2b, Table 1b). There was no difference in survivorship between treatments until Day 25 from the start of the experiment. Mussel survivorship suddenly declined, however, in the *Capitulum*-removal treatment after Day 25. By Day 60, 40% of mussels in the *Capitulum*-removal treatment died, and by Day 100 nearly 50%

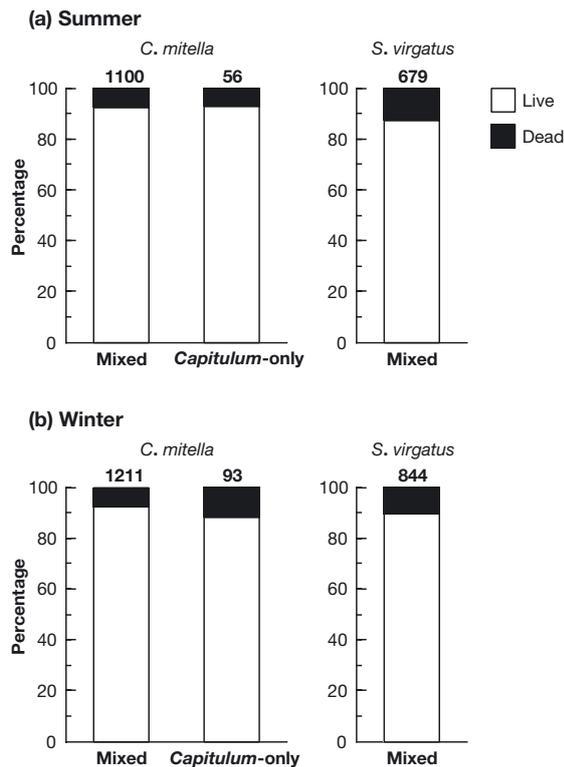


Fig. 1. *Capitulum mitella* and *Septifer virgatus*. Proportion of live and dead individuals in different types of patch. (Summer: mixed, $n = 15$; *Capitulum*-only, $n = 31$. Winter: mixed, $n = 16$; *Capitulum*-only, $n = 42$.) No *Septifer*-only patch occurred. Total numbers of individuals are given for each patch type above the bars

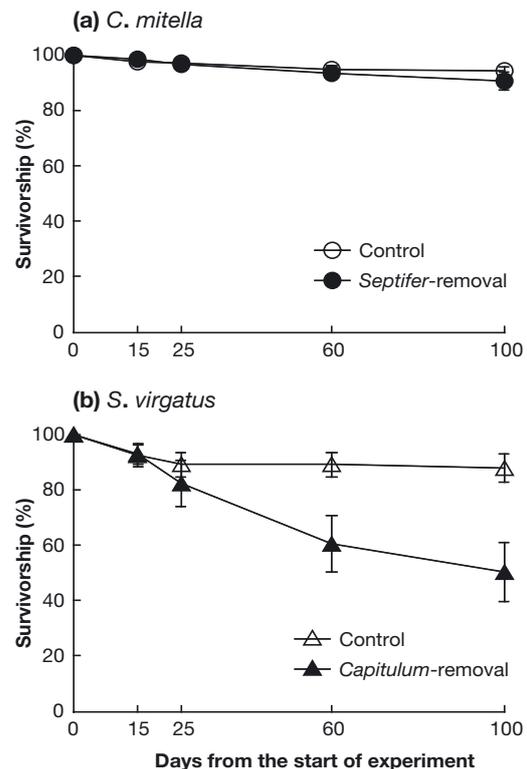


Fig. 2. *Capitulum mitella* and *Septifer virgatus*. Survivorship of (a) *C. mitella* and (b) *S. virgatus* in removal experiment. Values are untransformed means \pm 1 SE

Table 1. *Capitulum mitella* and *Septifer virgatus*. Results of 2-factor, repeated-measures ANOVA on the survivorship of (a) *C. mitella* and (b) *S. virgatus* in the removal experiment. Data were arcsine (square root) transformed before analysis. Denominator MS for the *F* ratios: b = Subject (group) error, c = Time × Subject (group) error

Source of variation	df	MS	<i>F</i>	MS	<i>p</i>
(a) <i>C. mitella</i>					
Treatment	1	32.02	0.20	b	0.658
Subject (group) error	22	158.90			
Time	4	646.56	24.69	c	<0.001
Time × Treatment	4	22.92	0.88	c	0.482
Time × Subject (group) error	88	26.19			
Total	119				
(b) <i>S. virgatus</i>					
Treatment	1	5089.91	5.05	b	0.035
Subject (group) error	22	1007.73			
Time	4	3567.30	17.50	c	<0.001
Time × Treatment	4	1434.60	7.04	c	<0.001
Time × Subject (group) error	88	203.80			
Total	119				

died. In contrast, the survivorship of mussels in the control treatment was uniformly high (nearly 90%) throughout the experimental period.

Transplant experiment

Almost all individuals of *Capitulum mitella* in the mixed treatment survived throughout the experimental periods in both seasons (Fig. 3). Mussel survivorship in summer varied with treatment × time interaction (Fig. 3a, Table 2a). The survivorship of mussels in the unshaded treatment rapidly declined. During the first 2 wk from the start of experiment, 60% of mussels in the unshaded treatment died. Moreover, by Day 42 nearly 80% of mussels died, while from Day 42 onwards no mussels died. In contrast, mussel survivorship in the mixed treatment was constantly high (over 80%) throughout the experimental period. Mussels in the shaded treatment also showed a high survivorship (~80%) during the first half of experimental period, in contrast to those in the unshaded treatment (Scheffé’s test: Day 14, *p* = 0.013; Day 28, *p* = 0.006; Day 42, *p* = 0.011). However, mussel survivorship in the shaded treatment gradually declined to ca. 50% and the difference with the unshaded treatment became non-significant towards the end of the experiment (Scheffé’s test: Day 84, *p* = 0.43).

Mussel survivorship in winter also varied with treatment × time interaction, though the pattern was slightly different from summer (Fig. 3b, Table 2b). During the first 14 d, only a few mussels (less than 10%) died in all treatments and there was no signifi-

cant difference among treatments. During the next 28 d, however, the magnitude of decrease in survivorship varied with treatments, the greatest being in the unshaded treatment, intermediate in the shaded treatment and smallest in the mixed treatment. In the unshaded treatment, nearly 80% of mussels died by Day 42 and continued to decline towards 0 at the end of the experiment. Mussel survivorship in the shaded treatment also declined rapidly after Day 14, reaching nearly 50% by Day 42 and 10% at the end. In contrast, although mussels in the mixed treatment showed a slight decreasing trend from Days 14 to 42, after that period mortality was low. In the end, over 70% of mussels in the mixed treatment survived through the experimental period. These results

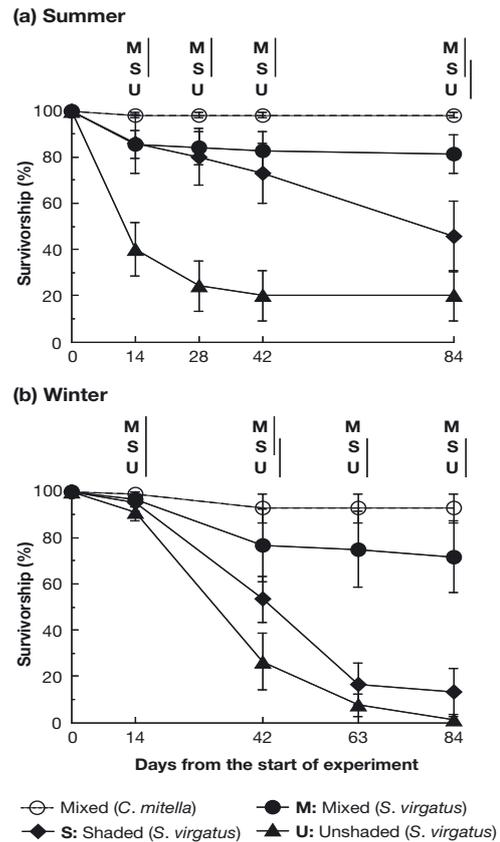


Fig. 3. *Capitulum mitella* and *Septifer virgatus*. Survivorship of *C. mitella* (dotted line) and *S. virgatus* (solid line) in transplant experiments in (a) summer and (b) winter. Values are untransformed means ± 1 SE. Vertical bars represent no significant difference (Scheffé’s test: *p* > 0.05) in the survivorship of *S. virgatus* between any pair of groups concerned

Table 2. *Septifer virgatus*. Results of 2-factor, repeated-measures ANOVA on the survivorship in the transplant experiment. Data were arcsine (square root) transformed before analysis. Denominator MS for the *F* ratios: b = Subject (group) error, c = Time × Subject (group) error

Source of variation	df	MS	<i>F</i>	MS	p
(a) Summer					
Treatment	2	13227.03	9.07	b	0.002
Subject (group) error	18	1457.65			
Time	4	6805.02	38.57	c	<0.001
Time × Treatment	8	1219.56	6.91	c	<0.001
Time × Subject (group) error	72	176.44			
Total	104				
(b) Winter					
Treatment	2	11203.47	12.14	b	<0.001
Subject (group) error	17	922.84			
Time	4	16237.42	78.06	c	<0.001
Time × Treatment	8	1726.87	8.30	c	<0.001
Time × Subject (group) error	68	208.02			
Total	99				

were consistent with the results of the removal experiment in which a higher survivorship of *Septifer virgatus* was recorded under the mixed situation with *Capitulum mitella* than in the single situation. Even in winter, however, the positive effect (of similar magnitude to summer) of *C. mitella* on *S. virgatus* was detected.

Growth and shell wear

Mussel growth was also positively affected by the presence of goose barnacles in the transplant experiment (Fig. 4a). The growth rate varied with treatments, but not with seasons nor with treatment × season interaction (Table 3). Only individuals in the mixed treatment showed positive growth in both seasons, while the shaded and unshaded treatment growth was negative, due probably to the faster rate of shell wear caused by wave action. Growth in the shaded treatment was negligibly negative in summer, while in winter the extent of negative growth was over 5 times larger than in summer. The growth rate of mussels in the unshaded treatment was the lowest, and similar in 2 seasons.

Almost all mussels that died during the experimental period had evidence of wear on their shells (Fig. 4b). The extent of shell wear in dead *Septifer virgatus* varied with treatments and seasons, with no treatment × season interaction (Table 4), with individuals in the mixed treatment showing the least shell wear. Shell wear in all 3 treatments was more pronounced in winter than in summer.

Thermal conditions

Overall, thermal conditions were more severe (e.g. high temperature and low humidity) in the unshaded treatment than in the mixed and shaded treatments (Figs. 5 & 6). The mixed and shaded treatments showed similar habitat-ameliorating effects in terms of reducing thermal stress under almost all situations. In winter, however, those differences among treatments were negligible.

Shell surface temperature was significantly higher in the unshaded treatment than in the mixed and shaded treatments in summer (ANOVA: 1 h, $F_{2,12} = 138.69$, $p < 0.0001$; 3 h, $F_{2,16} =$

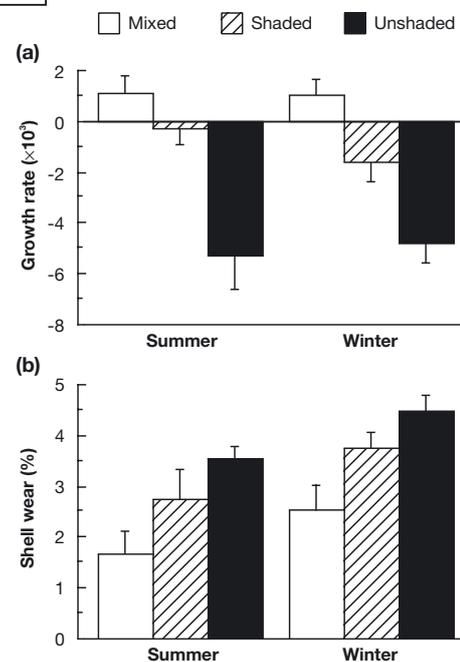


Fig. 4. *Septifer virgatus*. (a) Growth rate (relative size increase per day) and (b) shell wear (percentage) in dead *S. virgatus* in transplant experiments. Means ± 1 SE (vertical bars) are shown

Table 3. *Septifer virgatus*. Results of 2-factor ANOVA on the growth rate in the transplant experiment

Source of variation	df	MS	<i>F</i>	p
Treatment	2	1.00×10^{-3}	22.95	<0.001
Season	1	4.19×10^{-6}	0.18	0.671
Treatment × Season	2	1.31×10^{-5}	0.57	0.569
Residual	228	2.32×10^{-5}		
Total	233			

Table 4. *Septifer virgatus*. Results of 2-factor ANOVA on shell wear in dead *S. virgatus* in the transplant experiment

Source of variation	df	MS	F	p
Treatment	2	33.47	7.40	<0.001
Season	1	23.32	5.16	0.024
Treatment × Season	2	0.27	0.01	0.994
Residual	171	4.52		
Total	176			

14.39, $p < 0.001$; Fig. 5). The highest temperature was 38.6°C, recorded in the unshaded treatment after 3 h of exposure. In winter, shell surface temperature was low in all treatments and differences among treatments were either negligible or very small. The highest temperature was 11.0°C in the mixed treatment after 1 h of exposure.

The goose barnacle and the artificial shade could modify interstitial temperature within the transplanted patches (Fig. 6a). Interstitial temperature was similar among treatments at 1 h after low tide exposure in summer, while temperature in the unshaded treatment only increased from 1 to 3 h of exposure, and became significantly higher than in the mixed and shaded treatments (ANOVA: $F_{2,17} = 8.77$, $p = 0.002$). In contrast, the mixed and the shaded treatments were stable and remained at similar temperatures irrespective of time of exposure. The highest temperature was 39.5°C recorded after 3 h of exposure in the unshaded treatment. In winter, interstitial temperatures were very low, with no significant difference among treatments and very small variation from 1 to 3 h of exposure (~1.5°C). The highest temperature was 8.9°C in the unshaded treatment after 1 h of exposure.

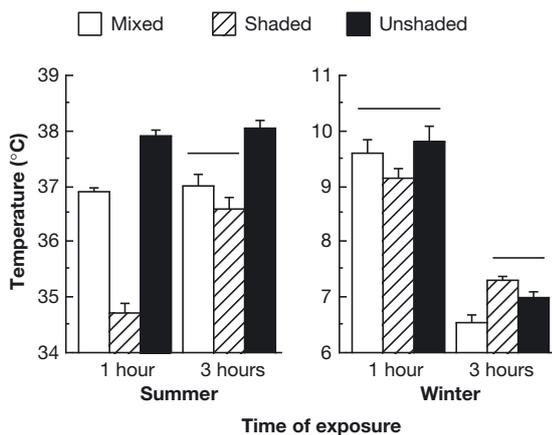


Fig. 5. *Septifer virgatus*. Shell surface temperature in transplant experiments after 1 and 3 h of low-tide exposure. Values are means \pm 1 SE. Horizontal bars represent no significant difference (Scheffé's test: $p > 0.05$) in temperature between any pair

The trends in interstitial humidity are shown in Fig. 6b. The significant difference among treatments was observed in summer, particularly at 3 h after low tide exposure (ANOVA: $F_{2,13} = 3.84$, $p = 0.049$). Humidity in the unshaded treatment decreased by 7% from 1 to 3 h of exposure, and tended to be lower than in other treatments (though differences did not become statistically significant by Scheffé's multiple comparisons test). Although humidity in the mixed and the shaded treatments also showed a decrease with increasing exposure time, the ranges (~5%) were smaller than in the unshaded treatment (~7%). The lowest humidity was 36.1% in the unshaded treatment after 3 h of exposure. In winter, humidity was very high in all treat-

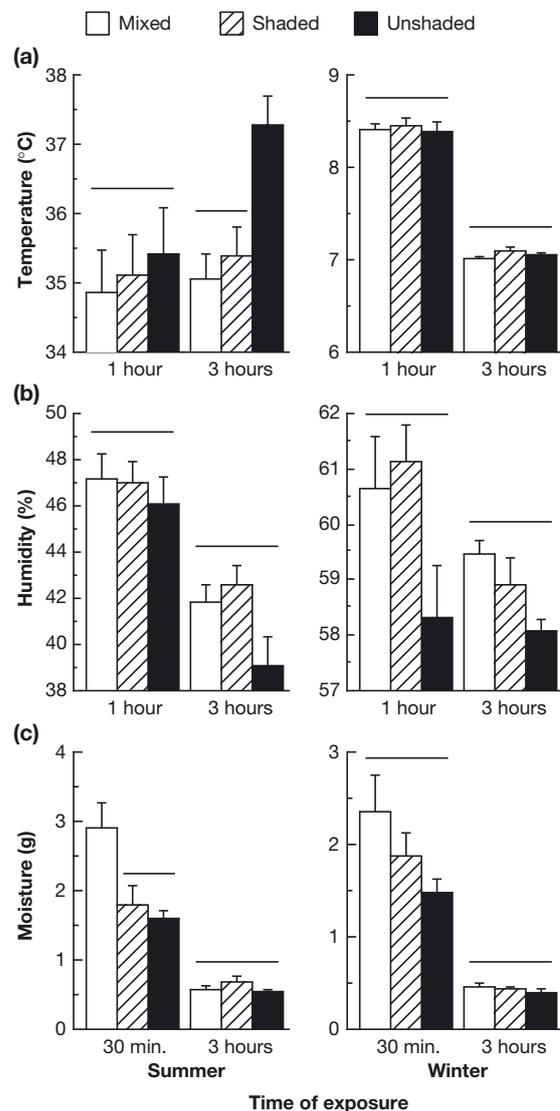


Fig. 6. (a) Interstitial temperature, (b) humidity and (c) the amount of water in transplant experiments after 1 h or 30 min and 3 h of low-tide exposure. Values are means \pm 1 SE. Horizontal bars represent no significant difference (Scheffé's test: $p > 0.05$)

ments, and the magnitude of its decrease from 1 to 3 h of exposure was very small (<3%). The lowest humidity was 56.3% in the unshaded treatment after 3 h of exposure; still a high value compared with summer.

Goose barnacles also contributed to increased water retention in an experimental patch, especially immediately after low-tide exposure (Fig. 6c). The amount of water was larger in the mixed treatment than in other treatments after 30 min of exposure, but the difference was significant only in summer (ANOVA: summer, $F_{2,15} = 6.29$, $p = 0.010$; winter, $F_{2,13} = 2.20$, $p = 0.15$). However, from 30 min to 3 h of exposure, the amount of water in all treatments declined to similar levels in both seasons, indicating that evaporative water loss is higher in the mixed treatment than in other treatments. In this case, different patterns were observed between the mixed and shaded treatments.

DISCUSSION

Coexistence in similar-sized sessile organisms

Body size differences are considered to facilitate species coexistence in some assemblages (Hutchinson 1959, Strong et al. 1979, Tokeshi 1999). Conversely, organisms with closely similar body sizes are more likely to compete for resources. In particular, interference competition for space is widespread among sessile organisms (Connell 1961, Paine 1984, Williamson 1990, Tokeshi & Romero 1995). The present study has demonstrated that 2 sessile organisms, the goose barnacle *Capitulum mitella* and the mussel *Septifer virgatus*, can coexist in the upper intertidal, despite having similar body sizes and similar modes of resource utilization (space and food; in particular, habitable space on microhabitat scales is limited in the upper intertidal).

A number of studies demonstrated intraspecific facilitation involving individuals of similar size ranges (Ottaway 1979, Taylor & Littler 1982, Bertness & Grosholz 1985, Bertness 1989, Pineda & Escofet 1989, Peterson & Black 1993). In contrast, studies showing interspecific facilitation in organisms of similar sizes are very rare, particularly in animals (Bertness & Yeh 1994, Lively & Raimondi 1987, Hodge & Arthur 1997). In the case of salt marsh plants living under hypersaline conditions, interspecific facilitation between seedlings occurred when salt tolerant species reduced substrate salinity, which in turn allowed salt intolerant but competitively superior species to survive (Bertness & Yeh 1994). As these species grew, the tolerance of the competitively superior individual to high salinity increased with habitat amelioration by neighbouring subordinate species, which led to a shift in the nature of interspecific

interactions from positive to negative. Lively & Raimondi (1987) also demonstrated transient facilitation between acorn barnacles and mussels, in which the former facilitated the latter's settlement and juvenile survival, but interference competition for space ensued as the latter grew up. In contrast, the present study suggests that the survival of adult *Septifer virgatus* depended on the presence of *Capitulum mitella* and the benefit of association exceeded the magnitude of negative effects from interspecific interference competition. If *S. virgatus* with a potentially faster growth rate (15 mm yr⁻¹ in shell length in Hong Kong: Morton 1995) outcompeted *C. mitella* that had a slow growth rate (2 mm yr⁻¹ in rostral-carinal length: Nakamura & Tanaka 1995) and/or increased its abundance vastly within mixed patches, *S. virgatus* would have become susceptible to harsh environmental conditions and suffered from a higher mortality. In conjunction with this, the morphological flexibility of *C. mitella* (a firm but flexible or even mobile peduncle of goose barnacles, Burnett 1987, Barnes 1996, Kugele & Yule 2000) that could buffer interference competition seems to enhance the stable coexistence of the 2 species. On the other hand, the relative importance of the negative effects of *S. virgatus* on *C. mitella* may increase with decreasing environmental harshness (Bertness & Callaway 1994, Brooker & Callaghan 1998, Bertness et al. 1999, Bruno et al. 2003). Actually, competitively superior *S. virgatus* was dominant on vertical rock surfaces and overhangs where environmental conditions (both thermal and physical stresses) were relatively benign. In Paine's (1974) study, relatively benign thermal conditions on the North American coast may have led to the competitive exclusion of the goose barnacle *Pollicipes polymerus* by the mussel *Mytilus californianus*.

Amelioration of multiple stresses

While the majority of past studies dealt with a single stress factor and its variation (Stachowicz 2001), our study revealed that coexistence may be affected by 2 different stress factors at different times of year.

The importance of ameliorating thermal stress was particularly evident in summer, as demonstrated by the higher survivorship (Fig. 3a) and growth (Fig. 4a) of *Septifer virgatus* within the mixed and the shaded treatments. As the time of low tide exposure was longer, the habitat-ameliorating effect of *Capitulum mitella* became more evident: lower interstitial temperature and higher interstitial humidity (Fig. 6a,b) within the mixed patches than the unshaded patches after 3 h of low tide exposure. The higher survivorship of *S. virgatus* under the mixed conditions in summer, in both the field observation (Fig. 1) and the removal

experiment (Fig. 2b), confirms this positive effect of *C. mitella* in mitigating thermal stress. Thermal conditions are closely linked to mussel body temperature and desiccation, which can affect mussel survivorship significantly (Helmuth 1998). Liu & Morton (1994) showed that *S. virgatus* did not survive a 6 h exposure to air temperature of 34°C and rock surface temperature of 40°C. In our case, interstitial air temperature constantly exceeded 35°C only in the unshaded treatment (Fig. 6a), and the maximum temperature was 39.5°C, recorded in the unshaded treatment at midday low tide in summer. In addition, time of exposure at spring tide was longer than 5 h in the upper intertidal in our study site. Therefore, the thermal condition in the unshaded treatment in summer was sufficiently severe to cause significant mortality in *S. virgatus*.

In winter when thermal stress was weak (Figs. 5 & 6) but physical stress by wave action was severe (Fig. 4b), the amelioration of physical stress was apparently more important. It is notable that during the first 14 d of the transplant experiment in winter, *Septifer virgatus* in all treatments showed a high survivorship in contrast to the summer season (Fig. 3b), probably due to calm sea and mild thermal conditions (Figs. 5 & 6). However, *S. virgatus* survivorship in the shaded and unshaded patches, but not in the mixed patches, rapidly declined from Day 14 onwards (Fig. 3b) when rough sea conditions prevailed. Thus, the presence of *Capitulum mitella* apparently mitigated the negative effects of wave-caused physical disturbance on mussels.

Structural characteristics of *Capitulum mitella* aggregations

The fact that *Capitulum mitella* has a higher tolerance of thermal stress than *Septifer virgatus* is demonstrated by its high survivorship under both natural and experimental conditions in summer (Figs. 1a, 2 & 3a) and by its wide range of distribution towards the upper elevation (Mori et al. 1985a,b, Tanaka et al. 1985). Further, *C. mitella* is also more tolerant of strong hydrodynamic forces than *S. virgatus*. While a lift force acting in a perpendicular direction is the most significant dislodgement agent for mussels (Denny 1987), it has little effect on a goose barnacle that is directly attached to the rock surface by solid cement, whereby no significant difference in hydrostatic pressure occurs between the upper and the lower side of its body (Denny 1995). In addition, the flexible peduncle of a goose barnacle (Burnett 1987, Barnes 1996) can buffer drag forces that act in the direction of flow more efficiently, like in algae (Gaylord et al. 1994), compared with mussels with inflexible shells. Consequently, *C. mitella* is less likely to

be dislodged by hydrodynamic forces than *S. virgatus*. Actually, *C. mitella* survivorship was constantly higher than *S. virgatus* under all situations in winter when physical stress was severe (Figs. 1b & 3b).

Living in either conspecific or heterospecific groups can reduce an individual's risk of being damaged and killed, because the presence of neighbours directly or indirectly buffers environmental extremes (e.g. acorn barnacles: Bertness 1989; mussels: Bell & Gosline 1997, Helmuth 1998; sea anemone: Ottaway 1979, Pineda & Escofet 1989; algae: Dayton 1975, Hay 1981, Bertness et al. 1999; marsh grasses: Leonard & Luther 1995, Bruno 2000; seagrasses: Orth et al. 1984, Irlandi & Peterson 1991; large polychaete tubes: Woodin 1978). In the present case, an aggregation of *Capitulum mitella* shielded the rock surface from irradiation so that it remained cooler than areas without *C. mitella*. Moreover, the magnitude of evaporative cooling, which is considered to be effective in lowering mussel equilibrium body temperature (Helmuth 1998), must be greater in *C. mitella* aggregations, as evidenced by a large amount of water loss from mixed patches compared with other patches, particularly in summer (Fig. 6c). In addition, *C. mitella* aggregation may modify hydrodynamic forces caused by pounding wave action due to *C. mitella*'s 3-dimensional and flexible structure. Consequently, *Septifer virgatus* can benefit greatly from being in a mixed patch, where both thermal conditions and hydrodynamic forces are ameliorated. The artificial shade could closely mimic the habitat-modifying effects of *C. mitella* in terms of reducing thermal stress, but failed to reduce hydrodynamic forces. Thus, the survivorship of mussels was substantially low in the shaded treatment and there was no difference between the shaded and the unshaded treatments in winter (Fig. 3b). Our experimental design used in the present study, however, could not separate the relative contributions of these 2 different habitat-modifying functions caused by goose barnacles precisely.

CONCLUSION

The results of this study give credence to a hypothesis that coexistence in the 2 species, the goose barnacle *Capitulum mitella* and mussel *Septifer virgatus*, was a consequence of seasonally variable modes of facilitation. *C. mitella* affected the survivorship and growth of *S. virgatus* positively through amelioration of thermal stress in summer and of physical disturbance in winter.

Thus, the present study has demonstrated that facilitation can occur even in potentially competing organisms with similar body sizes and feeding modes. It may

therefore be suggested that coexistence promoted by facilitation is not uncommon in many systems, particularly under harsh environmental conditions. Moreover, our study has indicated temporally variable modes of facilitation even in the same relationship. Our ongoing experiments using transparent physical barriers and facilitation 'mimics' (Bruno et al. 2003) are expected to further unravel the complex mechanisms underlying this temporally varying facilitation and the compound nature of species interactions. More investigation, coupled with a mechanistic approach, will be needed for a broader understanding of community organisation in different systems.

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